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

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Dionisios Youlatos *Editors*

Howler Monkeys

Behavior, Ecology, and Conservation

Springer

Developments in Primatology: Progress and Prospects

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M.K.: To Mariana and Bruno,
and to my parents and sisters

P.A.G.: To Seymour, Sylvia, Jenni, Sara,
and of course Chrissie

L.C.O.: To Paloma, Tommy, and Tom

B.U.: To my family, to my mentors, to Padmini

D.Y.: To Evangelos (Sr. and Jr.), Alexandra,
and Ioanna

Foreword

It is a privilege to be able to study wild howler monkeys, and an honor to have been invited to write the foreword to this volume of collected papers about them. Thank you to the howlers—everything I know, I learned from you—and thank you to the volume editors for this invitation and to all of the Latin American countries which so generously enabled me carry out research on howler monkeys in their forests.

Alouatta is considered the most successful New World primate genus in terms of ecological dominance as defined by overall biomass. Howler monkeys have a wide geographical distribution, which extends from southern Mexico through Central and South America and into northern Argentina. Their great success as a genus stems in large part from their ability, unusual in a neotropical primate, to use leaves as a primary food source. Fruits and flowers are also popular howler foods but it is their ability to survive for long periods on diets consisting largely of leaves that underlies their great ecological success. This ability has enabled howler monkeys to occupy a tremendous diversity of habitat types throughout the neotropics and to survive in small forest fragments that could not support other primates.

Despite being known for the loud sonorous howling vocalization produced by adult males, howler monkeys are quite subtle, secretive, and quiet monkeys most of the time. They spend a high percentage of their daylight hours throughout the year quietly resting or sleeping to conserve energy—this inactivity is an important feature of their overall foraging strategy. I have studied howler monkeys now for more than 40 years and to me they remain endlessly complex, fascinating, and endearing study subjects. I remember my parents asking me, after a decade or so of howler research and many missed holidays and family celebrations, if I hadn't answered just about all the questions that could possibly be asked about howler monkeys. But as the collection of papers in this volume clearly shows, there is thankfully no end in sight to the array of interesting questions that can be posed about members of the genus *Alouatta.*

Because of howlers' wide distribution and abundance, it's no surprise that over the decades an unusually large number of primatologists have carried out research on wild howler monkeys such that, today, it is considered one of the best studied of all primate genera. Indeed, though perhaps not well appreciated, the first successful systematic naturalistic study of *any* wild primate anywhere in the world was carried out on howler monkeys. In the early 1930s, C. Ray Carpenter travelled from the USA to Panama to begin a field study of mantled howler monkeys (*Alouatta palliata)* on Barro Colorado Island (BCI). Carpenter was motivated to study wild monkeys because he was convinced that a better understanding of primate behavior in the natural environment would provide important insights into key features of human biology and behavior. Though earlier attempts had been made to try and study wild chimpanzees and mountain gorillas, these study subjects proved elusive and little information was compiled. In contrast, Carpenter was able to spend long periods of time both in 1932 and 1933 observing howler monkeys at close range and amassed a wealth of detailed behavioral information. He also collected and identified many important howler food species and censused all individuals in every howler group on BCI two times during his fieldwork—providing invaluable baseline data for future studies of howler monkey population dynamics at this site. Carpenter produced an excellent and meticulously organized scholarly monograph from his field study, one filled with original information about howler monkey behavioral ecology—information as valid and interesting today as it was in 1934 when his original monograph *A Field Study of The Behavior and Social Relations of Howling Monkeys* was published. To say Carpenter was decades ahead of his time does not begin to do him justice.

After Carpenter's pioneering field study, world events intervened, leading to a hiatus in howler monkey research. But in the 1950s and 1960s, a number of young researchers followed in Carpenter's footsteps and travelled to BCI to observe howler monkeys—though generally only for short periods of time. During this period, field studies were also begun on red howlers at Hato Masaguaral in Venezuela and in 1972 on mantled howler monkeys at La Pacifica in Costa Rica. My howler monkey research began in 1974. Barro Colorado Island was an ideal study site because I was interested in dietary questions and by that time, a considerable amount of information was available on features of the BCI forest and the island had an excellent herbarium—essential tools for a dietary study. During my initial fieldwork, there were no other primate researchers on the island. But by 1978, a few short years later, primate field studies had begun to take off and so many graduate students began arriving on BCI to examine one or another attribute of howler monkeys that often we had to take turns collecting data on the more popular study groups near the laboratory buildings.

Though we now know a great deal more about howler monkeys than we did in the Carpenter's day, we still have much to discover about this engaging New World primate. Answering important questions about the ecology and behavior of living systems generally involves a long investment of time and effort and many years of continuous study at particular research sites. It is ironic that as this fact has become more apparent, funding to support long-term field studies has become increasingly difficult to secure. If our knowledge of living systems such as howler monkeys is to progress, researchers must not only ask the interesting questions but also have the time to compile the data needed to answer them. To enable the relevant studies to be carried out, however, our first task is to ensure the successful conservation of howler monkeys and their habitats throughout the neotropics. Without the habitats and monkeys, funding will not be necessary as there will be nothing left for us to study.

Editors Martín Kowalewski, Paul Garber, Liliana Cortés-Ortiz, Bernardo Urbani, and Dionisios Youlatos are to be commended for this timely and informative two-volume series on the genus *Alouatta.* What is particularly special and impressive about this and its companion volume is the international roster of countries represented by the volume's contributors and, in particular, the welcome contribution of so many Latin American scholars. This cohort of productive and dedicated Latin American primatologists represents the single most profound change that has occurred in my 40 years of studying wild howler monkeys. Every country in Latin America but Chile and perhaps Uruguay hosts at least one species of *Alouatta* and some countries are host to two, three, or more howler species. The conservation future of howlers and their habitats depends on the knowledge and expertise of these local Latin American scholars, who are in the best position to validate the importance of howler conservation and who understand the politics and policies of their own countries. Their influence is necessary to develop those policies and implement those decisions about conservation areas which will serve to ensure the survival of all howler monkey species into the indefinite future.

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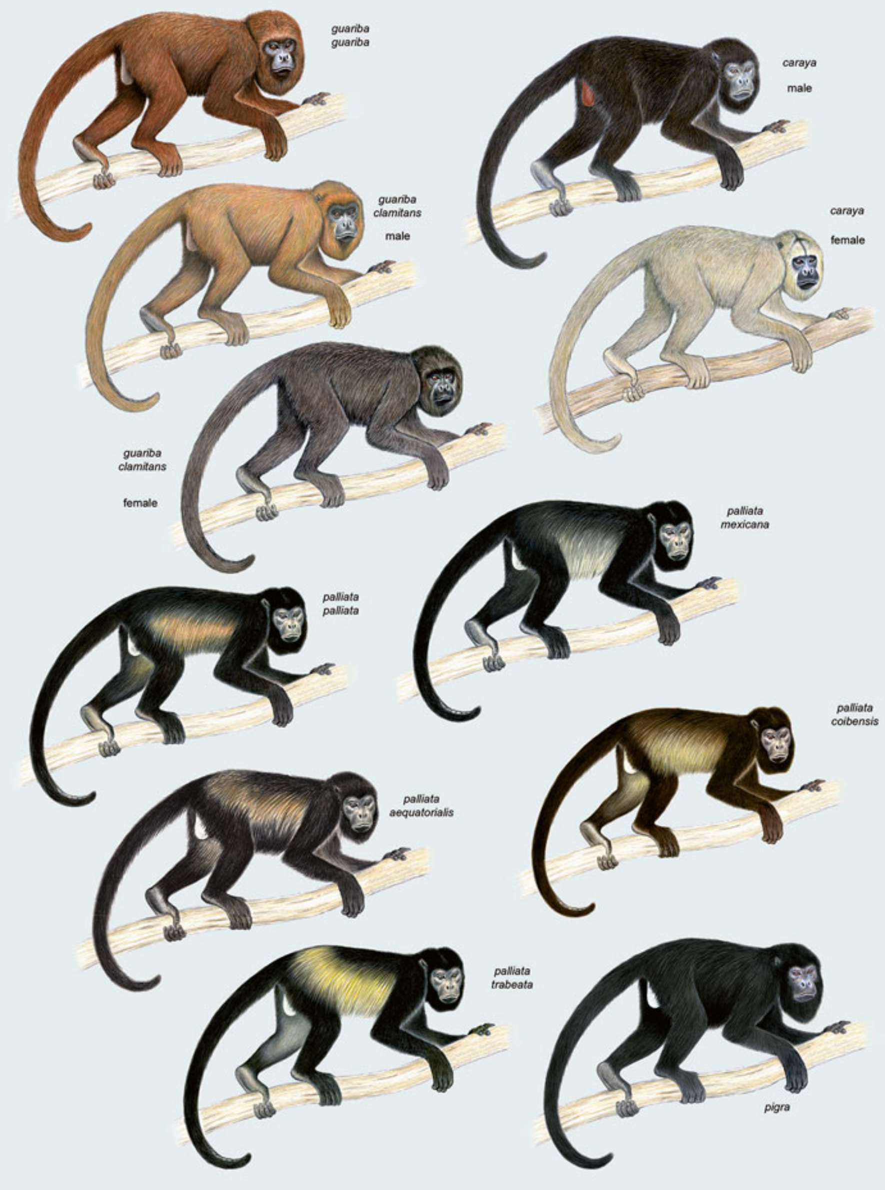
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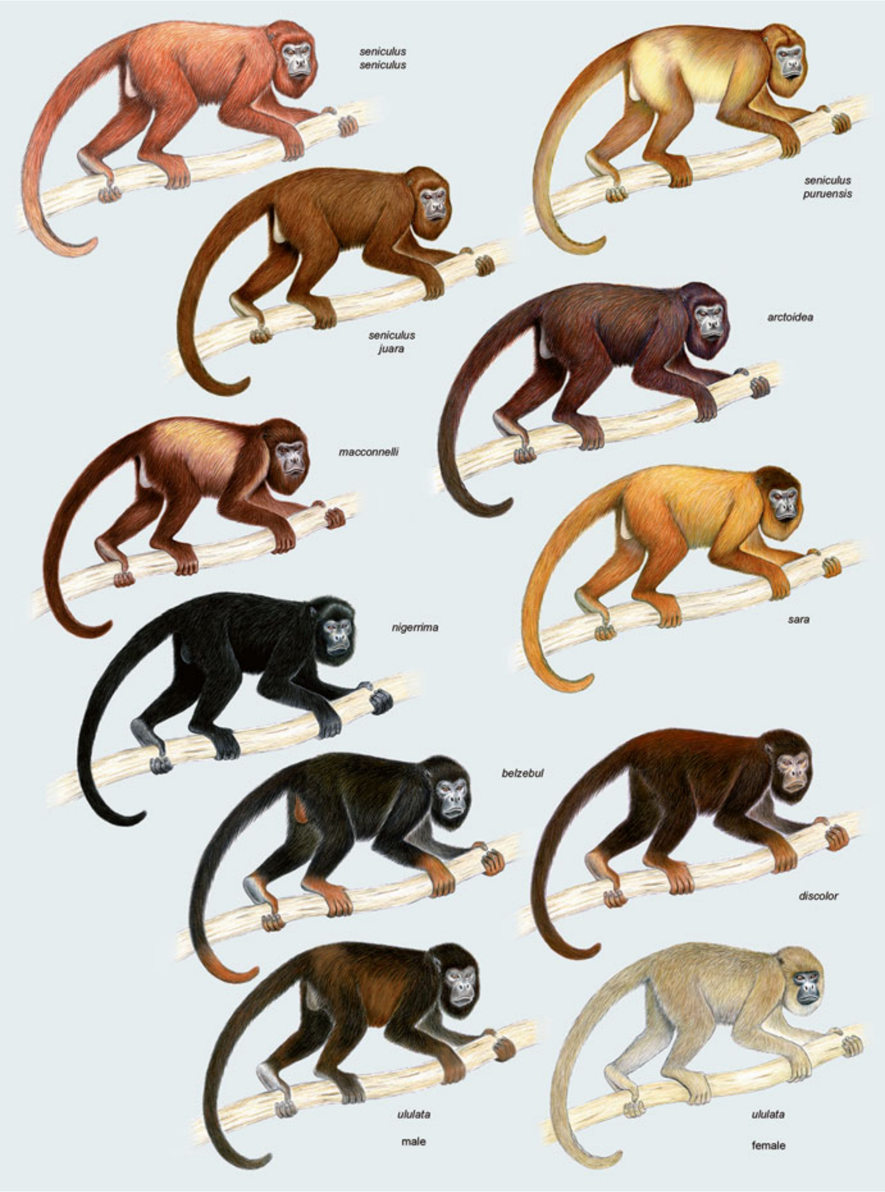
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Part I
Introduction

Chapter 1
Why Is It Important to Continue Studying the Behavioral Ecology and Conservation Management of Howler Monkeys?

Martín M. Kowalewski, Paul A. Garber, Liliana Cortés-Ortiz, Bernardo Urbani, and Dionisios Youlatos

1.1 Introduction

The goals of this first chapter to our volume "*Howler Monkeys*: *Behavior*, *Ecology, and Conservation*" are to highlight the importance of long-term studies for understanding howler behavioral ecology, evaluate the concept of howlers as a colonizing species, and to identify those aspects of howler behavior that are well studied from those that require further study. Although there have been numerous studies of individual species of howler monkeys, and several reviews of the genus *Alouatta*, there

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was only one volume dedicated to *Alouatta*. This was a special issue of the *International Journal of Primatology* (issue 3) published in 1998. This issue, edited by M. Clarke, was the result of a symposium entitled "*Howlers*: *Past and Present*," organized by K. Glander at the 1988 Congress of the International Primatological Society held at Brasilia, Brazil. In this seminal volume there are 11 contributions, four of them were reviews (two on the conservation status on howlers, one on parasites, and one on population characteristics), four were on *A. palliata*, and two on *A. arctoidea*. This issue was an important contribution to the study of howler monkeys, but also revealed our limited knowledge of the vast majority of howler species. Given significant advances in the tools available to primate researchers coupled with a dramatic increase in the number of howler species and groups studied, we have put together a single comprehensive volume that integrates our current knowledge of the behavioral, ecological, social, and evolutionary processes that have shaped the life history of this taxon. Our volume includes 15 chapters divided into four sections (1) introduction, (2) behavioral ecology, (3) conservation and management, and (4) conclusion.

This volume is best considered a companion volume to book we have just published entitled "*Howler Monkeys*: *Adaptive Radiation*, *Systematics*, *and Morphology*". Each chapter in both volumes identifies directions for further research on howler monkeys using a comparative framework. In developing both volumes, we have relied on the expertise of researchers from habitat countries. A total of 18 out of 28 (64 %) chapters in the two volumes were led by a Latin American or non-Latin-American that lives permanently in this region, and 25 out of the 28 chapters (89 %) have at least one Latin-American coauthor. Thus, we acknowledge the growing number of Latin American scholars who currently study Neotropical primates in situ and emphasize the importance of highlighting this research to ensure the continuity of long-term projects that can increase the understanding of Latin American primates.

1.1.1 The Relevance of Long-Term Studies

Since Carpenter's (1934) initial field investigation of mantled howler monkeys in Panama, studies of howler monkeys have been carried out across much of South and Central America. Some of these studies have resulted in the establishment of long-term research sites. Data from these long-term study sites are critical for developing a framework from which to understand behavioral variability, and demographic and life history patterns in howlers. To highlight the impact that long-term studies have made to our understanding of howler behavioral ecology, we describe a few examples and their contributions.

Milton's (1980) volume on the howler monkeys of Barro Colorado Island (hereinafter referred to as BCI), Panama, informed a generation of primatologists. In her book, she presented detailed quantitative data on mantled howlers feeding behavior, ecology, and nutritional strategies suggesting that these howlers were selective feeders, central place foragers, and behavioral folivores. Milton and colleagues went on to publish highly innovative studies of howler nutritional ecology, gut microbial ecology, digestive strategies, and food choice that stand today as primary references for researchers studying the feeding ecology of any primate. Milton also used howlers to address questions regarding the evolution of human and nonhuman primate cognition and intelligence and the challenges primates face when relying on group-based vs. individual-based ecological information. Today, Katie Milton remains an active researcher examining questions of howler genetics, social behavior, and mating strategies. Milton and colleagues (Ryan et al. 2008) also examined census data from 1974 and 2000 (except 1984) on the howler population on BCI. Their data suggest that the reproductive success of adult males and females decreased with group size (using both infants and immature individuals as a proxy for reproductive success—see Treves 2001). They also found a negative relationship between individual male reproductive success and the number of adult males in a group, but no relationship with the number of adult females in a group. In this regard, Ryan et al. (2008) suggest that female mantled howlers should choose groups that contain a high proportion of males, but males pay a cost for belonging to a group containing a high proportion of males because the presence of additional males will, on average, reduce the access of each male to reproductively active females. However, a single howler male needs the assistance of other adult males to successfully defend the group, resources, and mates within their home range, and this shifts the cost/benefit ratio in favor of the addition of multiple adult males and sharing group residence. This pattern has been also documented in long-term studies of *A. caraya* in northern Argentina (Kowalewski and Garber 2010, 2014; Garber and Kowalewski 2013). In this species, males in multimale groups appear to share access to adult females and participate collectively in group defense during intergroup encounters. Long-term studies give support to the idea that demographic changes in group size and adult sex ratio are the proximate drivers of male and female reproductive strategies.

Compared to other atelines, howlers are characterized by an earlier age at first reproduction and a shorter interbirth interval, and therefore a higher reproductive output (Di Fiore et al. 2011). Recent long-term data indicate that howler reproductive output is affected by food availability. For example, based on almost 6 years of data on more than 50 groups of *A. caraya* inhabiting two nearby study sites, Kowalewski and Zunino (2004) provide data that the observed variation in the timing of births was a facultative response to changes in food availability. The site characterized by a marked birth peak exhibited a long and pronounced cold season (4–5 months) during which several food items were limited, whereas groups inhabiting the site characterized by increased food availability and a shorter cold-dry season (2–3 months) had a more even distribution of births throughout the year. Groups living at these sites also differed in the proportion of multimale vs. unimale groups, the degree of home range overlap, and differences in the frequency of infanticide. These differences serve to identify a demographic-reproductive-resource pattern for black and gold howlers in which food availability across the year, the social structure of neighboring groups, and intergroup interactions directly influenced patterns of reproduction and mating.

Pavé et al. (2012) evaluated patterns of infant mortality across 8 years of data on 29 groups in the same population of *A. caraya*. The authors found that of 113 infants born during the study, 53 died prior to the age of 6 months. The cause of death for 24 was unknown. However, 19 infant deaths were attributed to periods of intense flooding, eight infants died/disappeared after the replacement of the breeding male, two infants died within 1–2 days after birth (presumably of disease or congenital effects), and one infant died from injuries received during an intergroup encounter. Thus, almost 20 % of infant deaths occurred in the context of male replacement. However, infants living in unimale–multifemale or age-graded male–multifemale groups experienced a higher risk of infanticide (0.15 male replacements/month) than infants living in multimale–multifemale groups (0.02 male/replacement/month). Thus, a benefit to *A. caraya* of living in a multimale group is male-collective action in mate, group, and infant defense (Kowalewski and Zunino 2004; Kowalewski and Garber 2010; Pavé et al. 2012). Finally, almost 20 years of group monitoring of *A. caraya* in disturbed forests under increasing fragmentation showed that group sizes and adult male: adult female ratios have remained virtually constant (Zunino et al. 2007). However, at these sites there is evidence that groups are composed of closely related females, possibly due to the difficulties of moving across a highly fragmented landscape (Oklander et al. 2010).

In sum, long-term data from BCI, Panamá as well as Isla Brasilera and Estación Biológica Corrientes, Argentina, indicate that (1) individual females and males may alternate reproductive strategies across different years based on the history of their individual social groups, (2) mortality caused by disease, natural disasters, and male replacement is an important regulator of population demography and group history, (3) within-group physical aggression is infrequent, and (4) individuals appear to solve everyday problems such as locating food, forming social bonds, and obtaining access to mating partners using a wide range of alternative behavioral tactics.

Since late 1970s and early 1980s, K. Glander and colleagues including Margaret Clarke, Evan Zucker, and Clara Jones, among others, have initiated pioneer studies on the behavior and ecology of mantled howler monkeys at Hacienda La Pacifica, Guanacaste, Costa Rica. The first studies at Hacienda La Pacifica concentrated on forest ecology and its effects on resource seasonality (i.e., 1978, 1979, 1980, 1981). This site was severely deforested in the 50s (Clarke et al. 2002), but small areas of upland and riparian deciduous forests remained relatively unchanged (see complete description in Glander 1992; Clarke and Glander 2008). Demographic studies began in the 1980s and have shown that mantled howlers of both sexes migrate when juveniles (Glander 1980, 1990, 1992; Clarke 1982, 1983, 1990; Clarke and Glander 1984), and that immigrants who are successful in entering a new group, remain in that group only if they can become dominant to all other same-sex residents. After leaving their natal group, males remained solitary for up to 4 years, whereas female were able to join established groups within a few months. In general, this immigration pattern produced a reversed, age-graded dominance hierarchy; older animals—those with the longest tenure in the group—generally were lower-ranking (based on agonistic interactions) but had higher reproductive success, while the more recent immigrants who were younger achieved a higher-rank (Glander 1980; Jones 1980b;

Clarke and Glander 1984). This pattern appears to differ from howlers at other sites, in which both younger and older adults behave as central or the most dominant male (Kowalewski and Garber 2010; Oklander et al. 2014). Clarke and Glander (2010) evaluated data from 1975 to 2009 to explore secondary transfer of adult mantled howlers. They found that secondary transfer does occur in both adult males and adult females. For example, evidence from seven groups indicate that 35 % of all of the adult male group members were potential secondary transfers, while 29 % of all of the adult female group members were potential secondary transfers. The mechanisms involved in the decision of howlers to attempt secondary transfer remain unclear. This long-term site also provided an extensive database on social and sexual behavior and inter-individual relationships in *A. palliata*. (i.e., Jones 1979, 1980a, b, 1985, 1995; Clarke and Glander 1984; Clarke and Zucker 1994). These studies have shown some behavioral patterns that are particular to this site. For example, only the alpha male in each social group appears to have access to estrous females (Glander 1980), whereas on BCI (Wang and Milton 2003) or in northern Argentina (Kowalewski and Garber 2010) all adult males in a given social group have access to resident adult females (see van Belle and Bicca Marques, 2014). As mentioned above, rank was reported to be inversely related to age in male and female *A. palliata* (Jones 1980a; Zucker and Clarke 1998). Jones (1980a) created dominance matrices based on the outcome of dyadic interactions over feeding and resting sites and male access to estrous females. This author reported a rate of 1.8 aggressive actions per hour per individual. Zucker and Clarke (1998) constructed dominance social hierarchies based on outcomes of dyadic agonistic interactions of adult females. They reported rates of female–female agonistic interactions of 0.0004 aggressive acts per hour per individual. It also has been argued that in *A. palliata* and *A. arctoidea*, male rank was correlated with reproductive success [*A. palliata* (Jones 1985), *A. arctoidea* (Pope 2000)]. Jones (1980a, 1985) also argued, based on limited observations, that male and female dominance hierarchies in *A. palliata* were related to reproductive success. Based on genetic studies in *A. arctoidea*, Pope (2000) found that the dominant male in multimale groups fathered all of the offspring during his tenure. She argues that although the reproductive success of a subordinate male is extremely low, his chance of establishing and maintaining a new bisexual group may be even lower. Zucker and Clarke (1998) suggested that the variability in female relationships in *A. palliata* at Hacienda La Pacifica could be attributable to the immigration of new females into the group, the presence of infants, or changes in male membership in the group. Finally, Clarke et al. (2002) present data on the effect of deforestation in this population from 1991 to 1998. Although they found that total population size (of 23 groups) was identical and group size similar, the number of adult males and females per group decreased (males 2.52 ± 1.95 vs. 1.59 ± 0.56; females 6.78 ± 5.13 vs. 4.79 ± 2.24) with a 12 % reduction in suitable habitat. However, the proportion of infants vs. adult female increased suggesting stabilization or recovery after deforestation.

Since the late 1970s, Alejandro Estrada has led an active research program on the behavior, ecology, and conservation of howlers. Estrada's work at the site of Los Tuxtlas, Mexico, on mantled howlers and more recently at Palenque National Park on black howlers has provided critical demographic data on group size and composition, howler feeding ecology, the role of howlers as agents of seed dispersal in rainforest communities, and on howler conservation (see Estrada 2014). Estrada's approach to howler conservation has focused on the human dimension of the problem including the understanding that without improving the economic, health, and social conditions of the local human population, most conservation efforts will fail. His research indicates that countries with the greatest income inequality, highest population density, and lowest human development index also have the highest rates of deforestation. A recent paper by Estrada and colleagues (Zarate et al. 2014) evaluated the viability of howler populations (*A. pigra*) in the context of agroforestry (groups inhabiting shade cacao plantations). They found that not only were howler populations sustainable in this type of modified landscape, but that across a range of differently disturbed forest fragments where other large mammals are absent, howlers play a major role in seed dispersal. Through seed dispersal, howlers influence forest regeneration and alter habitats in ways that can enhance their long-term sustainability, even in heavily impacted forests and agroforests. Other research by Estrada has looked at the role of dung beetles as secondary dispersers and predators of seeds voided by howler monkeys. Finally, Alejandro Estrada is the coeditor of two recent companion volumes on the behavior, ecology, and conservation of Mesoamerican primates (Estrada et al. 2006) and South American primates (Garber et al. 2009). Although these volumes focus on a taxonomically diverse set of platyrrhines, the genus *Alouatta* is featured prominently in each volume, and Estrada's commitment to rainforest conservation, protecting primate populations, and understanding the macro effects of deforestation and ecosystems health on the local human populations is central to the development of effective conservation action plans.

The value of maintaining long-term studies is that they provide an essential data base from which to evaluate how individual responses to natural perturbations in rainfall, food availability, temperature, sex ratio at birth, demography, disease, and predator pressure, in conjunction with anthropogenic change and human population increase affect fitness and population survivorship and ecosystem's health. The major problems faced by researchers in continuing long-term studies are difficulties in acquiring sufficient funding, obtaining local permits, and the political instability present in some countries. The number of long-term field sites where howlers have been studied is limited, and it is imperative to highlight the importance of continuing to gather data at these long-term sites because they are critical for answering questions on primate life history, adjustments to ecological changes, and population dynamics (Glander 1981).

1.1.2 Howler Monkeys as Colonizers

A number of studies and reviews (i.e., Crockett and Eisenberg 1987; Neville et al. 1988; Kinzey 1997; Sussman 2003; Di Fiore et al. 2011) of the genus *Alouatta* have suggested that howlers are characterized by marked variability in behavior, ecology, and social organization within and between species. In 1979, John Eisenberg proposed that howlers represent pioneer species given their ability to consume leaves, their widespread distribution, and their ability to survive in a wide variety of habitats. A pioneer species can be defined as a taxon that can effectively colonize new, changing, or open habitats (i.e., marginal habitats, areas of marked anthropogenic disturbance). The statement that howlers are pioneer or colonizer species has often been restated; however, this hypothesis has never been fully tested. Testing whether howlers are colonizing species would require long-term demographic, ecological, geographical data on population expansion, data on the success of individual howler species in founding stable populations in newly available landscapes, as well as detailed studies of behavioral change in populations that live in habitats transformed by anthropogenic activities. In the absence of such data, we need to rethink our research questions and define more clearly the limits of howler behavioral, ecological, and social variability in order to understand their widespread distribution. For example, certain aspects of howler behavior and ecology are characterized by very limited variability. At all sites and in all howler species, individuals rest 60–80 % of the time. Day range in virtually all howler groups averages less than 600 m. In most howlers species (*A. palliata* is the lone exception) established groups rarely contain more than 2–4 adult males and 2–4 adult females. Thus, certain important aspects of howler behavior, ecology, and group dynamics are highly conserved. Other aspects of howler behavior and ecology are more labile. New techniques in the fields of genetics, endocrinology, parasitology, food nutrient analysis, and microbiology (to understand gut microbiome community composition) can be used to better understand the basis and limits of the variation in howler monkey diet, group size, and ability to survive in high altitude/cold and highly fragmented landscapes. The goals of our volume are to present new empirical and theoretical research on this highly successful primate genus.

1.1.3 How Easy Is It to Study Howlers in the Field?

Howler monkeys were among the first primates described by naturalists visiting the Neotropics. For example, in the "Descent of Man and Selection in Relation to Sex", Darwin (1871) described howlers as an example of the evolution of sexual dimorphism. Darwin explains "….The vocal organs of the American *Mycetes caraya* are one-third larger in the male than in the female, and wonderfully powerful. These monkeys in warm weather make the forest resound at morning and evening with their overwhelming voices. The males begin their dreadful concert, and often continue it during many hours, the females sometimes joining in with their less powerful voices. An excellent observer, Rengeer, could not perceive that they were excited to begin by any special cause; he thinks that, like many birds, they delight in their own music, and try to excel each other…" (Darwin 1871: 546).

Given their relatively small home range, small day range, widespread geographical distribution, ability to exploit small forest fragments and anthropogenically disturbed habitats near human settlements, and the fact that they howl on most mornings, howlers would appear to be a relatively easy primate to study. A search of *Google academic* using the term *Alouatta* indicated that the number of published studies of howler monkeys (including journal articles, book chapters, and meeting abstracts) is comparable to the material published on *Ateles* and approximately 50 % less than the number of publications on *Cebus* (plus *Sapajus*). Naturalists such as Rengger (1830, cited in Carpenter 1934) reported that black and gold howlers were "…slow and sluggish in locomotion…", even Carpenter (1934: 20) described them as "serious, slothful, melancholy, phlegmatic, and peaceful". This early interpretation of howler behavior may have influenced researchers and graduate students in the decision to study howlers. In addition, given that genera such as *Cebus* or *Ateles* are considered by many as better models for the study of human behavior, cognition, ontogeny, and evolution, it is not surprising that these genera also are among the most commonly studied New World primates.

1.2 Book Organization

The current volume is organized into four sections that present original studies and comprehensive reviews, plus an introductory and a concluding chapter.

1.2.1 The Behavioral Ecology of Howlers

This section of the volume presents studies on howler behavioral ecology and reviews studies across species. In Chap. 2, Dias and Negrín present a comprehensive review of the howler diet based on the published literature. They present an overview of howler food resources and document dietary diversity across species, examining the effects of rainfall, group size, and forest size on dietary variation. Overall, howlers were found to use at least 1,165 plant species, belonging to 479 genera and 111 families as food sources. Rainfall patterns, group size, and forest size affected several dimensions of howler diet, such that the degree of frugivory increases with increased rainfall and forest fragment size, but decreases with increasing group size for individuals living in more productive habitats. These results provide new insights for future research on howler foraging strategies and nutritional ecology. It is possible that interspecific and inter-site variation in howler feeding behavior results from differences in food availability and digestive capabilities such as gut physiology, food transit time, and individual- and group-based differences in the diversity of the gut microbiome. This set of variables has seldom been modeled, and its understanding continues to be among the major challenges we face in howler research. In Chap. 3, van Belle and Bicca-Marques present a review on sexual selection in howler monkeys. Most of the data presented are based on a set of species that are generally characterized as having a polygynous (e.g., *A. arctoidea*, *A. seniculus* and *A. pigra*) and polygynandrous (e.g., *A. caraya* and *A. palliata*) mating system. Although there is variation in mating system both within and between species, females in all studied species copulate with multiple males within their group, with males in neighboring groups, and with solitary males, suggesting a "mixed mating strategy" characterized by periods of selective mating and periods of promiscuous mating (hormonal data come only from the study of *A. pigra* by van Belle). Due to mate guarding behavior, the number of adult males residing in the group, and male social hierarchies, central males may monopolize most breeding opportunities during the periovulatory period of the ovarian cycle when conception is most likely to occur by forming consortships with cycling females. These authors also discuss howler mating strategies in terms of intrasexual selection, mate choice, and intersexual conflict. In Chap. 4, Garber, Righini, and Kowalewski provide a new synthesis of published and unpublished data on the feeding behavior of several species of howler monkeys and provide evidence for three distinct dietary 'syndromes' that are generally consistent with phylogeny and biogeography. These include species with a fruit-dominated diet, species with a leaf-dominated diet, and species with a balanced fruit-leaf diet. These authors stress the importance of collecting data on feeding rates and nutritional composition of the diet, rather than to continue to use the indirect measure of feeding time, to obtain an accurate estimate of food intake, and a better understanding of species-specific dietary strategies. In addition, data presented in this chapter highlight the limitations of describing howlers as highly variable in the absence of defining the limits of variability and identifying traits that vary minimally from traits that are highly variable. In Chap. 5, Arroyo-Rodríguez and colleagues present an overview of the literature on seed dispersal by howler monkeys (*Alouatta* spp.) and assess the impact of howler seed dispersal for plant populations and communities. For many howler species 50 % of the amount of food ingested comes from fruit. For some plant species howlers are probably the primary dispersal agent (e.g., fruits with large seeds and/or with hard indehiscent husks), especially in small and anthropogenically disturbed forest fragments where other large-bodied frugivores tend to be absent or are locally extinct. In this regard, howlers contribute to secondary succession, aiding in the restoration of degraded habitats. Although certain components of howler seed dispersal such as seed shadows, post-dispersal seed fate, and seed/seedling survival need to be studied in greater detail, current information suggests that howler monkeys are effective seed dispersers for many plant species, with important consequences for plant communities and forest regeneration. In Chap. 6, Cristóbal-Azkarate and colleagues provide a review of howlers as members of an ecological community. These authors examined data from 10 howler species from 43 different neotropical sites. They found that howlers interacted with 10 other primate species, six mammalian predator species, five non-predatory mammals, 10 raptors, five nonraptor avian species, and one reptile species. Capuchin monkeys, spider monkeys, and coatis (*Nasua nasua*) were the most common species that howlers interacted with. The majority of all reported interactions occurred in fruiting trees and was, in general, pacific, although howlers were frequently harassed by other monkeys. An important aspect of these interactions involved predation, with large felids and harpy eagles being the most common predator of howlers. The authors conclude that anthropogenic effects have directly and indirectly transformed these interactions, increasing feeding competition and altering the nature and form of predator–prey relationships in howlers. Chapter 7 focuses on cooperation and collective action in howler monkeys. Kowalewski and Garber examined evidence of collective behavior across howler species, in particular black and gold howlers (*A. caraya*) in Argentina, and argue that collective action is not only beneficial for the actors but also for other members of the group. The authors present evidence for individual variation among males with regard to the frequency and context of male cooperative behavior and provide comparative data on male collective action in other howler species. The results indicate that individuals may adjust their participation during intergroup encounters in order to reduce the costs and enhance the benefits of collective action in maintaining reproductive access to resident females. In Chap. 8, Youlatos and Guillot review the current knowledge and present new unpublished data on howler postural and locomotor behavior and prehensile tail use. The authors argue that the positional behavior and tail use in different species of howler monkeys present a consistent pattern. Quadrupedal walk, clamber, vertical climb, sit and tail-hindlimb-hang compose the main positional modes, with Amazonian species emphasizing increased clamber, climb, and tail-assisted suspension more than species from Mesoamerica and the southern cone. Regarding the prehensile tail, the authors found that its use increased during feeding bouts and was associated with stability during food acquisition. Chapter 9 examines ranging behavior and spatial cognition in *Alouatta*. Barbisan Fortes and colleagues performed a multivariate analysis identifying the set of factors that exert the strongest influence on home range area and daily path length. Their results found that day range was negatively affected by population density and positively affected by group size. In addition, they found that *A. palliata* used significantly larger home ranges than other howler taxa. Finally their review of recent studies indicates that howlers use a route-based spatial representation when navigating in the forest.

1.2.2 Conservation and Management of Howlers

The third section of the volume focuses on howler monkey conservation and management under captive and wild conditions. Authors evaluate the impact of natural catastrophes and ecotourism on howler behavioral ecology, patterns of human interactions with howlers through history, and howler conservation in the twenty-first century. Urbani and Cormier (Chap. 10) review human–howler interaction based on evidence from the archaeological record and the ethnography of contemporary indigenous societies. The authors argue that although howlers represent a preferred prey species for many indigenous populations, their consumption is subject to cultural taboos in many contemporary indigenous societies. Furthermore, as revealed in an extensive array of myths, howlers play an important role in sacred and social symbologies, as subjects of contagion, transformation, and reflexivity.

In Chap. 11, McKinney and colleagues examine the affects of anthropogenic disturbance on howler diet and demography by discussing the use of matrix landscapes, effects of ecotourism, and the potential harmful affect of howlers as crop-raiders. The authors present three case studies from Suriname, Costa Rica, and Mexico. In all three cases, the local howler populations exhibited negative behavioral and health affects resulting from the presence of tourists and habitat modification that caused the howlers to raid crops. There also was a positive benefit to howler conservation through ecotourism. For example, the authors argue that the management of howler populations for ecotourism can be financially beneficial to local communities while maintaining favorable conditions for howler conservation. However, the effects of ecotourism on primate populations must be monitored carefully and re-evaluated frequently. In Chap. 12 on the health and welfare of howler monkeys in captivity, Pastor-Nieto outlines the conditions that should be met in order to achieve adequate captive management. Given that howlers can be difficult to maintain in captivity, proper management of different sex and age classes requires designing enclosures to stimulate natural social behavior and the creation of programs for captive enrichment, adequate nutrition, and proper diagnosis and treatment of health problems. Moreover, the maintenance of establishing healthy captive populations for *ex situ* conservation plans and future reintroductions back into the wild may become an important conservation tool. In Chap. 13, Behie and Pavelka analyze the effect of a hurricane on the population demography of *A. pigra* in Belize. These authors found that frugivory was an important part of the feeding ecology of this howler species and that periods of prolonged fruit shortage had a more significant impact on population survival and reproduction than the availability of leaves. These results are consistent with the studies by Amato and Garber (2014), Dias and Rangel-Negrín (2014), and Garber et al. (2014) that highlight the importance of fruit feeding in the howler diet. Thus, despite the fact that howlers can consume a leaf-based diet during many months of the year, as in other atelines, fruits are an essential dietary component. Given that both natural and anthropogenic habitat disturbance generally have a negative effect on fruit production, this could have important conservation implications for this primate genus. Finally, Estrada presents a review on howler monkey conservation that focuses on the human component of the problem (Chap. 14). He presents data from the Food and Agricultural Organization of the United Nations indicating that the high rates of human population growth have created unparalleled demands for food production and other goods and services resulting in increasing forest loss and habitat destruction. In addition, the human population in forested areas or near forests generally fails to profit from environmental change as poverty and health problems increase and longevity decreases. Estrada reports that 60 % of *Alouatta* populations in Central and South American exist outside of protected areas, suggesting that conservation efforts are needed at the landscape level. In his chapter, Estrada advises researchers to consider the social dimension of the human condition in Latin America when developing conservation strategies for the protection of howlers. Collaboration among local and foreign researchers is a critical step in understanding the complexities of political, social, and financial problems in habitat countries and in developing equitable solutions to these problems.

1.3 Conclusions

A major goal of each of our two volumes on *Alouatta* is to integrate published and unpublished data on howler monkeys into a framework that can be used to study other primate radiations. Thus, we feel that these books will be of strong interest to students and researchers examining a range of issues in tropical ecology, mammalian biology, anthropology, primatology, and conservation. In addition, it is relevant to point out that encounters with howler monkeys are common in the field, and most primatologists studying in tropical and subtropical America have observed one or more of the currently described taxa. Therefore, we foresee these two companion volumes as a centerpiece in contributing to the scientific literature on primates, neotropical community ecology, and conservation. Finally, we want to stress that, although many authors have contributed directly to this volume, there are other scholars who have contributed greatly to our knowledge and understanding of howler behavioral ecology, demography, and evolution. Their contributions have made this volume possible. Most certainly this includes Clarence Raymond Carpenter, Margaret Clarke, Kenneth Glander, Robert Horwich, Katharine Milton, Miguel Schön Ybarra, and Gabriel Zunino. Additionally absent are many graduate students currently gathering new and innovative data that will certainly broaden our knowledge in the near future.

So, why is it important to continue studying howlers? As for many other primate species, critical data remain to be collected. We need to promote the development and maintenance of long-term study sites that include populations of the same species living in diverse environments in order to understand the adaptability of the genus *Alouatta*. In addition, we need to collect data to define the set of conditions that promote phenotypic variability in howlers. Furthermore, long-term data on a broad set of taxa will facilitate comparative analyzes needed to explore the underlying mechanisms of behavioral, ecological, and genetic variability. Newly available methodologies are critical for addressing twenty-first century questions in primatology. These techniques include molecular genetics, GIS technology, portable high-definition and high-speed video recording, hormone analyses, nutritional analyses of plant foods, and the use of new tools to monitor and identify disease, the gut microbiome, and invertebrate and vertebrate DNA present in primate feces. Although these technologies may increase the cost of research, each will advance our understanding of howler monkey behavior, ecology, and evolution. These new studies also will require the collaboration of multidisciplinary research teams across countries. Many of the chapters in this volume are the result of such collaboration and irrefutable proof that we, as primatologists, are heading in the right direction.

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Part II
Behavioral Ecology

Chapter 2
Diets of Howler Monkeys

Pedro Américo D. Dias and Ariadna Rangel-Negrín

Abstract Based on a bibliographical review, we examined the diets of howler monkeys to compile a comprehensive overview of their food resources and document dietary diversity. Additionally, we analyzed the effects of rainfall, group size, and forest size on dietary variation. Howlers eat nearly all available plant parts in their habitats. Time dedicated to the consumption of different food types varies among species and populations, such that feeding behavior can range from high folivory to high frugivory. Overall, howlers were found to use at least 1,165 plant species, belonging to 479 genera and 111 families as food sources. Similarity in the use of plant taxa as food sources (assessed with the Jaccard index) is higher within than between howler species, although variation in similarity is higher within species. Rainfall patterns, group size, and forest size affect several dimensions of the dietary habits of howlers, such that, for instance, the degree of frugivory increases with increased rainfall and habitat size, but decreases with increasing group size in groups that live in more productive habitats. Moreover, the range of variation in dietary habits correlates positively with variation in rainfall, suggesting that some howler species are habitat generalists and have more variable diets, whereas others are habitat specialists and tend to concentrate their diets on certain plant parts. Our results highlight the high degree of dietary flexibility demonstrated by the genus *Alouatta* and provide new insights for future research on howler foraging strategies.

Resumen Con base en una revisión bibliográfica, examinamos las dietas de los monos aulladores para describir exhaustivamente sus recursos alimenticios y la diversidad de su dieta. Asimismo, analizamos los efectos de la pluviosidad, tamaño grupal y tamaño del bosque en que viven los grupos sobre la variación en su dieta. Los monos aulladores consumen casi todas las partes vegetales presentes en sus hábitats. El tiempo dedicado al consumo de diferentes tipos de alimentos varía entre especies y poblaciones, de tal manera que la conducta alimenticia de los monos aulladores puede ser altamente folívora o frugívora. Los monos aulladores usan como recurso alimenticio al menos 1,165 especies de plantas, pertenecientes a 479 génerosya 111

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familias. La similitud (medida con el índice de Jaccard) en el uso de taxa de plantas como alimento es mayor dentro que entre especies, aunque la variación en los índices de similitud es mayor dentro de una misma especie que entre diferentes especies. La pluviosidad, el tamaño grupal y el tamaño del bosque afectan diversas dimensiones de la conducta alimenticia de los monos aulladores, de tal modo que, por ejemplo, la frugivoría incrementa de manera directamente proporcional con la pluviosidad y el tamaño del bosque, pero disminuye en grupos grandes que viven en hábitats más productivos. Por otra parte, el rango de variación en los hábitos alimenticios se correlaciona positivamente con la variación en la pluviosidad, sugiriendo que algunas especies de monos aulladores son generalistas de hábitat y tienen dietas más variadas, mientras que otras son especialistas de hábitat y tienden a concentrar sus dietas en ciertas partes vegetales. Nuestros resultados subrayan el notable grado de flexibilidad alimenticia del género *Alouatta* y aportan nuevas perspectivas hacia futuras investigaciones sobre las estrategias de forrajeo de los monos aulladores.

Keywords *Alouatta* • Cross-species comparisons • Dietary diversity • Herbivory patterns

2.1 Introduction

In the 80 years following the pioneering study by C.R. Carpenter on the behavior of mantled howler monkeys (*Alouatta palliata*) of Barro Colorado Island in Panama, our knowledge of the howler diet has increased substantially. Current data provide evidence that members of the genus *Alouatta* are eclectic herbivores and present a very selective foraging profile combined with a highly diverse diet. This dietary pattern, a number of behavioral adaptations and digestive flexibility, allows howlers to efficiently solve the basic problem of meeting their nutrient requirements each day while staying below their maximum threshold for toxins. In this chapter we build on previous reviews of the diets of howlers (Crockett and Eisenberg 1987; Neville et al. 1988; Bicca-Marques 2003; Di Fiore and Campbell 2007; Cristóbal-Azkarate and Arroyo-Rodríguez 2007; Chaves and Bicca-Marques 2013) to better understand variation across species and populations for two main topics: (1) the food types and food taxa selected by howlers and (2) the extent and overall diversity of the howler diet. Additionally, we examine how the diet of howlers may vary throughout a gradient of high folivory to high frugivory as a function of rainfall, group size, and the size of the forests they inhabit. These three factors have been described as important determinants of the food habits of howlers, as: (1) rainfall is associated with habitat productivity and seasonality, and therefore, food availability (e.g., Dunn et al. 2010; Palma et al. 2001); (2) group size may affect within-group scramble competition for food, so that larger groups deplete food patches faster (e.g., Arroyo-Rodríguez et al. 2011); (3) forest size correlates positively with the number of food sources available for howler monkeys (e.g., Arroyo-Rodríguez and Dias 2010). Finally, we analyze the influence of rainfall, group size, and forest size on the dietary breadth (i.e., the patterns of plant species and plant family use) of howlers.

2.2 Literature Review

2.2.1 Database and Analyses

We reviewed all published articles, book chapters, and unpublished dissertations available on ProQuest Dissertations &Theses Database (ProQuest LLC, Ann Arbor, MI, USA) as well as those in digital libraries of Latin-American universities up to January 2012 that focused on the diet of *Alouatta*. When data from a thesis were published, we only used information presented in the publication. In this chapter we follow the howler taxonomy proposed by Cortés-Ortiz et al. (2003).

From each study, we extracted the following information for each sampled howler group: (1) the proportion of daily activity time spent feeding; (2) the proportion of feeding time dedicated to eat leaves (both mature and young leaves), fruits, flowers, and other food items (OFI); (3) the number of plant species and families used as food sources. Data on plant taxonomy were homogenized using relevant taxonomic literature and online databases (Tropicos, IPNI, ILDIS) by checking for synonyms and misspellings. The taxonomic treatment of plant families follows the Angiosperm Phylogeny Group II classification (APG 2003); (4) percentage of total feeding time dedicated to the top five plant species; (5) the number of plant species comprising >50 % of total feeding time; (6) the number of plant species used as sources of leaves and the number of plant species used as sources of fruits; (7) group size, calculated as the mean number of individuals present in each group during the sampling period; (8) average annual rainfall (in mm) at each study site. When this information was not provided by the authors, we consulted it at WorldClim (Hijmans et al. 2005); (9) forest size (in ha), calculated as the amount of continuous habitat available to each group.

To reduce the influence of seasonality, variation in study duration and differences in study design on our results, in analyses of the use of food items and similarity in the use of plant taxa as food sources, we only used studies that: (1) included ≥9 months and ≥140 h of observations; (2) included data collected in both wet and dry seasons; (3) sampled feeding behavior using focal or scan sampling methods. To analyze variation in dietary breadth (defined as the number of plant species and families used as sources of food), we similarly used studies with a duration ≥9 months and that sampled feeding behavior with focal or scan sampling, but divided the number plant species and families by the number of observation hours to obtain a measure of breadth that could be directly compared among studies with different observation effort.

We used paired *t*-tests to compare the proportions of time dedicated to consume different plant parts and one-way ANOVA to compare: (1) dietary variables among howler species (followed by LSD post hoc tests); (2) the number of plant species used as sources of leaves and the number of plant species used as sources of fruits. We used Pearson correlations to analyze associations between: (1) the proportion of time dedicated to the consumption of different plant parts; (2) the number of plant species included in the diet and the percentage of total feeding time dedicated to the top five plant species; (3) the number of plant species comprising >50 % of total feeding time and the time dedicated to the consumption of different plant parts. To explore variation in the howler diet (higher folivory to higher frugivory) as a function of rainfall, group size, and forest size, we first used a PCA to combine data on the proportion of feeding time dedicated to eat fruits with the proportion of feeding time dedicated to eat leaves in a single variable that could be used to describe the dietary habits of howlers. From this analysis we obtained a component that explained 88.4 % of the total variance in both variables (eigenvalue = 1.8). This component (dietary habits hereafter) correlated positively ($r = 0.94$) with fruit consumption and negatively with leaf consumption ($r = -0.94$). Values of this component ≥1 indicate a mainly frugivorous diet (i.e., >50 % of feeding time dedicated to fruits). Second, we used a backward stepwise regression analysis to predict variation in dietary habits as a function of rainfall, group size, and forest size. Third, to further understand the relationships between the predictive variables that were included in the stepwise analysis and dietary habits, we performed piecewise regressions. These regressions allowed identifying discontinuities in the relationships between each predictive variable and dietary habit by determining breakpoints. A new stepwise regression was then calculated for each slope defined by the breakpoints, in which we again included all predictive variables. To normalize distributions and homogenize variances, in these analyses percentage data was converted to proportions and proportions were transformed using the square root of the arcsine; and rainfall, group size, and forest size were log transformed.

We used backward stepwise regressions to predict variation in the proportion of time dedicated to consume flowers and OFI, as well as in the dietary breadth of howlers as a function of rainfall, group size, and forest size. In these analyses the proportions of time dedicated to feeding and the rates of consumption of plant species and families were transformed using the square root of the arcsine; and rainfall, group size, and forest size were log transformed.

We analyzed intra- and interspecific similarity in the use of plant taxa with the Jaccard's coefficient: S_{ij} = number of taxa consumed in both sites i and j/total number of taxa consumed in either site i or j. Similarity was calculated at the family, genus, and species level.

2.2.2 Sample Characteristics

The majority of studies (55.8 %) that have addressed topics related to the diet of howler monkeys have been conducted with groups living in Brazil and México, whereas in Ecuador, Peru, and Surinam, respectively, only a single study related to the howler diet could be found (Fig. 2.1). For Bolivia, Guiana, Paraguay, and Uruguay, countries where howler monkeys also occur, we could not find any dietary studies. *Alouatta palliata* has been the most thoroughly studied species, followed by *A. pigra* and *A. guariba*. Among the least studied species are *A. belzebul* and *A. macconnelli*, and no studies could be found on the diet of *A. nigerrima* and *A. sara* (Table 2.1).

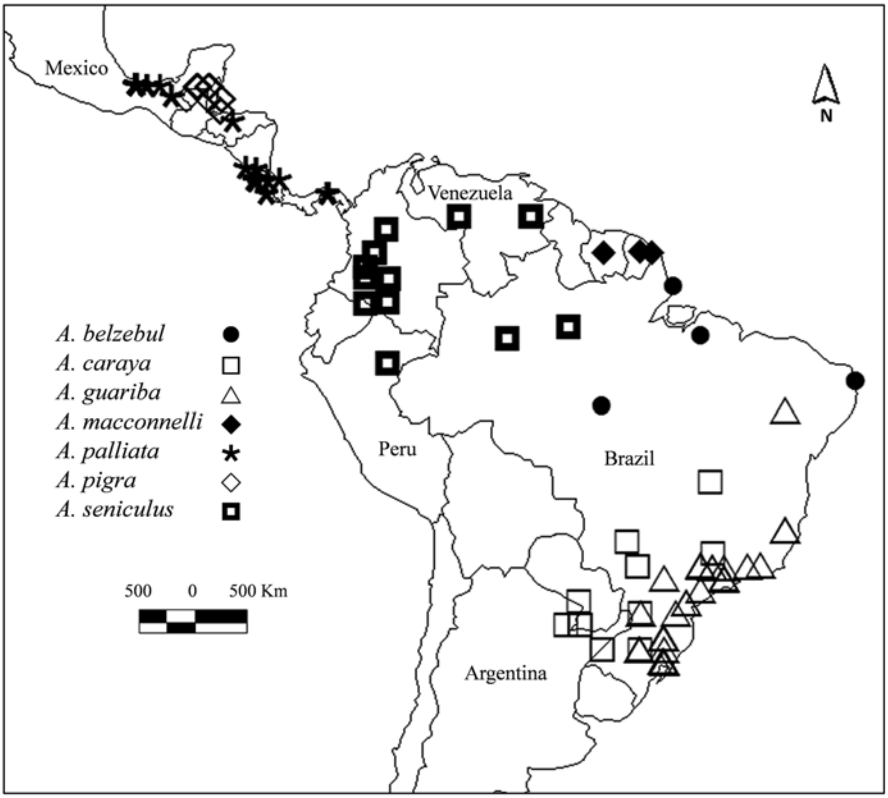


Fig. 2.1 Sites where the diets of howlers have been studied

More than half of all studies have been conducted with groups living in tropical dry forests (58.3 %; i.e., rainfall <2,000 mm), followed by groups in wet forests (27 %; i.e., rainfall >2,700 mm) and groups in moist forests (14.7 %; i.e., rainfall 2,000–2,700 mm). At the species level, all *A. belzebul* groups have been observed in moist forest, whereas all *A. caraya* and *A. guariba*, as well as the majority of *A. pigra* groups, live in dry forest. Conversely, the majority of *A. macconnelli*, *A. palliata,* and *A. seniculus* groups have been studied in wet forests. A similar number of groups have been studied in protected and unprotected forests (i.e., conservation status assigned by country's government), although most studies have been conducted in small forests: 47.1 % of studies were carried out in forests ≤100 ha, whereas only 18.5 % were carried out in forests ≥10,000 ha.

The diet of howler monkeys has been studied using a variety of different sampling methods. Most studies (98.2 %) relied on direct observations of the behavior of individuals within a discrete howler group or groups, and among these, the majority (72.4 %) used focal or scan sampling (Altmann 1974). Variation in the duration of studies is impressive, ranging from 1 week to 74 months and from 31 to 2,303

Table 2.1 Studies on the diet of howlers

Species	Study site	Year	Study length (months/h)	Sampling method	Group size	Rainfall (mm)	Forest size (ha)	Time feeding (%)^{a}	Plant items in diet (%)					No. species	No. families	%TFS^{b}	>50 % TFT^{c}	Sources fruits	Sources leaves	References^{d}
									Fruits	Leaves		Flowers	OFI^{e}							
										All^{f}	Young									
A. belzebul	Pacatuba, MG, Brazil	1985–1986	14/–	Scan	7	2,176	271	6.5	59.0	13.3	6.0	27.6	0.2	47	21	–	–	38	6	1
A. belzebul	Pacatuba, MG, Brazil	1998–1999	11/–	Scan	–	2,176	271	12.3	20.1	46.1	6.2	11.6	–	–	–	–	–	–	–	2
A. belzebul	Estação Científica Ferreira Penna, PA, Brazil	1997–1998	10/–	Scan	9	2,250	33,000	31.4	35.1	60.5	–	4.4	–	–	–	–	–	–	–	3
A. belzebul	Paranaíta, MT, Brazil	1999–2000	10/–	Scan	8	2,174	10,000	20	55.6	25.6	19.8	5.7	13.2	67	24	38.0	10	35	27	4
A. belzebul	Cauaxi, PA, Brazil	2000	10/1, 203	Scan	6	2,000	20,000	18.8	43.4	45.0	–	11.3	0.4	–	–	–	–	–	–	5
All *A. belzebul*^{g}					7.5 (6–9)	2,155.2 (2,000 –2,250)	12,708.4 (271–33,000)	17.8 (6.5–31.4)	42.6 (20.1–59)	38.1 (13.3 –60.5)	10.7 (6–19.8)	12.1 (4.4–27.6)	4.6 (0.2–13.2)	57 (47–67)	22.5 (21–24)	38	10	36.5 (35–38)	16.5 (6–27)	
A. caraya	Parque Nacional de Brasília, BSB, Brazil	1984	4/–	–	–	1,520	30,000	–	–	–	–	–	–	12	11	–	–	2	11	6
A. caraya	Ribeirão Preto, SP, Brazil	1980–1983	26/480	–	16	1,400	8.8	–	38.7	52.7	–	8.7	–	32	15	–	–	11	19	7
A. caraya	Riachuelo River, Corrientes, Argentina	1994–1995	2/200	Ad libitum	6	1,200	10	–	–	–	–	–	–	–	–	–	–	–	–	8
A. caraya	Riachuelo River, Corrientes, Argentina‡	1981–1982	15/528	Focal	7	1,200	7, 10, 12	–	29.0	71.0	–	–	–	23	17	~93	2	11	17	9
A. caraya	Isla Guáscara, Corrientes, Argentina‡‡	1981	3/58	Focal	10	1,200	40	–	–	–	–	–	–	12	10	–	–	5	12	10
A. caraya	El Piñalito, Misiones, Argentina*	2006–2007	12/734	Scan	10.8	1,952	3,796	–	19.0	64.0	25.0	6.0	10.0	56	–	40.4	9	7	9	11

A. caraya	Estabelecimento N.S[h] Conceição, RS, Brazil	2005–2006	12/699	Scan	13	1,500	0.7	14.9	12.3	82.4	–	2.7	2.6	14	13	61.7	2	9	12	12
A. caraya	Estância Casa Branca, RS, Brazil	1989–1990	12/745	Scan	16	1,500	2	–	28.9	60.9	15.6	2.7	7.5	27	18	77.4	3	20	18	13
A. caraya	Several locations in RS, Brazil	1989–1990/ 2005–2007	36/ 2,274	–	–	1,500	–	–	–	–	–	–	–	–	–	–	–	–	–	14
A. caraya	Isla Brasilera, Argentina*	1998–2000	17/ 1,680	Scan	18.5	1,230	141	18.9	19.0	64.0	13.0	12.0	5.0	22	13	–	–	17	12	15
A. caraya	San Cayetano, Corrientes, Argentina‡	2005–2008	–	Focal/ scan	6.75	1,230	–	–	–	–	–	–	–	–	–	–	–	–	–	16
A. caraya	Ilha Mutum, PR, Brazil	2004–2005	12/306	Scan	10	1,250	1,050	–	24.0	65.0	–	10.0	1.0	18	14	79.5	2	9	14	17
A. caraya	Rancho Praia Grande, PR, Brazil	2004–2005	12/288	Scan	12	1,250	–	–	46.0	49.0	–	4.0	1.0	18	11	84.4	3	9	13	18
A. caraya	N. Esperança and N. Querência, MS, Brazil	2002–2003	15/–	Scan	6	1,250	6,267	14.7	35.5	51.7	3.7	12.9	–	–	–	–	–	–	–	19
A. caraya	Corrientes, Argentina	–	–	–	6	1,200	12	15.2	26.7	70.5	–	0.8	2.0	–	–	–	–	–	–	20
A. caraya	Rancho Guaycolec, Formosa, Argentina	1988–1989	–	–	–	1,300	300	13.3	21.2	72.8	–	2.7	3.3	–	–	–	–	–	–	21
A. caraya	Tupanciretã, RS, Brazil	2006–2007	12/830	Scan	4.5	1,700	0.3	19	2.0	85.0	–	11.0	2.0	17	13	95.5	1	6	15	22
A. caraya	Corrientes, Argentina	1992–1993	20/421	Ad libitum	8.5	1,645	15	–	43.5	50.5	26.0	5.3	0.6	–	–	–	–	–	–	23
All *A. caraya*					10.1 (4.5 –18.5)	1,390.4 (1,200–1,952)	2.974.5 (0.3–30,000)	16 (13.3–19)	26.6 (2–46)	64.6 (49–85)	16.7 (3.7–26)	6.6 (0.8–12.9)	3.5 (0.6–10)	22.8 (12–56)	13.5 (10–18)	73.2 (40.4 –95.5)	3.1 (1–9)	9.6 (2–20)	13.8 (9–19)	
A. guariba	El Piñalito, Misiones, Argentina*	2006–2007	12/660	–	7.5	1,952	3,796	–	24.0	62.0	24.0	6.0	7.0	40	–	50.0	5	7	9	24
A. guariba	Montes Claros, MG, Brazil	1983–1984	10/–	Scan	7	1,250	970	15.6	15.6	70.6	18.0	8.4	5.4	–	–	–	–	–	–	25

(continued)

Table 2.1 (continued)

Species	Study site	Year	Study length (months/h)	Sampling method	Group size	Rainfall (mm)	Forest size (ha)	Time feeding (%)[a]	Plant items in diet (%)					No. species	No. families	%TFS[b]	>50 % TFT[c]	Sources fruits	Sources leaves	References[d]
									Fruits	Leaves		Flowers	OFI[e]							
										All[f]	Young									
A. guariba	Cantareira, SP, Brazil	1979	–	–	–	1,400	5,400	–	29.4	70.6	–	–	–	13	9	–	–	4	11	26
A. guariba	Sta. Genebra, SP, Brazil	1991–1992	12/ 718.5	Scan	6	1,366	250	18.5	5.0	76.0	59.0	12.0	8.0	68	30	49.3	6	12	60	27
A. guariba	Sta. Genebra, SP, Brazil	1988–1991	45/–	Allocurrence	–	1,366	250	–	15.0	75.0	–	10.0	–	52	24	37.0	9	18	42	28
A. guariba	Montes Claros, MG, Brazil	2003	6/–	Ad libitum	8	1,250	970	–	–	–	–	–	–	–	–	–	–	–	–	29
A. guariba	Mata Doralice, PR, Brazil†	2001–2002	12/ 122	Ad libitum	4.33	1,148	170	–	47.9	50.3	–	1.4	0.3	42	21	60.4	4	11	5	30
A. guariba	Fazenda Barreiro Rico, SP, Brazil	2001–2002	12/–	Scan	6	1,284	1,450	–	8.0	80.7	–	7.5	3.7	–	–	–	–	–	–	31
A. guariba	Parque Estadual Itapuã, RS, Brazil	–	–	–	8.5	1,200	35	20	36.0	54.0	27.0	10.0	0.0	45	–	–	6	32	37	32
A. guariba	Aracuri, RS, Brazil	1993–1994	13/765	Ad libitum	6	1,200	70	19	29.0	59.0	26.0	12.0	–	43	–	–	4	–	–	33
A. guariba	Fazenda Rio Claro, SP, Brazil	1992–1993	12/408	Scan	3.5	1,385	165	10	21.0	76.0	10.0	0.0	–	34	18	46.2	6	11	31	34
A. guariba	Floresta Nacional de Três Barras, SC, Brazil	–	–	–	7	1,300	4,458.5	19	34.0	38.0	–	–	–	–	–	–	–	–	–	35
A. guariba	Mata Boa Vista, RJ, Brazil	1993–1994	17/700	Scan	4	1,400	80	13	12.0	72.0	–	10.0	6.0	–	–	–	–	–	–	36
A. guariba	Ribeirão Cachoeira, SP, Brazil	1995–1996	12/228	Scan	8	1,409	234	16	12.0	74.0	–	9.0	6.0	–	–	–	–	–	–	37
A. guariba	Parque Estadual Intervales, SP, Brazil	1998–1999	12/ 918.3	Allocurrence	6	1,707	49,888	17	23.0	74.0	37.0	1.0	2.0	95	–	–	5	34	72	38
A. guariba	Chácara Payquerê, PR, Brazil*	2003–2004	12/393	Ad libitum	5	1,600	700	–	–	–	–	–	–	–	–	–	–	–	–	39

A. guariba	Chácara Payquerê, PR, Brazil	2002–2003	12/76.5	Scan	6	1,600	700	–	41.0	57.0	–	1.7	0.3	34	20	–	–	20	21	40
A. guariba	Floresta da Cicuta, RJ, Brazil‡	2002	5/165	Allocurrence	5.75	1,600	131	–	7.0	81.0	–	2.0	10.0	–	–	–	–	–	–	41
A. guariba	Montes Claros, MG, Brazil	1983	2/100	–	–	1,250	880	–	5.0	88.0	–	–	–	–	–	–	–	–	–	42
A. guariba	Sapiranga, RS, Brazil	1981	–/–	–	–	1,300	–	–	–	–	–	–	–	13	10	–	–	10	8	43
A. guariba	Fontes do Ipiranga, SP, Brazil	–	44/–	Feces	–	1,368	526.4	–	–	–	–	–	–	76	34	–	–	52	2	44
A. guariba	Morro da Extrema, RS, Brazil	2002–2003	12/609	Scan	12	1,300	27	12	19.0	66.0	–	4.0	–	–	–	–	–	–	–	45
A. guariba	Morro da Extrema, SP, Brazil	1998–1999	7/454	Scan	9.5	1,310	27	28.2	28.3	57.6	31.5	6.4	3.9	35	21	54.7	6	11	30	46
A. guariba	Lami, SP, Brazil	1998–1999	7/415	Scan	8.5	1,310	12	34.5	40.4	46.1	21.6	8.3	2.6	26	19	65.2	3	11	20	46
A. guariba	Campo de Instrução de Sta. Maria, RS, Brazil	2005	12/654	Scan	7	1,700	1.8	–	17.8	67.0	41.9	7.8	–	52	–	47.7	6	8	44	47
A. guariba	Campo de Instrução de Sta. Maria, RS, Brazil	2005	12/623	Scan	6	1,700	20	–	35.3	58.8	44.3	5.2	–	48	–	60.1	3	5	42	47
A. guariba	Campo de Instrução de Sta. Maria, RS, Brazil	2005	12/577	Scan	5	1,700	977	–	8.8	78.3	51.1	10.0	–	48	–	51.5	5	14	42	47
A. guariba	Barra do Ribeiro, RS, Brazil	2007	5/243	Focal	6.5	1,350	5	17.1	34.3	53.3	–	12.2	–	38	24	56.1	5	10	32	48
A. guariba	Ipê, RS, Brazil	2007–2008	12/636	Scan	6	1,900	2.2	20	15.0	78.0	–	2.0	5.0	42	22	56.0	4	13	41	49
A. guariba	Cantareira, SP, Brazil	–	–	–	9	1,400	7,900	21	15.0	55.0	50.0	29.0	–	41	–	–	6	–	–	50
A. guariba	Camaquã, RS, Brazil	2004/2005	13/–	Focal	5	1,200	10	30	29.5	70.5	38.9	–	–	–	–	–	–	–	–	51
All *A. guariba*					6.7 (3.5 –12)	1,426 (1,148–1,952)	2,670.2 (1.8–49,888)	19.4 (10–34.5)	22.5 (5–47.9)	66.3 (38–88)	34.3 (10–59)	7.7 (0–29)	4.3 (0–10)	44.3 (13–95)	21 (9–34)	52.9 (37 –65.2)	5.2 (3–9)	15.7 (4–52)	30.5 (2–72)	

(continued)

Table 2.1 (continued)

Species	Study site	Year	Study length (months/h)	Sampling method	Group size	Rainfall (mm)	Forest size (ha)	Time feeding (%)[a]	Plant items in diet (%)					No. species	No. families	%TFS[b]	>50 % TFT[c]	Sources fruits	Sources leaves	References[d]
									Fruits	Leaves		Flowers	OFI[e]							
										All[f]	Young									
A. macconelli	Petit Saut hydro-eletric dam, French Guiana	–	<1/70	Scan	5	2,600	–	26	–	55.0	–	–	45.0	–	–	–	–	–	–	52
A. macconelli	Les Nourages, French Guiana	1989	6/–	Feed frecuency	6	3,125	100,000	–	42.0	56.9	55.7	0.7	0.5	77	27	–	–	43	29	53
A. macconelli	Les Nourages, French Guiana	1988–1990	19/ 1,540	Feed frecuency	6	3,125	100,000	–	25.5	57.0	54.0	12.6	4.9	195	47	16.5	~40	97	96	54
A. macconelli	Saut Pararé, French Guiana	1977–1985	21/–	Stomachconts.	–	3,125	100,000	–	45.8	53.4	–	0.4	0.5	–	–	–	–	–	–	55
A. macconelli	Raleighvallen-Voltzbert Reserve, Surinam	1976–1977	12/–	–	–	2,375	56,000	–	69.0	28.6	14.3	2.4	–	–	–	–	–	–	–	56
All *A. macconelli*					5.7 (5–6)	2,870 (2,375 –3,125)	89,000 (56,000–100,000)	26	45.6 (25.5–69)	50.2 (28.6–57)	41.3 (14.3–55.7)	4 (0.4–12.6)	12.7 (0.5–45)	136 (77–195)	37 (27–47)	16.5	~40	70 (43–97)	62.5 (29–96)	
A. palliata	Isla Agaltepec, VER, Mexico	1989–1990	10/ 1,500	Focal	18	2,029	8.3	24	59.0	28.9	–	–	12.1	28	15	60.4	3	–	–	57
A. palliata	Isla Agaltepec, VER, Mexico	1989–1996	74/ 2,303	Focal	19.5	2,029	8.3	27	39.5	29.4	–	–	31.1	36	15	66.0	3	18	32	58
A. palliata	Isla Agaltepec, VER, Mexico	1989–1990	10/ 1,500	Focal	10	2,029	8.3	22.7	52.5	26.6	–	–	20.9	32	15	61.6	4	–	–	59
A. palliata	Isla Agaltepec, VER, Mexico	1997	10/630	Focal	57	2,029	8.3	16.9	31.0	33.0	–	–	37.0	30	13	45.9	6	–	–	59
A. palliata	Isla Agaltepec, VER, Mexico	1997–1998	11/300	Focal	59	2,029	8.3	29	21.4	57.1	48.5	5.3	16.3	56	23	43.2	7	15	52	60
A. palliata	Playa Escondida, VER, Mexico	1997–1998	11/300	Focal	7	3,500	40	25.9	57.3	36.9	32.6	0.2	5.6	49	26	66.8	3	22	42	60

A. palliata	Arroyo de Lisa, VER, Mexico	2000–2001	11/300	Focal	6	3,500	1.3	24.2	51.2	36.6	33.5	2.1	10.0	35	19	62.2	3	17	29	60
A. palliata	Barro Colorado Island, Panama	1932	5/–	Ad libitum	–	2,730	1,600	–	–	–	–	–	–	56	29	–	–	20	29	61
A. palliata	Barro Colorado Island, Panama	1974–1976	14/480	Scan	11	2,730	1,600	16.2	36.9	53.4	–	9.3	–	73	32	43.7	7	25	59	62
A. palliata	Barro Colorado Island, Panama	1974–1976	14/540	Scan	11	2,730	1,600	16.2	46.7	43.6	–	9.6	–	73	32	63.9	3	22	58	62
A. palliata	Hacienda La Pacifica, Costa Rica	1972–1973	14/ 2,078	Focal	13	1,431	9.9	21.3	12.5	63.6	44.2	18.2	5.7	62	25	44.7	6	15	51	63
A. palliata	Hacienda La Pacifica, Costa Rica	–	–/–	–	–	1,431	9.9	–	–	–	–	–	–	–	–	–	–	–	–	63
A. palliata	Sta. Rosa, Costa Rica	1983–1985	17/393	Focal	40	1,527	10,800	15.7	28.5	49.0	17.4	22.5	–	11	4	64.9	3	5	5	64
A. palliata	Sta. Rosa, Costa Rica	1996–1998	18/ 1,380	Scan	7.5	1,527	10,800	11.6	28.6	41.5	27.6	29.5	0.4	37	18	64.3	3	17	27	65
A. palliata	Refugio de Fauna Silvestre Curu, Costa Rica	1990	1/31	–	–	2,738	60	–	0.0	94.2	0.0	5.8	0.0	–	–	–	–	–	–	66
A. palliata	Barro Colorado Island, Panama§§	1966–1968	14/–	–	–	2,730	1,600	–	62.8	27.4	21.2	5.9	–	27	13	–	–	20	9	67
A. palliata	Barro Colorado Island, Panama**	1967–1968	6/407	Scan	–	2,730	1,600	21.6	38.8	53.7	–	5.6	1.8	–	–	–	–	–	–	68
A. palliata	Isla Ometepe, Nicaragua	1999	4/350	Focal/scan	7.1	1,550	4	21.5	11.0	54.0	–	33.0	–	–	–	–	–	–	–	69
A. palliata	Yumká, Tabasco, Mexico	2000–2001	7/302	Focal	28	2,159	33	13.2	15.0	72.0	38.0	13.0	–	21	13	–	3	5	20	70
A. palliata	Rancho Huber, Veracruz, Mexico	2003–2004	12/–	–	–	3,800	244.1	14	46.0	49.0	–	5.0	0.0	–	–	–	–	–	–	71
A. palliata	Montepío-G3, Veracruz, Mexico	2003–2004	12/–	–	–	3,800	63.8	14	23.0	77.0	–	0.0	0.0	–	–	–	–	–	–	71
A. palliata	Ruiz Cortinez, VER, Mexico	2003–2004	12/–	–	–	3,800	7.2	22	40.0	60.0	–	0.0	0.0	–	–	–	–	–	–	71

(continued)

Table 2.1 (continued)

Species	Study site	Year	Study length (months/h)	Sampling method	Group size	Rainfall (mm)	Forest size (ha)	Time feeding (%)[a]	Plant items in diet (%)					No. species	No. families	%TFS[b]	>50 % TFT[c]	Sources fruits	Sources leaves	References[d]
									Fruits	Leaves		Flowers	OFI[e]							
										All[f]	Young									
A. palliata	Flor de Catemaco, VER, Mexico	2004–2005	8/400	Focal	4	3,500	90	25.6	41.0	55.0	10.0	–	1.0	26	16	79.5	2	–	–	72
A. palliata	Montepío-T1, VER, Mexico	2002–2003	11/140	Focal	10	3,800	63.8	8	16.0	81.0	–	–	–	14	11	86.0	2	–	–	73
A. palliata	Montepío-T2, VER, Mexico	2002–2003	11/176	Focal	19	3,800	63.8	9	18.0	80.0	–	–	–	19	9	73.4	3	–	–	73
A. palliata	Sta. Martha, VER, Mexico	1986–1987	12/–	Focal	10	3,800	10	28	30.0	–	–	–	–	7	–	98.8	1	–	–	74
A. palliata	Sta. Martha, VER, Mexico	1996–1997	12/–	Focal	22	3,800	8	40	13.0	61.0	–	26.0	–	40	18	56.4	5	–	–	75
A. palliata	Rancho Huber, VER, Mexico	2006–2007	13/480	Focal	9	4,900	244	24.2	49.4	48.3	32.8	1.0	1.3	–	–	–	–	–	–	76
A. palliata	Ruiz Cortinez, VER, Mexico	2006–2007	13/480	Focal	8	4,900	7.2	17.9	39.1	58.3	49.6	2.2	0.4	–	–	–	–	–	–	76
A. palliata	EBT Los Tuxtlas, VER, Mexico	1977–1982	12/–	–	16	4,500	700	–	–	–	–	–	–	19	11	–	–	19	–	77
A. palliata	EBT Los Tuxtlas, VER, Mexico	1977–1978	12/883	Focal	14	4,500	700	–	51.0	49.3	39.3	0.2	–	27	16	79.6	2	12	24	78
A. palliata	EBT Los Tuxtlas, VER, Mexico	–	–	Focal	16	4,500	700	–	53.0	46.0	36.0	–	1.0	–	–	–	–	–	–	79
A. palliata	La Venta, TAB, Mexico	2001	5/448.5	Focal	15	1,800	6	–	19.0	76.0	57.0	5.0	–	31	17	57.5	4	9	30	80
A. palliata	F1, Los Tuxtlas, VER, Mexico	1994–1995	7/~840	Focal	6	4,900	3.7	12	29.0	65.0	56.0	0.4	6.0	44	19	82.8	3	–	–	81
A. palliata	F1, Los Tuxtlas, VER, Mexico	1999–2000	7/~840	Focal	6	4,900	2.2	13	20.0	80.0	78.0	0.1	0.1	33	17	82.4	2	–	–	81

A. palliata	F1, Los Tuxtlas, VER, Mexico	1999	6/–	Focal	5	4,900	3.2	24.3	1.9	98.1	81.9	0.0	0.0	–	–	–	–	–	–	82
A. palliata	F2, Los Tuxtlas, VER, Mexico	1999	6/–	Focal	7	4,900	35	16.4	44.1	45.2	34.2	10.7	0.0	–	–	–	–	–	–	82
A. palliata	F3, Los Tuxtlas, VER, Mexico	1999	6/–	Focal	8	4,900	250	28	71.8	23.5	22.5	4.7	0.0	–	–	–	–	–	–	82
A. palliata	Sta. Rosa, Costa Rica	1991–1992	11/577	Focal	5.7	1,527	10,800	23	14.3	58.5	31.8	27.3	–	37	16	74.9	3	5	25	83
A. palliata	Sta. Rosa, Costa Rica	1991–1992	11/532	Focal	11.7	1,527	10,800	23	18.0	63.0	33.8	19.0	–	30	18	71.7	3	17	28	83
A. palliata	Sta. Rosa, Costa Rica	1991–1992	11/628	Focal	20	1,527	10,800	24	22.3	58.0	36.3	19.8	–	29	18	72.2	3	7	25	83
A. palliata	Sta. Rosa, Costa Rica	1992	7/193	Focal	6	1,527	10,800	24	23.5	50.0	24.5	26.5	–	35	21	55.6	4	8	30	83
A. palliata	Cuero y Salado, Honduras	2000–2001	12/81	Focal	7	3,050	8,615.75	36.1	13.9	82.8	64.2	3.3	–	15	12	79.7	2	3	15	84
A. palliata	Cuero y Salado, Honduras	2000–2001	12/32.9	Focal	6	3,050	8,615.75	39.4	13.0	81.1	59.2	5.9	–	14	13	72.7	3	3	14	84
A. palliata	Finca La Luz, Mombacho, Nicaragua	1999–2000	14/396	Focal	25.9	1,490	650	11.1	29.0	58.0	19.0	10.0	3.0	50	~17	55.5	5	17	34	85
A. palliata	Finca La Luz, Mombacho, Nicaragua	1999–2000	14/451	Focal	15.3	1,490	650	13.5	42.0	50.0	22.0	5.0	3.0	43	~14	67.3	3	14	33	85
A. palliata	Finca La Luz, Mombacho, Nicaragua	1999–2000	14/461	Focal	20.2	1,490	650	15.4	34.0	56.0	38.0	8.0	2.0	45	~15	70.4	2	13	30	85
A. palliata	F1, Los Tuxtlas, VER, Mexico	–	12/–	Focal	7	4,900	3.6	17	38.0	62.0	–	1.0	–	–	–	–	–	–	–	86
A. palliata	La Selva, Heredia, Costa Rica	1991–1992	15/140	Scan	22	3,962	46,000	25	17.0	72.0	57.0	11.0	–	95	42	42.9	7	32	75	87
A. palliata	La Selva, Heredia, Costa Rica	1991–1992	15/208	Scan	12	3,962	46,000	27	29.0	65.0	57.0	6.0	–	65	36	67.3	2	24	49	87
A. palliata	Montepío 2, VER, Mexico	2009–2010	12/207	Focal	16	4,900	100	14.8	15.9	39.7	–	0.5	–	–	–	–	–	–	–	88

(continued)

Table 2.1 (continued)

Species	Study site	Year	Study length (months/h)	Sampling method	Group size	Rainfall (mm)	Forest size (ha)	Time feeding (%)^{a}	Plant items in diet (%)					No. species	No. families	%TFS^{b}	>50 % TFT^{c}	Sources fruits	Sources leaves	References^{d}
									Fruits	Leaves		Flowers	OFI^{e}							
										All^{f}	Young									
A. palliata	Balzapote, VER, Mexico	2009–2010	12/197	Focal	10	4,900	10	20.2	25.6	39.4	–	0.3	–	–	–	–	–	–	–	88
A. palliata	Chomes, Puntareas, Costa Rica	2005	6/–	Scan	8	1,725	–	27.7	26.0	39.8	31.5	29.0	5.1	19	8	65.7	3	4	16	89
A. palliata	Parque Nacional Palo Verde, Costa Rica	2005	6/–	Scan	38	1,725	19,804	35.7	26.0	45.0	41.5	28.0	0.2	24	9	70.8	3	6	22	89
All *A. palliata*					15.2 (4–59)	3,066.9 (1,431 –4,900)	3,911.3 (1.3–46,000)	21.3 (8–40)	31.1 (0–71.8)	55.5 (23.5–98.1)	38.7 (0–81.9)	9.9 (0–33)	5.9 (0–37)	36.5 (7–95)	18.2 (4–42)	66.2 (42.9 –98.8)	3.5 (1–7)	14.1 (3–32)	32 (5–75)	
A. pigra	El Tormento, CAM, Mexico*	2002	10/360	Focal	–	1,380	500	32.6	42.2	42.0	–	6.3	4.5	24	17	59.2	4	12	20	90
A. pigra	Cockscomb Basin Wildlife Sanctuary, Belize‡	1994	12/ 1,540	–	–	2,420	40,000	18	34.0	58.0	29.0	6.0	3.0	20	12	54.6	5	13	16	91
A. pigra	Tikal, Guatemala	1974	<1/84	Scan	7	1,350	56,700	22	–	–	–	–	–	7	6	96.5	1	4	7	92
A. pigra	Tikal, Guatemala	1973	3/1,147	–	–	1,350	56,700	–	–	–	–	–	–	2	1	–	1	2	1	93
A. pigra	Monkey River, Belize‡	2000–2001	8/368	Focal	–	2,500	52	17.5	38.8	56.7	25.8	4.5	–	28	21	59.2	4	7	25	94
A. pigra	Monkey River, Belize§	2002	4/149	Focal	–	2,500	52	15.3	0.0	99.7	85.3	0.3	–	15	10	83.9	2	0	15	94
A. pigra	Monkey River, Belize‡	2004	6/290	Focal	2	2,500	52	18	37.0	59.0	20.0	3.0	1.0	12	10	84.8	2	–	–	95
A. pigra	Monkey River, Belize	2004	6/290	Focal	3	2,500	52	20	22.0	70.0	27.0	7.5	0.5	11	9	81.2	3	–	–	95
A. pigra	Monkey River, Belize	2004	6/290	Focal	6	2,500	52	13	32.5	65.0	32.5	2.5	0.5	10	8	88.9	2	–	–	95
A. pigra	Monkey River, Belize	2004	6/290	Focal	4	2,500	52	15	67.0	29.0	24.0	3.5	0.5	12	9	83.6	2	–	–	95

A. pigra	Monkey River, Belize†	1999	2.5/ 125.7	Focal	10.7	2,500	52	16.3	68.0	30.0	–	2.0	–	21	16	64.0	4	11	15	96
A. pigra	Monkey River, Belize††	1999–2001	11/662	Focal	6.6	2,500	52	18.6	40.2	59.9	–	–	–	35	–	60.5	4	–	–	97
A. pigra	Baboon Santuary, Belize**	1999	12/–	Scan	6	1,650	1.25–75	–	–	–	–	–	–	–	–	–	–	–	–	98
A. pigra	Baboon Santuary, Belize**	1994–1995	12/ 1,160	Focal	5.9	1,955	25–50	24.4	40.8	45.1	37.2	10.2	3.4	74	10	42.8	7	19	20	99
A. pigra	Baboon Santuary, Belize	1995–1996	12/252	Scan	5	1,988	83	–	24.0	52.0	–	24.0	–	43	18	54.1	5	11	34	100
A. pigra	Baboon Santuary, Belize	1995–1996	12/252	Scan	7	1,988	24	–	20.0	68.0	–	11.0	–	44	–	64.3	3	17	36	100
A. pigra	Baboon Santuary, Belize	1995–1996	12/216	Scan	5	1,988	3.5	–	33.0	54.0	–	13.0	–	37	–	77.4	3	10	33	100
A. pigra	Baboon Santuary, Belize	1995–1996	12/264	Scan	5	1,988	1.25	–	34.0	57.0	–	9.0	–	51	–	65.3	4	19	39	100
A. pigra	Baboon Santuary, Belize	1995–1996	12/204	Scan	8	1,988	4.5	–	36.0	62.0	–	2.0	–	43	–	55.1	5	12	38	100
A. pigra	Baboon Santuary, Belize	1995–1996	12/216	Scan	6	1,988	121	–	63.0	33.0	–	4.0	–	32	–	85.1	1	8	24	100
A. pigra	Leona Vicario, Balancán, Mexico	2002–2003	12/499	Focal	9	1,906	0.2	19.6	17.4	55.7	49.2	5.3	21.6	15	8	65.8	4	7	13	101
A. pigra	Calakmul, CAM, Mexico†	2003	8/ ~201.6	Scan	6.3	1,750	147,915	–	–	–	–	–	–	10	8	96.3	1	–	–	102
A. pigra	Ejidos near Calakmul, CAM, Mexico*	2003	8/ ~134.4	Scan	6	1,750	12.8	–	–	–	–	–	–	16	13	80.6	3	–	–	102
A. pigra	Calakmul, CAM, Mexico	2001–2002	4/1,752	Feed.bouts	9	1,750	147,915	23	78.0	16.8	–	1.9	3.3	–	–	–	–	–	–	103
A. pigra	Calakmul, CAM, Mexico	2001–2002	4/1,752	Feed.bouts	10	1,750	147,915	23.2	62.0	20.0	–	18.0	–	–	–	–	–	–	–	103

(continued)

Table 2.1 (continued)

Species	Study site	Year	Study length (months/h)	Sampling method	Group size	Rainfall (mm)	Forest size (ha)	Time feeding (%)[a]	Plant items in diet (%)					No. species	No. families	%TFS[b]	>50 % TFT[c]	Sources fruits	Sources leaves	References[d]
										Leaves										
									Fruits	All[f]	Young	Flowers	OFI[e]							
A. pigra	Calakmul, CAM, Mexico	2001–2002	4/1,752	Feed.bouts	3	1,750	147,915	22.5	59.0	39.4	–	1.6	–	–	–	–	–	–	–	103
A. pigra	C G27 Calakmul, CAM, Mexico	2006	2/103	Focal	9	1,300	147,915	17.2	79.1	19.6	17.3	0.0	1.2	11	7	–	2	–	–	104
A. pigra	C G9 Calakmul, CAM, Mexico	2006	2/103	Focal	5	1,300	147,915	23.5	58.1	39.9	39.1	1.6	0.4	17	9	–	2	–	–	104
A. pigra	A GAA Álamo, CAM, Mexico	2005	2/103	Focal	4	1,400	96	21.6	0.0	72.8	51.3	2.4	24.7	34	21	–	3	–	–	104
A. pigra	A GR Álamo, CAM, Mexico	2005	2/103	Focal	7	1,400	96	22.1	13.1	77.0	69.3	4.5	5.4	24	13	–	4	–	–	104
A. pigra	Subestación, CAM, Mexico	2005	2/103	Focal	6	1,400	5.78	9.5	13.1	16.1	12.8	68.6	2.3	12	9	–	3	–	–	104
A. pigra	Oxcabal, CAM, Mexico	2006	2/103	Focal	5	1,400	7.99	16.3	62.5	24.7	24.2	0.9	11.9	12	8	–	2	–	–	104
A. pigra	Atascadero, CAM, Mexico	2005	1/103	Focal	4	1,400	1.14	7.2	0.0	100.0	100.0	0.0	0.0	14	9	–	3	–	–	104
A. pigra	Chilar, CAM, Mexico	2006	2/103	Focal	8	1,400	<1	10.5	41.7	37.8	28.3	19.7	0.8	4	2	–	1	–	–	104
All *A. pigra*					6.2 (2 –10.7)	1,873.2 (1,300 –2,500)	33,621.4 (0.2–147,915)	18.6 (7.2 –32.6	38.5 (0–79.1)	50.4 (16.1 –100)	39.6 (12.8–100)	8.3 (0–68.6)	5 (0–24.7)	23 (2–74)	10.6 (1–21)	71.6 (42.8 –96.5)	3 (1–7)	10.1 (0–19)	22.4 (1–39)	
A. seniculus	Finca Merenberg, La Plata, Colombia	1976	10/340	Focal	9	1,942	270	12.7	42.3	52.0	44.5	5.4	0.1	33	17	73.1	4	12	28	105
A. seniculus	Hato El Frío, Apure, Venezuela	1975–1976	13/–	Dissection/ scan	7.5	1,424	1,000	21.8	–	–	–	–	–	40	18	–	–	–	–	106
A. seniculus	Fazenda Esteio, AM, Brazil	1984–1985	5/491	Scan	8	2,900	13	22	13.5	56.0	39.0	4.0	27.0	93	30	–	–	22	93	107

A. seniculus	Río Peneya, Colombia	1971–1994	–	Ad libitum	–	3,000	1,000	–	–	–	–	–	–	–	–	–	–	–	–	108
A. seniculus	Tiputini, Orellana, Ecuador	2005–2008	–	Cameratraps	–	2,800	1,700,000	–	–	–	–	–	–	–	–	–	–	–	–	109
A. seniculus	Isla Iguana, Lago Guri, Venezuela	1999–2001	9/325	Allocurrence	6	1,100	0.6	–	2.0	73.0	52.0	14.0	11.0	–	–	–	–	–	–	110
A. seniculus	Isla Danto Machado, Lago Guri, Venezuela*	1999–2001	9/347	Allocurrence	6.5	1,100	190	–	22.0	55.0	26.0	18.0	5.0	–	–	–	–	–	–	110
A. seniculus	Tinigua, Meta, Colombia	1990–1991	13/672	Focal/scan	–	2,604	500	23	39.0	51.0	–	4.0	7.0	–	–	–	–	–	–	111
A. seniculus	Otún-Quimbaya, Colombia	2001	6/119.4	Scan	5	2,712	489	–	25.4	57.3	–	17.3	–	21	11	67.4	4	8	17	112
A. seniculus	Otún-Quimbaya, Colombia	2001	6/136.4	Scan	10	2,712	489	–	36.7	59.2	–	4.0	–	27	11	63.4	3	6	22	112
A. seniculus	Otún-Quimbaya, Colombia	2001	6/132	Scan	8	2,712	489	–	65.5	34.5	–	0.0	–	12	10	96.0	1	3	11	112
A. seniculus	Mamirauá, AM, Brazil	–	–	–	8	2,300	1,240,000	6	47.0	46.0	20.0	2.0	5.0	26	–	–	2	8	20	113
A. seniculus	A0 Yotoco, Valle del Cauca, Colombia	2004–2005	12/–	Focal	8	1,500	559	22.1	30.1	67.0	59.7	–	2.9	–	–	–	–	–	–	114
A. seniculus	A9 Yotoco, Valle del Cauca, Colombia	2004–2005	12/–	Focal	5	1,500	559	23.1	13.3	82.9	76.7	–	3.8	–	–	–	–	–	–	114
A. seniculus	Hacienda San Juan del Carare, Colombia	2008–2009	9/~475	Scan	–	3,496	65.87	7	35.1	61.4	22.8	0.8	2.5	–	–	–	–	–	–	115
A. seniculus	Estación Biológica de Cahuana, Peru§§	1979–1992	–/–	Ad libitum	5.5	3,000	720	–	40.0	53.0	–	6.0	–	–	–	–	–	–	–	116
All *A. seniculus*					7.2 (5 –10)	2,300.1 (1,100 –3,496)	184,146.5 (0.6–1,700,000)	17.2 (6–23.1)	31.7 (2–65.5)	57.6 (34.5–82.9)	42.6 (20–76.7)	6.9 (0–18)	7.1 (0.1 –27)	36 (12–93)	16.2 (10–30)	75 (75 –96)	2.8 (1–4)	9.8 (3–22)	31.8 (11–93)	
All *Alouatta*					9.9 (2 –59)	2,211.4 (1,100 –4,900)	30,596.4 (0.2–1,700,000)	19.7 (6–40)	31.4 (0–79.1)	56.7 (13.3–100)	36.2 (0–100)	8.4 (0–68.6)	5.6 (0–45)	35 (2–195)	16.4 (1–47)	65.6 (16.5 –98.8)	3.6 (1–10)	14.7 (0–97)	27.8 (1–96)	

(continued)

Table 2.1 (continued)

[a] % Time feeding = proportion of daily activity time dedicated to feeding

[b] %TFS = percentage of feeding time dedicated to feed from top five plant species

[c] >50 % TFT = number of plant species contributing >50 % of total feeding time

[d] References: 1. Bonvicino (1989); 2. Camargo et al. (2008); 3. de Souza et al. (2002); 4. Pinto (2002), Pinto and Setz (2004); 5. Pinto et al. (2003); 6. Lindberg and Santini (1984); 7. Alves and Guix (1992); 8. Bravo and Zunino (2000); 9. Rumiz et al. (1986); 10. Rumiz et al. (1986); 11. Agostini et al. (2010); 12. Prates (2007), Prates and Bicca-Marques (2008); 13. Bicca-Marques and Calegaro-Marques (1994a, b, c); 14. Bicca-Marques et al. (2009); 15. Bravo and Sallenave (2003); 16. Pavé et al. (2009); 17. Ludwig et al. (2008); 18. Ludwig et al. (2008); 19. Rímoli et al. (2008); 20. Zunino (1986, 1989); 21. Arditi (1992); 22. Muhle (2008); 23. Giudice and Mudry (2000); 24. Agostini et al. (2010); 25. Mendes (1989); 26. Silva (1981); 27. Chiarello (1993), (1994); 28. Galetti et al. (1994); 29. Almeida-Silva et al. (2005); 30. Aguiar et al. (2003); 31. Martins (2008, 2009); 32. Cunha (1994); 33. Biedzicki de Marques (1996); 34. Martins (1997); 35. Pérez (1997); 36. Limeira (1997); 37. Gaspar (1997); 38. Steinmetz (2000, 2001); 39. Miranda et al. (2005); 40. Miranda and Passos (2004); 41. Alves and Zaú (2007); 42. Young (1983); 43. Chitolina and Sander (1981); 44. Kuhlmann (1975); 45. Koch and Bicca-Marques (2007); 46. Fialho (2000); 47. Fortes (2008); 48. Pereira (2008); 49. Guzzo (2009); 50. Lunardelli (2000); 51. Damé (2006); 52. de Thoisy and Richard-Hansen (1997); 53. Simmen and Sabatier (1996); 54. Julliot and Sabatier (1993), Julliot (1996); 55. Guillotin et al. (1994); 56. Mittermeier and van Roosmalen (1981); 57. Serio-Silva (1995); 58. Serio-Silva et al. (2002); 59. Rodríguez-Luna et al. (2003); 60. Asensio-Herrero et al. (2007); 61. Carpenter (1934); 62. Milton (1980); 63. Glander (1978b, 1981); 64. Chapman (1987a, b, 1988); 65. Welker (2004); 66. Tomblin and Cranford (1994); 67. Hladik and Hladik 1969); 68. Smith (1977); 69. Devos (1999); 70. García del Valle et al. (2001), Muñoz et al. (2002); 71. Hervier (unpublished data *in* Cristóbal-Azkarate and Arroyo-Rodríguez 2007); 72. Sedden-González and Rodríguez-Luna (2010); 73. Bravo-Xicoténcatl (2003); 74. Jiménez-Huerta (1992); 75. García-Orduña (2002); 76. Dunn et al. (2009, 2010); 77. Estrada and Coates-Estrada (1984), Estrada et al. (1984); 78. Estrada (1984); 79. Estrada and Coates-Estrada (1986); 80. Fuentes et al. (2003); 81. González-Picazo et al. (2001); 82. Juan et al. (2000); 83. Larose (1996); 84. Snarr (2006); 85. Williams-Guillén (2003); 86. Juan et al. (1999), Ortiz-Martínez et al. (1999); 87. Stoner (1996); 88. Cuende-Fanton (2010); 89. Martínez-Esquivel (2010); 90. Barrueta (2003); 91. Silver and Marsh (2003); 92. Schlichte (1978); 93. Coelho et al. (1976); 94. Behie and Pavelka (2005); 95. Bridgett (2006); 96. Loudon (2000); 97. Pavelka and Knopff (2004); 98. Marsh and Loiselle (2003); 99. Silver et al. (1998); 100. Marsh (1999); 101. Pozo-Montuy and Serio-Silva (2006, 2007); 102. Rivera and Calmé (2006); 103. Rizzo (2004); 104. Coyohua-Fuentes (2008); 105. Gaulin and Gaulin (1982); 106. Braza et al. (1983); 107. Neves and Rylands (1991); 108. Izawa (1975); 109. Blake et al. (2010); 110. López et al. (2005); 111. Stevenson et al. (2000, 2002); 112. Giraldo et al. (2007); 113. Queiróz (1995); 114. Palma et al. (2011a, b); 115. Aldana-Saavedra (2009); 116. Soini (1992)

[e] OFI = other food items

[f] All = includes mature and young leaves, leave buds, bracts, petioles, pulvini, and tendrils

[g] Averages and ranges for each species and for the genus

[h] Length = months, observation hours

*Averages for two groups; [†] Averages for three groups; [‡] Averages for four groups; [§] Averages for five groups; **Averages for six groups; [††] Averages for eight groups; [‡‡] Averages for ten groups; [§§] Averages for an unspecified number of groups observation hours. However, the majority of studies (57.8 %) have included >300 h of observations, and 12.9 % had an observation effort >1,000 h. Finally, the majority of groups (65.1 %) were studied for ≥9 months, which allows controlling for and assessing the effects of seasonality on the diet.

2.3 Results

2.3.1 Howler Foods

Overall, howlers spend on average (±SD) approximately 19.7 ± 6.9 % of their daily activity time feeding, and time spent feeding does not vary significantly between species ($F_{5,49} = 0.891$, $p = 0.494$). As expected for an arboreal primate that occupies primarily the upper and middle portions of the canopy, howlers spend the majority of their feeding time (82 ± 17.1 %) consuming food items from trees.

Howlers consume both ripe and unripe fruits. Sometimes, they select and eat specific parts of fruits, such as seeds or arils (see Arroyo-Rodríguez et al. 2014). A significant proportion of the range of variation in time spent consuming fruits is shared by all howler species (Fig. 2.2a). This is particularly marked in species that

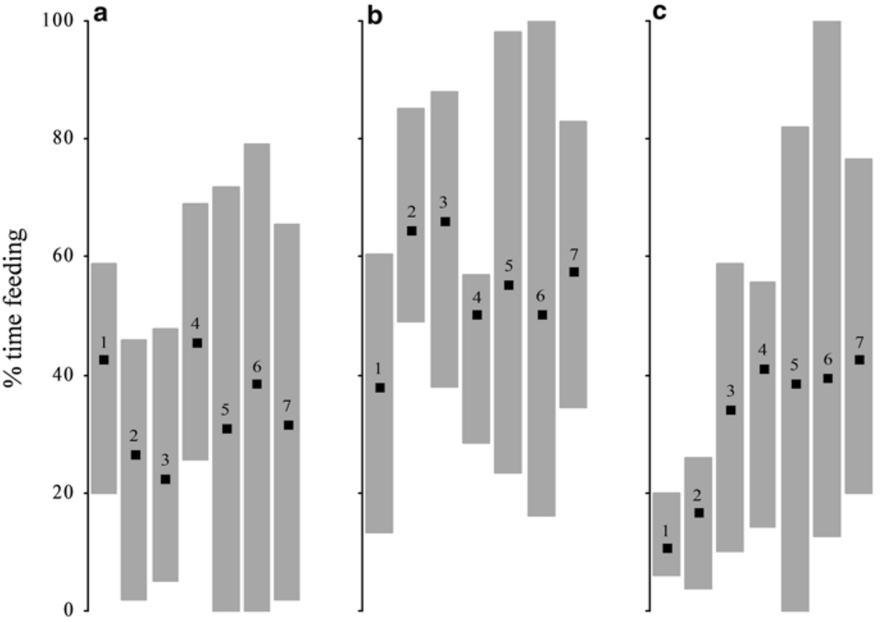


Fig. 2.2 Range (*gray columns*) and average (*black squares*) proportion of feeding time dedicated to the consumption of fruits (**a**), leaves of all ages (**b**) and young leaves (**c**). 1 = *A. belzebul*; 2 = *A. caraya*; 3 = *A. guariba*; 4 = *A. macconnelli*; 5 = *A. palliata*; 6 = *A. pigra*; 7 = *A. seniculus*

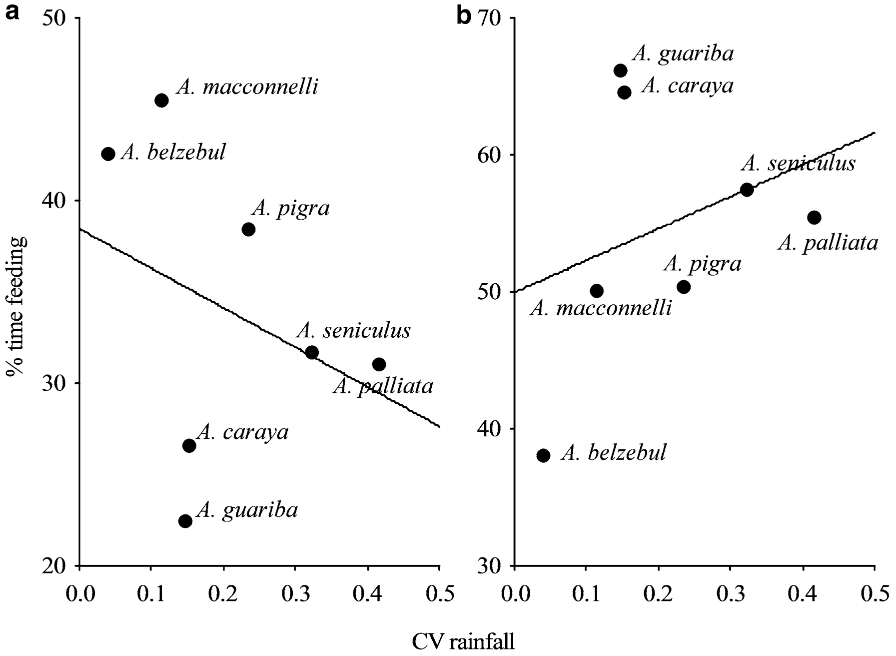


Fig. 2.3 Relationship between variation (CV = coefficient of variation) in rainfall and the proportion of time dedicated to the consumption of fruits (**a**) and leaves of all ages (**b**)

occupy a wider range of forest types (as assessed by variation in rainfall levels; Fig. 2.3a), such as *A. palliata*, *A. pigra,* and *A. seniculus*. In contrast, howler species that live in forests with low variation in rainfall levels (*A. belzebul* and *A. macconnelli*), and forests that are also more seasonal (*A. caraya* and *A. guariba*), present the highest and lowest values for fruit consumption, respectively.

Howlers eat young and mature leaves, leaf petioles, pulvini, and leaf buds. In contrast to fruit consumption, which for some species ranges from zero (e.g., *A. palliata*), howlers at all study sites always eat at least some leaves. As in the case of fruits, some howler species show higher variation in leaf consumption (including young leaves), which encompasses the range of other species (e.g., *A. palliata*; Fig. 2.2b, c). Species that are found in forests with low variation in rainfall tend to spend the highest (e.g., *A. caraya*) or lowest (e.g., *A. belzebul*) proportion of time consuming leaves, whereas species that live in more diverse forests in terms of rainfall levels (e.g., *A. palliata*) show intermediate proportions (Fig. 2.3b).

Besides fruits, leaves, and flowers, howlers consume lesser amounts of a variety of OFI. These include: other plant items, such as bark, gum, decayed and live wood, pine cones, pods, pseudobulbs (from epiphytes), roots, stems (including twigs) and herbs; chicken eggs; honey; insects (eggs, larvae, and adults); lichens; mushrooms; nectar; soil; and termitaria. Concerning the ingestion of insects, howlers inadvertently eat Hymenoptera (e.g., Blastophaga), Diptera, and Coleoptera (e.g., Curculionidae)

(Hladik and Hladik 1969; Milton 1980; Gaulin and Gaulin 1982; Alves and Guix 1992; Serio-Silva 1995; Bravo and Zunino 1998) that infest fruits, and these insects may be an important source of vitamins, minerals, and amino acids that can only be obtained from animal source foods (Urquiza-Haas et al. 2008).

Howlers have been observed ingesting soil from the forest floor (from "barreiros" or "salados": Izawa 1993; Stevenson et al. 2000, 2002; Blake et al. 2010), bird nests (Bicca-Marques and Calegaro-Marques 1994a, b, c), and termitaria (Julliot and Sabatier 1993; de Souza et al. 2002). It has been suggested that the main function of geophagy is as a digestive aid (e.g., detoxification of secondary compounds). This suggestion is supported by the observation that, in some howler populations, geophagy is positively correlated with leaf consumption, usually during the dry season (Julliot and Sabatier 1993; de Souza et al. 2002). Specifically, some soils consumed by howlers are rich in organic matter and clay, which may help to absorb secondary metabolites of plants, such as tannins, alkaloids, and terpenoids, and balance gastric acidity (Hirabuki and Izawa 1990; de Souza et al. 2002). Alternative explanations for geophagy by howlers include mineral supplementation (Izawa 1993) and to combat to endoparasite infestations (Bicca-Marques and Calegaro-Marques 1994a), although currently there is only very scarce data addressing both hypotheses.

The low proportion of time (<1 %) howlers dedicate to drinking water indicates that they acquire most water from their foods. However, howlers have been observed drinking rainwater accumulated in flowers, epiphytic bromeliads (Bonvicino 1989; Steinmetz 2000, 2001; Miranda et al. 2005), pools and holes in trunks (Glander 1978a; Silver et al. 1998; Giudice and Mudry 2000; Fialho 2000; Miranda et al. 2005; Pozo-Montuy and Serio-Silva 2006, 2007; Snarr 2006), as well as from ponds and rivers (Gilbert and Stouffer 1989; Almeida-Silva et al. 2005; Miranda et al. 2005). In several howler species (e.g., *A. guariba*, *A. palliata*, *A. pigra*), drinking is negatively correlated with precipitation, temperature, and fruit consumption and/or positively related to the consumption of mature leaves (Glander 1978a; Gilbert and Stouffer 1989; Bonvicino 1989; Steinmetz 2001; Miranda et al. 2005; Dias et al. 2014). Therefore, drinking water by howlers seems to relate to hydration when the climate is dryer or foods rich in water (i.e., new leaves, fruits) are unavailable.

Howlers consume significantly more leaves than fruits ($t_{71} = 7.86$, $p < 0.001$), and significantly more young leaves than mature leaves ($t_{37} = 2.47$, $p = 0.018$; Table 2.1). At the species level, *A. caraya* ($t_{8} = 4.53$, $p = 0.002$), *A. guariba* ($t_{11} = 11.72$, $p < 0.001$), *A. palliata* ($t_{30} = 4.15$, $p < 0.001$), and *A. pigra* ($t_{9} = 2.58$, $p = 0.003$) consume significantly more leaves than fruits, and only in *A. caraya* ($t_{3} = 4.08$, $p = 0.027$) and *A. palliata* ($t_{17} = 4.26$, $p < 0.001$) is the consumption of young leaves significantly higher than that of mature leaves. There are differences between species in the proportions of time dedicated to consume fruits ($F_{5,66} = 4.77$, $p < 0.001$), leaves ($F_{5,66} = 7.70$, $p < 0.001$), and young leaves ($F_{5,32} = 5.94$, $p < 0.001$), but not flowers ($F_{5,53} = 0.67$, $p = 0.649$) or OFI ($F_{5,33} = 0.85$, $p = 0.527$). These differences are determined by (LSD tests $p < 0.05$): (1) higher consumption of fruits by *A. belzebul* than by *A. caraya* and *A. guariba*; (2) higher consumption of fruits by *A. palliata* and *A. pigra* than by *A. guariba*; (3) lower consumption of leaves in *A. belzebul* than by all other species; (4) higher consumption of leaves by *A. guariba* and *A. caraya* than in *A. palliata* and *A. pigra*; (5) lower consumption of young leaves in *A. belzebul* and *A. caraya* than all other species, except for each other. Time spent eating fruits correlates negatively with the consumption of leaves ($r = -0.77$, $n = 72$, $p < 0.001$) and flowers ($r = -0.27$, $n = 59$, $p = 0.034$).

Dietary habits of howlers are significantly predicted ($R^2 = 0.22$, $F_{3,63} = 5.81$, $p = 0.001$) by rainfall ($\beta = 0.50$, $t = 3.09$, $p = 0.003$), group size ($\beta = 0.25$, $t = 2.81$, $p = 0.007$), and the interaction between rainfall and group size ($\beta = 0.22$, $t = 2.78$, $p = 0.007$). These results suggest that overall howlers tend to be more frugivorous when living in larger groups that occupy habitats with more rainfall (Fig. 2.4a, b). A piecewise regression of rainfall levels on the dietary habits of howlers resulted in a highly explicative model ($R^2 = 0.81$), which defined a breakpoint at 2,287.2 mm. For groups living in habitats with rainfall <2,287.2 mm ($R^2 = 0.40$, $F_{3,45} = 9.84$, $p < 0.001$), again rainfall was the most explicative variable, indicating that frugivory increases with increasing rainfall (rainfall $\beta = 0.59$, $t = 5.06$, $p < 0.001$; group size $\beta = 0.21$, $t = 1.79$, $p = 0.081$; forest size $\beta = 0.17$, $t = 1.48$, $p = 0.146$; Fig. 2.4c). For rainfall >2,287.2 mm ($R^2 = 0.27$, $F_{1,16} = 5.99$, $p = 0.026$), dietary habits tend to frugivory as group size decreases (group size $\beta = -0.52$, $t = 2.45$, $p = 0.026$; Fig. 2.4d). Concerning group size, a piecewise regression identified a breakpoint at 11.9 individuals ($R^2 = 0.64$). For groups <11.9 individuals, dietary habits were significantly predicted ($R^2 = 0.15$, $F_{2,43} = 3.74$, $p = 0.032$) by rainfall ($\beta = 0.47$, $t = 3.32$, $p = 0.001$) and forest size ($\beta = 0.20$, $t = 1.44$, $p = 0.156$), indicating that, at these group sizes, howler diets are more frugivorous in larger forests that receive more rainfall (Fig. 2.4e, f). For larger groups (i.e., >11.9 individuals) no model could be defined by the stepwise regression. Time dedicated to flower consumption is significantly predicted by rainfall and forest size ($R^2 = 0.30$, $F_{2,51} = 10.78$, $p < 0.001$). Specifically, howlers spend more time consuming flowers when they live in larger habitats ($\beta = 0.30$, $t = 2.51$, $p = 0.015$) that receive less rain ($\beta = -0.43$, $t = 3.68$, $p < 0.001$). The consumption of OFI is significantly predicted by group size and forest size ($R^2 = 0.34$, $F_{2,32} = 8.09$, $p = 0.001$). Howlers spend more time consuming OFI when living in larger groups ($\beta = 0.41$, $t = 2.83$, $p = 0.008$) and smaller forests ($\beta = -0.35$, $t = 2.43$, $p = 0.021$).

2.3.2 Dietary Diversity

Combined data show that howlers consume a total of 1,165 plant species, belonging to 479 genus and 111 families. If plant morphotypes are included in these calculations and we assume that no morphotypes are shared between studies, howlers consume 1,665 or more plant species. [A complete list of the plants used by howlers as food sources per study group and the plant parts used is available at http://goo.gl/F3ysf.] Fabaceae (200 species), Moraceae (104), Sapotaceae (56), and Bignoneaceae (53) are the families showing the highest number of plant species in the howler diet: together, these four families represent 35.5 % of all species consumed. At the genus level, *Ficus* and *Inga* are the taxa represented by more species in the howler diet, with 65 and 31 species, respectively. However, the majority of genera (ca. 50 %)

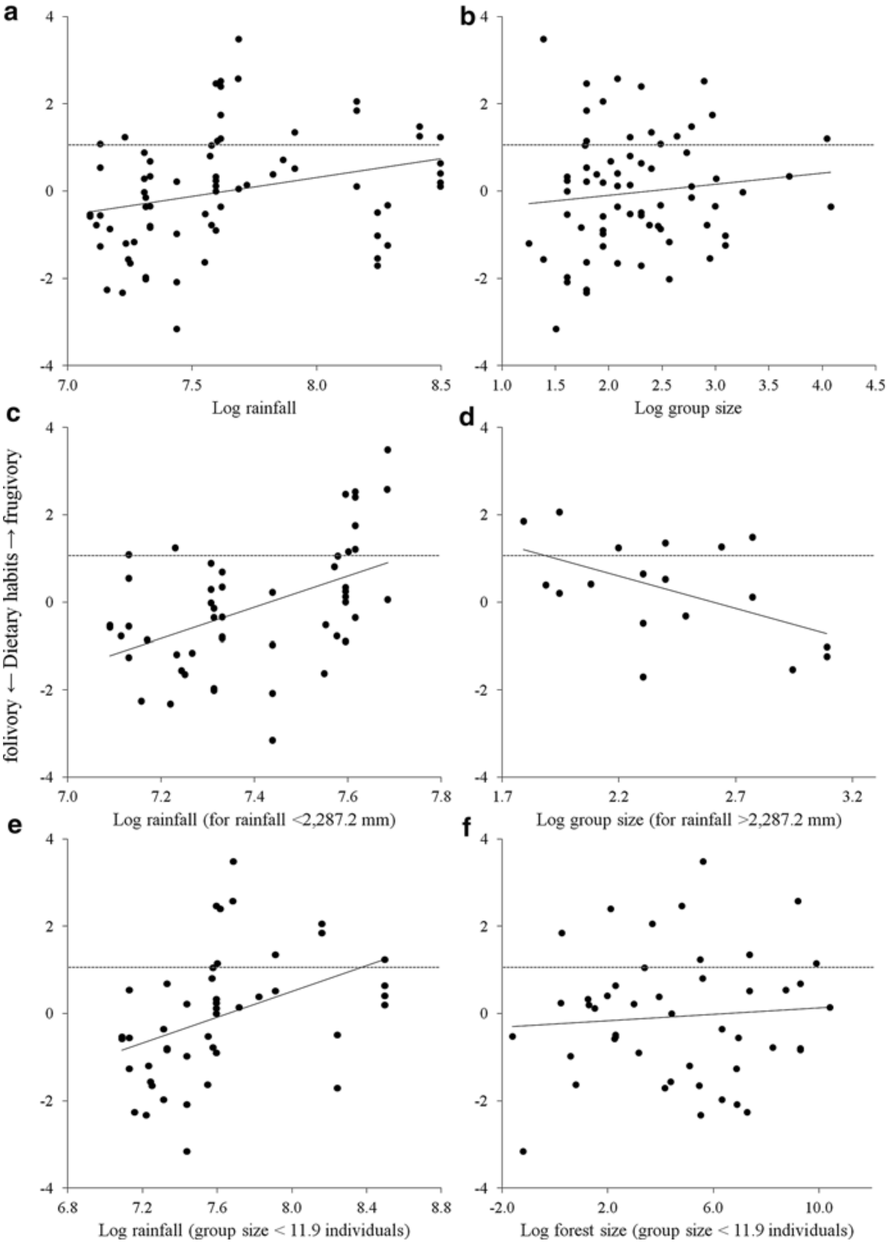


Fig. 2.4 Variation in the dietary habits of howlers as a function of: rainfall (**a**); group size (**b**); rainfall in groups that live in habitats that receive less than 2,287.2 mm of rainfall per year (**c**); group size in groups that live in habitats that receive more than 2,287.2 mm of rainfall per year (**d**); rainfall in groups with less than 11.9 individuals (**e**); forest size in groups with less than 11.9 individuals (**f**). The *dotted line* represents threshold for a balanced diet (i.e., equal amounts of time dedicated to consume fruits and leaves). Values higher than this threshold represent a mainly frugivorous diet, whereas lower values represent a mainly folivorous diet

are represented in the diet of howlers by only 1–3 species, and 78 % are represented by ≤10 species. Among known plant species used as food sources, 47 % are sources of fruit (548 species, 80 families), 64.8 % (754 species, 98 families) are sources of leaves, and 21.2 % (247 species, 59 families) are sources of flowers. The majority (>50 % of species) of fruits consumed by howlers belong to the Moraceae (83 species), Fabaceae (62), Sapotaceae (43), Myrtaceae (31), Urticaceae (24), Lauraceae (18) and Anacardiaceae (16) families; and to the genera *Ficus* (53 species), *Inga* (19), *Pouteria* (14), *Eugenia* (13), and *Cecropia* (11). The majority of leaves consumed by howlers belong to the Fabaceae (160 species), Moraceae (66), Bignoneaceae (36), Malvaceae (29), Sapotaceae (28), Myrtaceae (24), Lauraceae (19), and Chrysobalanaceae (18) families; and to the genera *Ficus* (41), *Inga* (23), *Protium* (13), *Licania* (11), *Eugenia* (10), *Lonchocarpus* (10), *Machaerium* (10), and *Pithecellobium* (10). Flowers are mainly consumed from the families Fabaceae (81), Bignoniaceae (29), and Malvaceae (14); 42 genera account for the majority of plant species serving as sources of flowers, led by *Inga*, which contributes 14 species.

Thirty-two percent of the plant families used as food sources are exclusively exploited by a single howler species, whereas 7 families (6.3 % of the total number of families utilized), Anacardiaceae, Bignoneaceae, Fabaceae, Malvaceae, Moraceae, Sapotaceae, and Urticaceae, are used by all howler species for which feeding data are currently available. At the genus level, the number of plant taxa used exclusively by a single howler species increases nearly twofold with respect to the previous taxonomic level, to 57 %, and only 4 genera are shared by all howler species (0.8 %; *Cecropia*, *Ficus*, *Inga,* and *Tabebuia*). At the species level, 81.5 % of all taxa are used by a single howler species, and no plant species is used by all howler species. Two plant species (0.2 %) are shared by five howler species, namely *Brosimum guianense* (Aubl.) Huber (*A. belzebul*, *A. guariba*, *A. macconnelli*, *A. pigra* and *A. seniculus*) and *Ficus insipida* Willd (*A. caraya*, *A. guariba*, *A. palliata*, *A. pigra* and *A. seniculus*). Interestingly, these two species are very different in terms of light requirements for their germination, as the first is shade-tolerant (i.e., typical of mature forests), whereas the second is a light-demanding species.

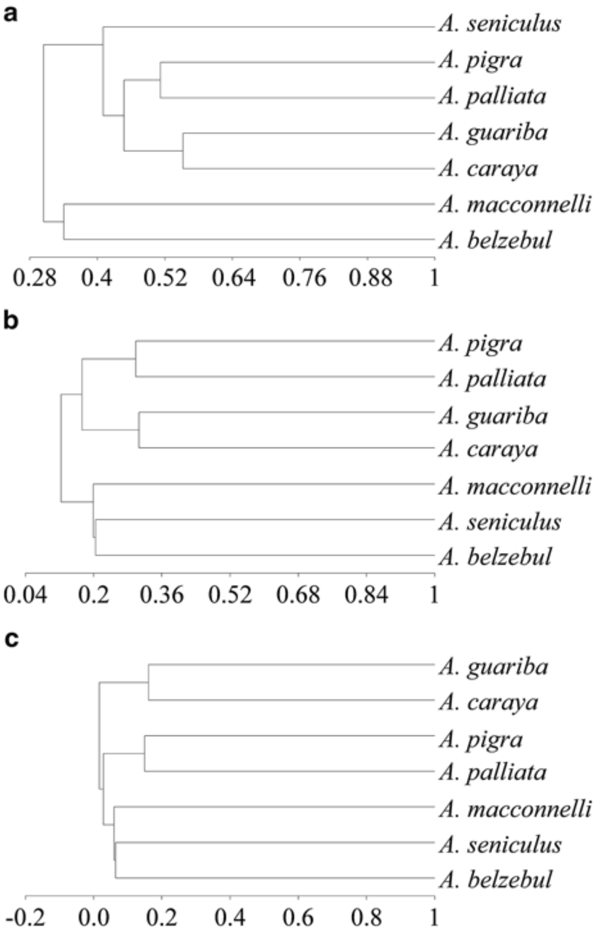
2.3.2.1 Similarity in the Use of Plant Taxa

Average similarity (as assessed by the Jaccard index) among howler species in the use of plants is low (Table 2.2) at the family, genus, and species level. Overall, *Alouatta pigra* shows the highest average similarity with other species, particularly with *A. palliata*; *A. caraya* and *A. guariba* show the highest similarity between each

Table 2.2 Similarity (*J* index) in the consumption of plant taxa between and within howler species

	Interspecific			Intraspecific		
Plants	Mean	SD	Range	Mean	SD	Range
Family	0.38	0.05	0.22–0.55	0.43	0.18	0.05–0.88
Genus	0.16	0.02	0.08–0.31	0.29	0.19	0.04–0.91
Species	0.04	0.007	0.007–0.16	0.22	0.19	0–0.93

Fig. 2.5 Interspecific similarity (Jaccard's index) in the use of plant families (**a**), genus (**b**), and species (**c**)



other than any other pair of species; and *A. belzebul* and *A. macconnelli* have the lowest average similarity with other species (Fig. 2.5). As expected by the distributional ranges of howler species, three major groupings may be identified in terms of similarity in the use of plant species, genus, and families as food sources: (1) trans-Andean howlers; (2) howlers from Amazonia and northern South America; (3) howlers from Chaco, Cerrado, and Atlantic forest. As an exception to this relationship between distributional range and use of similar plant taxa, *A. seniculus* groups with the first two groups at the plant family level. Average dietary similarity is higher intraspecifically than interspecifically (Table 2.2). Nevertheless, variation in similarity is higher within species than between species, particularly at the plant species level. In general, higher ($J > 0.75$) similarity levels are found between: (1) different groups of the same species living in the same (e.g., Refs. 85, 95 and 112 in Table 2.1) or different forests (e.g., Refs. 82 and 100 in Table 2.1) observed in the same study; (2) a single group observed at different moments (e.g., Ref. 78 vs. 79 in Table 2.1; Ref. 57 vs. 58 in Table 2.1).

2.3.2.2 Dietary Breadth

The average (±SD) rate of use of plant species and families as food resources by howler groups is 0.12 ± 0.1 and 0.06 ± 0.08 families/h, respectively. Plant species and families use is significantly predicted by rainfall and forest size (species: $R^2 = 0.26$, $F_{3,51} = 5.83$, $p < 0.001$; families: $R^2 = 0.32$, $F_{3,38} = 5.85$, $p < 0.002$). In both models rainfall (species: $\beta = 0.34$, $t = 2.80$, $p = 0.007$; families: $\beta = 0.34$, $t = 2.51$, $p = 0.017$), forest size (species: $\beta = 0.28$, $t = 2.29$, $p = 0.026$; families: $\beta = 0.33$, $t = 2.39$, $p = 0.022$), and group size (species: $\beta = -0.19$, $t = 1.59$, $p = 0.117$; families: $\beta = -0.22$, $t = 1.63$, $p = 0.112$) were included in the stepwise regression, but only the first two variables had significant effects, indicating that howlers use more plant species and families in extensive forests that receive more rainfall. The proportion of feeding time dedicated to top food species (TFS) varies significantly between howler species ($F_{5,44} = 2.74$, $p = 0.031$), a result that is mainly due to *Alouatta caraya* groups concentrating more feeding time to TFS than *A. belzebul*, *A. guariba,* and *A. palliata* (LSD tests $p < 0.05$). Time dedicated to the consumption of TFS increases when howlers use fewer plant species ($r = -0.68$, $n = 50$, $p < 0.001$). The number of plant species contributing >50 % of feeding time is negatively correlated with the percentage of time dedicated to consume fruits ($r = -0.20$, $n = 43$, $p = 0.05$), suggesting that higher fruit consumption is associated with a decrease in the use of plant species. Finally, howlers use significantly more plant species as sources of leaves than fruits ($t_{47} = 7.76$, $p < 0.001$) in a ratio of approximately 2:1 (Table 2.1).

2.4 Perspectives on the Diets of Howlers

The results from this review support previous classifications of howlers as folivore–frugivore primates, whose diets vary both inter- and intraspecifically. Furthermore, our analyses reveal several patterns in the diets of howlers that suggest that their degree of dietary variation is affected by both environmental (i.e., rainfall, forest size) and social (i.e., group size) factors.

Rainfall is a critical factor underlying variation in the diets of howlers. Water availability, through its limiting effects on plant physiology, determines the establishment of plant communities and their phenologies. Tropical forests with annual rainfall lower than 2,000–2,500 mm tend to be drier, more seasonal, and have lower fruit availability than forests with higher rainfall (van Schaik et al. 1993; Kay et al. 1997; Dirzo et al. 2011). Across the genus, howlers that live in wetter habitats have more frugivorous diets, consume fewer flowers, and show more diverse diets than those in drier habitats, although they concentrate a higher percentage of their total feeding time on a lower number of species. In particular, frugivory increases steadily with increasing rainfall up to the level of ≈2,200 mm and up to group sizes of ≈12 individuals; 47 % of all studied howler groups live under these circumstances. Furthermore, frugivory increases with increasing forest size (a proxy for availability of food sources: Arroyo-Rodríguez and Dias 2010) in groups with less than ≈ 12 individuals.

In habitats with rainfall higher than ≈2,200 mm, frugivory decreases with increasing group size, suggesting that in more productive habitats fruit sources are depleted faster. Therefore, overall and temporal fruit availability and perhaps indirect scramble competition for food (Sterck et al. 1997) in larger howler groups (Knopff and Pavelka 2006; Arroyo-Rodríguez et al. 2011) explain how the dietary habits of howlers vary throughout the folivore–frugivore gradient.

At the species level, howler species that are distributed exclusively in drier forests (*A. caraya* and *A. guariba*) show the highest consumption of leaves and lowest consumption of fruits across the genus. They also show a number of additional dietary similarities, including the use of many of the same plant taxa as food sources. Howlers that live in less seasonal moist forests (*A. belzebul* and *A. macconnelli*) are in turn the most frugivorous and least folivorous species and also share other features of their diets, such as the use of more plant species as sources of fruits than leaves. Contrasting with these habitat specialists, the remaining howler species occupy a large array of habitat types, and as a result, their dietary habits are more variable. Still, even among these species, rainfall patterns consistently explain variation in the consumption of leaves and fruits. Therefore, our analyses suggest that, although at the genus level howlers are primarily folivorous, their dietary habits range from higher folivory to higher frugivory depending on the rainfall patterns, group size, and forest size that a particular species or population faces. The fact that despite these differences time dedicated to feeding is not significantly variable across species supports previous suggestions that howlers' time-budgets are either phylogenetically or metabolically constrained (Bicca-Marques 2003; Pavelka and Knopff 2004). It is interesting to observe that similarity in dietary habits seems to parallel proximity in geographic distributions more than phylogenetic relationships within the genus (e.g., Cortés-Ortiz et al. 2003; Gregorin 2006).

As discussed above, in addition to rainfall, group size and habitat size explain variation in several traits of howler diets. Across the genus, larger groups spend more time eating fruits and OFI. Furthermore, frugivory increases steadily with increased group size up to the level of ≈12 individuals per group. This suggests that larger groups deplete patches of preferred foods faster and increase the consumption of alternative food sources. At the species level, however, the relationship between fruit consumption and group size stands only for *A. palliata*, probably because this is the species with the highest mean group size, and in which some groups eat fruits more intensively (only second to *A. pigra*). This result coincides with previous evidence that some *A. palliata* populations experience reduced access to food sources when living in large groups (Arroyo-Rodríguez et al. 2011). In other species, the effects of group size on the consumption of seasonal plant items are more variable, probably because the interaction among dietary preferences, availability of seasonal foods, and food-patch depletion varies within and between species as a function of habitat characteristics. Among these, habitat size is particularly important as it is positively related to food availability throughout the forests occupied by howlers; small forests have less food sources that are additionally smaller (Arroyo-Rodríguez and Dias 2010). As a consequence, howlers eat less fruits, more flowers, and OFI, and their diets are less diverse. As discussed elsewhere, these relationships have important consequences for the conservation of howlers in disturbed habitats (Bicca-Marques 2003; Cristóbal-Azkarate and Arroyo-Rodríguez 2007; Arroyo-Rodríguez and Dias 2010).

Howlers have a number of anatomical and physiological adaptations that enable the use of leaves as a primary food resource. In addition to dental morphology and other craniomandibular features (e.g., Anapol and Lee 1994), the caecum and proximal colon of howlers are enlarged (Fooden 1964; Milton 1998) and harbor extensive communities of symbiotic microorganisms that degrade the structural components of plant cell walls through fermentation (Milton and McBee 1983). Due to the slow transit and long retention times of digesta associated with the kinetics of caeco-colic fermentation (Crissey et al. 1990; Milton 1998; Edwards and Ullrey 1999), and an important dependence on fermentation end products to meet daily energy requirements (Milton and McBee 1983), the ability of howlers to exploit non-leaf foods is probably limited. However, all species of howlers consume some non-leaf foods which, in some cases, may represent their main food resource (e.g., *A. belzebul*). In fact, it has been demonstrated that howlers prefer eating fruits when these are available (e.g., Silver et al. 1998; Stevenson et al. 2000; Palma et al. 2001), and our own data indicates that during peak fruiting *A. pigra* may spend up to 95 % of their feeding time consuming fruits for at least two week periods and may consume no leaves at all up to 3 consecutive days. Data from a reduced number of captive *A. caraya*, *A. palliata,* and *A. seniculus* individuals suggests that, independent of fiber concentrations in the diet, digestive capabilities vary among howler species (Edwards and Ullrey 1999). Therefore, it is possible that interspecific variation in feeding behavior results from differences in the interplay between food availability and digestive capabilities. In the future it will be interesting to compare the digestive flexibility of howlers that tend to be more highly frugivorous with those showing stronger folivorous tendencies.

In summary, howlers exploit some proportion of nearly all types of plant parts that are available in their habitat and their diets tend to be highly diverse. In the present study we concentrated on the description of the dietary habits of howlers and on analyzing the influences of rainfall, group size, and forest size on its variation. However, in a broader context, the feeding behavior of howlers is part of a foraging strategy that essentially relies on an intricate interplay between food availability and nutrient requirements that vary individually (e.g., Dias et al. 2011), a relatively non-specialized digestive tract and a number of mechanisms that allow behavioral modulation of their active metabolism (e.g., Milton 1998). This set of interaction has seldom been modeled, and its understanding continues to be among the major challenges we face in future howler research.

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Chapter 3
Insights into Reproductive Strategies and Sexual Selection in Howler Monkeys

Sarie Van Belle and Júlio César Bicca-Marques

Abstract The genus *Alouatta* is characterized by a flexible social system in which the reproductive strategies of males and females show great variability both within and between species. Even though the mating system of some species is more frequently polygynous (e.g., *A. arctoidea*, *A. seniculus,* and *A. pigra*) and that of other species more often polygynandrous (e.g., *A. caraya* and *A. palliata*), females in all species whose reproductive behavior has been studied have been reported to copulate with multiple males within their group, with males in neighboring groups, and with solitary males, suggesting a "mixed mating strategy" characterized by periods of selective mating and periods of promiscuous mating. Central males, however, may be able to monopolize most breeding opportunities during the periovulatory period (POP) of the ovarian cycle when conception is most likely to occur by forming consortships with cycling females. Females do not avoid these consortships as they sexually solicit the central male frequently during their POPs. All howler monkey species are sexually dimorphic in body size, canine size, and hyoid apparatus, suggesting high male–male competition. In addition, four taxa present degrees of sexual dichromatism. Infanticide has been observed in various howler monkey species and might play an important role in shaping their social systems. We review the reproductive behavior of *Alouatta*, discuss male and female reproductive strategies that are associated with sexual selection via intrasexual selection, mate choice, or intersexual conflict, and propose a model for the evolution of reproductive behavior in atelid primates.

Resumen El género *Alouatta* se caracteriza por un sistema social flexible en cual las estrategias reproductivas de los machos y las hembras muestran una gran vari-

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abilidad dentro y entre las especies. A pesar de que el sistema de apareamiento de algunas especies es más frecuentemente poligínico (por ejemplo, *A. arctoidea*, *A. seniculus* y *A. pigra*) y el de otras especies más a menudo poligínándrico (por ejemplo, *A. caraya* y *A. palliata*), se ha observado en todas las especies cuyas reproducción se ha estudiado que hembras copulan con varios machos de su grupo, con machos en grupos vecinos y con machos solitarios, lo que sugiere una "estrategia de apareamiento mixto" caracterizado por períodos de apareamiento selectivo y períodos de apareamiento promiscuo. Sin embargo, los machos con una posición central pueden monopolizar la mayoría de las oportunidades reproductivas durante el período periovulatorio del ciclo ovárico, cuando la concepción es más probable, al formar un consorte con una hembra ciclando. Las hembras no evitan estos consortes y solicitan sexualmente al macho central con más frecuencia durante sus períodos periovulatorios. Todas las especies de monos aulladores son dimórficos sexualmente en el tamaño corporal, tamaño de los caninos y huesos hioides, sugiriendo una competencia intra- e intergrupal alta entre machos. Además, cuatro taxa presentan grados de dicromatismo sexual. Infanticidio se ha observado en varias especies de monos aulladores y podría jugar un papel importante en la conformación de sus sistemas sociales. En este capítulo revisamos el comportamiento reproductivo del género *Alouatta*, discutimos las estrategias reproductivas de los machos y de las hembras, examinando si éstas son compatibles con los procesos asociados a la selección sexual, como la selección de pareja ("mate choice"), la selección intrasexual y el conflicto intersexual, y proponemos un modelo hipotético sobre la evolución de las conductas reproductivas en los primates atélidos.

Keywords Intrasexual selection • Mate choice • Intersexual conflict • Dimorphism • Dichromatism • Sexual solicitation • Copulation • Extragroup mating • Interbirth interval • Infanticide

3.1 Sexual Selection Theory and Howler Monkeys

The sexual selection theory (Darwin 1871) aims at explaining the evolution of traits unrelated to survival but that impact an individual's reproductive success. Recent reviews of sexual selection have stressed the intricate interaction of the role of the three major mechanisms: intrasexual selection, intersexual selection, and intersexual conflict (Manson 2003; Kappeler and van Schaik 2004). Intrasexual selection or mating competition refers to male–male and female–female competition for access to mates via contests, scrambles, sperm competition, or suppression of sexual function (Andersson 1994; Bicca-Marques 2003; Kappeler and van Schaik 2004). Intersexual selection or mate choice involves strategies individuals of one sex apply to attract (or be chosen by) individuals of the other sex for breeding purposes. They may include signaling social status, genetic quality, and age or health, provisioning resources, and providing infant care or protection against conspecifics or predators, as well as cryptic female choice that influences the outcome of sperm competition via anatomical, physiological, or behavioral adaptations (Bicca-Marques 2003; Reeder 2003; Shanoor and Jones 2003; Manson 2011). A third mechanism, intersexual or mating conflict, operates when the mating interests of males and females or their consequences to each sex diverge (Muller and Wrangham 2009). The most obvious forms of mating conflict involve males sexually coercing females through physical attacks, intimidation, harassment, sequestering, forced copulation, copulation interruption, and infanticide (Smuts and Smuts 1993; van Schaik and Janson 2000; van Schaik et al. 2004; Muller et al. 2009; Watson-Capps 2009; Stumpf et al. 2011).

Whereas we may never fully understand the precise contribution of each of these mechanisms to the evolution of morphological, behavioral, and physiological traits observed in living species (Hunt et al. 2009), it is well established that sexual selection contributes importantly to sex differences in secondary sexual characters (e.g., ornaments, weapons, conspicuous colors, and large body size) that are believed to increase its bearers' (principally males) fitness (Gerald 2003; Kappeler and van Schaik 2004). Among anthropoid primates, body and canine size are probably the most widespread sexually selected traits that have been associated with polygynous mating systems (Plavcan 2004; but coalition formation may lower the selective pressures on weaponry development, Plavcan and van Schaik 1992). Sexual dimorphism in these traits is argued to be a consequence of male–female differences in parental investment and the variance of individual reproductive success within these mating systems (Plavcan 2004; Manson 2011). Whereas females' ability to produce offspring is more constrained by resource availability than by access to mates (a single male can inseminate many females), the variance in reproductive success among males is generally greater, especially when a single or a few males can monopolize access to ovulating females (Strier 2007). Among primates, the main exceptions to this trend may be monogamously breeding species such as gibbons (Hylobatidae), owl monkeys (*Aotus* spp.), and titi monkeys (*Callicebus* spp.) in which variance in male and female reproductive success is minimized, and in polyandrously breeding tamarins and marmosets (Callithrichinae) in which variance in female reproductive success may be greater than in males (Strier 2007).

The strength of this intrasexual competition and its consequences are also affected by the dispersal pattern (Strier 2003). For example, when males disperse from their natal groups and attempt to enter a new group, they are likely to encounter high levels of resistance and aggression from resident males (van Hooff 2000). This might select for large canine and body size if these traits enable males to avoid injury and increase access to mating partners, but may also involve behavioral strategies. In primate species such as anubis baboons (*Papio anubis*), for example, Smuts (1985) presents data showing that immigrant males may remain on the periphery of the group, bond with females with young offspring, and assist these females in caring for their young as part of a behavioral strategy to enter the group, resulting in lower levels of male–male competition over access to females.

In addition, in species in which the likelihood of competing for access to receptive females with kin is high, such as in spider monkeys (*Ateles* spp.), muriquis (*Brachyteles* spp.), and chimpanzees (*Pan troglodytes*), less risky forms of competition may be favored, such as sperm competition and its association with an increase in testes size relative to body size, increased sperm production, and sperm plugs (Strier 2007; Dixson 2012).

In this chapter, we review the reproductive behavior of howler monkeys (*Alouatta* spp.) and explore how mating competition, mate choice, and sexual conflict may shape it. Howler monkeys represent an instructive model for exploring the operation of sexual selection on reproductive behavior because the genus is characterized by a highly flexible social system with all species exhibiting marked variability in group size and composition, and regardless of the species, most populations contain unimale and multimale bisexual groups (Di Fiore et al. 2011). Resident males in multimale groups rarely engage in agonistic interactions (Wang and Milton 2003; Van Belle et al. 2008; Rangel-Negrín et al. 2011; Garber and Kowalewski 2011), and generally no clear dominance hierarchies can be discerned (but see Jones 1980; Dias et al. 2008). Nevertheless, one resident male, herein referred to as the "central" male, can be recognized based on his closer spatial association with resident females, his priority of access to fertile females, and increased participation in howling bouts compared to "noncentral" males (Wang and Milton 2003; Kitchen et al. 2004; Kowalewski 2007; Van Belle et al. 2008). In addition, howler monkeys (1) are sexually dimorphic in body, canine, and hyoid size (see chapters by Youlatos et al. 2014 and da Cunha et al. 2014 for details on the importance of the hyoid bone in the production of vocalizations), (2) four taxa also show sexual dichromatism (Table 3.1; see also Youlatos et al. 2014), (3) females may mate with multiple males, including extragroup males (Kowalewski and Garber 2010), (4) species differ in relative testes size (Kelaita et al. 2011), (5) both males and females may disperse from their natal groups (Glander 1992; Calegaro-Marques and Bicca-Marques 1996; Pope 2000a; Van Belle et al. 2008, 2011; Di Fiore et al. 2011), (6) immigrant males may commit infanticide after successfully taking over groups (Crockett 2003), (7) males exhibit very limited direct investment in offspring care (Bolin 1981; Neville et al. 1988; Calegaro-Marques and Bicca-Marques 1993a), and (8) adults may react to same-sex immigrants with intense hostility (Pope 2000a; Van Belle et al. 2008, 2011).

3.2 Sexual Solicitations

Solicitation for sexual interactions in howler monkeys involves establishing eye contact with a preferred mate (i.e., exaggerated gaze only observed within sexual context), tongue flicking at the mate (i.e., rhythmic movement of the tongue in and out and up and down the mouth observed almost exclusively within sexual context), presenting one's genitals while looking back over their shoulder at the solicitee, or touching, smelling, and/or licking the genitals of the mate (*A. belzebul*: Bonvicino 1989;

Table 3.1 Body and hyoid size and dimorphism (estimated as the ratio of the mean value of the male trait divided by that of the female) in *Alouatta* spp.

Taxon	Adult body mass (kg)		Body mass dimorphism	Hyoid length (mm)[1]		Hyoid dimorphism	Sexual dichromatism?
	Male	Female		Male	Female		
A. arctoidea	6.3 (19)	5.1 (8)[2,3]	1.24				No
A. belzebul				58.1 (20)	41.4 (13)	1.40	No
A. caraya	6.8 (113)	4.4 (141)[4–8]	1.54	51.6 (13)	34.5 (21)	1.50	Yes
A. discolor				63.2 (29)	40.0 (8)	1.58	No
A. guariba clamitans	6.7 (4)	4.4 (5)[9]	1.55	63.8 (8)	38.5 (12)	1.66	Yes
A. guariba guariba				35.3 (9)	24.2 (6)	1.46	No
A. juara				63.2 (3)	34.7 (2)	1.82	No
A. macconnelli				68.7 (22)	38.0 (15)	1.81	No
A. nigerrima				66.1 (6)	40.8 (8)	1.62	No
A. palliata	6.0 (369)	4.9 (775)[10,11]	1.22	36 (2)	27 (1)[12]	1.33	No
A. pigra	7.6 (37)	5.7 (32)[11]	1.33				No
A. seniculus puruensis							Yes[1]
A. sara							No
A. seniculus	5.6 (31)	4.0 (29)[13]	1.40				No
A. ululata				63.7 (1)	30.0 (1)	2.12	Yes[1]

Sources: [1]Gregorin (2006), [2]Rodríguez and Bohrer (1988), [3]Thorington et al. (1979), [4]Aguiar et al. (2007), [5]Almeida et al. (2005), [6]Redford and Eisenberg (1992), [7]Rumiz (1990), [8]Thorington et al. (1984), [9]Smith and Jungers (1997), [10]Glander (2006), [11]Kelaita et al. (2011), [12]Hill (1962), [13]Braza et al. (1983)
Values shown are mean and sample size (in parentheses)

A. caraya: Calegaro-Marques and Bicca-Marques 1993b; Kowalewski and Garber 2010; *A. palliata*: Carpenter 1934; Jones 1985; *A. pigra*: Horwich 1983; Van Belle et al. 2009; *A. seniculus*: Neville 1972; Izawa and Lozano 1989; Izawa 1997). In addition, *A. pigra* females have been observed to rhythmically move their hands or the tip of their tails over their erected clitoris (Van Belle pers. obs.). Whether this behavior is related to sexual stimulation is unknown.

Both sexually mature males and females have been observed to solicit sexual interactions in various howler species. In two study groups at Hacienda La Pacifica, Costa Rica, *A. palliata* males solicited significantly more frequently than females relative to their numbers in the groups, and central males solicited significantly more frequently than noncentral males. Similarly, females solicited both central and noncentral males, but central males were solicited significantly more frequently (Jones 1985). In a subsequent study of one *A. palliata* group at the same site, females solicited the majority (94 %, $N=88$ of 94) of copulations, and females solicited both central and noncentral males at equal rates (Ford 2010). *Alouatta caraya* and *A. pigra* females also solicited significantly more frequently than males (Van Belle et al. 2009; Kowalewski and Garber 2010). *Alouatta pigra* females of two multimale-multifemale groups solicited the central male in their groups almost exclusively (Van Belle et al. 2009), while *A. caraya* females solicited all resident males of their groups, as well as extragroup males (Kowalewski and Garber 2010).

Male and female sexual solicitations across the ovarian cycle were examined in *A. palliata* (Jones 1985) and *A. pigra* (Van Belle et al. 2009). The *A. palliata* population at La Pacifica, Costa Rica, is the only known howler monkey population for which females experience consistent cyclic changes in vulvar size and coloration (Jones 1985; Glander 1980; but see Kowalewski and Garber 2010 for the possibility of slight genital changes in *A. caraya*). Jones (1985) discriminated four stages of tumescence and detumescence based on 37 ovarian cycles: E0: no tumescence (mean = 3.3 days), E1: minimal tumescence when vulvae is swollen, but not pinkish (mean = 4.0 days), E2: moderate tumescence when vulvae is swollen and pinkish, but not "ruddy" (mean = 6.8 days), and E3: maximum tumescence when vulvae is swollen, pinkish, and has a "ruddy" appearance (mean = 1.8 days), which is assumed to coincide with the periovulatory period (POP) when conception is most likely to occur. However, this assumption has not been verified using hormonal data. Males more frequently (84 %, $N=37$ of 44) solicited females who were at or near peak tumescence (E2 and E3) compared with females at stages E0 or E1. Furthermore, most male solicitations directed toward E3 females were initiated by the central male (72 %, $N=13$ of 18), while those directed toward E2 females were initiated by any resident male in the group (central males accounted for 42 % ($N=8$ of 19) of solicitations during E2). Females at the E2 stage of their ovarian cycle solicited males more frequently (69 %, $N=81$ of 118) compared with E3 females (20 %, $N=24$ of 118), while E0 and E1 rarely solicited (11 %, $N=13$ of 118). Similar to the male pattern, E2 females solicited males of all ranks, while E3 females directed their solicitations most frequently to their central male (75 %, $N=18$ of 24). Thus, the most observed sexual solicitations were between central males and females at peak tumescence (E3) (Jones 1985).

In *A. pigra*, ovarian cycles were assessed by fecal estrogen and progesterone profiles in two groups (*N* = 4 females), and the occurrence of male and female sexual solicitations was compared during the POPs and outside these periods (nonPOPs). The POP (*N* = 18) was defined as the estimated day of ovulation ± 3 days based on elevated levels of fecal progesterone and estradiol (reviewed in Van Belle et al. 2009; Van Belle 2014). Females solicited central males significantly more frequently during POPs than nonPOPs, but not noncentral males, whom they rarely solicited. Males were seldom observed to solicit sexual interactions, but central males groomed cycling females more frequently than cycling females groomed them. Nonetheless, central males groomed cycling females at equal rates during the POPs and nonPOPs, suggesting that although central males were actively involved in establishing and maintaining social relationships with cycling females, grooming females were not associated with copulations per se and therefore grooming is not a true indicator of solicitation by the central male. Central males sniffed females' genitals significantly more frequently during POPs than nonPOPs, suggesting that males might be able to monitor females' reproductive status through olfactory cues and coordinate their sexual activities accordingly.

Furthermore, central males spent significantly more time in close proximity (0–1 m) to cycling females during POPs than nonPOPs and were largely responsible for maintaining this association, providing opportunities for consortships and mate guarding at times when conception was most likely to occur. Also in *A. caraya*, *A. palliata*, and *A. arctoidea*, central males, but not other resident males, have been reported to form consortships by persistently following a presumably ovulating female and engaging in sexual interactions (Pope 1990; Calegaro-Marques and Bicca-Marques 1993b; Jones 1995; Kowalewski and Garber 2010; but see Wang and Milton 2003). In *A. palliata*, a consorting pair frequently (73 %, *N* = 29 of 38) engaged in concomitant feeding before sexual interactions and central males who defend food resources against other male group members more successfully (Jones 1980) have been hypothesized to be preferred mating partners (Jones 1985, 1995). In *A. pigra*, females might also play an active role in choosing their consort partners. Females significantly increased their approach rate toward central males during their POPs compared with nonPOPs and compared to noncentral males (Van Belle et al. 2009). Female mate choice also is expressed when females choose to mate exclusively with one particular noncentral male or with extragroup males (Jones 1985; Kowalewski and Garber 2010) (see "Copulations and Mating Patterns" below).

It is important to point out that not all sexual solicitations are successful. Fifty one percent (*N* = 55) of male genital sniffing and 49 % (*N* = 52) of female solicitations were ignored or rejected by the solicitee in *A. pigra* (Van Belle Unpublished data). Furthermore, of the 53 events in which a male sniffed the genitals of a female and the female responded by soliciting back, only 23 % (*N* = 12) led to copulations despite the fact that both the male and female showed sexual interest in each other. However, of the 54 female solicitations in which the solicited male responded by smelling her genitals or tongue flicking, 76 % (*N* = 41) led to copulations (Van Belle Unpublished data). Thus, copulations were more frequently (77 %) initiated by females than by males (Van Belle et al. 2009). *Alouatta caraya* and *A. palliata* females also initiated copulations more frequently (89 % and 68 %, respectively) than resident males (Jones 1985; Kowalewski and Garber 2010). However, when considering the percentage of successful sexual solicitations across the ovarian cycle in *A. palliata*, solicitations by central males directed to E3 females were more successful than those by E3 females toward central males. Sex of the solicitor did not influence solicitation success at other times (Jones 1985). The central male also rejected female solicitations more frequently (7 of 36) than did noncentral males (1 of 31 and 0 of 25; Jones and Agoramoorthy 2003). Finally, young adult female *A. palliata* and *A. arctoidea* were quite successful in avoiding forced copulations (Jones and Agoramoorthy 2003), suggesting that such male sexual coercion in these species is not a common or successful male strategy.

3.3 Copulations and Mating Patterns

Copulations in howlers are reported to last an average of 49 s and include an average of 34 pelvic thrusts (Table 3.2). Males have been observed to pause after a series of pelvic thrusts before ending intromission, which might coincide with ejaculation (*A. arctoidea*: Neville 1972; *A. caraya*: Calegaro-Marques and Bicca-Marques 1993b; *A. palliata*: Jones 1985; Jones and Cortés-Ortiz 1998; *A. pigra*: Van Belle pers. obs.; *A. seniculus*: Izawa and Lozano 1989; Izawa 1997). Jones (1985) reports that central males ($N=2$) of two *A. palliata* groups ejaculated in 88 % and 80 % of their copulations, while noncentral males ($N=3$) of these groups ejaculated in 82, 77, and 67 % of their copulations. However, because the ejaculate does not coagulate into a sperm plug in howler monkeys (Moreland et al. 2001), it has not been confirmed whether these pauses truly reflect ejaculation or whether the male failed to ejaculate during copulations without pauses.

Table 3.2 Copulation duration (seconds) and number of pelvic thrusts (mean ± standard deviation, range and sample size) in *Alouatta* spp.

		Copulation duration(s)			Pelvic thrusts		
Taxon	Site	Mean ± SD	Range	*N*	Mean ± SD	Range	*N*
A. belzebul	Fazenda Pacatuba, Brazil[1]	–	<120	3	–	–	–
A. caraya	Estância Casa Branca, Brazil[2]	41 ± 11	25–70	18	45 ± 12	25–65	12
	Isla Brasilera, Argentina[3]	48 ± 17	13–140	219	–	–	–
A. palliata	Hacienda La Pacifica, Costa Rica[4]	–	<50	25	32	>22	25
A. pigra	Palenque National Park, Mexico[5]	55 ± 27	21–152	76	29 ± 17	30–70	25

Sources: [1]Bonvicino (1989), [2]Calegaro-Marques and Bicca-Marques (1993b), [3]Kowalewski and Garber (2010), [4]Jones (1985), [5]Van Belle (Unpublished data)

3.3.1 Intragroup Mating Patterns

The mating system of *A. caraya* and *A. palliata* generally involves females promiscuously mating with several males of their group, while that of *A. arctoidea*, *A. pigra*, and *A. seniculus* appears more frequently to involve females concentrating mating with only one resident male (Table 3.3). However, in all species whose reproductive behavior has been studied, adults of both sexes have been reported to copulate with more than one mate within their group (Table 3.3), suggesting a "mixed mating strategy" characterized by periods of selective mating and periods of promiscuous mating depending on the social and ecological environments (Kowalewski and Garber 2010). For example, whereas females of two multimale-multifemale *A. pigra* groups were observed to copulate almost exclusively with the central male during a 14-month field study (June 2006–July 2007; Van Belle et al. 2008), virtually all females of the same groups and of a third multimale-multifemale group were observed to copulate with two or three resident males in a subsequent 16-month study (September 2010–December 2011; Van Belle et al. 2014). A similar pattern of variability was observed in *A. arctoidea* and *A. seniculus* (Table 3.3).

Despite multimale mating, the central male might still be able to monopolize the majority (47–85 %) of mating opportunities (Table 3.3), or might be able to monopolize mating opportunities during POPs. Similar to the patterns of sexual solicitation, 66–75 % of copulations by central *A. palliata* males in Jones' two study groups involved females with vulvae at peak tumescence (E3), while the majority (60–86 %) of copulations by subordinate males were with females with moderate sexual swellings (E2; Jones 1985). Similarly, copulations of central males in *A. pigra* were almost exclusively (89 %) restricted to POPs, although the three copulations by one noncentral male also occurred during POPs (Van Belle et al. 2009). In addition, paternity assignment analyses in *A. arctoidea* revealed that the male of five unimale groups and the central male of four multimale groups sired all infants ($N = 28$) conceived during their tenure (Pope 1990); however, the central male in *A. palliata* groups could be excluded as a potential sire in three of five cases where DNA samples were available for the offspring, its mother, and the males present at the time of conception (Ellsworth 2000). Also in *A. pigra*, two males were observed to have sired offspring (N = 7) in two multimale groups, while only one resident male sired offspring (N = 11) in two additional multimale groups and one unimale group (Van Belle et al. 2014).

Variability in reproductive opportunities and success among howler monkey males and the associated male–male competition for access to fertile females are believed to have resulted in sexual dimorphism in body and canine size in this genus (Plavcan 2004, see Table 3.1). Interestingly, of the six species for which body size measurements exist, *A. caraya* and *A. guariba clamitans* show the highest degree of sexual dimorphism, while *A. arctoidea*, *A. palliata*, *A. pigra*, and *A. seniculus* have lower degrees of sexual dimorphism (Table 3.1, see also Kelaita et al. 2011). Based only on the pattern of female promiscuity, a lower degree of sexual dimorphism might be expected in *A. caraya* and *A. palliata*, whose females mate promiscuously on a more regular basis than those of *A. arctoidea*, *A. guariba*, *A. seniculus*, and *A. pigra*. However, a species' degree of sexual dimorphism may be multifactorial and

Table 3.3 Intragroup mating patterns in *Alouatta* spp.

Taxon	Study site	Study duration	# of groups	Mating pattern	Central male monopolization	# of copulations
A. arctoidea	Hato Masaguaral, Venezuela[1]	12 months	3 MMG	UMM	Yes (100 %)	26
	Hato Masaguaral, Venezuela[2]	10 years	5 UMG/4 MMG	UMM/UMM	Yes	–
	Hato Masaguaral, Venezuela[3]	25 months	8 MMG	MMM	–	14
A. belzebul	Fazenda Pacatuba, Brazil[4]	14 months	1 UMG	UMM	–	3
A. caraya	Isla Brasilera, Argentina[5]	20 month	2 MMG	MMM	Yes (55–78 %)	149
	Estância Casa Branca, Brazil[6]	12 months	1 MMG	MMM	Yes (85 %)	40
A. palliata	Barro Colorado Island, Panama[7]	9 months	1 MMG	MMM	No (15 %)	27
	La Pacifica, Costa Rica[8]	17 months	2 MMG	MMM	Yes (47–62 %)	42
	La Pacifica, Costa Rica[9]	12 months	1 MMG	MMM	Yes	148
	Agaltepec Island, Mexico[10]	4 months	1 MMG	MMM	–	45
A. pigra	Palenque National Park, Mexico[11]	14 months	2 MMG	UMM	Yes (91–100 %)	72
	Palenque National Park, Mexico[12]	28 months	1 UMG/4 MMG	UMM/MMM	No (33–62 %)	59
	Campeche, Mexico[13]	10 month	1 MMG/1 UMG	MMM/UMM	–	
A. seniculus	La Macarena, Colombia[14]	12 months	1 UMG	UMM	Yes	–
	La Macarena, Colombia[15]	28 months	1 MMG	MMM	No	–

Sources: [1]Sekulic (1983), [2]Pope (1990), [3]Agoramoorthy and Rudran (1995), [4]Bonvicino (1989), [5]Kowalewski and Garber (2010), [6]Calegaro-Marques and Bicca-Marques (1993b), [7]Wang and Milton (2003), [8]Jones (1985), [9]Ford (2010), [10]Jones and Cortés-Ortiz (1998), [11]Van Belle et al. (2009), [12]Van Belle et al. in press, [13]Rangel-Negrín et al. (2011), [14]Izawa and Lozano (1989), [15]Izawa (1997)

UMG unimale groups, *MMG* multimale groups, *UMM* unimale mating, *MMM* multimale mating express, for example, both the intensity of precopulatory male–male competition and female–female competition (Kelaita et al. 2011).

Female howler monkeys may compete to avoid infanticide risk (Crockett and Janson 2000), and such female–female competition may increase female body and canine size, reducing size differences between the sexes (Plavcan and van Schaik 1992). In *A. arctoidea*, groups with three to four adult females become increasingly more attractive targets to coalitions of extragroup males that attempt to take over the group by evicting resident males and may commit infanticide (Crockett and Janson 2000). Resident females aggressively prevent extragroup females from immigrating, thereby maintaining limited group size (Crockett and Pope 1993; Crockett 1984). Resident females compete to recruit their own daughters as additional breeding females and other females' daughters are forcefully evicted as juveniles. When adult female group size has reached four all juvenile females are evicted (Pope 2000b). In addition, *A. arctoidea* females in coalitions with kin enjoy higher reproductive success than those in coalitions with unrelated females (Pope 2000b). Similar forms of female–female competition have also been observed in *A. caraya* (Calegaro-Marques and Bicca-Marques 1996) and *A. pigra* (Van Belle et al. 2011; Brockett et al. 1999), and females have been reported to co-reside with kin in some groups of *A. pigra* (Van Belle et al. 2012), *A. caraya* (Oklander et al. 2010), and *A. palliata* (Milton et al. 2009). It is unknown to what extent female–female competition in howler monkeys has selected for weaponry and larger bodies, and how it influences sexual dimorphism. Comparisons of body size and canine dimorphism among all howler monkey species, along with estimates of the intensity of male–male and female–female competition, are needed to better understand sexual dimorphism in this genus.

Because intragroup copulations often occur in full view of other group members and copulations are seldom interrupted or challenged by others (see examples in *A. caraya*, Calegaro-Marques and Bicca-Marques 1993b), central males seem to tolerate the mating activities of other resident males (Wang and Milton 2003; Van Belle et al. 2009; Kowalewski and Garber 2010; Garber and Kowalewski 2011). Such tolerance is fully compatible with the formation of male coalitions and appears to be reinforced by mutual howling (Kitchen et al. 2004; Van Belle et al. 2008, in press) and social embracing (Wang and Milton 2003; Dias et al. 2008; Garber and Kowalewski 2011). Compared to single males, male coalitions increase the chances of successfully taking over groups or the likelihood of resident males repelling intruding males (Sekulic 1983; Crockett 2003; Van Belle et al. 2008). These coalitions in howler monkeys are compatible with concession models that assume that dominant individuals allow subordinates to copulate (i.e., paternity expectation) in order to increase the chances that they will stay and cooperate in the social group (Hager 2003). Here, post-copulatory male–male competition in the form of sperm competition may play a prominent role. This is especially true for howler monkey species whose groups are commonly composed of multiple males and hence have more frequently a polygynandrous mating system, such as *A. palliata* and *A. caraya*. According to Kelaita et al. (2011), the relative testes size in *A. palliata* was on average twice as large as those in *A. pigra*, suggesting more intense sperm competition in the first. Compared to other anthropoids, *A. palliata* testicular volume relative to body size is consistent with the ratio documented for primates living in large multimale-multifemale groups such as savannah baboons (*Papio* spp.), while *A. pigra* relative testicular volume is slightly higher than that reported for unimale-multifemale groups of gorillas (*Gorilla* spp.), hamadryas baboons (*Papio hamadryas*), and orangutans (*Pongo pygmaeus*) (Kelaita et al. 2011). Mean values of relative testes size in *A. caraya* are between those of *A. palliata* and *A. pigra* (Moreland et al. 2001), suggesting intermediate levels of sperm competition in this species.

In addition to the sexual interactions during a 2–5 day period that coincides with the POP (*A. pigra*: Van Belle et al. 2009; *A. arctoidea*: Herrick et al. 2000), or is assumed to coincide with this period in other species for which hormonal and sexual behavior data were not collected simultaneously (e.g., *A. caraya*: Calegaro-Marques and Bicca-Marques 1993b; Kowalewski and Garber 2010; *A. palliata*: Jones 1985), females have also been observed to copulate when they are pregnant or lactating (*A. caraya*: 27 % of observed copulations, Kowalewski and Garber 2010; *A. palliata*: Glander 1980; *A. seniculus*: Izawa 1997), suggesting that these non-procreative matings might represent a female strategy to foster affiliative or protective social bonds with males (see "Interbirth Interval, Infanticide, and Female Counterstrategies" below; see also Zinner and Deschner 2000; Kowalewski and Garber 2010).

3.3.2 Extragroup Mating Patterns

The central male's capacity to monopolize reproductive opportunities can be further undermined by females mating with males of neighboring groups. High rates of extragroup copulations with neighboring males have been reported for *A. caraya*, where 32 % ($N=70$ of 219) of observed copulations involving females ($N=8$) of two study groups were with males ($N=14$) belonging to five neighboring groups (Kowalewski and Garber 2010). These extragroup copulations occurred during either intergroup encounters (54 %) or during resting periods (46 %) when females left their groups to search for mates in neighboring groups. This activity took a female an average of 8 min before returning to her group. In both cases, females solicited virtually all (96 %) extragroup sexual interactions, and extragroup copulations were observed during both periods of female receptivity (86 %) and female infertility (pregnancy or lactation, 14 %). Unlike the pattern of within-group mating, copulations with extragroup males occurred out of sight of the female's group mates. In the only two cases in *A. caraya* in which a male of the female's group was reported to witness the sexual interaction, he promptly approached and threatened the pair interrupting the copulation without physical contact (Kowalewski and Garber 2010).

Extragroup copulations between neighbors also have been observed, though at considerably lower rates, in *A. guariba clamitans* (three of six observed copulations between the same adult female and the same adult male of a neighboring group, Fialho and Setz 2007; seven copulations between the same couple distributed over the course of 2 days, Lopes and Bicca-Marques 2011; a single extragroup copulation during an intergroup encounter out of 19 observed encounters over 54 days distributed over 7 months, Decker and Bicca-Marques 2013), *A. pigra* (nine of 139 observed copulations involving four adult females from three social groups, Van Belle et al. 2008; Van Belle Unpublished data; three of eight observed copulations between the same adult female and the same adult male of a neighboring group over the course of 4 days, Horwich 1983), and *A. arctoidea* (nine copulations involving seven adult females of six social groups, Agoramoorthy and Hsu 2000). The neighboring males involved in the nine extragroup copulations observed in *A. arctoidea* were heavier than the female's resident males, suggesting that females might prefer high quality males as mate (Agoramoorthy and Hsu 2000). As was observed for *A. caraya*, females of *A. guariba clamitans*, *A. pigra*, and *A. arctoidea* also initiated the majority of extragroup sexual interactions, and resident males of the female's group interrupted some, but not all, of the extragroup copulations. Females engaging in extragroup copulations belonged to groups containing a single adult male (17 % of groups), two (44 %), three (29 %), or four (11 %) adult males ($N=14$ groups).

Resident males and females may also copulate with solitary individuals during encounters. Solitary *A. palliata* females may use such copulations with resident males of the group they attempt to join as a tactic to form a social bond with one male group member and gain protection against resident females who aggressively chase them away (Glander 1992). One solitary adult female *A. arctoidea* was observed to copulate 17 times with four adult and subadult males of two social groups. However, despite her sexual interactions with these males, she did not succeed in gaining entrance into either group over a period of at least 17 months (Sekulic 1982). Similarly, extragroup copulations ($N=3$) with a solitary individual were observed in *A. pigra*, involving both solitary males ($N=1$) and females ($N=2$, Van Belle et al. 2009; Van Belle Unpublished data), and in *A. caraya* between a solitary male and a resident female during her fertile period ($N=2$, Kowalewski and Garber 2010).

3.4 Interbirth Interval, Infanticide, and Female Counterstrategies

The interbirth interval can be divided into three components: gestation, lactation, and ovarian cyclicity. Gestation length is considered to be the least variable component of the interbirth interval (Strier 2001) and was determined to be 184 days for *A. pigra* based on hormonal profiles of one female (Van Belle et al. 2009). Comparable hormonal data for other howler species are not available, but estimates of the time interval between the last observed POP based on patterns of copulatory behavior and parturition are similar for *A. arctoidea* (mean = 191 days, range = 186–194, $N=6$; Crockett and Sekulic 1982), *A. caraya* (152–195 days, $N=2$; Calegaro-Marques and Bicca-Marques 1993b), and *A. palliata* (mean = 186 days, range = 180–194, $N=4$; Glander 1980).

Although gestation and lactation are temporally distinct components in most primates due to the hormonal inhibition of ovulation during these stages (Strier 2001), howler monkey females may become sexually receptive when still lactating 6–12 months after parturition (Glander 1980; Van Belle et al. 2009; Pavé et al. 2010; Dias et al. 2011). By that time, the nursing demands of the infant/young juvenile are significantly reduced, suckling decreases, and offspring are consuming larger amounts of solid food (Clarke 1990; Miranda et al. 2005; Pavé et al. 2010; reviewed in Raguet-Schofield and Pavé 2014), which could potentially release the hormonal inhibition of ovulation. Hormonal studies are needed to understand ovarian cyclicity during lactation. In addition to variability in the duration between postpartum acyclicity and ovarian cyclicity, the period during which females cycle and engage in sexual interactions also varies due to the fact that females may experience one to eight ovarian cycles before becoming pregnant, with each ovarian cycle lasting an average of 16–19 days (reviewed in Van Belle 2014).

This variability results in an interbirth interval after the survival of 1-year old infants of, on average, 18.3 months, ranging from 10 to 38 months (Table 3.4). Differences in mean interbirth interval among species and populations might be attributed to differences in seasonal abundance and quality of food resources across diverse habitats, as was suggested for a 2-month mean difference in the interbirth interval between *A. arctoidea* populations inhabiting woodland versus gallery forests (Crockett and Rudran 1987). Furthermore, when a female loses an infant younger than 1-year old, the period of postpartum acyclicity ends abruptly and the female starts soliciting sexual interactions from 1 day to 3 weeks after the loss of the infant (Glander 1980; Van Belle et al. 2009), significantly shortening the interbirth interval to an average of 11.3 months (Crockett and Sekulic 1984; Fedigan and Rose 1995; Crockett 2003; Pavé et al. 2012).

Table 3.4 Interbirth interval (months; mean, range, and sample size) in *Alouatta* spp.

		Interbirth interval (months)		
Taxon	Site	Mean	Range	*N*
A. arctoidea	Hato Masaguaral, Venezuela[1]	17	10.5–26	131
A. caraya	Corrientes, Argentina[2]	21	17–27	
	Río Riachuelo, Argentina[3]	15.8	12–26	30
	Isla Brasilera, Argentina[4]	14.1	11–17	15
A. guariba clamitans	Estação Biológica de Caratinga, Brazil[5]	23.9	19–38	11
A. palliata	Isla Agaltepec, Mexico[6]	19.5		8
	Hacienda La Pacifica, Costa Rica[7]	22.5	18–25	16
	Barro Colorado Island, Panama[8]	17		
	Santa Rosa National Park, Costa Rica[9]	21.1		23
A. pigra	Palenque National Park, Mexico[10]	14		1
	Several sites, Campeche, Mexico[11]	15.5		

Sources: [1]Crockett and Rudran (1987), [2]Zunino (1996), [3]Rumiz (1990), [4]Pavé et al. 2012, [5]Strier et al. (2001), [6]Dias (2005), [7]Glander (1980), [8]Milton (1982), [9]Fedigan and Rose (1995), [10]Van Belle (Unpublished data), [11]Dias et al. (2011)

This shortening of the interbirth interval after the premature death of an unweaned young infant is the major evidence supporting the adaptive value of infanticide committed by males (Struhsaker and Leland 1987; van Schaik and Janson 2000; Crockett 2003). Infanticide by howler males has been directly observed 17 times and was almost observed on three additional occasions when infants with severe and fresh wounds were seen close to a potentially infanticidal male (reviewed in Crockett 2003). Of these, seven cases were observed in *A. seniculus* (Izawa and Lozano 1991, 1994; Kimura 1992; Izawa 1997; Palacios 2000), six in *A. arctoidea* (Rudran 1979; Agoramoorthy and Rudran 1995), four in *A. pigra* (Knopff et al. 2004; Van Belle et al. 2010), two in *A. caraya* (Zunino et al. 1985; Aguiar et al. 2005), and one in *A. palliata* (Clarke 1983). Data on infanticide in howler monkeys is compatible with the sexual selection hypothesis (Hrdy 1979; Hausfater and Hrdy 1984) in that victims were seldom suspected to be related to their killers, almost all deaths led to early resumption of sexual activity by the victims' mothers, and infanticidal males were observed to copulate with these females and were often the most likely sire of the mother's next offspring (reviewed in Crockett 2003).

Formerly considered a form of intrasexual selection via male–male competition, infanticide is currently seen as a mechanism of male sexual coercion, a form of intersexual conflict (van Schaik and Janson 2000; Clarke et al. 2009; Stumpf et al. 2011; Palombit 2012). The risk of infanticide is seen as the driving force of the evolution of female counterstrategies (Palombit 2012). Female counterstrategies include promiscuity that allows them to increase paternity confusion among several males and hence decrease males' ability to evaluate their actual likelihood of siring an offspring (Struhsaker and Leland 1987; Wolff and Macdonald 2004; Clarke et al. 2009; Palombit 2012). The promiscuous mating of female howler monkeys with multiple resident males, males in neighboring groups, and solitary males, along with copulations during pregnancy, seems to fit the hypothesis of howler females employing such counterstrategies against infanticide threats that may occur during group takeover attempts and central male replacements.

However, changes in male breeding positions in howler monkeys most frequently come from outside when extragroup males take over the social group and assume the breeding position (Crockett 2003; Van Belle et al. 2008). In this situation, as opposed to changes in the male central position within the social group, mating promiscuously with both central and noncentral males might not significantly lower the risk of infanticide coming from outside the group (Pradhan and van Schaik 2008). In that regard, it is unclear whether the low rate of extragroup copulations reported for most populations (except for *A. caraya* at Isla Brasilera, Argentina; Kowalewski and Garber 2010) represents an effective strategy against infanticide in howler monkeys. Instead, mating promiscuously with both central and noncentral resident males in howler monkeys might be a female strategy to reinforce sociosexual bonds with all resident males resulting in resident males acting collectively to repel an intruding male (see Kowalewski and Garber 2014).

Multimale mating in howler monkeys also could promote genetic variability among successive offspring (Wolff and Macdonald 2004), as has been suggested for *A. caraya* (Kowalewski and Garber 2010). These authors argue that the genetic variability, and hence phenotypic variation, among a female's offspring resulting from promiscuous mating might increase the likelihood that at least some individuals will be able to successfully colonize and exploit the diverse range of forest types and associated extreme seasonal variation in temperature and food availability characteristic of the southernmost geographic distribution of howler monkeys. Data on the mating patterns in northern populations of *A. caraya* and southern and northern populations of *A. guariba clamitans* are needed to test their hypothesis. Considering that the southern populations of both species face similar environmental conditions, Kowalewski and Garber's (2010) hypothesis leads to the prediction that southern populations of *A. guariba clamitans* should behave similarly to Argentinean *A. caraya*, whereas northern populations of both species that live in less seasonal habitats (at least in terms of temperature variation) should engage in lower levels of promiscuity and extragroup copulations.

Multimale mating in primates also has been hypothesized to be a female strategy to guard against male fertility (Manson 2011), to promote female cryptic choice through sperm competition (Reeder 2003), and to insure gene quality and compatibility for offspring (Schwenson et al. 2008; Setchell et al. 2010). It is very likely that no single explanation will best predict the mating behavior of female howler monkeys across species, populations, individuals, and over the course of a female's reproductive career (Kowalewski and Garber 2010). Clearly, additional research on intra- and intergroup mating patterns, along with paternity assignment analyses, long-term male and female reproductive success, and the costs and benefits of social relationships are needed to further elucidate male and female reproductive strategies.

3.5 A Model for the Evolution of Sociosexual Behavior in Atelids

We propose a model for the evolution of sociosexual behavior within the family Atelidae based on our review on howler monkeys and on Di Fiore et al.'s (2011) review of ateline social and reproductive behavior (Fig. 3.1). Our model follows the phylogenetic arrangement accepted by Di Fiore et al. (2011) in which *Alouatta* is the most basal extant genus and *Brachyteles* and *Lagothrix* are the most derived sister taxa (*Oreonax* is not included). Based on the similarity of the dentition of *Stirtonia*, an extinct basal atelid (Kay et al. 2012), with that found in *Alouatta* (Kay and Cozzuol 2006), the model assumes that the ancestral atelid consumed a folivorous-frugivorous diet like modern howler monkeys do (Crockett and Eisenberg 1987). It also considers that a small polygynous multimale-multifemale social organization represented the primitive platyrrhine condition (Garber et al. 1993). The small size and estimated canine dimorphism in *Homunculus*, the basal taxon of the extinct basal platyrrhine lineage, similar to the median found in extant platyrrhines suggest different levels of selection among males and females and low levels of within-sex contest competition or an increased importance in same-sex coalition

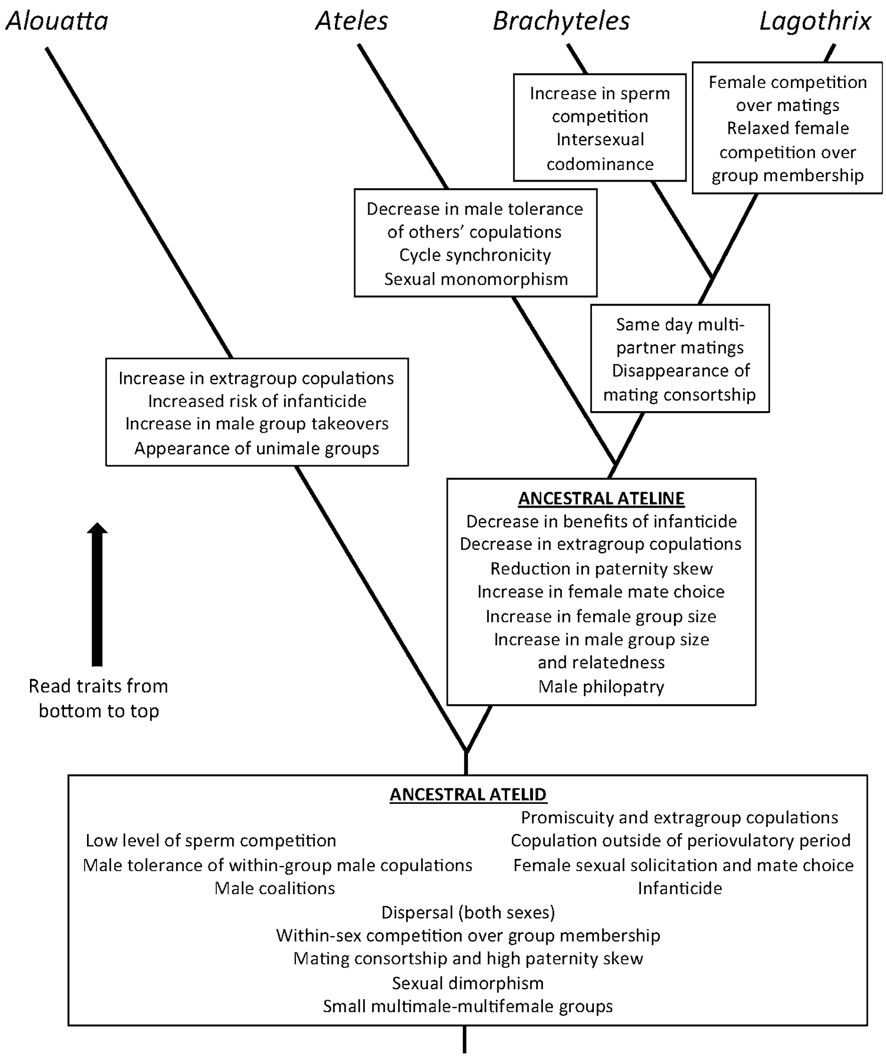

Fig. 3.1 A model for the evolution of sociosexual behavior in atelids. See text for details

formation for defending access to mates or food resources (Kay et al. 2012). These traits are compatible with Garber et al.'s (1993) hypothesis.

We propose that ancestral atelids were sexually dimorphic and lived in small multimale-multifemale groups in which central males formed consortships with receptive females, thereby resulting in high paternity skew. A lack or low level of seasonal reproduction (as seen in *Alouatta*; Di Bitetti and Janson 2000; Kowalewski and Zunino 2004) allowed males to influence the reproductive success of females via infanticide, selecting for male dispersal, as proposed by Strier (1996). Therefore, within-sex competition for group membership in both males and females led to a bisexual dispersal pattern. Male dispersal created a conflict between resident and extragroup males that favored the formation of male coalitions (kin or non-kin) to defend the group or to increase the likelihood of taking over a group. Resident kin coalitions benefitted both central and noncentral males via direct and inclusive fitness, decreased the likelihood of contest competition over mates, facilitated central male tolerance of noncentral male copulations, and selected for low levels of sperm competition. The decrease in direct competition among related males favored a longer or more successful tenure of kin coalitions, has been reported in extant *A. arctoidea* (Pope 1990). The killing of dependent infants would be an advantageous strategy particularly when a new central male, who could not have sired the young reached the top of the male hierarchy either via an intragroup ranking reversal, the filling of the vacancy of a deceased former central male, or the successful takeover of a group by invading male(s). Therefore, selection may have favored a series of female strategies aimed at confusing paternity, such as ovulation concealment, female sexual solicitation and copulation outside of the POP, within-group promiscuity, and copulations with extragroup males from neighboring groups or solitary individuals. The reinforcement of female–male bonds could be a complementary benefit of within-group promiscuity.

The appearance of unimale groups in the *Alouatta* lineage increased the risk of male group takeovers and infanticide, leading to an increase in the occurrence of extragroup copulations. In a population dominated by unimale groups, extragroup copulations may serve (a) as a mechanism of paternity confusion as an anti-infanticidal strategy, (b) to increase the genetic diversity of offspring, and/or (c) to avoid mating with related males. If male tenure under these conditions is shorter than the time required for a female to reach sexual maturity, the incest avoidance hypothesis would not represent a strong alternative. The lineage of *A. palliata*, on the other hand, diverged from its South American ancestral form (Ford 2006) in the opposite direction. In terms of social structure, mantled howlers live in larger multimale-multifemale groups more similar to those found in the atelines. Compatible with our hypothesis, despite being the most studied howler species, only one case of infanticide and no event of resident females involved in extragroup copulations have been reported for *A. palliata*.

The shift to a more frugivorous diet in the ateline lineage (supported by the dentition of the extinct basal taxon *Solimoea*; Kay and Cozzuol 2006) triggered a series of changes in the socio-reproductive strategies of atelines, including the evolution of seasonal reproduction (as seen in *Ateles*, *Brachyteles* and *Lagothrix*; Di Bitetti and Janson 2000). The older age at first reproduction and longer interbirth interval of atelines also support the contention that their reproduction is more ecologically constrained than that of *Alouatta* (Strier 2001). The temporal restriction of fertile matings decreased the ability of ateline males to manipulate female reproductive physiology to their advantage, thereby changing the balance between the risks of dispersal and the benefits of group takeover in favor of male permanence in their natal groups (Strier 1996). The evolution of male philopatry promoted an increase in male group size and their relatedness, furthering the importance of inclusive fitness. Larger male groups may have been more attractive to females because they were more successful in defending food resources and/or allowed for increased mate choice opportunities. This increase in male and female group sizes and female mate choice reduced paternity skew (Di Fiore et al. 2009; Strier et al. 2011) and extragroup copulations. Together, these changes significantly reduced the potential advantages of infanticidal behavior.

In the *Ateles* lineage females appear to have evolved ovarian synchronicity, sexual monomorphism, and resident male tolerance of others' copulations decreased significantly or disappeared, resulting in some copulations occurring in seclusion (Campbell and Gibson 2008). In the common ancestral of *Brachyteles* and *Lagothrix* mating consortship disappeared, allowing males and females to engage in sexual interactions with multiple partners on the same day. Finally, *Brachyteles* evolved male–female codominance and an increase in sperm competition, whereas females appear to be indifferent to same-sex immigrants but compete over matings in *Lagothrix* (see Di Fiore et al. 2011).

3.6 The Evolutionary Basis of Sexual Dichromatism

The evolution of sexual bi-phasic dichromatism in the most austral howler monkey taxa, *A. guariba clamitans* and *A. caraya*, has been hypothesized by Thorington et al. (1979) as a consequence of between-sex seasonal differences in energetic and thermal requirements. Crockett (1987), on the other hand, argued that the coat color change of maturing males may have been positively selected for signaling sexual identity and allowing female choice of distinctively colored males. Data on the resting behavior of both species over a wide range of ambient temperatures (ca. 5–35 °C) did not support postural and microhabitat selection differences between adult males and females, lending no support to Thorington et al.'s thermoregulatory hypothesis (Bicca-Marques and Calegaro-Marques 1998; Bicca-Marques and Azevedo 2004). Sex-based seasonal differences in thermoregulatory needs also do not offer a good explanation for the evolution of dichromatism in *A. seniculus puruensis* and *A. ululata* in the thermally more homogeneous environment of their northern tropical distribution.

Bicca-Marques and Calegaro-Marques (1998) proposed two alternative, not mutually exclusive, hypotheses to explain the evolution of dichromatism in *A. caraya*. According to these authors, during the evolution of male black coat color, (1) color variation among males signaled fighting ability and/or aggressiveness, health status, maturity, or resource occupancy, and/or (2) helped in long-distance sex recognition by individuals dispersing between habitat patches in a fragmented landscape. Whereas the first hypothesis also may apply to *A. s. puruensis*, whose males are dark red and females are golden (Gregorin 2006), the validity of the latter is weakened by the likely divergence (and early evolution) of this species from its sister taxon before the debated Pleistocene forest shrinking in the Amazon (Cortés-Ortiz et al. 2003; see also Lynch Alfaro et al. 2012). Information on the ecology, behavior, and evolutionary history of *A. ululata* is very scanty for addressing the significance of its sexual dichromatism.

The recent discovery of contact zones and the several cases of hybridization between the two austral taxa in south Brazil and Argentina (Cortés-Ortiz et al. 2014), including a case in captivity (Jesus et al. 2010), suggest that differences in coat color are not effective reproductive barriers between howler males and females (Silva 2010). This finding weakens Crockett's mate choice hypothesis for explaining the evolution of sexual dichromatism because in both interbreeding possibilities (male *A. guariba clamitans* x female *A. caraya* and male *A. caraya* x female *A. guariba clamitans*) the color of males and females is more similar between species than within-species. This is in concordance with Bradley and Mundy (2008: 108), who state that "female choice for pelage color has yet to be widely tested in primates."

Male color change in both austral howler monkeys is a developmental process (no information on this aspect is available for *A. s. puruensis* and *A. ululata*). The observation of a delay of at least 24 months in the onset of the development of a darker coat in two juvenile male *A. caraya* residing in an unimale group isolated in a 0.3 ha orchard forest in south Brazil is compatible with the hypothesis that male–male competition may have played a critical role in the evolution of dichromatism in this species (Bicca-Marques and Calegaro-Marques 1998). Teasing apart the influence of intrasexual and intersexual selection is not a trivial task, however, because females may also prefer the trait also favored in male–male competition. Nevertheless, the occurrence of interbreeding (mentioned above) casts doubt on this possibility.

Finally, the observation of a color polymorphism in males and females within *A. macconnelli* populations (Gregorin 2006), including pelage patterns similar to those found in male and female *A. s. puruensis*, highlights the complexity of the task of studying the evolution of sexual dichromatism within this genus. Thus, overall we conclude based on present evidence that the strongest explanation for the evolution of dichromatism in austral howlers is that adult male color is a by-product of developmental (hormonal) changes related to male fighting ability and/or aggressiveness for within-sex competition.

3.7 Conclusions and Prospects

We can conclude that all three mechanisms of sexual selection (intrasexual selection, intersexual selection, and intersexual conflict) influence the reproductive behavior of howler monkeys. For example, the high degree of sexual dimorphism suggests that males experience high levels of intra- and intergroup competition over access to fertile females. Although males in unimale groups should experience limited intragroup male–male competition, such groups are more attractive targets to dispersing males who attempt to join or take over groups by evicting resident males, resulting in high levels of intergroup competition (Pope 2000a; Van Belle et al. 2008; Rangel-Negrín et al. 2011). In contrast, multimale groups should experience lower intergroup competition, yet intragroup competition should increase with the number of resident males. Intragroup male–male competition in multimale groups might be considerably lower among resident male who are kin compared to those who are not, as males accrue inclusive fitness benefits as a consequence of the mating behavior of relatives. Genetic studies have revealed that adult males who are closely related co-reside in some bisexual groups in *A. pigra* (Van Belle et al. 2012), *A. caraya* (Oklander et al. 2010), *A. palliata* (Milton et al. 2009), and *A. arctoidea* (Pope 1990). In addition, male coalitions of related individuals in multimale *A. arctoidea* groups last longer and accrue greater fitness than coalitions of unrelated resident males (Pope 1990).

Central males are generally able to monopolize the majority of sexual opportunities by mate guarding and copulating with females during their POPs, when conception is most likely to occur. Females do not avoid these consortships with the central male, whom they solicit for sexual interactions most frequently during their POPs, suggesting that the reproductive strategies of central males and resident females generally coincide in howler monkeys. Notwithstanding, females also sexually solicit and copulate with other resident males particularly outside the POPs, undermining the central males' ability to monopolize all reproductive opportunities, and suggesting that females can exercise mate choice. The mixed mating strategy characterized by periods of selective mating and periods of promiscuous mating may be employed during a single ovarian cycle, across different cycles within the same fertile period preceding conception, or across different fertile periods. Studies are needed to understand how demographic, social, physiological, and ecological factors influence the degree to which the reproductive strategy of a given female at a given point in time inclines toward selective or toward promiscuous mating, and how these vary across the genus. The occurrence of copulations with males in neighboring groups or solitary males, generally solicited by females and, whenever witnessed, often precluded by their group mates, further attests that female howler monkeys can exercise mate choice. Such mating could reduce the risk of infanticide, but might also be driven by inbreeding avoidance or female's preference for high quality males (Agoramoorthy and Hsu 2000).

As a final point, it is important to highlight that studies on the reproductive behavior and strategies have encompassed less than half of the *Alouatta* species and were conducted under a limited range of environmental and social conditions. There also exist only a handful of sites with data from long-term studies. We are still far from understanding the effect of group size and composition, demography, dispersal patterns, social status, and social relationships on patterns of sexual solicitation, mating, male coalition, paternity distribution, and infanticide. Much remains to be investigated on the role played by sexual selection on the evolution of physiological and morphological traits (e.g., sexual dichromatism, body, canine, hyoid, and testes size). Modern techniques of noninvasive genetic, endocrine and nutritional analyses, GIS, and mathematical modeling are becoming increasingly accessible to help us fill these gaps.

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Chapter 4
Evidence of Alternative Dietary Syndromes and Nutritional Goals in the Genus *Alouatta*

Paul A. Garber, Nicoletta Righini, and Martín M. Kowalewski

Abstract Howler monkeys exploit difficult-to-digest and potentially toxic food items such as mature leaves and unripe fruits; persist across an extreme range of habitat types, including highly disturbed forests; and have the most widespread geographical distribution of any genus of New World primate. Given evidence of dietary variability in the amount of monthly fruit, leaf, and flower consumption, howler monkeys provide an instructive model for examining relationships among foraging strategies, activity budgets, and patterns of habitat utilization. In this chapter we examined evidence for interspecific differences in dietary patterns and nutritional ecology within the genus *Alouatta* and identified three dietary "syndromes" that are generally consistent with howler monkey phylogeny and biogeography. Specifically, we show that Mesoamerican howler monkeys and *A. seniculus* are characterized by a balanced leaf and fruit diet, Amazonian species by a fruit enriched diet, and Atlantic Forest and southern howler monkeys by a leaf-enriched diet. Finally, to be able to identify species-specific dietary strategies and syndromes across the primate Order, we recommend an approach that includes collecting data on feeding rates and the nutritional composition of the diet.

Resumen Los monos aulladores consumen alimentos difíciles de digerir y que potencialmente contienen compuestos secundarios tóxicos como hojas maduras y frutos inmaduros; habitan en tipos de ambientes muy variados, incluyendo áreas altamente fragmentadas, y tienen la distribución geográfica más amplia de cualquier otro género de primates neotropicales. Debido a las conspicuas fluctuaciones mensuales en las cantidades de frutos, hojas y flores consumidos, los monos aulladores constituyen un modelo útil para examinar las relaciones entre estrategias de forrajeo,

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patrones de actividad y de utilización de hábitat en otros primates, incluyendo a los folívoros. En este capítulo examinamos la evidencia de diferencias interespecíficas en los patrones alimentarios y nutricionales dentro del género *Alouatta*, e identificamos tres “síndromes” alimentarios consistentes con los patrones filogenéticos y biogeográficos. En particular, mostramos que los monos aulladores de Mesoamérica y *A. seniculus* se caracterizan por tener una dieta balanceada de hojas y frutos, las especies del Amazonas por una dieta en la que predominan los frutos, y aquellas de la Foresta Atlántica y del Sur por una dieta en la que predominan las hojas. Finalmente, subrayamos la importancia de colectar datos sobre las tasas de ingestión de los alimentos y sobre la composición nutricional de la dieta para poder identificar estrategias y síndromes alimentarios especie-específicos en los primates.

Keywords Behavioral syndromes • Diet • Feeding rates • Folivory • Frugivory • Nutrition

Abbreviations

°C	Celsius degrees
Df	Degrees of freedom
DQ	Dietary quality index
F	ANOVA’s F statistic
HSD	Honest Significant Difference
kg	Kilograms
kJ	Kilojoules
MA	Million years ago
MBM	Metabolic Body Mass
mtDNA	Mitochondrial DNA
P	Significance value
S	South
SE	Standard Error
TNC	Total non-structural carbohydrates
unpubl. Data	Unpublished data
W	West

4.1 Introduction

Howler monkeys show extreme variability in terms of monthly differences in time spent consuming different food types, such as fruits, leaves, and flowers. In a comparison of 26 primate species, Chapman and Chapman (1990) found that monthly dietary variability in *Alouatta palliata* was only exceeded by one other primate species, *Macaca fascicularis*. Similarly, Estrada (1984) reported that monthly variation in time spent feeding on ripe fruit in *A. palliata* varied from 0 % in some months to over 70 % in other months. In the case of young leaves, monthly time spent feeding varied from a high of 90 % to a low of 20 %. Similar variation in monthly feeding patterns has been reported in other howler monkey species (Bonvicino 1989; Zunino 1989; Pavelka and Knopff 2004). Given evidence of marked temporal variability in feeding behavior, and evidence of a highly selective feeding pattern (Milton 1980; Chapman 1988), howler monkeys provide an instructive model for examining guild-based (Root 1967) or parallel ecological relationships among foraging strategies, nutritional ecology, activity budgets, and patterns of habitat utilization in other lineages of fruit-eating and leaf-eating primates.

The goals of this chapter are to (1) examine evidence for species differences in dietary patterns and feeding ecology within the genus *Alouatta*; (2) highlight the role of phylogeny in evaluating taxonomic differences in howler monkey behavioral and nutritional ecology; (3) discuss the importance of using data on feeding rates in conjunction with data on time spent feeding to estimate the amount of each food type consumed; and (4) present a nutrient mixing framework for evaluating dietary "syndromes" in howler monkeys.

Howler monkeys exploit difficult-to-digest and potentially toxic food items such as mature leaves and unripe fruits, persist across an extreme range of habitat types (including highly anthropogenically disturbed forests, cloud forest (up to 3,200 m), lowland rainforest, seasonally deciduous dry tropical forest, and areas of gallery, woodland, cerrado, and caatinga forest), and have the most widespread geographical distribution of any genus of New World primate (Crockett 1998; Di Fiore et al. 2011; IUCN 2012). The genus *Alouatta* is currently divided into 12 species of medium-sized (average adult female body mass 4.3–6.4 kg, Rosenberger et al. 2009; Kelaita et al. 2011; Di Fiore et al. 2011, Table 4.1) New World monkeys that are distributed from southeastern Brazil (29° 56′ S, 55° 59′ W) and northern Argentina (29° 08′ S, 59° 38′ W) throughout the Amazon Basin, Guiana Shield, and into Central America as far north as the state of Veracruz in Mexico (20° 06′ N, 96° 42′ W) (Bicca-Marques 1990; Cortés-Ortiz et al. 2003). Although howler monkey species are principally allopatric across this range, researchers have identified areas of sympatry and possible zones of hybridization in southern Mexico (*A. pigra* and *A. palliata*; Cortés-Ortiz et al. 2010, 2014; Kelaita and Cortés-Ortiz 2013) and southern Brazil and northern Argentina (*A. guariba* and *A. caraya*, Aguiar et al. 2007; Agostini et al. 2010; de Souza et al. 2010; Cortés-Ortiz et al. 2014).

Based on fossil and molecular evidence (mtDNA), howler monkeys appear to have diverged from a common ateline ancestor approximately 16 million years ago (Cortés-Ortiz et al. 2003; Di Fiore et al. 2011). Cortés-Ortiz et al. (2003) suggest that the ancestors of modern *Alouatta* species underwent a period of initial diversification some 6.8 MA splitting into two separate populations to the east and west of the Andes (Fig. 4.1). This appears to have coincided with the end of a geologically and ecologically active period in which uplifting of the Andes led to the development of a massive wetland system of swamps and mega-lakes (Pebas lake) across Amazonia (Campbell et al. 2006). In western and central Amazonia, this system of mega-lakes was present until about 7 MA, when the current Rio Amazonas and

Table 4.1 Characteristics of different howler monkey species, including the proposed behavioral syndrome they fit in, body weights, dietary quality indices (DQ), molar shearing quotients, gut passage times, and coefficients of gut differentiation[a]

Species	Behavioral syndrome	Male wt (kg)	Female wt (kg)	Body mass dimorphism	Mean DQ	Mean shearing quotient[b]	Mean gut transit time (h)[c]	Mean retention time (h)	Coefficient of gut differentiation
A. belzebul	Fruit-enriched diet	7.27	5.52	1.31	162.07 ± 21.6	–	23	–	–
A. macconnelli		–	–	–	157.49 ± 14.2	–	–	–	–
A. caraya	Leaf-enriched diet	6.42	4.33	1.48	136.49 ± 14.9	15.26	7.5 ± 2.2[d]	38.4 ± 17.1[e]	–
A. guariba		6.73	4.35	1.54	133.14 ± 14.4	14.26	7.5 ± 1.7[a]	–	–
A. palliata	Fruit and leaf-balanced diet	–	–	–	151.23 ± 16.4	19.11	20.4	30.6 ± 3.8[e]	1.55
A. p. aequatorialis		7.56	6.44	1.17	–	–	–	–	–
A. p. mexicana		5.80	4.39	1.32	–	–	–	–	–
A. p. palliata		5.79	4.72	1.22	–	–	–	–	–
A. pigra		7.60	5.68	1.33	151.59 ± 11.5	–	22.7 ± 0.8[f]	36.9 ± 7.4[f]	–
A. seniculus		7.20	5.60	1.28	150.25 ± 13.4	24 ± 1.6	20.6	53.3 ± 40.6[e]	0.82

[a] Data from: Chivers and Hladik (1980), Milton (1984), Rumiz (1990), Anthony and Kay (1993), Julliot (1996), Smith and Jungers (1997), Edwards and Ullrey (1999), de Souza (2003), Glander (2006), Espinosa-Gomez et al. (2009), de Sousa and Bicca-Marques (2010), Kelaita et al. (2011), Ramdarshan et al. (2011), Di Fiore et al. (2011)

[b] Shearing quotients correspond to a relative measure of molar shearing (relation between the total length of molar crests and the length of the tooth)

[c] Time of first appearance of markers

[d] Captive individuals were fed fruits and vegetables. Forty plastic markers (diameter: 7 mm) were fed to each individual

[e] Captive individuals were fed diets containing 42 % neutral detergent fiber (NDF) on a dry matter basis. Na Co-ethylenediaminetetraacetic acid (EDTA) was used as marker

[f] Individuals consumed a natural diet containing 49.9 % NDF

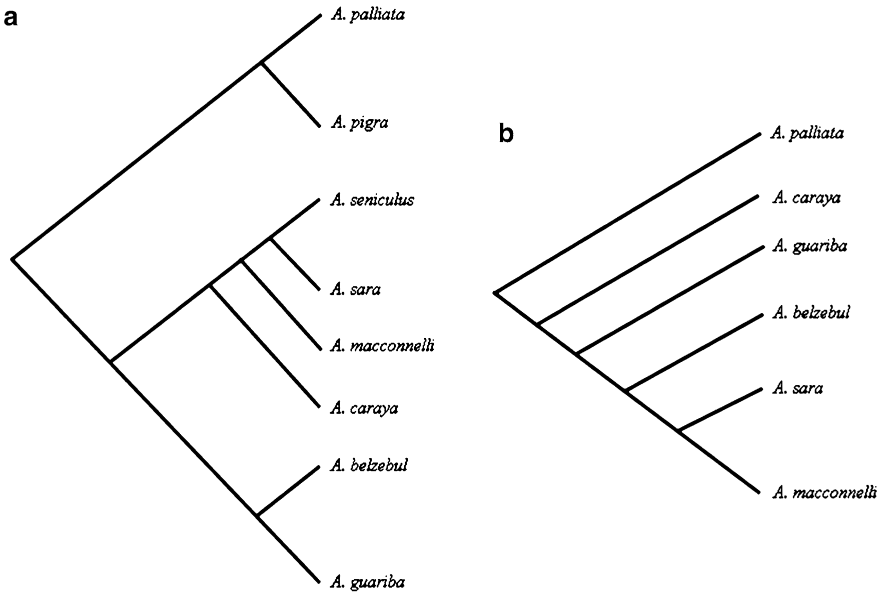

Fig. 4.1 Simplified cladograms showing the evolutionary relationships among *Alouatta* species. (**a**) Cortés-Ortiz et al. 2003 (modified from their Fig. 3, p. 71) and (**b**) Villalobos et al. 2004 (modified from their Fig. 1)

drainage system emerged (Antonelli et al. 2009; Wesselingh et al. 2010). According to Cortés-Ortiz et al. (2003), at approximately 5.1 MA, the eastern group of howler monkeys further differentiated into two groups (Fig. 4.1). In contrast, the evolutionary history and biogeography of the Central American howler monkeys was strongly influenced by more recent volcanic activity and the emergence of the Panamanian isthmus. *Alouatta palliata* and *A. pigra* are reported to have crossed the land bridge into Central America in two distinct waves, with the ancestors of *A. pigra* entering some 3.0–3.5 MA and the ancestors of *A. palliata* entering in an independent dispersal event some 2 MA (Ford 2006).

These evolutionary/dispersal events are generally consistent with karyotypic, morphological, and DNA evidence that support three main howler monkey clades. There is a strong consensus that the sister taxa *A. palliata* and *A. pigra* represent a closely related group. Among South American howler monkeys, Villalobos et al. (2004) argue for an *A. seniculus* group that includes *A. belzebul* and *A. guariba*, as well as four other species, and places *A. caraya* in a separate radiation (Fig. 4.1). In contrast, based on mtDNA evidence, Cortés-Ortiz et al. (2003) place *A. caraya* within the *A. seniculus* clade and support a distinct *belzebul*-*guariba* lineage. These authors note, however, that the bootstrap values supporting the position of *A. caraya* with *A. seniculus* are not very strong. It is worth noting that the position of *A. caraya* still falls within the *A. seniculus* clade when a large number of markers are analyzed (Perelman et al. 2011); however, the support for its placement within this clade continues to be low. Thus, the phylogenetic position of *A. caraya* remains unclear.

Given the evidence for biogeographic and taxonomic differences among howler monkey clades, we begin by describing dietary and behavioral "syndromes" within *Alouatta* in an attempt to identify the degree to which sets of related or unrelated species are best characterized by similar or divergent patterns of behavior. In this regard we use the framework of a behavioral syndrome which is defined as "a suite of correlated behaviors expressed either within a given behavioral context …. or across different contexts" (Sih et al. 2004a, p. 241). The strength of this concept rests in identifying a set of behavioral and anatomical traits that covary and therefore are best understood as an integrated or functional unit (Cheverud 1996; Sih et al. 2004b). The developmental and evolutionary integration of several traits can result from the pleiotropic effect of a single gene on multiple systems or from linkage disequilibrium, a situation in which genes affecting the same trait or trait complex are inherited together (Cheverud 1996; Thierry et al. 2008). Finally, "characters can also evolve together even when they are not inherited together if they are co-selected for participation in a common function" (Cheverud 1996, p. 46).

In general, the presence of a package of traits resulting in a behavioral syndrome is expected to place boundaries on behavioral plasticity by limiting the set of effective solutions to a particular ecological problem. Using this model, a forager would be expected to express the same or related set of behavioral responses under a broad range of ecological conditions (Sih et al. 2004b; Thierry et al. 2008). Although the concept of behavioral syndromes has been used to examine consistent differences in behavior or personality (e.g., aggressiveness, risk-taking) among individuals in the same population, the concept also can be applied to compare differences in patterns of behavior and ecology among closely related species (Sih et al. 2004a, b). For example, Thierry et al. (2008) found that within the genus *Macaca*, interspecific differences in social styles and modes of conflict resolution covaried with particular sets of behavioral traits. In some cases, these were strongly related to phylogeny (Thierry et al. 2000), whereas in other cases these associations may have resulted from parallel evolutionary responses to similar selective pressures (Thierry et al. 2008). These interdependent traits were argued to form functional links or "behavioral syndromes" that constrained macaque responses to proximate changes in their ecological and social environments.

4.2 The Howler Monkey Adaptive Pattern

Researchers over the past several decades have proposed that the defining suite of behavioral and anatomical traits that distinguish the feeding ecology of howler monkeys from other atelines include an energy-minimizing foraging strategy (Milton 1980, 1998, 2000), small day range (Di Fiore et al. 2011), efficient hindgut fermentation of structural carbohydrates (Milton 1981; Milton and McBee 1983; Edwards and Ullrey 1999; Amato and Righini 2014), incisal reduction and prominent molar shearing crests that aid in the efficient processing of leafy material (Kay 1975, 1990; Rosenberger et al. 2011), slow rate of food passage (Nagy and

Milton 1979; Milton 1984), extended periods of resting/digesting (Milton et al. 1979; Lambert 1998; Milton 1998), and a dietary commitment to leaf-eating. Rosenberger et al. (2009, 2011) hypothesized that many of these traits are likely to have co-evolved in highly seasonal, dry, less productive, and patchily forested habitats outside of the Amazon basin. These authors describe *Alouatta* as a pioneer or colonizing genus that is ecologically resilient, able to exploit difficult to digest foods, and "comparatively undeterred by ecological barriers that biographically limit other monkeys" (Rosenberger et al. 2009, p. 97). If this is the case, then an energy-minimizing behavioral strategy, dental and digestive adaptations associated with exploiting difficult to process or high fiber foods, and the ability to concentrate feeding time on either fruits, flowers, or leaves depending on local availability may represent a functionally integrated set of traits (i.e., a behavioral syndrome) that serve to define the genus *Alouatta*.

Howler monkeys are hindgut fermenters, and they appear to overcome difficulties associated with digesting the structural carbohydrates (fiber) present in leaves by having a relatively long food transit time compared to most other platyrrhines (Lambert 1998) [20.4 ± 3.5 h for first appearance of markers in the feces for *A. palliata* (Milton 1981)]. Milton (1981) reported that howler monkeys have a capacious colon compared to other atelines, and in fact colon and cecum volumes in *A. palliata* are larger than that predicted for a primate of its body size. Howler monkeys also have larger whole gut volumes (stomach + small intestine + cecum + colon) than expected based on their body mass (Chivers and Hladik 1980; Amato and Righini 2014). However, in comparing the ratios of intestine (small intestine + cecum + colon) length to body length, howler monkeys exhibit values considerably smaller than other hindgut fermenters such as indriids (*Propithecus* spp. have a ratio of intestine length to body length of 15.5:1), and instead show greater similarity with spider monkeys (2.8:1 for *A. palliata* and 2.7:1 for *Ateles geoffroyi*) (Milton 1981).

Animals with relatively short intestines are expected to consume more easily digestible foods including ripe fruits and insects (Barboza et al. 2009). In this regard, Glander (1981) suggested that nutritional and, in particular, phytochemical differences in available foods play an important role in howler monkey dietary selectivity. In contrast, Milton (1979, 1998) proposed that the most important factor influencing leaf choice in howler monkeys is the protein:fiber ratio. However, in the absence of data on the nutrient composition and secondary compound profile of the specific foods consumed, caution must be exercised in assuming that a given food type or plant tissue is more or less nutritious or toxic than another. For example, Gaulin and Gaulin (1982) found that mature leaves (0.375 g protein/min) and ripe fruits (0.230 g protein/min) eaten by *A. seniculus* inhabiting a montane wet forest in Colombia (altitude 2,300 m) provided more protein per unit feeding time than did young leaves (0.076 g protein/min) or immature fruit (0.214 g protein/min). Despite their relatively high protein content, however, mature leaves accounted for only 7.5 % of *A. seniculus* feeding time (Gaulin and Gaulin 1982). These authors also point out that time spent feeding on a food item or food type was not a strong predictor of the amount of food consumed and that "differences in mean item weight, [nutritional] composition, and distribution all combine to alter total and individual nutrient harvest rates" (Gaulin and Gaulin 1982, p. 25). Gaulin and Gaulin (1982) report that the ratio of time spent consuming leaves to dry weight of leaves ingested was 2.1, whereas the ratio of time spent consuming fruit to the dry weight of fruit ingested was only 0.58. Thus, given such potentially important differences in measures of time spent feeding relative to the quantity of food consumed, and differences in the nutritional content of fruits or leaves from the same plant taxa across different habitats or study sites (Conklin and Wrangham 1994; Carlson et al. 2013), the precise nutritional factors affecting food choices in howler monkeys remain poorly understood.

Using a framework of behavioral syndromes and trait covariation, we explore evidence for species differences in howler monkey feeding ecology. Different howler monkey lineages appear to have modified an initial *Alouatta* adaptive pattern and evolved new trait complexes in response to in situ environmental conditions. For example, data presented by Chivers and Hladik (1980) suggest that based on a "coefficient of gut differentiation" (surface area of the stomach + caecum + colon divided by the small intestine, independent of body mass), *A. palliata* groups with species of Old World folivores, whereas *A. seniculus* fits within the category that contains primate frugivores. Similarly, molar shearing crests in *A. palliata* are reported to be higher than those found in *A. caraya* and *A. guariba* (Rosenberger et al. 2011). The presence of these traits plus the fact that adult female *A. palliata* are heavier than adult female *A. caraya* or *A. guariba* (Table 4.1) suggest the possibility that *A. palliata* are more reliant on difficult to digest foods than are these other howler monkey species. If this is correct, then behavioral/anatomical tradeoffs imposed by different sets of functionally integrated traits are expected to result in alternative patterns of habitat utilization and diet among howler monkey species. What remains less clear from these data is whether *A. palliata* is expected to consume greater amounts of leaves, greater amounts of mature leaves, greater amounts of unripe fruits, or more commonly supplement their diet with other difficult to digest foods compared to other howler monkey species. Although in some instances, constraints imposed by trait covariation can lead to a reduction in behavioral plasticity and a decrease in an ability to exploit novel or changing environments, in other cases these trait "packages" can expand a species diet and niche breadth (Sih et al. 2004b). In the case of *Alouatta*, behavioral and anatomical traits associated with energy minimization, slow passage rate, and the ability to consume difficult to digest foods (mature and immature leaves, unripe fruits, bark) appear to have expanded the ability of howler monkeys to successfully exploit a wide range of ecological conditions.

4.3 Evidence of Behavioral Syndromes in *Alouatta*

Based on their anatomical, ecological, and behavioral characteristics, howler monkeys have been traditionally considered to be "ecospecies", which, according to Peres and Janson (1999, p. 56), are defined as "a few ecologically equivalent (and mutually exclusive) congeners, usually representing parapatric replacements across sharp biogeographical boundaries". Some authors have considered interspecific differences in howler monkey dietary patterns to be smaller than intraspecific variability linked to local habitat characteristics or patterns of seasonality (Agostini 2009; Di Fiore et al. 2011). However, here we argue that recognizing interspecific differences in howler monkey anatomy, behavior, and ecology offers important insights into the evolution and behavioral ecology of the genus.

Although *Alouatta* represents one of the most commonly studied genera of New World primates, a major obstacle in evaluating evidence of interspecific differences in howler monkey behavior and ecology is that, as is the case for many primate taxa, researchers have often used different methods of data collection and different definitions of behavioral categories, studies have varied in length from a few months to several years, and the ecological conditions of study sites have varied from highly disturbed forest patches of 1–2 ha to continuous and relatively undisturbed forests of thousands of hectares. Despite these limitations, we can identify three distinct dietary patterns across howler monkey species. This is particularly apparent when patterns are calculated based on feeding rates (dry weight of plant tissues consumed/unit time), rather than solely on the proportion of time spent feeding on particular food types. Using average feeding rates calculated by Gaulin and Gaulin (1982) for *A. seniculus* and by Righini (2014) for *A. pigra* (Table 4.2), we transformed data on time spent feeding from over 80 published field studies of howler monkeys into an estimate amount (in grams) of each food type consumed. In accomplishing this, we only selected studies in which data were collected for a period of 9 months or greater (Table 4.3, modified from Dias and Rangel-Negrin 2014).

The first dietary pattern within *Alouatta* is characterized by an increased commitment to fruit-eating (fruit-enriched diet) and is most evident in *A. belzebul* and *A. macconnelli*. Based on four studies, time spent feeding on leaves (47.3 % ± 12.8) in *A. macconnelli* was, on average, slightly greater than time spent consuming fruits (44.2 % ± 18.5) (Mittermeier and van Roosmalen 1981; Julliot and Sabatier 1993; Guillotin et al. 1994; Westin 2007). However, recalculating the percentages based

Table 4.2 Mean feeding rates (g dry weight/min) for different food items consumed by howler monkeys

	Feeding rates *A. pigra*[a]	Feeding rates *A. seniculus*[b]	Average (g/min)
YL	2.11	1.17	1.64
ML	3.56	3.7	3.63
Leaves	2.66	2.43	2.55
RF	2.57	6.35	4.46
UF	2.13	3.7	2.91
Fruits	2.47	5.02	3.75
FL	1		1

YL young leaves, *ML* mature leaves, *RF* ripe fruits, *UF* unripe fruits, *FL* flowers and inflorescences

[a] Righini (2014)

[b] Gaulin and Gaulin (1982)

Table 4.3 Diet composition of different howler monkey species (modified from Dias et al., this volume)

		% based on feeding time								% based on grams ingested						
Species	N	Fruits			Leaves			Flowers	Other	Fruits			Leaves			Flowers
		All	RF	UF	All	YL	ML			All	RF	UF	All	YL	ML	
A. belzebul	5	**42.64**			**38.1**	10.67	17.67	**12.12**	4.6	**57.66**			**37.93**	6.6	25.68	**4.41**
Range		20.1–59			13.3–60.5			0.2–13.2		31.1–77.8			12.7–64			1.5–9.6
A. caraya	15	**24.92**			**64.03**	20.61	38.26	**9.06**	3.17	**33.3**			**63.51**	13.08	48.82	**3.19**
Range		2–46			49–85			0–31		3.2–57.2			41.4–92.1			0–12
A. guariba	23	**21.67**			**67.43**	35.6	31.17	**7.74**	3.97	**30.4**			**66.85**	24.43	41.44	**2.75**
Range		5–47.9			38–88			0–29		7.7–58.1			41.4–92.2			0–15.6
A. macconnelli	4	**44.19**			**47.33**	34.15	22.54	**6.16**	2.7	**55.06**			**42.51**	24.81	25.42	**2.43**
Range		25.5–69			28.6–57			0.4–12.6		41.6–76.8			22.4–55.6			0.1–6
A. palliata	38	**33.75**	32.55	8.98	**53.97**	38.29	16.27	**9.58**	7.85	**47.99**	50.7	9.53	**48.77**	25.44	22.87	**3.24**
Range		12.5–62.8			26.6–82.8			0–29.5		21–78.8			19.2–77.5			0–13.6
A. pigra	14	**36.33**	20.14	14.27	**53.51**	37.21	16.54	**8.66**	4.74	**48.45**	33.43	15.22	**48.41**	26.18	21.75	**3.14**
Range		17.4–63			33–77.3			0–24		32–72.8			25.9–66.8			0–9.7
A. seniculus	6	**35.28**			**58.65**	50.23	11.75	**4.35**	3.76	**49.24**			**49.74**	35.56	15.86	**1.02**
Range		13.3–42.3			46–82.9			0–6		25.1–61.3			36.7–74.8			0–2

Percentages (%) are calculated based on feeding rates[a] (g dry matter/min) of plant parts consumed (on the right), and on feeding time (on the left)

[a] Feeding rates are averages of the mean feeding rates from Gaulin and Gaulin (1982) and Righini (2014) (see Table 23.2)

on feeding rates, these relationships changed, and the amount of fruit consumed by *A. macconnelli* accounted for over 55 % (±15.7) of dietary intake, whereas the amount of leaves consumed was 42.5 % (±14.2). Data from five populations of *A. belzebul* similarly indicate that this species is characterized by a fruit-enriched diet, with fruits accounting for 57.6 % (±20.3) of the amount consumed, leaves 37.9 % (±21.6), and flowers 4.4 % (±3.2) (Bonvicino 1989; Pinto 2002; Pinto et al. 2003; Pinto and Setz 2004). *Alouatta belzebul* also is reported to devote a substantial component of its feeding time to flowers during certain months of the year, reaching 41 % of feeding time in the dry season, which corresponds to 17 % of the total amount of food consumed (the rest being 69 % fruits and 13.8 % leaves) (Bonvicino 1989). Given that neotropical flowers and inflorescences can contain 9–29 % crude protein (Milton 1980, 1999; Oftedal et al. 1991; Silver et al. 2000; Williams-Guillén 2003; Felton 2008; Norconk et al. 2009; Behie and Pavelka 2012), flower feeding may provide howler monkeys with an important dietary source of protein when other protein-rich foods are less available. For example, protein present in flowers may be comparable to protein present in leaves (crude protein percentage of inflorescences ($n=18$) and young leaves ($n=25$) consumed by *A. pigra* in Mexico was 19.6 ± 4.9 % and 20.5 ± 5.7 % of dry weight, respectively [Righini 2014]). In addition, Norconk et al. (2009) report that flowers consumed by primates generally contain lower amounts of insoluble fiber and yield a greater amount of metabolizable energy than either young or mature leaves. However, we found no correlation between the amount of leaves consumed and the amount of flowers consumed by *A. belzebul* per month, suggesting leaves and flowers do not represent complementary resources and therefore the consumption of one had no effect on the consumption of the other.

A second feeding pattern was found in *A. caraya* and *A. guariba.* These species exhibited an alternative foraging strategy in which dietary emphasis has shifted to leaves (leaf-enriched diet) (Table 4.3). Both species are sexually dichromatic and distributed across northern Argentina and southern Brazil. The distribution of *A. caraya* also extends into Paraguay, and eastern Bolivia continuing north of the *A. guariba* distribution in Brazil and south of the *A. guariba* distribution in Argentina. *Alouatta caraya* occupies a set of marginal habitats associated with gallery semideciduous forests, flooded forests on islands, chaco forests, and cerrado habitats across certain parts of its range. *Alouatta caraya* also is found in subtropical forests—Selva Paranaense, but at lower densities (Brown and Zunino 1994; Holzmann 2012). Two factors may help explain why *A. caraya* is present at low density in certain habitats. First, they are highly susceptible to outbreaks of yellow fever and periodically suffer extremely high mortality from this disease (Holzmann et al. 2010). Second, *A. caraya* appears to be more successful in extremely dry forests, deciduous forests, and forests of low productivity; these conditions appear to result in increased reproductive success (M Kowalewski, unpubl. data).

Alouatta guariba is endemic to the Atlantic forest region of southern Brazil and northern Argentina (Kinzey 1982). Its distribution relative to habitat types is limited. Individuals of this species are found principally in small forest fragments and relicts of the Atlantic Forest in Brazil and at low densities in the Selva Paranaense in

Argentina (Chaves and Bicca-Marques 2013). In terms of their body mass, *A. caraya* and *A. guariba* have the lowest average body weight among howler monkey species (Table 4.1).

In the southern-most distribution of their range, *A. caraya* and *A. guariba* are the largest arboreal mammal present, and despite the fact that there exist few primate competitors across their range, fruits account for only a limited proportion of their diet. Based on transformed data using feeding rates and feeding time from 15 field studies, leaves accounted for approximately 63 % (±14.9) (and specifically, mature leaves for 49 %), fruits for 33 % (±15.9), and flowers for 3.2 % (±3) of food consumption in *A. caraya*. Individuals of this species supplement their diet with a variety of other food types such as bark, burnt wood, honey, moss, lichen, soil (Bravo and Sallenave 2003; Kowalewski 2007), eggs (Bicca-Marques et al. 2008), aphid infested leaves (Bravo and Sallenave 2003), ants (M Raño, pers. comm.), and mealy bugs (A Perez-Rueda, pers. comm.). Although the ingestion of these items is rare, they are generally consumed during food-limited periods of the year (Kowalewski 2007; Bicca-Marques et al. 2008; except ants and mealy bugs). At a study site in which *A. caraya* and *A. guariba* are sympatric, only *A. caraya* was observed to feed on bark, whereas both species consumed male pine cones and moss (Agostini et al. 2010).

A third pattern found in howler monkeys is present in *A. palliata, A. pigra,* and *A. seniculus*. Based on 58 studies, time spent feeding on leaves (54–58 %) was on average greater than time spent consuming fruit (33–36 %) (Table 4.3). However, after transforming the data using feeding rates, each of these three species was found to exploit a balanced diet in terms of the amount of fruit (~48 %) and leaf (~49 %) tissue consumed (fruit and leaf balanced diet). The ancestors of both *A. pigra* and *A. palliata* appear to have independently colonized Central America over the past 2–3 million years and are likely to be descended from an ancestral *Alouatta* population that was isolated on the west side of the Andes. Thus, it seems parsimonious that the fruit and leaf balanced dietary pattern present in *A. palliata* and *A. pigra* was inherited from a common ancestor also shared with *A. seniculus*.

The concept of a behavioral syndrome requires an attempt to define the limits or range of variation that characterize or distinguish a set of species that adopts one dietary pattern from another set of species that adopts an alternative dietary pattern. Given differences in the methods used by researchers to collect data on howler monkey feeding ecology (see above), we cautiously compare one measure of variance (% grams of each food type consumed) between *A. pigra*, the northernmost distributed howler monkey species, and *A. caraya*, the southernmost distributed howler monkey species. *Alouatta pigra* is characterized by a fruit and leaf-balanced diet, whereas *A. caraya* is characterized by a leaf-enriched diet. In the case of *A. caraya*, we use data from four groups (each group was studied for 11–12 months) inhabiting two nearby research sites (Corrientes and Isla Brasilera) in Argentina during the same 2-year period (Delgado 2006; Kowalewski 2007). The data for *A. pigra* were collected over 15 months on two neighboring groups studied by Righini (2014) in Mexico and two groups studied by Silver et al. (2000) for 12 months in Belize. A comparison of the coefficient of variation indicates that the percentage of grams of each major food type in the diet of *A. caraya* varied between

21.8 % in fruits and 24.0 % in leaves. For *A. pigra* these values were 37 and 29.7 %. Although it is difficult to fully evaluate the implications of these differences, it appears that the dietary syndrome of *A. pigra* is characterized by greater site-to-site or year-to-year dietary variability than found in *A. caraya*. There are several possible explanations. These data could mean that *A. pigra* is more flexible or plastic in its feeding behavior, tolerating a leaf-enriched, a fruit-enriched, or a more balanced fruit and leaf-based diet. This might occur if particular fruit and leaf species consumed by *A. pigra* in northern Mesoamerican forests are similar to each other in nutrient content (e.g., protein to fiber ratio, percent nonstructural carbohydrates). This would result in greater dietary flexibility in switching between fruits and leaves depending on availability. It is equally possible that the nutritional composition of fruits and leaves in northern Mesoamerica is more variable or of lower quality (higher ratio of fiber to protein, see below Sect. 4.4), which requires howler monkeys to modify their diet based not on the type of plant tissues consumed, but on the specific nutrient content of individual food items. Finally, differences in dietary syndromes between *A. pigra* and *A. caraya* might result from the fact that many of the forests occupied by *A. caraya* experience periodical flooding which deposits rich alluvial soils into the region. Site-specific differences in soil chemistry, which relates to the nutrient content of tree foliage, could help to explain the taxonomic and biogeographical differences in the proposed dietary patterns in *Alouatta*. Clearly, future studies of howler monkey diet and feeding ecology need to focus on questions of soil chemistry and strategies of nutrient balancing in order to better understand species differences in howler monkey diet.

4.4 Geometric Framework for Nutrition

Recently, several researchers have examined primate food choice using a geometric framework for nutrition (Felton et al. 2009a, b, c; Rothman et al. 2011; Raubenheimer and Rothman 2013). This model assumes that macronutrient regulation is a major goal of individual foraging decisions and that given differences in the nutritional and energy content of different food types and individual plant and animal species (see Rothman et al. 2012 for a more complete discussion of primate nutritional ecology), a forager can achieve its nutritional target "by mixing its diet from individually imbalanced but complementary foods" (Simpson et al. 2003, p. 124). A geometric framework examines in multidimensional space an individual's nutritional goals and feeding behavior by comparing patterns of food intake and the nutrient content of individual food items across several axes in "nutritional" space (Felton et al. 2009a, b, c). Examining feeding behavior and food choice from a nutritional perspective (e.g., nutrients/g of dry matter), rather than a categorical one based on the amount of time spent eating a particular food type (e.g., fruit, leaves, flowers), offers critical insight into howler monkey dietary strategies. In this regard, Sailer et al. (1985) developed a dietary quality index (DQ) that takes into account the relative energy content and abundance of food types consumed by primate foragers, assuming that in general insect prey and ripe fruits contain greater metabolizable energy than leaves or other difficult to digest foods. This index ($DQ = 1\,s + 2r + 3.5a$) is based on the percentage of structural plant parts (s), reproductive plant parts (r), and animal prey (a) in the diet and ranges from 100 to 350, with lower values representing a "nutrient-poor" diet (energy derived principally from difficult to digest carbohydrates) and higher values representing a "nutrient-rich" diet (energy derived principally from animal protein and lipids). The DQ indices calculated for seven howler monkey species using our diet database (Table 23.3) differed significantly (One-way ANOVA, $F = 6.16$, $df = 6$, $P < 0.0001$) (Table 23.1). In particular, the low index of *A. guariba* differed from the values of *A. palliata* (HSD unequal N, $P = 0.002$) and *A. pigra* (HSD unequal N, $P = 0.03$), which were intermediate, consistent with these two species' more balanced dietary profile. The relatively high DQ indices of *A. belzebul* and *A. macconnelli* reflected a nutrient-richer diet than all the other species, due to their increased reliance on fruits and flowers (i.e., reproductive plant parts). Surprisingly, the relatively high DQ index of *A. belzebul* ($DQ = 162 \pm 21.6$) and the relatively low DQ index of *A. guariba* ($DQ = 133.1 \pm 14.4$) did not differ statistically. This is likely to result from the high variation shown by *A. belzebul*'s DQ values across studies. In particular, one study, by Camargo et al. (2008), resulted in an extremely low DQ value of 135.9 for *A. belzebul*. In that study, fruits accounted for only 20.1 % of feeding time. Removing this one outlier, there was a statistical difference between *A. guariba* and *A. belzebul* (HSD unequal N, $P = 0.02$).

Several explanations can be offered to account for differences in dietary emphasis among *Alouatta* spp. First, ripe fruits represent a major component of the diet of all atelines and can account for or exceed 70 % of yearly feeding time in *Ateles*, *Lagothrix*, and some groups of *Brachyteles* (see Table 11.3 in Di Fiore et al. 2011). Thus, a nutrient foraging strategy designed to obtain energy derived from nonstructural carbohydrates and lipids present in ripe fruit pulp (relative to that present in either young or mature leaves) by all howler monkey species may resemble the ancestral condition for atelines. In this regard, Rosenberger et al. (2011) have hypothesized that during the course of alouattin evolution, there was a shift in dietary emphasis from fruit-eating to "semifolivory". These authors define semifolivory as a strategy adopted by primates that show leaf-eating habits, but possess only a subset of the typical morphological and physiological adaptations of strict folivores (e.g., foregut fermentation, robust mandibles, sharp molar crests). They further argue that feeding competition with other fruit-eating primates in Neotropical forests provided the selective pressure that moved ancestral howler monkeys to a greater reliance on leaves as a dietary staple. Although the precise set of ecological factors that enabled ancestral alouattins to expand their diet to include a greater emphasis on difficult to digest food remains unclear, leaves account for a critical component of the diet of all atelines ranging from 7 to 17 % of feeding time in *Ateles*, 9–16 % of feeding time in *Lagothrix*, and 21–57 % of feeding time in *Brachyteles* (Di Fiore et al. 2011). Thus, a commitment to leaf eating appears also to be present in the common ancestor of all atelines.

Among howler monkeys, *A. caraya* and *A. guariba* exploit diets in which metabolizable energy is derived principally from leaves. *Alouatta caraya* occupies the southernmost distribution of the genus *Alouatta* (29 °S) and exploits flooded and semideciduous gallery and naturally fragmented forest habitats characterized by plant species that lose their leaves in winter and have relatively shorter and highly seasonal periods of flowering and fruiting (generally late spring and summer) (Zunino 1989; Kowalewski 2007). Based on a study using mtDNA, *A. caraya* appears to have experienced a demographic expansion in southern Argentina during the Holocene (15,500–17,000 years ago) by colonizing forested corridors of the Parana and Paraguay Rivers (Ascunce et al. 2007). This expansion moved *A. caraya* into habitats characterized by daytime temperatures as low as −2 °C, nighttime temperatures even lower, and increased seasonal variation in day length (sunset to sunrise) from 14 h in the summer to 10 h in the winter. These semideciduous forests are characterized by limited food availability during the winter. For example, at the San Cayetano study site, Corrientes Province, Argentina (27° 30′ S 58° 41′ W), leaves, petioles, and shoots accounted for 100 % of *A. caraya* feeding time, and presumably the overwhelming majority of energy acquisition during the winter months of July and August (Zunino 1989). At a nearby site (27° 20′ S and 58° 40′ W), *A. caraya* invested more than 90 % of their feeding time consuming leaves during the winter month of August (Kowalewski 2007). At another site (26° 54′ S and 58° 13′ W), leaves and petioles accounted for between 98 and 100 % of *A. caraya* feeding time during the autumn and winter (Arditi 1992). As indicated in Table 4.4, based on feeding rates over 55 % of metabolizable energy and over 71 % of energy from available protein in the *A. caraya* diet is derived from leaves. At these sites, it is worth noting that mature leaves provided considerably more energy from protein (55 %) than did immature leaves (19 %; Table 23.4). We calculated Metabolizable Energy as the sum of the energy contributions of total non-structural carbohydrates, available protein, and lipids in the foods consumed (Conklin-Brittain et al. 2006).

Alouatta guariba in Northern Argentina (26° 30′ S, 53° 50′ W) shows a similar nutritional pattern with almost 70 % of total feeding time in the winter month of July devoted to leaf eating and almost 30 % devoted to the consumption of pollen-filled male cones (*Pinus* sp.) (Agostini et al. 2010). In a second study (Campo de Instrução de Santa Maria, Municipio de Santa Maria, 29° 43′–29° 44′ S; 53° 42′–53° 44′ W), three groups of *A. guariba* spent 66–99 % of their feeding time consuming leaves in July and August, and 94–100 % in September (late winter) (Fortes 2008). As indicated in Table 23.4, 59 % of metabolizable energy and more than 78 % of energy from available protein in the *A. guariba* yearly diet was derived from leaves. In contrast to *A. caraya*, however, *A. guariba* obtains a considerably greater proportion of its energy from immature leaves. It is possible that the changes in the Pleistocene climate in southern South America leading to natural forest fragmentation, a reduction in forest productivity, and limited and highly seasonal fruit production (especially during the winter months of June, July, and August) resulted in southern howler monkeys (*A. guariba* and *A. caraya*) shifting to a leaf-enriched diet (Bravo and Sallenave 2003; Kowalewski 2007).

Cortés-Ortiz et al. (2003) place *A. guariba* and *A. caraya* in two distinct howler monkey clades, with *A. guarib*a grouped in the *A. belzebul* clade and *A. caraya* in the *A. seniculus* clade. This would suggest that *A. guariba* and *A. caraya* have independently

Table 4.4 Percentages of available protein energy (kJ) and metabolizable energy (kJ) in the diet of different howler monkey species

	% available protein energy (kJ)							% metabolizable energy (kJ)						
Species	Fruits			Leaves			Flowers	Fruits			Leaves			Flowers
	All (%)	RF (%)	UF (%)	All (%)	YL (%)	ML (%)	(%)	All (%)	RF (%)	UF (%)	All (%)	YL (%)	ML (%)	(%)
A. belzebul	43.24			51.07	11.77	31.46	5.69	65.04			30.95	5.05	21.47	4.01
A. caraya	21.00			71.71	18.99	54.77	3.52	41.19			55.55	10.77	42.81	3.26
A. guariba	18.82			78.48	32.63	44.93	2.95	37.75			59.24	23.74	33.32	3.01
A. macconnelli	39.42			57.89	36.42	32.31	2.70	63.35			34.33	20.08	20.67	2.32
A. palliata	32.58	33.48	7.86	63.96	35.88	25.31	3.86	56.46	62.60	8.01	40.35	20.78	18.92	3.19
A. pigra	32.20	19.57	11.29	64.33	33.05	22.19	3.47	57.45	44.81	13.89	39.55	20.92	17.69	3.01
A. seniculus	32.36			66.43	39.17	15.20	1.20	58.33			40.74	29.74	12.70	0.93

Metabolizable Energy includes energy obtained from available protein (AP), total non-structural carbohydrates (TNC), and lipids. Energy content was calculated using standard conversions: 16 kJ/g for TNC, 17 kJ/g for AP, and 37 kJ/g for lipids (Conklin-Brittain et al. 2006). Nutritional data for all the food categories (YL, ML, RF, UF, FL) were obtained from average values of 8–20 plant species per category reported by Righini (2014) and Felton (2008), who carried out nutritional analyses on plant items included in the annual diets of *A. pigra* in Campeche, Mexico, and *Ateles chamek* in Bolivia, respectively shifted to a greater dependence on leaves in their diet as a response to exploiting more seasonal temperate and xeric forests. However, Villalobos et al. (2004) suggest that *A. guariba* and *A. caraya* are part of a single radiation. If this is correct then their increased reliance on leaves and seeds represents the retention of a common behavioral-ecological syndrome.

4.5 Conclusion

Many primate species (e.g., indriids, callithrichines, African and Asian colobines, gorillas) exploit low quality and/or difficult to process resources including woody plants, mature leaves, unripe fruits, lichen, and plant exudates year-round or during food-limited times of the year (Garber 1987; Rogers et al. 1990; Waterman and Kool 1994; Lambert 1998, 2007; Powzyk and Mowry 2003; Marshall and Wrangham 2007; Porter et al. 2009). Although different primate taxa have followed alternative pathways to successfully exploit difficult to process foods, efficient exploitation of these resources has been correlated with species-specific changes in behavior and anatomy (Lambert 1998). Changes in gut size, morphology, and food passage rate have enabled these taxa to support a rich symbiotic bacterial and protozoan microflora and thereby more efficiently ferment foliage, seeds, and other plant parts containing complex polysaccharides (Kay and Davies 1994). In addition to anatomical specializations of their masticatory apparatus that aid in breaking food into smaller particles, many primate taxa have developed behavioral and cognitive solutions that serve to increase foraging efficiency or reduce energetic requirements when exploiting low quality foods (Milton 1978, 1980, 1998; Strier 1992; Ganas et al. 2008; Lambert 2011). Food quality has been defined as the amount of available digestible material, such as protein, relative to indigestible or difficult to digest material (e.g., fiber and complex sugars) present in a food item (Milton 2006). However, since the digestibility of a food item varies as a function of the manner in which the consumer processes food orally as well as in its gut, a more accurate definition of food quality should refer to the capacity of food to yield energy to a given individual (Lambert 2007). This could vary across species and within species as well (Amato and Righini 2014).

All species of howler monkeys consume various proportions of fruits, leaves, and flowers. This highlights the limitations of terms such as frugivores and folivores when describing the howler monkey diet. Depending on local environmental conditions and the nutritional composition of the particular plant tissues consumed, all howler monkey species can subsist for periods of days, weeks, or in some cases months, on a diet composed principally of leaves, including mature leaves, a diet principally of fruits, or a diet principally of flowers. This depends both on the local ecological conditions of the forest, the nutritional content of the available foods, and the howler monkey dental and digestive traits. According to data from Conklin and Wrangham (1994), Conklin-Brittain et al. (1998), and Norconk et al. (2009), there is clear evidence that leaves and fruits of even congeneric plant species can vary markedly in their nutritional content. Although in general mature leaves of many plant species consumed by primates are higher in crude protein, secondary compounds, and fiber than whole fruits, and lower in crude protein and higher in fiber and secondary compounds than immature leaves, this is not always the case. Therefore, in the absence of obtaining data on the nutritional composition of the particular plant tissues consumed by howler monkeys, as well as the diversity and abundance of microbial populations present in the howler monkey gut (Amato and Righini 2014) we cannot equate time spent feeding on a particular resource with the nutritional importance of that resource in the diet (Schuelke et al. 2006; Felton et al. 2009a, b, c). Moreover, given differences in the nutritional content between leaves of individual plant species and between fruits of individual plant species, it may be possible for howler monkeys to balance nutrient intake over periods of days, weeks, or months by principally consuming a single food type. That is; consume leaves or fruits of different plant species that offer complementary nutrients.

In this sense, the use of a geometric nutrient framework and the analysis of individual macronutrient regulation (lipids, protein, carbohydrates) are essential for understanding diet selection in different species of free-ranging primates. Recent research on wild spider monkeys (*Ateles chamek*) in Bolivia (Felton et al. 2009a, b, c) revealed that individuals regulated their daily intake of available protein by supplementing a fruit-rich diet with small daily amounts of leaves. Thus, spider monkeys were able to maintain a relatively stable protein intake across seasons independent of food availability, while total energy intake fluctuated according to the nutritional content of available food items. In contrast, mountain gorillas (*Gorilla beringei*) have been found to prioritize non-protein energy (i.e., energy derived from lipids and nonstructural carbohydrates) and selectively consumed plant tissues and food types that enabled them to maintain a relatively constant lipid and nonstructural carbohydrate intake throughout the year, in spite of drastic changes in food availability (Rothman et al. 2011). During periods of fruit scarcity, gorillas were found to over-eat protein (31 % of available energy intake vs. 19 % during periods of fruit availability) and altered their diet to include a greater proportion of leaves and herbaceous vegetation (Rothman et al. 2011). This feeding pattern enabled them to achieve a consistent level of carbohydrates and lipids throughout the year.

Given the close evolutionary relationship between howler monkeys and other atelines, and the fact that all atelines include fruits, leaves, and flowers as the primary components of their diet (Rosenberger and Strier 1989; Rosenberger et al. 2011), we anticipate that *Alouatta* will exhibit a nutritional strategy of protein regulation more similar to that of spider monkeys than to gorillas (Rosenberger and Strier 1989; Rosenberger et al. 2011). Preliminary data for *A. pigra* (which exploits a fruit and leaf-balanced diet) in Mexico and *A. caraya* (which exploits a leaf-enriched diet) in Argentina support this hypothesis, since individuals of these two species consumed relatively consistent daily amounts of available protein energy (averaging 102 kJ/Metabolic Body Mass ± 4.6 SE and 186 kJ/MBM ± 19 SE, respectively), while daily non-protein energy intake varied to a much greater extent (e.g., from 65 to 3,900 kJ/MBM in *A. caraya*) (Fernandez and Righini, unpubl. data). We hypothesize that this pattern is also present in howler monkey species characterized by a fruit-enriched diet (*A. belzebul* and *A. macconnelli*); however, it also may be possible that during periods of fruit scarcity, all howler monkey species increase their non-protein energy intake by supplementing their diet with difficult to digest food items that provide a balance of macronutrients in terms of the average intake ratio of protein and non-protein energy (Felton et al. 2009b). In this regard, additional data on differences in dental morphology, gut proportions, transit time, and gut microbiota across howler monkey species are necessary to better define behavioral syndromes in *Alouatta* and to better understand the challenges that individual taxa face in exploiting a leaf, flower, and fruit diet.

In conclusion, based on our analysis of published data on the feeding ecology (time spent feeding on a given food type multiplied by feeding rates based on the amount consumed) of howler monkeys, there is evidence of three dietary "syndromes". These syndromes are generally consistent with howler monkey phylogeny and biogeography, with Mesoamerican howler monkeys plus *A. seniculus* characterized by a balanced leaf and fruit diet, Amazonian howler monkeys with a fruit-enriched diet, and Atlantic Forest and southern howler monkeys characterized by a leaf-enriched diet. Although our analysis represents a first step in advancing studies of howler monkey nutritional ecology, we strongly encourage researchers studying primate diet to collect data on (1) feeding rates (in addition to time spent feeding) in order to estimate the amount (in grams) of different plant and animal tissues consumed and (2) the nutritional content of individual plant and animal tissues in order to identify and analyze species-specific dietary strategies across the Order (for example see Felton et al. 2009a, b, c; Rothman et al. 2011). Such an approach highlights the limitations of terms such as frugivore, folivore, folivore-frugivore, frugivore-folivore, omnivore, and insectivore-frugivore and redirects the analysis of primate feeding ecology to social, ecological, physiological, and cognitive questions associated with patch choice, decision-making, nutrient-balancing, resource-mixing, and spatial and temporal changes in the local availability of nutrients in their home range.

Finally, although evidence presented here of behavioral syndromes in *Alouatta* is based primarily on diet and feeding ecology, we suggest that anatomical/physiological differences in gut microbiota, food passage rates, and gut morphology are also likely to vary across howler monkey species, and we encourage researchers to initiate studies to identify possible behavioral-ecological-anatomical relationships.

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Chapter 5
Seed Dispersal by Howler Monkeys: Current Knowledge, Conservation Implications, and Future Directions

Víctor Arroyo-Rodríguez, Ellen Andresen, Susana P. Bravo, and Pablo R. Stevenson

Abstract Primate seed dispersal has been increasingly recognized as having a potentially profound impact on tropical forest regeneration and plant species composition. Confirming and quantifying this impact, however, has proven to be an important challenge. We review the literature on seed dispersal by howler monkeys (*Alouatta* spp.) throughout their geographical range and assess the impact for plant populations and communities. Howler monkeys spend ca. 50 % of their feeding time eating fruits from many plant species and different life forms. For some plant species they are probably the only or primary dispersal agent (e.g., fruits with large seeds and/or with hard indehiscent husks), especially in anthropogenically disturbed forests, where other large-bodied frugivores tend to be absent or are locally extinct. In this regard, howlers contribute to secondary succession, aiding in the restoration of degraded habitats. *Alouatta* spp. swallow most (>90 %) of the seeds they handle, defecating them undamaged. Studies indicate that passage through the howler gut has a positive effect on rates of seed germination. In addition, studies of secondary dispersal indicate that seeds voided in howler dung attract secondary seed dispersers such as rodents and dung beetles. Also, nutrients in the dung may enhance seedling establishment. Although certain components of howler seed dispersal such as seed shadows, post-dispersal seed fate, and seeds/seedlings survival need to be better studied, current information suggests that howler monkeys are effective seed dispersers for many plant species, with important consequences for plant communities and forest regeneration.

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Resumen La dispersión de semillas por primates puede tener un gran impacto potencial sobre la regeneración y composición de especies de plantas en bosques tropicales. Sin embargo, la confirmación y cuantificación de dicho impacto ha constituido un importante reto. Nosotros hacemos una revisión de la literatura sobre dispersión de semillas por monos aulladores (*Alouatta* spp.) en su rango de distribución geográfica y evaluamos su impacto sobre las poblaciones y comunidades de plantas. Encontramos que los aulladores dedican ca. 50 % de su tiempo a alimentarse de frutos de muchas especies de plantas y varias formas de vida. Ellos pueden ser los únicos o principales dispersores primarios para algunas especies (por ejemplo, frutos con semillas grandes y/o con exocarpo duro e indehiscente), especialmente en bosques perturbados, donde otros frugívoros de tamaño grande tienden a desaparecer. De hecho, estos primates pueden contribuir a la sucesión secundaria, ayudando a la restauración de hábitats degradados. Ellos tragan la mayoría de las semillas que manipulan, defecándolas sin dañarlas. Usualmente, el paso por el tracto digestivo tiene un efecto positivo en la germinación. Además, las semillas que se encuentran en las heces de monos aulladores pueden ser dispersadas por dispersores secundarios como roedores y escarabajos. Sus heces enriquecen el suelo y pueden favorecer el establecimiento de plántulas. Aunque algunos componentes de este mutualismo, como el destino final de las semillas dispersadas y la supervivencia de semillas/plántulas, necesitan ser mejor estudiados, la información actual sugiere que los monos aulladores son dispersores efectivos para muchas especies de plantas, con importantes consecuencias para las comunidades vegetales y la regeneración de bosques.

Keywords Forest regeneration • Seed-dispersing animals • Seed dispersal effectiveness

5.1 Introduction

More than 60 % and up to 94 % of woody plant species in tropical forests have their seeds dispersed through endozoochory by frugivorous animals. Hence, studying the interactions between frugivores and plants is critical for understanding the dynamics of these ecosystems (Jordano 2000). Frugivory and the consequent dispersal of seeds constitute a key ecological interaction that is mostly mutualistic, and that has important ecological, evolutionary, and conservation implications for both the animal and plant species involved, as well as for the ecosystems in which they occur (Herrera 2002; Schupp et al. 2010).

From a plant's perspective, seed dispersal has three main, non-mutually exclusive, advantages (Howe and Smallwood 1982): (1) escape from areas of high mortality; (2) colonization of suitable sites which occur at random locations; and (3) directed dispersal to suitable sites. The 'escape hypothesis', which was derived from the mechanistic part of the Janzen–Connell hypothesis (Janzen 1970; Connell 1971), predicts that seed/seedling mortality will be higher under the parent plant, due to predators and/or pathogens that act in a density- and/or distance-dependent fashion, resulting in greater recruitment with increasing distance from the parent plant. In turn, according to the 'colonization hypothesis', widespread dispersal of seeds may be critical for some species, because it allows the arrival of at least some seeds into favorable sites, whose occurrence is unpredictable in space and time. Finally, according to the 'directed dispersal hypothesis', some dispersal vectors, and in particular animal vectors, can promote the arrival of seeds into specific non-random habitats (or microsites), where survival of seeds/seedlings will be predictably higher.

As mentioned above, these and other advantages of seed dispersal are not mutually exclusive, and the relative importance of each is species- and context-dependent (Andresen 2000; Vulinec and Lambert 2009; Chaves et al. 2011). In this regard, the theoretical framework most extensively used to assess the contribution of seed dispersal agents to plant fitness is the 'Seed Dispersal Effectiveness' framework (Schupp 1993; Schupp et al. 2010). Dispersal effectiveness is defined in terms of the contribution that dispersal agents make to the reproduction of a given plant species (Schupp et al. 2010). However, seed dispersal not only affects plant demography or the number of saplings present in a given area (e.g., recruitment); it can also play an important role in determining the spatial distribution of individuals in a given population, and it can have important consequences at the plant community level (Schupp et al. 2010; Russo and Chapman 2011). Regarding the latter, seed dispersal not only plays a role in determining the species composition of local plant communities through its effect on individual species, but it will also affect emerging properties such as community structure and diversity (Schupp et al. 2010; Russo and Chapman 2011).

In tropical forests, the most prominent taxa of seed-dispersing frugivores are birds, bats, and primates (Fleming and Kress 2011). While the former two have been the focus of seed dispersal studies for many decades, it has only been during the last two decades that primates have been recognized as important seed dispersers, with an increasing number of evidences from species within the Strepsirrhini and Haplorrhini suborders of primates (Chapman 1995; Lambert and Garber 1998; Koné et al. 2008; Chaves et al. 2011; Russo and Chapman 2011; Stevenson 2011; González-Zamora et al. 2014). This may reflect the fact that although many primates act as seed dispersers, they also act as seed predators. Seed consumption is reported in a large number of primate taxa including *Lagothrix*, *Ateles*, and *Alouatta* (Stevenson et al. 2002). In addition, since larger bodied primates tend to disperse many seeds together in a large fecal clump (Chapman 1989; Russo et al. 2006; González-Zamora et al. 2012, 2014), which may attract fungal pathogens or other seed predators (rodents), post-dispersal survivorship of voided seeds can be low (Howe and Smallwood 1982).

Frugivorous primates can disperse viable seeds of many plant species. However, evidence shows that the effects of seed dispersal on plant populations and communities can be highly variable among and within primate species (see Russo and Chapman 2011 for a thorough review). Primate species also differ in their vulnerability to disturbances such as hunting or habitat loss. While some primate species are highly sensitive, others are known to be particularly resilient (e.g. howler monkeys in the Neotropics; Arroyo-Rodríguez and Dias 2010; Estrada 2014), becoming the main or only seed dispersal agent for many plant species in areas where other frugivores have disappeared (Andresen 2000).

This chapter focuses on seed dispersal by howler monkeys (*Alouatta* spp.) throughout their geographical range. As is the case with primates in general, studies of seed dispersal by howler monkeys have focused on one or a few aspects of the seed dispersal process (e.g., frugivory, seed-handling, gut-passage effects, seed deposition patterns, post-dispersal seed fate, among others; Table 5.1). Thus, clearly establishing the effects of howler monkey seed dispersal on plant populations (demography, spatial distribution), and on plant communities (composition, structure, diversity), has been difficult.

As an attempt to fill these gaps of information, we first assess the effects of seed dispersal by howler monkey on plant populations. To do so, we follow the seed dispersal effectiveness framework by identifying general patterns of the two primary components of effectiveness, i.e., quantity and quality of dispersal. Then, we discuss how seed dispersal by howler monkeys also can affect the spatial distribution of plant individuals in a population. At present, however, we know very little regarding the degree to which seeds dispersed by howlers actually survive the seedling, sapling, and pole stages of development and live to become fruiting and reproductive adults. In the second section, we evaluate the impact that howler monkey seed dispersal may have on plant community properties. Finally, in the last section we draw some conclusions on the roles that howler monkeys may play in forest conservation and restoration. Although this genus represents a radiation of some 12 species (Cortés-Ortiz et al. 2014), this review is focused on 6 howler monkey species due to the lack of data on the remaining species (Table 5.1).

5.2 Implications of Howler Monkey Seed Dispersal for Plant Populations

5.2.1 Seed Dispersal Effectiveness and its Effects on Demography

Seed dispersal effectiveness depends on both the quantity and the quality of seed dispersal (Schupp 1993). Dispersal quantity is simply given by the number of seeds that are dispersed. In turn, the number of dispersed seeds depends on the number of visits to the plant by a disperser and the number of seeds swallowed per visit. The quality component is given by the probability that a dispersed seed germinates and the developing sapling survives to become a reproductive adult. The quality of seed dispersal is determined by two sub-components: the quality of the treatment given to the seed in the animal's mouth/gut, and the quality of seed deposition (Schupp 1993). This latter is influenced by primary dispersal, as well as in many cases secondary dispersal.

Table 5.1 Aspects of seed dispersal by howler monkeys (*Alouatta* spp.) studied throughout their geographic range in both continuous forest (CF) and forest fragments (FF). References are indicated inside parentheses

	A. caraya		*A. fusca*	*A. guariba*		*A. palliata*		*A. pigra*		*A. seniculus*		*A. puruensis*	*A. macconnelli*
Aspects	CF	FF	CF	CF	FF	CF	FF	CF	FF	CF	FF	CF	CF
Frugivory [a]	–	Argentina (4[b], 51[b])	–	Brazil (49)	–	Costa Rica (13) Mexico (15, 16, 22)	–	Guatemala (25) Mexico (22, 28)	Mexico (28)	Colombia (33, 35, 48)	Colombia (50)	Peru (47)	Brazil (29) French Guiana (38, 39, 41, 44)
Seeds in feces	Brazil (7)	Argentina (4[b])	–	Brazil (11)	–	Costa Rica (13, 14) Mexico (15, 16, 22)	Mexico (23)	Guatemala (25) Mexico (22, 28)	Mexico (28)	Colombia (33, 34, 35)	Colombia (36, 37)	Peru (47)	Brazil (29, 30, 31, 32) French Guiana (40, 42, 43, 44, 45)
Gut passage time	–	Argentina (1)	–	–	–	Costa Rica (14) Mexico (15, 16, 18, 19)	Mexico (18, 19)	–	–	Colombia (33, 34)	–	–	French Guiana (40)
Gut passage effect on seed germination	–	Argentina (1, 3, 5[b])	Brazil (8, 9, 10)	Brazil (11)	Brazil (12)	Mexico (15, 17, 18, 19)	Mexico (17, 18, 19, 21)	Mexico (27, 28)	Mexico (27, 28)	Colombia (34)	–	–	Brazil (30) French Guiana (40, 44)
Ranging patterns[a]	–	Argentina (5[b])	–	–	–	Mexico (15, 17, 18, 19, 22)	Mexico (17, 18, 19)	Mexico (22)	Belize (24)	Colombia (33, 35, 48)	–	–	Brazil (29) French Guiana (38, 39, 40, 41)

(continued)

Table 5.1 (continued)

	A. caraya		*A. fusca*	*A. guariba*		*A. palliata*		*A. pigra*		*A. seniculus*		*A. puruensis*	*A. macconnelli*
Aspects	CF	FF	CF	CF	FF	CF	FF	CF	FF	CF	FF	CF	CF
Defecation pattern	Brazil (7)	Argentina (1, 3, 5[b])	–	Brazil (11)	–	Costa Rica (14)	Mexico (23)	Guatemala (26)	–	Colombia (35, 33)	–	Peru (47)	Brazil (31) French Guiana (40, 41, 43, 45, 46)
Seed dispersal distance	–	Argentina (1, 3, 5[b])	–	Brazil (11)	–	Mexico (15, 16, 18, 19)	Mexico (18, 19)	–	–	Colombia (33, 35)	–	–	French Guiana (40)
Post-dispersal seed fate	–	Argentina (2)	–	–	–	Costa Rica (13, 14) Mexico (16)	Mexico (20)	Guatemala (25, 26)	–	–	Colombia (36, 37)	Peru (47)	Brazil (30, 31, 32) French Guiana (42, 43, 44, 45)
Seedling/ sapling recruitment	–	Argentina (6[b])	–	–	–	Mexico (15)	Mexico (23)	Mexico (27, 28)	Belize (24) Mexico (27, 28)	–	–	–	Brazil (32) French Guiana (41)

References: (1) Bravo et al. (1995), (2) Bravo and Zunino (1998), (3) Bravo and Zunino (2000), (4) Bravo (2008), (5) Bravo (2009), (6) Bravo (2012b), (7) Moura and McConkey (2007), (8) de Figueiredo (1993), (9) Pedroni and Sanchez (1997), (10) De Figueiredo and Longatti (1997), (11) Martins (2006), (12) Graeff et al. (2007), (13) Chapman (1989), (14) Wehncke et al. (2004), (15) Estrada and Coates-Estrada (1984), (16) Estrada and Coates-Estrada (1991), (17) Serio-Silva and Rico-Gray (2002a), (18) Serio-Silva and Rico-Gray (2002b), (19) Serio-Silva and Rico-Gray (2003), (20) Martinez-Mota et al. Martínez-Mota et al. (2004), (21) Righini (2004), (22) Amato and Estrada (2010), (23) Anzures-Dadda et al. (2011), (24) Marsh and Loiselle (2003), (25) Ponce (2004), (26) Ponce et al. (2006), (27) Gonzalez-Di Pierro et al. (2011), (28) González-Di Pierro (2011), (29) Santamaría (1999), (30) Andresen (2001), (31) Andresen (2002a), (32) Andresen and Levey (2004), (33) Yumoto et al. (1999), (34) Stevenson et al. (2002), (35) Giraldo et al. (2007), (36) Santos-Heredia et al. (2010), (37) Santos-Heredia et al. (2011), (38) Julliot and Sabatier (1993); (39) Julliot 1996av (40) Julliot 1996b, (41) Julliot 1997, (42) Feer (1999), (43) Feer et al. (2001), (44) Feer and Forget (2002), (45) Pouvelle et al. (2009), (46) Ratiarison and Forget (2011), (47) Andresen (1999, (48) Stevenson et al. (2000), (49) Martins (2008), (50) Palma et al. (2011), (51) Bravo (2012a)

–: Unavailable data

[a] We only included in this review those studies focusing on howler monkey seed dispersal. Consequently the lists of studies addressing frugivory and ranging patterns, presented here, are not comprehensive. For additional information on these aspects please refer to other chapters in this volume

[b] Study carried out on an island

5.2.1.1 Quantity of Seed Dispersal

Considering that the number of visits to a particular feeding site is directly related to the abundance of the dispersers, their dietary preferences, and the reliability of visitation (Schupp 1993), howler monkeys can contribute notably to this component of seed dispersal effectiveness. First, because of their high population densities (densities vary widely, but values of up to 283 ind/km^2 have been reported) (reviewed in IUCN 2012), howler monkeys constitute one of the most common vertebrate species in many Neotropical forests (Peres 1997; Garber et al. 2006). Second, although howler monkeys have been typically considered the most folivorous of Neotropical primates, they spend approximately half of their feeding time consuming ripe fruits when this resource is available (reviewed by Bicca-Marques 2003; Cristóbal-Azkarate and Arroyo-Rodríguez 2007; see also Dias and Rangel-Negrin 2014), generally being ‘as frugivorous as possible and as folivorous as necessary’ (Silver et al. 1998). Finally, howler monkeys spend most of their time feeding on the fruits of a small number of plant families (e.g. Moreaceae, Fabaceae, Lauraceae and Sapotaceae; Bicca-Marques 2003; Cristóbal-Azkarate and Arroyo-Rodríguez 2007; Dias and Rangel-Negrin 2014). These species are consistently used year after year (e.g. Estrada and Coates-Estrada 1984), such that howler monkeys can be considered highly reliable seed dispersers for these plant taxa. Therefore, these evidences indicate that howlers are able to disperse very large quantities of seeds.

The number of seeds dispersed per visit depends on the number of seeds handled and swallowed per visit and the probability of dispersing a handled seed (Schupp 1993). In general, howler monkeys disperse, through defecation, most of the seeds they handle. Also, there is a trend showing that, in general, the larger the frugivorous animal, the higher the amount of fruits (and seeds) it can handle, and the larger the size of fruits/seeds it is able to swallow (e.g., Cramer et al. 2007). However, some important exceptions have been published (e.g., tamarin monkeys: Lambert and Garber 1998).

Studies indicate that howlers disperse large numbers of seeds from both small-seeded species and from large-seeded (>10 mm) plant species (Tables 5.2 and 5.3). For example, Andresen (2002a) found that up to 560 seeds >3 mm long can be found in a defecation sample of *A. macconnelli* in Brazil, although 20 % of the defecation samples with seeds had less than 30 seeds. Similarly, Giraldo et al. (2007) analyzed 60 fecal samples of *A. seniculus* in Colombia, finding 290,174 seeds (1–33 mm long), of which 99.9 % belonged to three small-seeded light-demanding tree species (*Ficus* spp., *Cecropia telealba*, and *Miconia acuminifera*). Martins (2006) assessed seeds larger than 2 mm in length and reported an average of 18 seeds (range: 1–97 seeds) per fecal sample (from 1 or 2 tree species) in 147 fecal samples of *A. guariba* in a semideciduous forest in Brazil. In Argentina, one *A. caraya* group can remove up to 1,070 fruits from a tree of *Ocotea diospyrifolia* (Lauraceae) in a day (Bravo 2012a). *Ocotea diospyrifolia* seeds are 13.2 mm long (7 mm in diameter) and the howlers were reported to swallow 100 % of removed seeds.

The ability to swallow large seeds (up to 4.6 cm length; Table 5.2) that are unlikely to be swallowed by smaller frugivorous animals makes the dispersal services offered

Table 5.2 Ranging pattern and gut passage time (GPT) of howler monkeys (*Alouatta* spp.), and characteristics of seeds in monkeys' feces

	Ranging pattern[b]			Characteristics of seeds in monkeys' feces[c]			
Howler species and references[a]	DR (m)	HR (ha)	GPT (hour)	No. spp. (*n*)	Seed length (cm)	SDD (m)	% FWS (*n*)
A. caraya							
1	–	–	24	–	–	5–290	–
3	–	–	–	–	–	20–1,200	–
4	–	–	–	–	0.9–1.4	–	–
5	500–600	–	–	–	–	0–360	–
7	–	–	–	19 (19)	0.6–1.9	–	–
A. fusca							
9	–	–	–	–	1.5	–	–
A. guariba							
11	–	–	19	14 (147)	–	> 100	45 (66)
A. macconnelli							
29	688	21	–	12 (103)	1.1–2.2	–	80 (103)
30	–	–	–	–	1.8	–	–
31	–	–	–	137 (263)	1–3.3	–	9–61 (263)
32	–	–	–	–	0.4–2.7	–	–
38, 39, 40, 41	–	45	35	86 (236)	<0.1–4	0–550	–
42	–	–	–	47 (100)	up to 4.6	–	–
43, 44	–	–	–	–	2.5	–	–
45	–	–	–	37 (–)	–	–	–
46	–	–	–	–	–	–	–
A. palliata							
13	–	–	–	12 (53)	<0.1–2.5	–	15 (53)
14	–	–	16–25	8 (–)	<0.1–2.4	–	46 (68)
15	10–893	60	18	15 (250)	<0.1–3.6	10–811	–
16	–	–	18–20	28 (–)	<0.1–3	10–1,000	–
17, 18, 19	–	10–75	20–30	–	–	65.7–217 means	–
22	127 (±66)	6	–	31 (167)	4	–	–
23	–	–	–	13 (–)	0.4–3.3	–	–
A. pigra							
24	–	1–4	–	–	–	–	–
25, 26	–	–	–	2 (–)	0.1–1.5	–	–
22	202 (±149)	33	–	13 (156)	2.1	–	–
27, 28	–	–	–	8 (–)	1–3	–	–
A. s. puruensis							
47	–	–	–	14 (27)	–	–	21 (27)

(continued)

Table 5.2 (continued)

Howler species and references[a]	Ranging pattern[b]		GPT (hour)	Characteristics of seeds in monkeys' feces[c]			
	DR (m)	HR (ha)		No. spp. (*n*)	Seed length (cm)	SDD (m)	% FWS (*n*)
A. seniculus							
33	560–1,660	17	19–20	8 (–)	0.8–2.1	up to 1,875	0.65 (153)
34, 48	633 (±261)	79	35	80 (–)	<0.1–3.2	–	–
35	554	8–14	–	9–13 (60)	<0.1–3.4	116 (±92)	–
36	–	–	–	–	0.68	–	–
37	–	–	–	–	0.8–1.4	–	–

[a] References are the same as in Table 5.1

[b] Day range (DR) and home range (HR)

[c] Number of species (no. spp.) in *n* fecal samples, seed length, seed dispersal distances (SDD) and percentage of *n* fecal samples without seeds (%FWS)

– unavailable data

by howler monkeys particularly relevant for large-seeded plants (Julliot 1996a; Andresen 2002a; Bravo 2009; Anzures-Dadda et al. 2011). For example, 83 % of the large-seeded fruit species (i.e., 5–25 mm in length) in the Paraná flooded forest (e.g., Lauraceae species) are dispersed by *A. caraya* (Bravo 2009). Also, genera such as *Garcinia* and *Inga* and many Sapotaceae species have seeds >3 cm long and are commonly found in howler monkeys' defecations (Table 5.3). Ramos-Obregon (2007) found that howler monkeys disperse a larger biomass of seeds >4 mm (in width) than the smaller sympatric brown capuchins, and that the mass of seeds dispersed per fecal sample was also higher (12.1 g vs. 1.3 g). In addition, she found that adult howler monkeys defecated a larger biomass of seeds than juveniles (mean adult female: 15 g/sample, adult male: 12, and juvenile: 7), consistent with the idea that body size can limit seed dispersal abilities within a primate species (Stevenson et al. 2005). Given that juveniles, in general, eat the same species with the adults, this difference between age classes can be explained by higher seed spitting rates in juveniles than in adults.

Plant species with indehiscent hard-husked fruits also tend to have a limited assemblage of dispersers. This is due to the fact that small bats and avian frugivores have limited handling abilities to open protected fruits in comparison with primates and other mammals (Janson 1983). For such plant species, howler monkeys and non-flying mammals with biting and manipulative abilities will likely play a very important role in seed dispersal (Andresen 2000). This is again the case for most species in the Sapotaceae family, which are very diverse and dominant in the forests of the Guiana Shield and in Central Amazonia and are frequently dispersed by Guianan red howler monkeys (*A. macconnelli*; Julliot 1996b; Andresen 2002a). For example, during a 2-years period *A. macconnelli* in Brazil defecated seeds from 47 species of Sapotaceae with large seeds (average size ± SD: 19.6 ± 0.7 mm in length, and 11.2 ± 0.4 mm width; Andresen 2002a). Other species with hard indehiscent

Table 5.3 Plant taxa dispersed by howler monkeys (*Alouatta* spp.) throughout their geographic range[a]

Family	Species[b]	Life form	Howler species[c]	References [d]
Anacardiaceae	*Spondias* spp. (>2)	Tree	Apa, Api, Ase	13–15, 24, 34
	Tapirira peckoltiana	Tree	Ama	40
Annonaceae	*Duguetia* sp.	Tree	Ama	42
	Rollinia edulis	Tree	Ase	36
Apocynaceae	*Parahancornia fasciculata*	Tree	Ama	40–42
	Stemmadenia obovata	Tree	Apa	14
Aralicaceae	*Dendropanax* spp. (3)	Tree	Api, Ase	22, 34
	Schefflera paraensis	Tree	Ama	42
Arecaceae	*Iriartea deltoidea*	Palm	Ase	34
	Oenocarpus bataua	Palm	Ase	34
	Syagrus sancona	Palm	Ase	34
Boraginaceae	*Cordia* spp. (3)	Tree	Agu, Apa, Api	11, 14, 24
Bromeliaceae	*Bromelia plumieri*	Epyphite	Aca	7
Burseraceae	*Bursera simaruba*	Tree	Apa	13, 15
	Protium spp. (4)	Tree	Ase	33, 34
	Tetragastris sp.	Tree	Ama	42
Cannabaceae	*Celtis* spp. (2)	Tree	Agu, Ase	11, 34
Celastraceae	*Salacia* cf. *cordata*	Tree	Ama	40
Chrysobalanaceae	*Chrysobalanus icaco*	Shrub	Api	24
	Hirtella racemosa	Tree	Apa	13
Clusiaceae	*Garcinia* sp.	Tree	Ase	35
Dilleniaceae	*Doliocarpus* sp.	Liana	Ama	40, 42
Erythroxylaceae	*Erythroxylum* sp.	Tree	Aca	7
Fabaceae	*Cynometra retusa*	Tree	Apa, Api	22
	Dialium guianense	Tree	Apa	15
	Geoffroea striata	Tree	Aca	5
	Inga spp. (7)	Tree	Api, Ase	22, 24, 34
	Pithecelobium lanceolatum	Tree	Api	24
	Samanea saman	Tree	Apa	14
	Swartzia arborescens	Tree	Ase	34
Icacinaceae	*Dendrobangia boliviana*	Tree	Ama	40
Lamiaceae	*Vitex* sp.	Liana	Aca	7
Lauraceae	*Nectandra* spp. (3)	Tree	Aca, Apa	3, 5, 15
	Ocotea spp. (4)	Tree	Aca, Api	2, 4–5, 7, 22
Lecythidaceae	*Gustavia hexapétala*	Tree	Ase	34
Malpighiaceae	*Byrsonima gardneri*	Tree	Aca	7
Malvaceae	*Belotia mexicana*	Tree	Apa	15
	Guazuma ulmifolia	Tree	Api	24

(continued)

Table 5.3 (continued)

Family	Species[b]	Life form	Howler species[c]	References [d]
Melastomataceae	*Miconia* spp. (>2)	Tree	Aca, Api, Ase	7, 24, 35
Meliaceae	*Guarea* sp.	Tree	Apa	15
	Trichilia pleeana	Tree	Ase	34
Moraceae	*Bagasa guianensis*	Tree	Ama	40
	Brosimum spp. (4)	Tree	Aca, Apa, Api, Ase, Apu	7, 14–15, 22, 34, 47
	Castilla ulei	Tree	Ase	33, 34
	Clarisia racemosa	Tree	Ase, Apu	37, 47
	Ficus spp. (>22)	Tree	Aca, Apa, Api, Ase, Apu	1–3, 7, 13–14, 17–18, 20–21, 24, 26, 33–35, 47
	Maclura tinctoria	Tree	Apa	14
	Perebea spp. (2)	Tree	Ase	33, 34
	Poulsenia armata	Tree	Apa	15, 22
	Pseudolmedia spp. (4)	Tree	Apa, Api, Ase	15, 22, 33–34, 37
	Trophis racemosa	Tree	Api	24
Muntingiaceae	*Muntingia calabura*	Tree	Apa	13
Myristicaceae	*Virola* spp. (2)	Tree	Ama, Apu	41, 47
Myrtaceae	*Eugenia* spp. (3)	Tree	Aca, Agu	4, 5, 7, 11
	Psidium guajava	Tree	Aca	5
	Syzygium spp. (2)	Tree	Api	24
Olacaceae	*Minquartia guianensis*	Tree	Ama	41
Phytolaccaceae	*Phytolacca dioica*	Tree	Aca	3
	Trichostigma octandra	Liana	Api, Apu	22, 47
Polygalaceae	*Diclidanthera* sp.	Liana	Agu	11
	Coccoloba spp. (5)	Tree	Api, Ase	24, 33, 34
Primulaceae	*Cybianthus* sp.	Shrub	Aca	7
Quiinaceae	*Quiina obovata*	Shrub	Ama	41
Rhamnaceae	*Zizyphus* sp.	Tree	Aca	7
Rubiaceae	*Alibertia* sp.	Tree	Ase	34
	Genipa americana	Tree	Apa, Ase	13, 34
	Morinda panamensis	Tree	Api	24
	Psychotria carthagenensis	Tree	Aca	5
Salicaceae	*Banara arguta*	Tree	Aca	4, 5
	Zuelania guidonia	Tree	Apa	13
Sapindaceae	*Allophylus mollis*	Tree	Ase	35
	Cupania guatemalensis	Tree	Apa	13
	Paullinia spp. (2)	Liana	Aca	3, 5
	Talisia sp.	Tree	Ama	40

(continued)

Table 5.3 (continued)

Family	Species[b]	Life form	Howler species[c]	References [d]
Sapotaceae	*Chrysophyllum* spp. (2)	Tree	Ama, Apu	40–42, 44, 47
	Sideroxylon portoricense	Tree	Apa	15
	Ecclinusa lanceolata	Tree	Ama	40
	Manilkara spp. (2)	Tree	Apa	13, 15
	Micropholis spp. (5)	Tree	Ama, Apu	30, 40, 42, 47
	Pouteria spp. (>10)	Tree	Aca, Apa, Api, Ama	5, 15, 26, 40–42
Simaroubaceae	*Simarouba* spp. (2)	Tree	Api, Ase	24, 34
Smilacaceae	*Smilax* sp.	Vine	Apa	22
Solanaceae	*Solanum* sp.	Liana	Ama	42
Ulmaceae	*Ampelocera hottlei*	Tree	Apa, Api	15, 27
Urticaceae	*Cecropia* spp. (8)	Tree	Aca, Apa, Api, Ase, Ama	5, 7, 15, 22, 33, 34–35, 40
	Coussapoa spp. (3)	Tree	Apa, Ase, Apu	22, 34, 47
	Pourouma spp. (3)	Tree	Ase	33, 34
	Urera aurantiaca	Shrub	Aca	5
Violaceae	*Leonia glycycarpa*	Tree	Ase	34
Vitaceae	*Cissus* sp.	Liana	Aca, Api	5, 22

[a] Plant nomenclature followed the Missouri Botanical Garden nomenclatural update data base (http://mobot.org/W3T/search/vast.html). We only include plant taxa with seeds swallowed and/or defecated by howler monkeys for studies listed in Table 5.1. The species list, however, is not complete, as several papers only report the total number of species swallowed and/or defecated by howler monkeys, and not the complete species list

[b] For the plant genera with several species we only indicate the genus (and the number of species in parenthesis). The symbol '>' indicates that the number of species could be higher, as one or more studies report taxa identified only to genus level (e.g. *Ficus* sp.)

[c] Species of howler monkeys: Aca: *Alouatta caraya*; Agu: *A. guariba*; Ama: *A. macconnelli*; Apa: *A. palliata*; Api: *A. pigra*; Apu: *A. s. puruensis*; Ase: *A. seniculus*

[d] References are the same as in Table 5.1

husks and for which howler monkeys provide important dispersal services include *Dialium guianense*, *Inga* spp., *Genipa americana*, and *Gustavia hexapetala* (Table 5.3).

The number of seeds dispersed per visit also depends on the length of a visit, and howler monkeys tend to have long feeding bouts. For instance, the time fruit feeding in a single tree by a group of *A. palliata* in Los Tuxtlas, Mexico, can reach 40 min (mean ± SD, 19.0 ± 7.0 min; Dunn et al. 2012), whereas *A. caraya* in Argentina can spend up to 2 h feeding on fruit in a single laurel tree (*Ocotea diospyrifolia*; Bravo 2012a). In fact, *A. seniculus* in Colombia spends on average 14 min (±15.6, SD) per tree feeding on fruits, which represent longer feeding bouts than those reported for three other sympatric primates (mean bout length: *Cebus apella*: 8.4 ± 10.3 min, *Lagothrix lagothricha*: 7.8 ± 9.3 min, and *Ateles belzebuth*: 6.9 ± 9.0 min; Stevenson et al. 1998). As argued by these authors, the stronger group cohesion in howler monkeys compared to *Ateles* and *Lagothrix* results in larger feeding subgroup sizes and longer feeding bouts (more fruits consumed per group feeding bout). This stable grouping pattern can result in howlers exploiting larger food patches (to accommodate all group members; group size in *A. seniculus* in Colombia averaged 9.3 ± 0.9 individuals), allowing individuals to spend more time feeding on each food patch (Stevenson et al. 1998) and minimizing thus the energy cost related to traveling between food patches.

5.2.1.2 Quality of Seed Dispersal

Seed treatment in the mouth and gut determines both the proportion of seeds destroyed (due to mastication and/or digestion) and the germination ability (percentage of seeds that are not destroyed) (Schupp 1993; Schupp et al. 2010). In general, researchers have considered howler monkeys as high quality seed dispersers because, despite a long transit time (18–35 h), seeds remain viable after passing through their gut (e.g., Milton 1980; Estrada and Coates-Estrada 1984; de Figueiredo 1993; Julliot 1996a; Santamaría 1999; Gonzalez-Di Pierro et al. 2011). Howler monkeys generally swallow seeds and rarely chew or spit out seeds (e.g., *A. caraya*: Bravo 2009; *A. palliata*: Wehncke et al. 2004). Occasionally, however, howler monkeys include unripe fruits in their diet, and in these cases they act as seed predators by selecting seeds before they are fully mature and capable of germination. In some cases these seeds are digested in the gut (Giraldo et al. 2007). However, several studies of howlers indicate that individuals show a marked preference for consuming mature fruits (80–90 % of fruit feeding time: Estrada and Coates-Estrada 1984, 1991; Giraldo et al. 2007; Amato and Estrada 2010), which implies a reduced likelihood of seed predation.

Gut passage can also positively affect germination and early seedling establishment through at least two mechanisms (Traveset et al. 2007): (1) scarification (i.e., removal or thinning of the seed coat); and (2) deinhibition (i.e., separation of the seeds from the pulp). The scarification process increases the permeability of seeds, allowing the exchange of gases and water, which in turn triggers germination in many seed species (Traveset et al. 2007). It has been reported that gut passage in howler monkeys can have a positive, neutral, or negative effect on germination (Table 5.4). On the other hand, the impact of deinhibition has not been assessed for seeds dispersed by howler monkeys, and studies focusing on how howlers treat, process, and void seeds are needed to gain a better understanding of all possible implications of gut passage on seed germination. It is important to note that deinhibition occurs not only for defecated seeds, but also for seeds that are spat or dropped. Therefore, although howler monkeys disperse most seeds through defecation, in future studies it would be very useful to analyze the effect of pulp removal on seed fate, not only for defecated seeds, but also for spat and dropped seeds.

Another positive effect of gut passage on seed survival and germination is the control of insect larvae present in the ingested fruits/seeds. For example, the passage of seeds through the gut of howler monkeys can kill insect larvae that infest seeds of *Ocotea diospyrifolia* (Lauraceae), increasing the probability of seed survival and germination (Bravo 2008). In other cases, larvae are not killed, and seed dispersal by monkeys actually favors insect dispersal (Hernández 2011). Both phenomena are probably widespread, but have so far received little attention. Finally, gut passage may also have effects beyond germination, i.e., on seedling survival and growth; however, the available evidence on this topic is very limited (e.g., Gonzalez-Di Pierro et al. 2011; Table 5.1).

While the quality of seed treatment is relatively easy to quantify and has thus received more attention (Tables 5.1 and 5.4), the quality of seed deposition is much harder to evaluate, as it requires an assessment of seed and seedling fate through the primary and secondary post-dispersal and post-germination phases (Schupp et al. 2010). Seed deposition quality can be affected by many variables. Some of these can be directly linked to characteristics of the primary disperser (e.g., howlers), while others cannot. Variables affecting deposition quality, which can be directly associated to the primary disperser, include movement, foraging, and defecation patterns (whether seeds are voided singly or in large clumps), diet, social structure, and frugivore gut size and food passage rates (Schupp 1993). These aspects of animal behavior will determine many specific circumstances of seed deposition which are known to affect seed fate, such as: (1) presence/absence of dung surrounding the seeds; (2) amount and type of dung surrounding the seeds; (3) amount of seeds and number of seed species dispersed together; and (4) dispersal distance with respect to conspecific fruiting trees (Andresen 1999). Most of these variables will affect seed/seedling fate indirectly, i.e., through the effect they have on the behavior of secondary seed dispersers and/or predators and fungal pathogens, which in turn will determine what happens to a seed or seedling. These biotic post-dispersal agents will be discussed separately in the next section.

In terms of dispersal distances, howler monkeys are able to disperse seeds far from the parent plant due to their high daily travel distances (mean = 497 m, range = 50–1,564 m: Bicca-Marques 2003; also see Table 5.2) and long retention times (up to 35 h; Table 5.2). Evidence indicates that seeds dispersed by howler monkeys are deposited at distances of up to 1,000 m or more from the parent plant (Table 5.2). Nevertheless, howler monkeys may also defecate or drop fruits underneath conspecific fruiting trees; a reason why some authors have considered these primates as low-quality dispersers (e.g., Howe 1980).

In fact, due to their cohesive social structure, and their digestive physiology, howler monkeys spend most of their time resting in large sleeping trees [mean = 64.2 %, range = 8–97 %; from Cristóbal-Azkarate and Arroyo-Rodríguez (2007) and Bicca-Marques (2003) reviews]. After the resting period, and before moving to another tree, all or most of the individuals in the group usually defecate simultaneously (this occurs 2–4 times in a 24 h period; *A. palliata*: Wehncke et al. 2004; *A. s. puruensis*: Andresen 1999; *A. seniculus*: Giraldo et al. 2007). This behavior results in high amounts of feces and seeds being deposited in latrines located under the sleeping trees (e.g., Chapman 1989; Julliot 1996a, 1997; Andresen 2002a; Wehncke et al. 2004; Pouvelle et al. 2009, Table 5.2). For example, Wehncke et al. (2004) report that 67 % of *A. palliata* feces in a tropical dry forest in Costa

Table 5.4 Gut passage net effect on seed germination rates (i.e., percentage of defecated vs. control seeds that germinated in trials) and latency period of seeds[a]

Howler species	Country	Germination rate			Latency period			Germination trials[b]	Refs.[c]
		Higher	Similar	Lower	Shorter	Similar	Longer		
A. caraya	Argentina	1	0	0	1	0	0	Lab	1
A. caraya	Argentina	1	2	0	0	3	0	–	3
A. caraya	Argentina	0	3	1	3	1	0	Lab	5
A. fusca	Brazil	1	0	0	–	–	–	Lab	8
A. fusca	Brazil	1	0	0	–	–	–	Lab	9
A. fusca	Brazil	0	0	1	–	–	–	–	10
A. guariba	Brazil	3	1	1	0	3	1	Lab	11
A. guariba	Brazil	0	0	1	0	0	1	Lab	12
A. palliata	Mexico	5	1	0	3	2	0	Mix	15
A. palliata	Mexico	1	0	0	–	–	–	Field & Lab	17,18,19
A. palliata	Mexico	0	1	0	–	–	–	Field & Lab	21
A. pigra	Mexico	1[e]	0	0	1	0	0	Field	27, 28
A. macconnelli	Brazil	0	1	0	–	–	–	Field	30
A. macconnelli	French Guiana	4	7	6	2	12	1	Mix	40
A. macconnelli	French Guiana	0	1	0	–	–	–	Field	44
A. seniculus	Colombia	4	2	1	4	2	0	Mix	34
	Total percentages[d]	42 %	37 %	21 %	35 %	58 %	8 %		

[a] Cells indicate the number of plant species that showed a significant effect (positive or negative) and those that showed no effect of gut passage on germination rate and latency period

[b] Germination trials were performed in the field (Field), in the laboratory (Lab), and/or in the field by controlling some variables such as light, water and/or soil (Mix)

[c] References are the same as in Table 5.1

[d] Percentages are based on the number of plant species used for testing germination rates (52 species) and latency periods (40 species)

[e] Although the cumulative germination percentage of *Ampelocera hottlei* seeds after the 60 days trial was significantly higher for control seeds in fragments, in continuous forest this percentage was higher for ingested seeds

–unavailable data

Rica are deposited under sleeping trees. Similar percentages have been reported for *A. caraya* in Argentina (65 %, Bravo 2009). Larger percentages have been reported, but these are usually related to howler monkeys living in smaller habitat patches (e.g., 90 % of *A. caraya* feces are deposited in latrines in a small tropical dry forest patch in Argentina; Bravo and Zunino 2000).

Despite this large aggregation of feces and seeds under sleeping trees and/or underneath conspecific fruiting trees, howler monkeys can also disperse a substantial fraction (33–35 %) of seeds in individual scats distributed across the forest (e.g., scattered pattern; Wehncke et al. 2004; Bravo 2009). Furthermore, during periods in which howler monkeys are eating large amounts of leaves, relative to fruits, seeds are reported to be dispersed in low densities (Andresen 2002a). Therefore, seed deposition patterns produced by howler monkeys can be considered mixed, i.e., a fraction clumped and another one scattered. However, given that clumped fecal deposits generally contain many more seeds than scatted fecal deposits, and there exist very few studies on the seedling survivorship of seeds voided by howlers, the specific impact of howler monkeys as seed dispersers relative to other fruit eating tropical vertebrates remains unclear (Russo and Chapman 2011).

The clumped defecation and seed deposition pattern produced by howler monkeys may be important in terms of soil nutrient enrichment. Evidence indicates that latrines are enriched in nutrients (e.g., N, P, and several minerals) compared to surrounding areas (Feeley 2005; Pouvelle et al. 2008; Neves et al. 2010), and may have positive effects on establishment, growth, and survival of seedlings arising from howler-dispersed seeds. For example, Bravo (2012b) found that the *per capita* survival of saplings taller than 1 m was higher in latrines than in control sites. This result is unlikely to be solely related to a higher rate of seed arrival and the possible saturation of biotic mortality agents, but is probably also affected by the higher nutrient availability in latrines (Russo and Augspurger 2004; Bravo 2012b). Thus, consistent with the 'directed dispersal hypothesis' (Howe and Smallwood 1982), howler monkeys may be depositing a large proportion of seeds in specific non-random habitats (i.e., latrines), where survival of seeds/seedlings could be relatively high. In fact, Bravo (2012b) also reports four times more saplings (and from more species) in latrines of *A. caraya* than in randomly selected areas within the forest, and that saplings >1 m tall of three tree species (*Ocotea diopyrifolia*, *Nectandra megapotamica*, and *Eugenia punicifolia*) have higher densities in latrines than below parent trees. Nevertheless, available evidence on this topic is very scarce and needs to be investigated more deeply.

5.2.1.3 Post-dispersal Seed Fate: Seed Predation and Secondary Seed Dispersal

Seed predation and secondary seed dispersal are considered key processes in the seed dispersal cycle (Wang and Smith 2002). These processes can greatly alter the initial seed shadow created by the primary seed dispersal agent, thus affecting the patterns of seedling recruitment (Forget et al. 2005; Russo and Chapman 2011).

The behavior of seed predators and secondary dispersers is often directly affected by the particular characteristics of the seed deposition patterns produced by the primary seed dispersal agent. For howler monkeys in particular, seed density and the presence/amount of dung in individual dung piles, as well as the overall seed/dung density produced by scatter vs. clumped defecation patterns, are known to affect post-dispersal seed fate (Chapman 1989; Andresen 2002a, b; Wehncke et al. 2004; Santos-Heredia et al. 2010).

Rodents, ants, and dung beetles are known to be attracted to howler monkey defecations and to affect, positively or negatively, the fate of the seeds in them (e.g., Chapman 1989; Estrada and Coates-Estrada 1991; Andresen 1999, 2001; Martínez-Mota et al. 2004; Wehncke et al. 2004). While granivorous rodents and ants may act both as seed predators and secondary seed dispersers by actively searching for seeds in defecations, dung beetles act solely as secondary seed dispersers, as they search and use the fecal material, and move and bury accidentally seeds imbedded in it (Andresen and Feer 2005).

In general, rodents are known to be highly efficient in locating seeds dispersed by monkeys, and removal rates of 90 % or more are not uncommon (Chapman 1989; Estrada and Coates-Estrada 1991; Andresen 1999). Moreover, seeds embedded in relatively large quantities of feces have a higher probability of removal by rodents than seeds in small quantities or without feces (Chapman 1989; Andresen 1999, 2002a; Wehncke et al. 2004). Seed density can be another factor affecting seed removal by rodents, but much variation exists among microhabitats, seed species, and/or seasons/years (see Hulme 2002 and references therein). Although seed removal by rodents has been traditionally considered equivalent to seed predation, it is clear now that not all seeds removed by rodents are consumed. Depending on the rodent species, the seed species, and the overall fruit availability in a given moment, the probability of secondary seed dispersal by rodents, rather than predation, can be quite high (Forget et al. 1998; Feer and Forget 2002).

Secondary seed dispersal by dung beetles is characterized by burial and/or small horizontal movements (generally <1 m, Andresen and Feer 2005; Vulinec and Lambert 2009) of the seeds imbedded in the fecal material. In general, Neotropical dung beetles bury small and large seeds (up to approximately 3 cm), but there is a negative relationship between seed size and the percentage of seeds buried (Estrada and Coates-Estrada 1991; Feer 1999; Andresen and Feer 2005). Burial depth also varies greatly, but in general, most seeds are buried <5 cm (e.g., Andresen and Feer 2005). Seed burial by dung beetles greatly increases the probability of seed survival (Estrada and Coates-Estrada 1991; Andresen 1999, 2001, 2002b; Santos-Heredia et al. 2010) and, while seed burial may in some cases hinder seedling emergence (Feer 1999), it has been shown to have a significant net positive effect on seedling establishment of large-seeded species (Andresen 2001; Andresen and Levey 2004). In particular, twice as many seedlings emerged from seeds buried by beetles compared to defecated seeds that remained on the surface (Andresen and Levey 2004).

As with rodents, seeds surrounded by larger amounts of dung (as is often the case with seeds defecated by howler monkeys compared to seeds defecated by other frugivorous mammals including some other primates such as tamarins; Garber 1986) also have a higher probability of being removed by dung beetles (Andresen and Feer 2005). However, seed density per fecal clump does not seem to affect the probability of seed burial by dung beetles (Andresen 2002a; Culot et al. 2009). Regarding the influence of defecation patterns (clumped vs. scattered), results are not conclusive. Some studies report no significant effect of the defecation pattern on seed burial by dung beetles (Andresen 2002a; Ponce et al. 2006), but one study has reported increased seed burial rates for the clumped defecation pattern, but only for spider monkey dung, and not so for howler monkey dung (Santos-Heredia et al. 2010).

Although less studied, ants are likely to play very important roles as both predators and secondary dispersers of seeds defecated by howler monkeys, in particular of small seed species (<3 mm). A very extensive literature exists on seed predation and seed dispersal by ants in many different ecosystems. These studies illustrate how important these insects can be in plant–animal interactions (see Beattie and Hughes 2002 and references therein). For seeds defecated by howler monkeys, one study has shown that ants transport seeds to moist sites, rich in organic material, such as cracks in bark, ant gardens, and tunnel-like nests (Martínez-Mota et al. 2004). As argued by Martínez-Mota et al. (2004), these microsites may favor germination of some important epiphytic fig trees (*Ficus* spp.) and may thus constitute an example of directed seed dispersal.

Finally, post-dispersal seed fate is not only affected by rodents, dung beetles, and ants. Other biotic factors, such as pathogens (e.g., fungi) and other insect predators (e.g., bruchid beetles) also are responsible for the death of many dispersed seeds (Jones 1994). For example, Lambert (2002a, b) demonstrated that red-tailed guenons (*Cercopithecus ascanius schmidti*) consume fruits and spit out cleaned seeds of the tree *Strychnos mitis*, and that these seeds are significantly less likely to be attacked by seed predators and fungus than the unprocessed seeds. Further studies are needed to assess the impact of insect predators and fungus on post-dispersal fate of seeds dispersed by howler monkeys.

5.2.2 Effects on the Spatial Distribution of Individuals in a Plant Population

The implications of primary seed dispersal at the level of plant populations go beyond determining the number of seeds that are dispersed and affecting the probability those seeds have on producing a reproductive adult. While effective dispersal is necessary for the successful recruitment of new individuals, dispersal will also play an important role in determining the spatial distributions of those recruits, and possibly the spatial structuring of reproductive adults in a population or metapopulation. The spatial distribution of dispersed seeds is generally assessed by describing the seed shadow (number of seeds at different distances from the parent plant) and/or estimating the seed dispersal kernel (probability distribution of dispersed seeds relative to distance). Although the shape and size of seed shadows are recognized as having profound implications for population/metapopulation dynamics and community structure (see below), accurately estimating seed shadows, particularly for vertebrate-dispersed trees, remains an important challenge (Russo et al. 2006).

One of the main difficulties researchers face is how to incorporate complex animal behavior and their spatially explicit movement patterns, when estimating seed dispersal shadows (Russo and Augspurger 2004). Yet, the behaviors and movements of dispersers are known to create highly structured seed deposition patterns, often with no distance relationship to the parent plant (Schupp et al. 2002). Studies on tamarins, spider monkeys, and tapirs show evidence of how these animals, through their behavior and movement patterns, are responsible for the spatial distribution of individuals for some of the plant species they disperse (Garber 1986; Fragoso et al. 2003; Russo and Augspurger 2004).

No study has yet explicitly assessed the seed shadows created by howler monkeys for particular plant species, and only one has focused on the possible implications (Bravo 2012b). However, the potential impact that howler monkeys are having through their seed dispersal on the spatial distribution of local plants is repeatedly mentioned by authors. Indeed, since the seminal study by Milton (1980), it has been suggested that seed dispersal by howler monkeys could create a patchy spatial distribution of preferred fruit-tree species. Studies reporting ranging and defecation patterns for these primates (e.g., Julliot 1996a; Andresen 2002a; Bravo 2009), together with studies quantifying seedling abundance in howler latrines (e.g., Julliot 1997; Anzures-Dadda et al. 2011; Bravo 2012b), suggest that seed dispersal by howler monkeys may have strong effects on the spatial distribution of howler-preferred plants. This constitutes a very important avenue for future research, in particular for those plant species for which howler monkeys constitute the only or main seed dispersal agent.

5.3 Implications of Howler Monkey Seed Dispersal for Plant Communities

At the plant community level, howler monkeys are considered important seed dispersers because they can disperse the seeds of many plant species from different life forms (e.g., trees, lianas, palms, and epiphytes; Tables 5.2 and 5.3). Although most studies have reported fruit diets consisting of less than 40 species (Bicca-Marques 2003), studies of *A. macconnelli* indicate that in some areas howler monkeys are able to disperse the seeds of more than 100 plant species (110 species, French Guiana: Julliot and Sabatier 1993; Julliot 1996a; 137 species, Central Amazonia: Andresen 2002a). In general, howler monkeys can feed and disperse a fewer number of plant species than other primates in pristine habitats. For instance, in Tinigua Park, during the same year of observations, red howlers fed on 52 species, while capuchins fed on 106, woolly monkeys on 137, and spider monkeys on 97 (Stevenson et al. 2000, 2002). However, the number of species dispersed depends, in part, on local tree diversity and, hence, in forests with fewer tree species or due to their smaller home range howler monkeys may disperse seeds of a small number of fruit species (Ramos-Obregon 2007). The length of the study can also affect the number of species reported in the diet of primates. Many plant species fruit every two years, while most primate research studies last one year or less. Not surprisingly, the studies reporting >100 fruit species in howler monkey diet had a duration of two years.

As already mentioned, howler monkeys, as well as other arboreal mammals and a few large birds species such as toucans, may serve as the main dispersers of large-seeded plants (>10 mm, seed length) and/or plants with hard indehiscent husks. These plants may constitute a large proportion of the total tree species richness and stem density (e.g., Sapotaceae in Central Amazonia and the Guiana Shield); therefore, by dispersing seeds of these species, howler monkeys may affect the abundance and distribution of structurally important tropical plant populations, directly impacting the structure of plant communities and forest dynamics.

Seed dispersal by howler monkeys also may have important implications for the maintenance of high tree species diversity in tropical forests. For other primate species, in particular highly frugivorous atelines, it has been shown that primate density is positively associated with the diversity of regenerating plants (Stevenson 2011). Although the effect of less frugivorous primates, such as howler monkeys, is probably less strong, the effect of these primates still remains positive in models that predict the diversity of regenerating plants (Stevenson 2011).

Howler monkeys and other primates may promote species diversity not only through effective seed dispersal, but also through the highly structured seed shadow they produce (see above). Due to their behavior and ranging patterns, the seed shadow created by howler monkeys is characterized by areas of very high seed density in latrines, which are used repeatedly over time (Julliot 1997; Bravo 2009). It has been argued that such patterns of seed dispersal will create dissemination limitation for other potential plant recruitment sites, and consequently recruitment limitation, which is defined as the failure to establish seedlings in a suitable site (Schupp et al. 2002). In turn, recruitment limitation is one of the main mechanisms that are assumed to prevent competitive exclusion by superior competitors, and thus favoring the coexistence of many plant species (see Schupp et al. 2002 and references therein). Nevertheless, much research is still needed to clearly establish the relative importance of different aspects of recruitment limitation (Terborgh et al. 2011), as well as to ascertain its role in the maintenance of high plant species richness.

5.4 Implications of Howler Monkey Seed Dispersal for Conservation and Restoration

Large-bodied, seed-dispersers have been shown to be particularly vulnerable to hunting pressure and habitat destruction, with potentially severe cascading effects for plant regeneration (Peres and Palacios 2007; Stoner et al. 2007; Wilkie et al. 2011). Studies increasingly show that such disturbances disrupt plant-animal dispersal systems, causing changes in plant recruitment, and potentially changing forest composition and structure in sites without primates and/or with lower primate population sizes (Chapman and Onderdonk 1998; Stevenson and Aldana 2008; Gonzalez-Di Pierro et al. 2011; Stevenson 2011). In this sense, understanding the long-term effects that primate disappearance and/or population declines could have on the composition and structure of plant communities represents an important challenge for ecologists, primatologists, and conservation biologists (Chapman 1989; Russo and Chapman 2011; Stevenson 2011).

In this chapter we have shown that howler monkeys can have negative effects on seed dispersal. For example, they can deposit a large number of seeds in clumps, which can result in high seed and seedling mortality. Also, in some cases, howler monkeys can act as seed predators. Nevertheless, the positive effects are more frequently reported, indicating that they play an important role in Neotropical forest regeneration due to a combination of factors: (1) they are one of the most abundant frugivorous arboreal mammals; (2) they can spend ca. 50 % of their monthly or yearly feeding time consuming fruits, swallowing most of the seeds they handle, and defecating them undamaged; (3) gut passage rarely has a negative effect on germination and often has a positive one; (4) their behavior and ranging patterns create a highly structured seed shadow, i.e., a spatially heterogeneous distribution of seeds, that may enhance plant species diversity; (5) they disperse seeds of many plant species from different life forms, including trees, lianas, palms, and epiphytes; (6) they are likely to be the main seed dispersers of certain tree species (e.g., large-seeded species and/or with indehiscent hard-husked fruits), especially in small forest fragments in which other primates are absent; and (7) their dung enriches the soil (that is commonly poor in many tropical forests), and attracts secondary seed dispersers that move the seeds to microsites with higher probability of survival and seedling establishment.

Howler monkeys not only play an important role as seed dispersers in conserved habitats, but they can also be playing a crucial role in disturbed habitats. Unlike most large Neotropical mammal species, howler monkeys are highly resilient to disturbance, being able to maintain populations in disturbed habitats, such as forest fragments, secondary forests, and some types of agroecosystems (Vulinec et al. 2006; Williams-Guillén et al. 2006; Arroyo-Rodríguez and Dias 2010; Zárate et al. 2014). For example, in a small fragment in the Orinoco basin in Colombia without other large atelines, howler monkeys were estimated to disperse approximately 40,900 g of dry weight of seeds per km^2 in 4 months (Ramos-Obregon 2007), equivalent to the dispersal rate of more frugivorous ateline primates at other sites (Stevenson 2007). Thus, it has been increasingly recognized that howler monkeys play a key role for local plant regeneration in disturbed habitats (e.g. Gonzalez-Di Pierro et al. 2011). However, in smaller and/or disturbed habitat patches, howler monkeys tend to spend a lower percentage of time feeding on fruits (Dias and Rangel-Negrin 2014) and exploit a smaller number of plant species (Bicca-Marques 2003; Cristóbal-Azkarate and Arroyo-Rodríguez 2007). This has also been found for other frugivorous primate species (e.g. *Ateles geoffroyi*; González-Zamora et al. 2009). Thus, in terms of the quantity of seeds dispersed, as well as the number of species dispersed, the role played by howler monkeys as seed dispersers at both the plant population and the plant community level appears to be lower in highly disturbed habitats. Nevertheless, the role played by these primates in such habitats will depend on the extent to which their populations are able to compensate for lost dispersal services due to the local extinction of other seed-dispersing animals and may thus be proportionally large. Such compensatory role, however, still remains to be assessed in future studies.

Howler monkeys can transport seeds among different forest types and conditions (e.g., continuous and fragmented forests, old-growth and secondary forests), contributing to secondary succession and thus aiding in the restoration of degraded habitats (e.g., Giraldo et al. 2007). Particularly relevant for forest restoration in degraded habitats is the fact that howler monkeys disperse seeds of both pioneer and old-growth forest species. Abundant dispersal of light-demanding and pioneer tree species, such as *Ficus*, *Cecropia*, *Inga*, and many liana species (Julliot 1996a; Cristóbal-Azkarate and Arroyo-Rodríguez 2007; Pouvelle et al. 2009) could favor rapid recruitment of vegetation in open areas. At the same time, dispersal of long-lived pioneer and old-growth forest species could favor the incorporation of such species in the seed and seedling bank, allowing for the continuation of succession.

Finally, soil nutrient enrichment through defecation is an important factor that may affect forest regeneration, particularly in degraded areas. Only three studies are available on this topic (Feeley 2005; Pouvelle et al. 2008; Neves et al. 2010), and all agree that howler monkeys' dung contributes considerably to the horizontal and vertical redistribution of nutrients. For example, the clumped defecation pattern of howler monkeys can enrich the soil in nutrients such as phosphorus and nitrogenous, which are important for vegetation growth (Feeley 2005). Also the physical characteristics of the soil are improved due to increased activity of the soil microbial and microfaunal communities (Neves et al. 2010). Whether the improvement of soil characteristics in defecation sites actually translates into positive effects for plants (seedling survival, establishment, growth), either in conserved or disturbed habitats, is still unknown. This is a highly promising avenue for future research.

5.5 New Directions for Future Research

Overall, we found that several aspects of seed dispersal by howler monkeys (*Alouatta* spp.) have been studied throughout their geographic range (Table 5.1), but there are some important questions that need to be addressed to improve our understanding on the importance of howler monkeys as seed dispersers. First, we found that current evidence comes exclusively from studies of eight of 14–18 howler monkey species, and therefore studies of other species are needed to accurately determine (e.g., through meta-analyses) whether there are inter-specific differences in their contribution as seed dispersers. This is likely given differences in diet found across the genus *Alouatta* (see Dias and Rangel-Negrin 2014). Second, most studies have so far focused on well-conserved forests. Thus, more research is needed in fragmented/degraded forests in order to assess, for example, if seed dispersal effectiveness can be lower in these habitats, if primate disappearance and/or population declines can negatively affect forest regeneration, and the potential compensatory role of howlers in sites lacking other dispersal agents. Third, while the quantity component of seed dispersal has received much attention, some aspects of the quality component require further research (Table 5.1). These include: (1) the effect of pulp removal (deinhibition) on seed fate, not only for defecated seeds, but also for spat and dropped seeds; (2) the effect of gut passage on the control of insect larvae present in the ingested fruits/seeds; and (3) the impact of gut passage on seedling survival and growth.

Regarding the impact of howler monkeys on the spatial distribution of plants, no study to date has yet explicitly assessed the seed shadows created by howler monkeys for particular plant species. Also, the post-dispersal seed fate is not well understood. Studies are needed to fully assess the importance of ants, dung beetles, rodents, insect predators, and fungal pathogens in determining the fate of small-seeded species dispersed by howler monkeys and other primates. Finally, more investigation is also needed to assess the differences between clumped (e.g., in latrines) and scattered seed deposition patterns on seeds/seedlings survival and plant recruitment. Also, an interesting hypothesis that needs to be tested in future research is whether seed dispersal by howler monkeys creates a patchy spatial distribution of preferred fruit-tree species, creating food gardens within the forests (Milton 1980). This is possible if seeds deposited in latrines regenerate in greater density than seeds deposited in other areas, but evidence on this topic is scarce, and it is still unclear whether the improvement of soil characteristics in latrines actually translates into positive effects for plants (seedling survival, establishment, growth).

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Chapter 6
Interactions of Howler Monkeys with Other Vertebrates: A Review

Jurgi Cristóbal-Azkarate, Bernardo Urbani, and Norberto Asensio

Abstract Understanding the way howler monkeys interact with other vertebrates has critical ecological, evolutionary, cognitive, and conservation implications. In this review, we completed an extensive search of the available data on interspecific howler encounters, including individual communications from field primatologists, in order to gain insight into how howlers share their habitat and interact with other species, the pressure that predators and potential competitors may exert on them, and the potential benefits and costs that howlers may represent for other species. Howlers interacted with several vertebrates throughout their distribution range, including birds and mammals, particularly capuchin monkeys, spider monkeys, and coatis. A great deal of these interactions occurred in fruiting trees and were, in general, pacific, although howlers were frequently harassed by other monkeys, and they were observed behaving aggressively with coatis and birds. Howlers were also targets of multiple predators. Among them, large felids and harpy eagles are ranked as the prevalent natural predators of this primate taxon. Finally, evidence indicates that the transformation of natural habitats can have important effects on the interaction patterns of howlers with other species. Fragmentation can increase competition for food and in extreme cases even force them to predate on eggs to compensate for the reduction in food availability. On the other hand, natural predators are often absent in anthropogenic landscapes, but there are increasing reports of predation by dogs and coyotes, which could potentially have very negative effects on the already highly threatened populations of howler monkeys in fragmented landscapes.

Resumen Comprender cómo los monos aulladores interaccionan con otros vertebrados tiene importantes implicaciones ecológicas, evolutivas, cognitivas y de

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conservación. En esta revisión, realizamos una búsqueda extensiva de la información disponible, además de comunicaciones con primatólogos de campo, en torno a encuentros interespecíficos de aulladores. Nuestro objetivo es elucidar cómo los monos aulladores comparten su hábitat e interactúan con otras especies, la presión que potenciales depredadores y competidores ejercen sobre ellos, así como los potenciales beneficios y detrimentos que tienen los aulladores en relación a sus vinculaciones con otras especies. Los monos aulladores interactúan con múltiples vertebrados a lo largo de su distribución, entre ellos aves y mamíferos, en particular, monos capuchinos, monos araña y coatis. Gran parte de esas interacciones ocurrieron en árboles frutales, siendo en su mayoría interacciones pacíficas, mientras que en otras ocasiones fueron agredidos por otros monos. Igualmente, los aulladores se comportaron agresivamente con aves y coatis. Los monos aulladores son también presa de varios depredadores. Entre ellos, felinos de gran tamaño y águilas arpía serían los principales depredadores naturales de este taxón de primates. Para finalizar, existe evidencia de que la transformación de los hábitats naturales puede tener repercusiones importantes sobre los patrones de interacción de los aulladores con otras especies. Puede incrementar la competencia por el alimento, y en casos extremos incluso forzar a los aulladores a depredar huevos a fin de compensar la reducción en la disponibilidad de alimento. Por otra parte, los depredadores naturales de los aulladores regularmente no están presentes en los paisajes antropogenizados, pero existe un número creciente de observaciones de deprecación por perros y coyotes, los cuales podrían tener un efecto muy negativo sobre las ya altamente amenazadas poblaciones de aulladores en paisajes fragmentados.

Keywords *Alouatta* • Interspecific interactions • Predation • Platyrrhine • Neotropics

6.1 Introduction

Interactions between species are thought to be a major force structuring ecological communities (e.g., species distribution and abundance) as they affect phenotypic divergence, speciation processes, and survival. Consequently, they play a critical role in natural selection, niche separation, metapopulation dynamics, cognition, and community structure (Schoener 1983; Bengtsson 1989; Isbell 1994; Boinski et al. 2000; Holekamp 2006).

From the perspective of fitness effects, interspecific interactions can be classified as neutralism, commensalism, mutualism, competition, amensalism, and predation (Wallace and Mitchell 1989). With the exception of predation, identifying the nature of interspecific interactions is often difficult due to the complexity of quantifying their fitness costs. On the other hand, the nature of biological interactions between species is variable, so that two species may interact differently under different circumstances. For example, predators may prey or not on a particular species depending on the availability of other preferred prey species. In addition, potential competition between species at the same trophic level of an ecosystem may increase if the availability of a resource, such as food or water used by the two species, decreases due to seasonal fluctuations or habitat transformation.

Howlers (*Alouatta* spp.) have the broadest distribution among the Neotropical primates, with 12 recognized species (Cortés-Ortiz et al. 2003) inhabiting the tropical and subtropical forests of the continent from northern Argentina to southern Mexico (Cortés-Ortiz et al. 2003). Consequently, the genus shares its habitat with a great number and diversity of vertebrates with which they are likely to interact directly or indirectly. Although they are regarded as the most folivorous Neotropical primates (Milton 1980), howlers are partly frugivorous, and thus their diet may overlap considerably with other species, particularly other primates, creating the possibility for food competition (e.g. Klein and Klein 1973; Mendes-Pontes 1997; Dias and Strier 2000; Asensio et al. 2007).

One way of inferring the nature of interspecific relationships is from direct observations of the way species behave in the presence of one another. However, the generally low rates of interactions that howlers display (Neville et al. 1988) have made a systematic analysis difficult, and little is known in this regard.

In this review we conducted an extensive search of the available data in the existing literature, and a survey of field primatologists regarding direct observable interactions between howlers and other vertebrate species. We also included indirect evidence of howler predation (i.e., remains in predator feces or nests) as these episodes are seldom witnessed due to their rarity, short duration, and the tendency of predators to avoid humans (Cheney and Wrangham 1987; Isbell 1994; Di Fiore 2002; Urbani 2005; Ferrari 2009). With this review we aim to gain insight into the way howlers share their habitat with other vertebrate species, the pressure that predators and potential competitors may exert on them, and the conditions that modulate these relationships.

6.2 Data Survey

We conducted an extensive search of published information regarding interspecific interactions. Additionally, we conducted a survey using a semi-structured questionnaire directed to primatologists doing research in the Neotropics. This was composed of nine questions focused on understanding the species with which howlers interacted, the characteristics of the interactions, the context, and the characteristics of the habitat in which they occurred.

We considered an interspecific interaction as any behavior that howlers directed to a different vertebrate species, or vice versa, independently of the result of that behavior. In addition, behaviors such as simultaneous feeding, traveling and resting, or alternate feeding between howlers and other species were also considered as interactions as they involved direct space sharing, and thus the behavior of one species was likely to be affected by the others.

With all the individual reports we constructed a database that included: researcher name, study site, country, howler species, age/sex of individuals involved in the interaction (if reported), directionality of interaction (howler to other species, other species to howler, or simultaneous), type of interaction, and context. Interactions were classified into different kinds: agonistic, approach, play, grooming, simultaneous feeding, simultaneous resting, simultaneous traveling, and alternate feeding. Agonistic behaviors were further divided into high intensity aggression or overt attacks and low intensity agonistic interactions. Overt attacks were characterized by physical contact between species in which biting, grabbing and pulling behaviors occurred, whereas low intensity agonistic interactions were restricted to vocalization, rapid approaches, signs of arousal (e.g., piloerection), and threats (e.g., branch shaking and breaking) without physical contact. Simultaneous feeding and resting occurred every time two or more species fed or rested in the same tree at the same time, while alternate feeding occurred when one species arrived at a tree and began to feed after the other departed within a 5-min period. Simultaneous traveling occurred when the two species traveled together.

We collected 499 individual reports for wild vertebrates: 406 from 28 published studies and 93 from personal communications of 20 field researchers. These included: Norberto Asensio (N.A.), Julio Cesar Bicca-Marques (J.C.B.M.), Xyomara Carretero (X.C.), Carlos Andrés Chica-Galvis (C.C.G.), Lisa Corewyn (L.C.), Anthony Crease (A.C.), Carolyn Crockett (C.C.), Linda M. Fedigan (L.M.F.) (cited in Chapman 1986), Denisse Goffard (D.G.), Anamélia de Souza Jesus (A.S.J.), Carolina Gómez-Posada (C.G.P.), Shawn Lehman (S.L.), Miguel Marquina (M.M.), Tracy McKinney (T.M.), Katherine Milton (K.M.), Sylvana Peker (S.P.), Gilberto Pozo-Montuy (G.P.M.), Melissa Raguet-Schofield (M.R.S.), Germán Rios (G.R.), and Bernardo Urbani (B.U.) (Table 6.1). The sources consulted in this work did not always provide or could not always recall the precise frequency and context of the interspecific interactions, so we did not include their observations in Tables 6.2, 6.3, and 6.4, but we considered them separately. For the same reason, we did not include the indirect evidence of predation from felid scats or data from eagles' nests in Tables 6.2, 6.3 and 6.4.

Overall, howlers interacted with 43 different wild vertebrate species (Tables 6.1–6.4). This included 11 primate species, 6 mammalian predator species, 5 nonpredator mammals, 12 raptors, 7 nonraptor bird species, and 2 reptile species. In addition, there was evidence of interaction with another five domestic vertebrates.

Reports originated from 44 different sites covering Argentina, Bolivia, Brazil, Colombia, Costa Rica, French Guiana, Guatemala, Guyana, Mexico, Nicaragua, Panama, Peru, Suriname, and Venezuela, comprising a total of 10 howler taxa: ursine (*Alouatta arctoidea*), red-handed (*A. belzebul*), black-and-gold (*A. caraya*), brown (*A. guariba*), Guianan red (*A. macconnelli*), mantled (*A. palliata*), Central American black (*A. pigra*), Purús red (*A. s. puruensis*), Bolivian red (*A. sara*), and red (*A. seniculus*) howlers (Tables 6.1, 6.2, 6.3, and 6.4; Fig. 6.1).

Table 6.1 Reported vertebrate species that interact with howler monkeys (see Fig. 19.1 for locations)

Vertebrate class	Vertebrate species	Howler species	Habitat	Country	Reference
Primates	*Ateles belzebuth*	*A. macconnelli*	Continuous	Brazil	Mendes-Pontes (1997)
		A. sara	Fragment	Colombia	Klein and Klein (1973)
	Ateles geoffroyi	*A. palliata*	Continuous, Fragment	Mexico, Panama	N.A., K.M.
		A. pigra	Fragment	Mexico	G.P.M
	Ateles paniscus	*A. macconnelli*	Continuous	French Guiana	Simmen (1992)
	Brachyteles hypoxanthus	*A. guariba*	Fragment	Brazil	Mendes (1989), Dias and Strier (2000), Bianchi and Mendes (2007)
	Cebus capucinus	*A. palliata*	Continuous, Island	Costa Rica, Nicaragua, Panama	B.U, K.M., N.A., M.S.R., T.M., Phillips (1995), Rose et al (2003)
		A. seniculus	Fragment	Colombia	C.A.C.G., C.G.P.,
	Cebus olivaceus	*A. macconnelli*	Riparian forest	Venezuela, French Guiana	C.C., S.L., Mendes-Pontes (1997), Lehman (2000)
	Sapajus apella	*A. seniculus*	Fragment	Colombia	X.C.
		A. macconnelli	Continuous	French Guiana	J.C.B.M., Richard-Hansen and Bello (1998), Lehman (2000)
		A. s. puruensis	Continuous	Brazil	Haugaasen and Peres (2009)
	Sapajus libidinosus	*A. s. puruensis*	Fragment	Bolivia	D.G.
	Sapajus nigritus	*A. guariba*	Fragment	Brazil	Mendes (1989)
	Saimiri sciureus albigena	*A. seniculus*	Fragment	Colombia	C.G.P., X.C.
	Saimiri sciureus sciureus	*A. macconnelli*	Continuous	French Guiana	Lehman (2000)
	Saimiri ustus	*A. s. puruensis*	Continuous	Brazil	Haugaasen and Peres (2009).

(continued)

Table 6.1 (continued)

Vertebrate class	Vertebrate species	Howler species	Habitat	Country	Reference
Mammalian predators	*Canis familiaris*	*A. caraya*	Fragment	Brazil	J.C.B.M
		A. palliata	Fragment	Nicaragua	M.R.S.
		A. pigra	Fragment	Mexico	G.P.M.
		A. seniculus	Fragment	Colombia	C.G.P., X.C.
		A. arctoidea	Riparian forest	Venezuela	Braza (1980)
	Canis latrans	*A. pigra*	Fragment	Mexico	Pozo-Montuy and Serio-Silva (2007)
	Eira barbara	*A. belzebul*	Island	Brazil	Camargo and Ferrari (2007)
		A. palliata	Fragment	Mexico, Panama	Phillips (1995), Asensio and Gómez-Martín (2002)
	Felis catus	*A. caraya*	Fragment	Brazil	A.S.J.
	Puma yagouaroundi	*A. caraya*	Island	Argentina	S.P.
	Panthera onca	*A. palliata*	Zoo	Mexico	Cuarón (1997)
Other mammals	*Bos taurus*	*A. pigra*	Fragment	Mexico	G.P.M.
	Choloepus didactylus	*A. macconnelli*	Island	Guyana	Richard-Hansen and Bello (1998)
	Didelphis spp.	*A. palliata*	Fragment	Mexico	N.A.
Other mammals	*Nasua narica*	*A. caraya*	Island	Argentina	S.P.
		A. palliata	Fragment, Anthropogenic	Costa Rica, Mexico	L.C., Asensio et al. (2007)
	Procyon lotor		Anthropogenic	Costa Rica	L.C.
	Sciurus yucatanensis	*A. pigra*	Fragment	Mexico	G.P.M.
	Sus scrofa domesticus	*A. pigra*	Fragment	Mexico	G.P.M.
Raptors	*Busarellus nigricollis*	*A. caraya*	Continuous	Brazil	S.P.
	Buteogallus urubitinga	*A. arctoidea*	Riparian forest	Venezuela	Braza (1980)
	Caracara plancus	*A. caraya*	Anthropogenic	Brazil	Calegaro-Marques (1992)
		A. palliata	Anthropogenic	Costa Rica	McKinney (2009)
	Cathartes aura	*A. palliata*	Island	Panama	Young (1982)
	Coragyps atratus	*A. caraya*	Island	Argentina	S.P.
		A. palliata	Fragment	Panama	N.A.
		A. seniculus	Fragment	Colombia	G.R.

(continued)

Table 6.1 (continued)

Vertebrate class	Vertebrate species	Howler species	Habitat	Country	Reference
	Geranospiza caerulescensa	*A. caraya*	Island	Argentina	S.P.
	Harpia harpyja	*A. arctoidea*	Continuous	Venezuela	M.M., Urbani et al. (2012)
		A. belzebul	Continuous	Brazil	Ferrari (2009)
		A. macconnelli	Continuous	Venezuela	A.C.
		A. palliata	Island	Panama	Touchton et al. (2002)
		A. s. puruensis	Continuous	Peru, Brazil	Eason (1989), Peres (1990), Sherman (1991)
	Milvago chimachima	*A. arctoidea*	Riparian forest	Venezuela	Braza (1980)
	Morphnus guianensis	*A. macconnelli*	Island	French Guiana	Julliot (1994)
	Otus choliba	*A. caraya*	Fragment	Brazil	Calegaro-Marques (1992)
	Spizaetus tyrannus	*A. guariba*	Fragment	Brazil	Miranda et al. (2006)
	Large eagle	*A. macconnelli*	Continuous	Brazil	Mendes-Pontes (1997)
		A. guariba	Fragment	Brazil	Mendes (1989)
	Medium-sized raptor	*A. caraya*	Island	Argentina	S.P.
Non-raptor	*Aratinga pertinax*	*A. arctoidea*	Riparian forest	Venezuela	Braza (1980)
Birds	*Crax alector*	*A. macconnelli*	Continuous	French Guiana	Richard-Hansen and Bello (1998)
	Cyanocorax sp.	*A. caraya*	Fragment	Argentina	S.P.
	Furnarius rufus	*A. caraya*	Fragment	Brazil	Calegaro-Marques (1992)
	Gallus gallus	*A. caraya*	Fragment	Brazil	Bicca-Marques et al. (2009)
	Pitangus sulphuratus	*A. arctoidea*	Riparian forest	Venezuela	Braza (1980)
	Ramphastos sulfuratus	*A. palliata*	Fragment,	Mexico	N.A.
	Unidentified columbiforme	*A. caraya*	Fragment	Brazil	Calegaro-Marques (1992)
Reptiles	*Boa constrictor*	*A palliata*	Fragment	Costa Rica	L.M.F. (in Chapman 1986)
		A. s. puruensis	Fragment	Brazil	Quintino and Bicca-Marques (2013)
	Ctenosaura similis	*A. palliata*	Anthropogenic	Costa Rica	L.C.
	Iguana iguana	*A. pigra*	Fragment	Mexico	G.P.M

Table 6.2 Interspecific interactions initiated by howler monkeys

	Alternating feeding	Approach	Low intensity agonistic	High intensity agonistic	Play	Egg inspection	Egg predation
Primate							
Ateles panicus	3 ff		2[c]				
Cebus spp.				1[c]ff; 14u	1[d] r; 6u 6u		
Sapajus sp.					1[d]		
Mammalian predators							
Eira barbara				1[a]			
Puma yagouaroundi			1[a]				
Other mammals							
Choloepus didactylus					1* r		
Didelphis sp.				1[a] r			
Nasua narica	8[d]ff	1[d] r;1[d] fu	1[c]fl; 1[c]	1[c] ff			
Procyon lotor				1[a] t			
Raptors							
Busarellus nigricollis			1[a]				
Buteogallus urubitinga		1[a]					
Cathartes aura				5[d]			
Coragyps atratus		3[a]	2[a]				
Geranospiza caerulescens			2[a]				
Milvago chimachima			1[a]				
Morphnus guianensis			1[a]				
Otus choliba		3[a]					
Medium-sized raptor			2[a]				
Non-raptor birds							
Aratinga pertinax		1[a]					
Crax alector					1[a]		
Furnarius rufus		1[b]				1[d]	

(continued)

Table 6.2 (continued)

	Alternating feeding	Approach	Low intensity agonistic	High intensity agonistic	Play	Egg inspection	Egg predation
Ramphastos sulfuratus	1[c]ff						
Gallus gallus		1[b]				1[d]	19
Non-raptor birds							
Unidentified bird							2
Unidentified columbiforme		1[a]					
Reptile							
Boa constrictor				1[d]			

Letters represent both the result of the interaction and the context in which they occurred
The context of the interaction is only provided for those species whose diets overlap with the diet of howler monkeys
1. Result of the interaction: [a]displacement, [b]agonistic response, [c]supplanting feeding, [d]no effect.
2. Context of the interaction: *ff* feeding on fruit, *fl* feeding on leaves, *fu* feeding on unidentified items, *r* resting, *t* traveling, *u* unspecified

6.2.1 Interactions with Other Primate Species

6.2.1.1 Capuchin Monkeys (Genera *Cebus* and *Sapajus*)

Capuchin monkeys (*Cebus* spp. and *Sapajus* spp.) were the primates with whom howlers interacted the most (254 interactions in total, Tables 6.2–6.4). The majority of these reports derive from Rose et al. (2003) in Santa Rosa and Lomas Barbudal, Costa Rica. According to the authors, the most common type of interactions were attacks by white-faced capuchins on mantled howlers (40 %). On several occasions, these attacks inflicted severe wounds to the latter, especially in Lomas Barbudal. B.U. also observed a juvenile white-faced capuchin throwing branches at a mantled howler twice. In eight occasions capuchins aggressively supplanted howlers from feeding trees (T.M., M.R.S., X.C., N.A.), a behavior also observed by J.C.B.M. between *S. apella* and *A. macconnelli* in French Guiana. However, on one occasion, M.R.S. saw a group of mantled howlers chasing a male capuchin monkey that had entered a fruit tree where howlers were feeding, and K.M. also reported mantled howlers acting aggressively towards white-faced capuchin monkeys in Barro Colorado, Panama.

Rose et al. (2003) did not relate the agonistic interactions between capuchin and mantled howlers to any particular context, but rather to the aggressive temperament of capuchins. Interestingly, the intensity of the aggression varied between their two study-sites in western Costa Rica, Lomas Barbudal and Santa Rosa being highest in Lomas Bardubal, where densities of howlers were also the highest. The lower

Table 6.3 Interspecific interactions not initiated by howler monkeys

	Alternating feeding	Approach	Grooming solicitation	Play	Low intensity agonistic	High intensity agonistic	Contact	Predation attempt	Predation	Vocalization
Primates										
Ateles sp.	1^{d}ff		1^{e} fu;1^{d}fu	1^{d}ff	1^{b}ff	8^{b}ff; 3^{d} ff				
Brachyteles sp.	4^{b}fu	1^{a}			7^{a}t, 2^{a}; 3^{a}r; 16^{b}u; 5^{f}u					
Cebus sp.	1^{d}ff			1^{d} r; 1^{c}r; 6u	3^{b}ff; 4^{b}u	179 u				
Saimiri spp.					14^{b}					5^{d}t
Sapajus sp.	1^{d}ff				4^{b}u; 2^{b}fu					
Mamalian predator										
Eira barbara								1^{ac}		
Other mammal										
Sciurus granatensis		1^{a}								
Raptors										
Caracara plancus								1g		
Geranospiza caerulescens							1^{d}			
Harpia harpyja								1^{c}	1	
Large raptor		1^{b}						1^{d}		
Non-raptor birds										
Pitangus sulphuratus						1^{a}				
Reptile										
Boa constrictor									1	
Iguana iguana					1^{a}fl					
Ctenosaura similis		1^{a} r								
Livestock										
Canis familiaris								2	3	

The context of the interaction is only provided for those species whose diets overlap with the diet of howler monkeys.

Letters represent both the result of the interaction and the context in which they occurred

1. Result of the interaction: ^{a}displacement, ^{b}supplanting feeding, ^{c}howling, ^{d}no effect,^{c}agonistic response,^{e}grooming received, ^{f}infant play, ^{g}low intensity aggression
2. Context of the interaction: *ff* feeding on fruit, *fl* feeding on leaves, *fu* feeding on unidentified items, *r* resting, *t* traveling, *u* unspecified

Table 6.4 Simultaneous interspecific interactions between howler monkeys and other vertebrate species

	Feeding	Low intensity agonistic	High intensity agonistic	Play	Resting	Traveling	Vocalization
Primates							
Ateles sp.	1ff; 2; 14u	1u		5ffu	1u	2u	
Brachyteles sp.				5u			
Cebus sp.	13u	1u	1u	1tu	3u		
Saimiri spp.	2ff;12u			1u			
*Sapajus*sp.	1ff	3u		1u			
Cebus sp. + *Saimiri* spp.	2u				2u		
Sapajus sp.+*Saimiri* spp.	1fu						
Other mammals							
Nasua narica	9ff						
Raptors							
Geranospiza caerulescens						1u	
Non-raptor birds							
Cyanocorax sp.							1u

Context of the interaction: *ff* feeding on fruit, *fl* feeding on leaves, *fu* feeding on unidentified items, *r* resting, *t* traveling, *u* unspecified
The context of the interaction is only provided for those species whose diets overlap with the diet of howler monkeys

intensity of aggression in Santa Rosa is consistent with the reports of N.A. at the same site, McKinney (2009) at Refugio de Vida Silvestre Curú also in Costa Rica, *S. apella* at San Martín Meta in Colombia (X.C.), and *S. nigritus* at Caratinga, Brazil (Mendes 1989).

Mantled howlers and capuchins fed simultaneously on 18 occasions (Lehman 2000; Rose et al. 2003). X.C., C.G.P., C.C., K.M., and Haugaasen and Peres (2009) also observed these primates feeding peacefully in the same tree occasionally. South American howlers (*A. sara* and *A. macconnelli*) rested peacefully in the same tree with capuchins in three instances (D.G.; Mendes-Pontes 1997). On one occasion, Bolivian red howlers feeding on fruits went into inactivity immediately after a group of tufted capuchins (*S. libidinosus*) arrived to eat fruit from the same tree, and howlers did not resume eating until the capuchins left the tree (D.G.). Immature mantled howlers played with capuchins on 13 occasions (X.C.; T.M.; Rose et al. 2003). C. Julliot (in Richard-Hansen and Bello 1998) observed a juvenile Guianan red howler playfully pulling the tail of an adult capuchin, and S.L. saw a juvenile wedge-capped capuchin touching the tail of an adult howler.

Fig. 6.1 Location of the interspecific interactions of *Alouatta* spp. The locations indicated in the map are: ^{1}Los Tuxtlas (N.A.; Asensio and Gómez-Martín 2002, Asensio et al. 2007); ^{2}Balacán (G.P.M.); ^{3}Macuspana (G.P.M.); ^{4}Punta Laguna (N.A.); ^{5} Mayan Biosphere Reserve (Novack et al. 2005); ^{6}Isla de Ometepe (M.R.-S.); ^{7}Santa Rosa (N.A., Rose et al. 2003); ^{8}Lomas Barbudal (Rose et al. 2003); ^{9}Refugio de Vida Silvestre Curú (McKinney 2009); ^{10}La Pacífica (L.C.); ^{11} La Suerte Biological Station (BU); ^{12}Corcovado National Park (Chinchilla 2007); ^{13}Barro Colorado (Touchton et al. 2002; Phillips 1995; Izor 1985; Young 1982); ^{14}Calcedonia (C.G.-P.; G.R.); ^{15}Santuario de Flora y Fauna Otún Quinbaya (C.G.P.); ^{16}Valle de Yocoto (C.A.C.); ^{17}San Martín del Meta (C.A.C.); ^{18}Tinigua National Park (X.C.); ^{19}La Macarena (Klein and Klein 1973); ^{20}Hato Masaguaral (C.C.); ^{21}Guatopo National Park (M.M); ^{22}Guarapiche River (Urbani et al. 2012); ^{23}Imataca Mountain Range (Álvarez-Cordero 1996); ^{24}Guri Lake (Peetz et al. 1992); ^{25}Berbice River (S.L.); ^{26}(Lehman 2000); ^{27}Central Guyana (Richard-Hansen and Bello 1998); ^{28}Rupununi River (Retting 1978); ^{29}Central Suriname (Ford and Boinski 2007); ^{30}Central Amazon (Haugaasen and Peres 2009); ^{31}Nouragues Station (Julliot 1994; Simmen 1992); ^{32}Northeastern Amazon (Ferrari 2009); ^{33}Tucurui Reservoir (Camargo and Ferrari 2007); ^{34}Sena Madureira (Peres 1990); ^{35}Manú National Park (Sherman 1991; Eason 1989); ^{36}Fazenda Acurizal (Schaller 1983); ^{37}Santa Cruz (D.G.); ^{38}Caratinga Biological Station (Bianchi and Mendes 2007; Bianchi 2001; Dias and Strier 2000; Mendes 1989); ^{39}Chacará Payrequé (Miranda et al. 2006); ^{40}Isla Brasileira (S.P.); ^{41}San Cayetano (S.P); ^{42}Estancia Casa Branca (Bicca-Marques et al 2009; Calegaro-Marques 1992; A.S.J.); ^{43}Santa Elena-Ikabarú Road (A.C.); ^{43}Hato El Frío (Braza 1980)

Phillips (1995) observed a group of mantled howlers and white-faced capuchins directing threats and vocalizations to a tayra (*Eira* sp.). C.A.C.G. reported a similar situation in Valle de Yotoco, Colombia, but this time vocalizations from *A. seniculus* and *C. capucinus* were directed towards a human observer.

6.2.1.2 Spider Monkeys (Genus *Ateles*)

White-bellied spider monkeys (*A. belzebuth*) fed simultaneously with red howlers on 16 occasions (Klein and Klein 1973; Mendes-Pontes 1997). On four occasions, spider monkeys tried to aggressively supplant howlers, but they were unsuccessful (G.P.M.; Klein and Klein 1973). However, they aggressively displaced howlers from feeding trees on nine occasions (Klein and Klein 1973; N.A.), and howlers were once seen waiting for a group of spider monkeys to leave a fruiting tree before they could reenter and eat (Klein and Klein 1973). K.M. also observed that mantled howlers actively retreated when Geoffroy's spider monkeys approached them, and that this usually occurred in fruiting trees. Contrary to this pattern of howlers avoiding spider monkeys or being displaced by them in feeding contexts, Simmen (1992) observed that howlers (*A. macconnelli*) in French Guiana displaced spider monkeys (*Ateles paniscus*) twice, and in other three occasions spider monkeys avoided howlers by leaving the tree or waiting in the vicinity until howlers left to enter the food tree. However, it should be noted that howler monkeys clearly outnumbered spider monkeys in Simmen's observations; whereas the group of howlers was of eight, spider monkeys were only two individuals.

Immature red howler and white-bellied spider monkeys played together on five instances (Klein and Klein 1973), and an infant Geoffroy's spider monkey was observed touching the tail of a male Central American black howler once (N.A.). Klein and Klein (1973) reported that in two occasions female white-bellied spider monkeys solicited grooming from red howlers (in one case successfully). They also saw solitary howler males following subgroups of spider monkeys twice.

According to Klein and Klein (1973) the great majority of interactions between howlers and spider monkeys occurred in fruiting trees, which is supported by observations of N.A., K.M., Simmen (1992), and Mendes-Pontes (1997).

6.2.1.3 Woolly Spider Monkeys (Genus *Brachyteles*)

Interactions between brown howlers (*A. guariba*) and northern woolly spider monkeys (*B. hypoxanthus*) have only been reported by Mendes (1989) and Dias and Strier (2000) in Brazil (Tables 6.1–6.4). Mendes (1989) observed woolly spider monkeys displacing howlers from feeding trees in four occasions, and in one instance from a non-feeding tree. Also, according to the author, two woolly spider monkey males chased away a female howler from his study group. Similarly, the behavior of northern woolly spider monkeys towards howlers reported by Dias and Strier (2000) was always agonistic, although never involved overt attacks. On 16 occasions these interactions resulted in howlers being displaced from feeding trees, but agonistic interactions also occurred while both species were resting ($n=3$) and traveling ($n=7$). In five instances, woolly monkeys reacted aggressively against brown howlers after immature individuals of both species played together.

6.2.1.4 Squirrel Monkeys (Genus *Saimiri*)

Squirrel monkeys (*Saimiri* spp.) were observed supplanting red howlers from feeding trees on 14 occasions (X.C.; Table 6.3). Squirrel monkeys also fed simultaneously with red howlers on other 14 occasions, and immature individuals of both species played together once (X.C.). C.G.P. observed a male *S. sciureus* vocalizing and displaying aggressively to a group of red howlers (*A. seniculus*) on five occasions, but howlers never reacted to this. Howlers interacted simultaneously with squirrel monkeys and capuchins. On those occasions they were either feeding ($n=2$) or resting ($n=2$) (Mendes-Pontes 1997; Lehman 2000; X.C.).

6.2.2 Interactions with Non-primate Mammals

6.2.2.1 Predators

Dogs attacked howlers on four occasions in fragmented landscapes in Colombia and Nicaragua (C.G.P., M.R.S.), Raguet-Schofield (2008) and in one occasion in the *Llanos* of Venezuela (Braza 1980) (Table 6.3). On two occasions howlers were able to escape (once with the help of people), but they were killed on the other two occasions. Pozo-Montuy and Serio-Silva (2007) reported the attack of a coyote (*Canis latrans*) on an immature *A. pigra* that was traveling on the ground between forest fragments, and G.P.M. also reported frequent attacks of dogs over *A. pigra* in similar circumstances in Mexico, and X.C. in Colombia. Probably for this reason, J.C.B.M., in Brazil, observed that *A. caraya* avoided coming to the forest floor in the presence of dogs, but not when other domestic animals were nearby. At the same study site, A.S.J. observed that a group of howlers only descended to drink from a water source situated on the ground after a domestic cat (*Felis catus*) had left the place.

Asensio and Gómez-Martín (2002) reported a predation attempt by tayras (*Eira barbara*) on mantled howlers, which was successfully defended by group members, and Camargo and Ferrari (2007) reported two attacks of tayras on red-handed howlers. In the first attack, a tayra bit the lower dorsum of an infant howler that was hanging from a liana, 1.5 m above the ground, while a second tayra watched it from the ground. In the second case, four tayras attacked a subadult female howler on the ground. In both cases, the attacks were interrupted by the presence of the researchers and the howlers were able to escape. Camargo and Ferrari (2007) observed howlers howling toward nearby tayras, a behavior also reported by Phillips (1995) in Panama. However, in the case observed by Phillips (1995), mantled howlers vocalized towards a tayra together with white-faced capuchins.

S.P. reported black-and-gold howlers vocalizing aggressively to a jaguarundi (*Puma yagouaroundi*). However, the only report of a felid actually preying on a howler comes from Cuarón (1997), who observed a jaguar (*Panthera onca*) attacking a howler monkey that entered its enclosure at a zoo (ZOOMAT) in Tuxtla Gutierrez, Chiapas, Mexico. Besides this report, all information regarding howler predation by felids is indirect, and mostly occurred in continuous forests of southern Brazil (Miranda et al. 2005; Bianchi and Mendes 2007; Ludwig et al. 2007), Guatemala (Novack et al. 2005), and Costa Rica (Chinchilla 2007). Traces of howlers (bone fragments, hair, nails, and teeth) were found in 4 % ($n=22$) and 2.6 % ($n=76$) of feces of jaguars (*Panthera onca*) (Chinchilla 2007; Novack et al. 2005, respectively), 18 % ($n=11$), 12.4 % ($n=145$), and 50 % ($n=8$) of feces of pumas (*Puma concolor*) (Chinchilla 2007; Novack et al. 2005; Ludwig et al. 2007, respectively), and in 20 % of ocelot feces (*Leopardus pardalis*) (Bianchi and Mendes 2007). This corresponds to 4.4 % and 2.9 % of the biomass consumed by jaguars in a year (Chinchilla 2007 and Novack et al. 2005, respectively), and 19.6 and 8.7 % of the biomass consumed by pumas in a year (Chinchilla 2007 and Novack et al. 2005, respectively). It is important to note that Novack et al. (2005) were not able to distinguish between howler and spider monkey body remains. Miranda et al. (2005) also confirmed the presence of howler body parts in feces of ocelots. Peetz et al. (1992) inferred that jaguars preyed on howlers after finding five howler carcasses in an area frequented by this felid in the Venezuelan Guayana. Finally, Braza (1980) reported hairs of howlers in feces of ocelots in the Venezuelan *llanos.*

6.2.2.2 Non-predators

Reports of interactions of howlers with other non-predator mammalian species were mostly restricted to coatis (*Nasua narica*). These interactions included nine and eight episodes of simultaneous and alternate fruit feeding respectively (coatis feeding after mantled howlers) (Asensio et al. 2007), two approaches of black-and-gold howler to coatis (S.P.) (while feeding and resting), two low intensity agonistic interactions (L.C.; S.P.) (one while feeding on leaves), and one overt attack of a male adult mantled howler over a coati in a fruiting tree (Asensio et al. 2007). N.A. also observed an overt attack of an adult male mantled howler over an opossum (*Didelphis* sp.), and L.C. of a male and female mantled howler on a raccoon (*Procyon lotor*). Richard-Hansen and Bello (1998) observed an adult male Guianan red howler using a stick to, softly but repeatedly, hit a two-toed sloth (*Choloepus didactylus*). The last three episodes occurred while howlers where resting. Similarly, G.P.M. observed immature Central American black howlers chasing playfully squirrels that were feeding in the same fruit tree.

Finally, Central American black howlers have been observed interacting with pigs and cows in a fragmented landscape of Mexico (G.P.M.; www.vozsaraguato.blogspot.com). These episodes were pacific and occurred when howlers descended to the ground to travel from one forest fragment to another (Fig. 22.3). These interactions included immature howlers touching the cows, or brief chases of pigs and cows over howlers. Braza (1980) reported that ursine howlers showed certain avoidance for cows and horses (*Equus ferus caballus*), as they tended to reach the upper parts of the trees when the two species occurred nearby while using live fences (i.e., several strands of barbed wire held up by a line of trees); however, no contact or evident interaction was observed.

6.2.3 Interactions with Birds

6.2.3.1 Raptors

On 14 occasions, mantled howlers displayed low intensity agonistic behavior to black vultures (*Coragyps atratus*) (N.A.; G.R.; S.P.), a small owl (*Otus choliba*) (Calegaro-Marques 1992), three medium-sized raptors (*Busarellus nigricollis*, *Geranospiza caerulescens* and an unidentified medium-sized raptor) (S.P.), a crested eagle (*Morphnus guianensis*) (Julliot 1994), a yellow-headed caracara (*Milvago chimachima*) (Braza 1980), and a black hawk-eagle (*Spizaetus tyrannus*) (Miranda et al. 2006). On all occasions, the raptor flew away when approached by or vocalized to by the howlers. Young (1982) reported five episodes of intense howling and approaches of mantled howlers to turkey vultures (*Cathartes aura*), which he interpreted as competition for sunbathing sites. Braza (1980) reported that ursine howlers displaced turkey vultures and one black hawk (*Buteogallus urubitinga*). Miranda et al. (2006) and Eason (1989) reported unsuccessful howler predation attempts by five black hawk-eagles (*Spizaetus tyrannus*) and a harpy eagle (*Harpia arpyja*), respectively. In another report, brown howlers moved away after the approach of a falconid (Mendes 1989).

Successful predations by harpy eagles (Fig. 6.2) have been reported on 12 occasions (A.C.; M.M.; Peres 1990; Sherman 1991; Touchton et al. 2002; Ferrari 2009; Urbani et al. 2012), and by a large eagle (probably a harpy eagle) once (Mendes-Pontes 1997). McKinney (2009) observed what seemed to be a predation of two crested caracaras (*Caracara plancus*) on an infant mantled howler in Costa Rica. However, Calegaro-Marques (1992) in Brazil observed a group of *A. caraya* approaching inquisitively a crested caracara, a behavior that suggests howlers did not recognize it as a potential predator.

Besides direct observations of harpy eagles preying on howlers, remains of *A. macconnelli* and *A. palliata*, including postcranial elements, have been identified inside harpy eagle nests located in the Guiana Shield and Panama, respectively (Izor 1985; Retting 1978; Álvarez-Cordero 1996; Ford and Boinski 2007). Of these studies, only Retting (1991) provides information regarding the frequency of howler remains. According to the author, of a total of 57 captured individuals, only one was a howler monkey. Ford and Boinski (2007), on the other hand, report that harpy eagles prefer pitheciines and capuchins over howlers.

The observations of harpy eagles (or similar raptors) predating on howlers occurred in continuous forest (A.C., M.M., Eason 1989; Peres 1990; Sherman 1991; Mendes-Pontes 1997; Ferrari 2009; Urbani et al. 2012) or on the large island of

Fig. 6.2 An ursine howler (see *arrow*) preyed by a harpy eagle in northeastern Venezuela (Photograph: M. R. González-Alentorn; see also Urbani et al. 2012)

Barro Colorado (Touchton et al. 2002). In the last case, the harpy eagles were reintroduced to the island, but they abandoned it once they reached sexual maturity (K.M.). Predation by smaller size raptors, a black hawk eagle (Miranda et al. 2006), and a presumed attempt by a crested caracara (McKinney 2009) have been observed in forest fragments. Finally, Mendes-Pontes (1997) observed a group of *A. macconnelli* and a group of *Ateles belzebuth* that were resting together in a tree, aggressively and simultaneously vocalizing at a large raptor after it had attacked and killed an adult female howler.

6.2.3.2 Non-raptors

The most striking interactions between howlers (*A. caraya*) and non-predatory birds were the 19 episodes of chicken (*Gallus gallus*) egg predation, wild bird egg predation (two occasions), and the inspection of a *Furnarius rufus* nest (one occasion) observed by Calegaro-Marques (1992) and Bicca-Marques et al. (2009) in a highly transformed landscape in Brazil. Other interactions include the approach of mantled howlers to a keel-billed toucan (*Ramphastos sulfuratus*) that was eating fruit and to pigeons (undetermined columbiform) by N.A. and Calegaro-Marques (1992), respectively. In addition, a juvenile Guianan red howler pulled the tail of a black curassow (*Crax alector*) (J.C. Vié, in Richard-Hansen and Bello 1998). In the

Venezuelan *Llanos*, Braza (1980) observed two kiskadees (*Pitangus sulphuratus*) displacing a group of ursine howlers from their nesting tree (Braza 1980), and a group of ursine howlers displacing a flock of brown-throated parakeets (*Aratinga pertinax*).

Finally, S.P. reported a black-and-gold howler responding to a vocalization of a crow (*Cyanocorax* sp.), which resulted in further vocalization by the rest of the howler group.

6.2.4 Interactions with Reptiles

Quintino and Bicca-Marques (2013) reported a predation episode of an adult female Purús red howler by a *ca.* 2-m long boa (*Boa constrictor*) in a 2.5 ha forest fragment in Brazil. This female howler belonged to a group of six individuals, but only one female responded to her distress calls, running towards the boa, vocalizing and hitting the snake with her hands. However, the boa did not react and the female howler watched how it swallowed her group mate from a nearby tree. Meanwhile the rest of the group remained completely oblivious to the attack, 15 m above the victim. Boas have also been observed attempting to prey on mantled howlers in Costa Rica (L.M.F. cited in Chapman 1986), supporting the idea that boas may be a common predator of howlers.

Besides boas, the only reports of a howler interacting with reptiles refer to iguanas. L.C. observed a black iguana (*Ctenosaura similis*) approaching and displacing a mantled howler in Costa Rica. G.P.M. recorded a male green iguana (*Iguana iguana*) responding aggressively to the proximity of Central American black howlers that were feeding on leaves.

6.3 Discussion and Future Directions

Our study indicates that howlers interact with a wide range of vertebrates throughout their distribution (Table 6.1–6.4; Fig. 6.1). However, the frequency of these episodes was very low and mainly restricted to species that either share their diet, namely primates and coatis, or are potential predators, particularly raptors. Therefore, howlers' interactions with other species were limited to circumstances directly related to their survival such as feeding and predation avoidance. This low rate of interaction is consistent to the general energy saving strategy that howlers display to cope with a diet based on plant matter (Milton 1980). Exceptions to this pattern were the interactions of immature howlers who frequently played with other primate species (of the same age or older) and behaved playfully and inquisitively with birds and non-primate mammals. This is a trait shared with other immature primates who spend a great deal of their time playing, interacting, and exploring their environment (Fagen 1992). This activity decreases with age, as juvenile howlers become dependent on plant matter which requires time and energy for its digestion (Baldwin and Baldwin 1978).

Evidence of supplantation from and aggression in feeding trees suggests that howlers may compete directly for food, and particularly for fruit, with other sympatric primate species, but also with other species that consume fruits such as coatis and curassows. While in the later cases howlers appear to dominate these contests, other primates regularly force howlers out of feeding trees. This lower 'aggressiveness' is probably a consequence of their relatively poorer diet and associated energy saving strategy (Milton 1980). Accordingly, howlers exhibit some of the lowest levels of conspecific agonism among social primates (Klein 1974). However, howlers are sometimes able to resist, and even displace, other competitors from feeding trees, which tends to occur when howlers outnumber the other species. The consequences that withdrawing in such competitive situations may have over the fitness of howlers are not clear. It is commonly regarded that howlers can compensate low fruit consumption by supplementing their diet with leaves and reducing energy expenditure (Milton 1980). However, recent studies suggest that fruit consumption helps howlers maintain low traveling costs (Dunn et al. 2009, 2010) and reduced levels of stress (Behie et al. 2010; Dunn et al. 2013), which in turn supports the idea that howlers may compete for fruit with other species. Accordingly, we consider that it is necessary to study the consequences of competition over fruit with other primates and coatis may have on howlers. This could be achieved by modeling the effect that densities of other primates, in addition to habitat characteristics, have over the consumption of fruit, nutritional stress levels, and ultimately population densities of howlers.

Describing the relationship of howlers with other primates and coatis as competitive would, nevertheless, be over simplistic, as howlers were also observed on several occasions feeding, resting, and interacting peacefully together with other primates and co-feeding with coatis. The conditions that allow peaceful living between howler and other species, that is neutralism, need further attention, particularly how they may fluctuate seasonally, and how they may be related to population density and habitat characteristics. For example, the degree of frugivory of howlers, other primates, and coatis varies throughout the year, which may modulate the competition between these species (Asensio et al. 2007). Moreover, the size of the feeding trees is apparently a key factor in this regard, as interspecific associations of howlers with other primates (Defler 1979; Terborgh 1983; Mendes-Pontes 1997; Haugaasen and Peres 2009) and with coatis (Asensio et al. 2007) tend to occur in large trees. In this sense, compared to other Neotropical primates, howlers do not tend to form stable associations with other species (Mendes-Pontes 1997; Lehman 2000; Haugaasen and Peres 2009) which has been attributed to their largely folivorous diet and associated low mobility as they limit the probability of overlap within other species in food sources (Haugaasen and Peres 2009). Nevertheless, punctual evidence in our review suggests that they may get some anti-predatorial benefit from these mutualistic associations.

The behavior of howlers towards raptors suggests that in general they regard them as predators, but direct observations of successful howler attacks by 'natural' predators are restricted to harpy eagles and to a "harpy eagle-like" large raptor (e.g. Mendes-Pontes 1997). Although harpy eagles may be the principal predators of howlers in their natural habitats, the evidence available from nest watching indicates that these eagles may prefer other primates to howlers (Ford and Boinski 2007) and that they may constitute a small part of their diet (Retting 1978). Concerning terrestrial predators, direct evidence suggests that tayras may be the most important threat for howlers, but there is also indirect evidence (carcasses and/or corpse remains in feces) suggesting that howlers can constitute a very significant part of the diet of ocelots (Bianchi 2001; Miranda et al. 2005; Bianchi and Mendes 2007), and more particularly pumas and jaguars (Schaller 1983; Peetz et al. 1992; Ludwig et al. 2007). Everything considered, the information regarding predation on howlers is insufficient to draw any conclusion on the effect that both terrestrial and aerial predators may have on their population structure and dynamics. Further fecal analyses of potential terrestrial predators and the monitoring of raptor nests may be the most effective way to gain insight on the howler-predators' ecology, as predation events, particularly by felids, are very difficult to witness. These studies should be conducted in different types of habitat, with different availability of potential prey (i.e. habitats with a high diversity of primates versus habitats in which only howlers are present), and with varying diversity of predators. However, the presence of howler remains in feces or nests have to be interpreted with care as they may represent episodes of scavenging rather than predation.

Finally, our review indicates that the transformation of natural habitats may also affect howler interaction patterns with other species in several ways. One of the results of habitat transformation is the reduction in the availability of fruit and large trees (Arroyo-Rodriguez and Mandujano 2006), factors that may influence food competition and coexistence of howlers with other species. The ability of howlers to consume large quantities of leaves appears to provide them with a competitive advantage over other more frugivorous primate species in smaller forest fragments (Bicca-Marques 2003), and accordingly, howlers can be found in forest patches in which other primate species, i.e. spider monkeys, have gone extinct (Estrada and Coates-Estrada 1996). On the other hand, Bicca-Marques et al. (2009) observed how habitat impoverishment and very high densities (7–20 ind./ha) may force howlers to predate on eggs as a response to reduced availability of food sources, a phenomenon also probably induced by access of howlers to chicken eggs, being in close proximity to human settlements.

Howlers in fragmented landscapes are also often forced to go down on the ground to access isolated forest patches (see Arroyo-Rodríguez et al. 2011). While doing so, they may come in contact with domestic animals and with wild predators that like open areas such as coyotes. Howler interactions with pigs and cows are neutral (Fig. 6.3), although they may facilitate the transmission of parasites and infectious diseases, but we consider very worrying the reports of coyote and dog attacks on howlers. The absence of harpy eagles and/or large felids in fragmented landscapes has been suggested to favor large densities of howlers in forest fragments (Ferrari 2009; Arroyo-Rodríguez et al. 2011), but increasing evidence supports that coyotes and dogs may counteract this positive effect. Also, encounter rates of howlers with

Fig. 6.3 Mantled howlers flanked by a cow in a forest fragment surrounded with pasture for cattle ranching in southern Mexico (Photograph: N. Asensio)

boas might be higher in small forest fragments (Quintino and Bicca-Marques 2013). Given the negative consequence that predation may have over the already highly threatened populations of howlers in fragmented landscapes, we believe that this is an issue that should be addressed by primatologists working with howlers in this context; first by quantifying the rates of predation and, if necessary, by implementing conservation initiatives that can range from the control of 'free ranging' dogs to the increase of landscape connectivity.

Despite the evidence provided in this review, further studies are necessary to fully understand the way howlers share their habitat with other species due to its potential effect on their ecology and conservation. Of particular urgency are studies on food competition and predation in fragments, given that howlers are clearly affected by habitat transformation.

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Chapter 7
Solving the Collective Action Problem During Intergroup Encounters: The Case of Black and Gold Howler Monkeys (*Alouatta caraya*)

Martín M. Kowalewski and Paul A. Garber

Abstract Growing evidence from field studies highlights the importance of social affiliation, social bonds, and cooperation in understanding primate behavior and social structure. In several platyrrhine species, intersexual and intrasexual cooperation and tolerance in the form of dyadic and group-level social interactions are reported to serve a critical role in the ability of individuals to obtain access to mates, effectively patrol and defend home ranges and feeding sites, and increase offspring survivorship. Howler monkeys constitute an instructive model for testing hypotheses concerning the costs and benefits of collective action as they usually live in cohesive social groups composed largely of unrelated or distantly related adults. We explored evidence of collective action focusing on Argentina black and gold howlers (*Alouatta caraya*). We investigated the participation of individually recognized resident adult males in howling, vigilance, and fighting bouts during intergroup encounters, an event during which extragroup males (either lone males or males from neighboring groups) attempt to enter established groups and mate with resident females. During these encounters, some or all resident adult males responded by howling and approaching the intruder. Based on data on individual male participation during intergroup encounters, we argue that the collective action of several males benefits both actors and other group members by reducing opportunities for extragroup male takeovers, infanticide, and social disruption in established groups. Individuals may adjust their participation during these encounters in order to reduce the costs and enhance the benefits of collective action in maintaining reproductive access to resident females. We suggest that intergroup encounters are platforms

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where collective action problems may arise, are negotiated, and are solved through joint actions by central males and noncentral males. We also present limited data on male collective action in other howler monkey species.

Resumen Cada vez hay más evidencia proveniente de estudios de campo que sugiere la importancia de la afiliación social, los lazos de amistad y la cooperación para entender el comportamiento y la estructura social de los primates. En varias especies de platirrinos, la cooperación y tolerancia entre individuos del mismo o diferente sexo, en la forma de interacciones de diadas, cumplen un papel crítico en la habilidad de los individuos para obtener acceso a parejas, patrullar y defender áreas de acción y de sitios de alimentación y aumentar la probabilidad de incrementar la supervivencia de los infantes. Los monos aulladores constituyen un buen modelo para probar hipótesis relacionadas con los costos y beneficios de la acción colectiva ya que usualmente viven en grupos sociales compuestos por individuos generalmente no relacionados. En este trabajo se explora la existencia de acción colectiva en aulladores focalizándonos en los aulladores negros y dorados (*Alouatta caraya*) de Argentina. Se investiga la participación individual de los machos residentes en eventos de aullidos, vigilancia y peleas durante encuentros intergrupales, momentos durante los cuales los machos extragrupales intentan ingresar en grupos establecidos y copular con hembras residentes. Durante estos encuentros, algunos o todos los machos residentes adultos responden con aullidos y aproximándose al intruso. Basados en datos sobre la participación individual en machos durante encuentros intergrupales, se sugiere que la acción colectiva de varios machos beneficia tanto a los actores como a otros miembros del grupo, reduciendo las oportunidades para la toma de grupo por machos extragrupales, de infanticidio y de disrupción social de grupos establecidos. Los individuos pueden ajustar su participación durante estos encuentros para reducir los costos y aumentar los beneficios de la acción colectiva, manteniendo el acceso reproductivo a hembras residentes. Se sugiere que los encuentros intergrupales son plataformas donde los problemas de acción colectiva pueden surgir y ser negociados y resueltos a través de acciones conjuntas entre machos centrales y otros machos residentes. Además se presenta una revisión sobre acción colectiva de machos en otras especies de monos aulladores.

Keywords Collective action • Intergroup encounters • Howlers • Mate defense

7.1 Introduction

Based on field observations across several primate taxa (see for example, Clutton-Brock 2009; Sussman and Garber 2011), there exists a growing consensus highlighting the importance of social affiliation, partner preferences, and cooperation in understanding the benefits to individuals of living in an effectively functioning social group; e.g., *Saguinus mystax* (Garber et al. 1993; Garber 1997), *Alouatta palliata* (Wang and Milton 2003; Bezanson et al. 2008), *Alouatta arctoidea* (Pope 2000a, b), *Brachyteles arachnoides* (Strier 1994; Strier et al. 2002), *Cercopithecus* *mitis* (Cords 1997, 2002), *Papio cynocephalus* (Silk et al. 2006), *Pan troglodytes* (Mitani et al. 2002a, b; Lukas et al. 2005). For example, long-term data on social interactions and offspring survivorship in *P. cynocephalus* indicate that females who invested more time in affiliative social interactions were characterized by increased reproductive success (Silk et al. 2003). Baboon females that had more social alliances and were more socially integrated into the group experienced higher lifetime reproductive success than females who were less socially connected. Findings in other primate species also suggest that living in social groups has positive fitness benefits (*P. hamadryas ursinus* Barrett and Henzi 2002; *C. mitis* Cords 2002; *A. arctoidea* Pope 2000a, b, see also Kapsalis 2003). And, although many authors have tended to highlight the costs of social group living in terms of feeding and mating competition, both competitive and cooperative behaviors occur in all group living primates, and there are strong selective benefits to individuals of establishing predictable long-term social bonds and alliances (Silk et al. 2006).

Two general classes of coordinated or joint affiliative social interactions have been described. One is reciprocity (Trivers 1971), which is analogous to a tit-for-tat strategy in which each of the two actors repeats the last affiliative interaction engaged in with that partner. Reciprocity typically involves behaviors that have low cost to the actor such as grooming, with the expectation that the act will be reciprocated in the near future. A second form of joint affiliative social interaction is associated with the co-operative behavior of two or more individuals. In this regard, Clutton-Brock (2002, 2009) has argued that mutualism, a class of coordinated social interactions in which participating individuals directly and simultaneously obtain benefits from their joint actions, plays an important role in promoting the evolution of cooperative behavior. Moreover, a specific type of mutualism termed by-product mutualism, which may be the most common form of cooperative behavior, involves no additional cost to an actor because that individual is expected to perform the behavior in the presence or absence of conspecifics. Examples of by-product mutualism are predator vigilance or resource monitoring, in which each individual is expected to benefit from performing this behavior effectively, but the collective action of several individuals is likely to provide additional benefits to all participants (Dugatkin 1997, 2002). Therefore, both reciprocity and mutualism result in the formation of stable and long-term social bonds and friendships and are expected to have adaptive value to both actors and recipients (Boccia et al. 1989; Sapolsky et al. 1997; Castles and Whiten 1998; Das et al. 1998; Aureli and Smucny 2000; Silk 2000; Silk et al. 2003; Sussman and Garber 2011; MacKinnon and Fuentes 2011). Sussman and Garber (2004:178,180) suggest "…cooperation and affiliation represent behavioral tactics that can be used by group members to obtain resources, maintain or enhance social positions, increase reproductive opportunities, and reduce stress of social isolation…," moreover "…social affiliation and cooperative behaviors provide psychological, physiological, and ecological benefits that are reinforced by hormonal and neurological systems…".

Although the role of adult male primates in intrasexual competition, sexual coercion, mate guarding, infanticide, and home range defense has received considerable attention, less is known concerning the costs and benefits to individual males of collective or mutually beneficial action (Nunn 2000; Kappeler and van Schaik 2002; Wrangham and Muller 2009). In the case of common chimpanzees, Mitani and Watts (2001) and Watts (2002) present data indicating that as the number of males participating in hunts of red colobus monkeys increases, there is a correlated increase in capture success, weight of prey obtained, and the amount of meat consumed by each hunter. Chimpanzees cooperatively hunt with reciprocating partners regardless of kin relationships and cooperative hunting appears to be best described in terms of a mutually beneficial behavior (Mitani and Watts 2001; Boesch et al. 2006).

However, when male chimpanzees engage in coordinated activities such as hunting or patrolling behavior, there is the possibility of a collective action problem (CAP). A CAP occurs when non-participants receive the benefit of collective action but incur none of the costs. For example, a CAP may occur when some but not all community chimpanzee males participate in boundary defense or territorial incursions, which has a potential high cost or risky behavior in terms of injury or death to those who participate (Watts and Mitani 2001). Watts and Mitani (2002) suggest that chimpanzee patrolling could result in “free riders,” individuals that patrol less frequently or stay behind during patrols and incur no costs. The presence of free riders is expected to discourage collective action unless free riders face sanctions such as directed aggression or reduced access to reproductive partners (Nunn 2000).

Collective action during intergroup encounters has been documented in several species of primates that live in multimale and multifemale groups and, therefore provides an opportunity to assess the costs and benefits to individuals of joint participation (Cheney 1987; Nunn 2000; Watts and Mitani 2001; Fashing 2001a, b; Kitchen and Beehner 2007). Given that individuals within the same group may differ in age, rank, reproductive success, and access to resources, the specific set of social and ecological factors that serve to promote within-group tolerance, affiliation, and collective action among resident group members is likely to differ among individuals and groups. In the case of adult male primates, individuals may compete directly over a limited resource such as ovulating females or indirectly by differentially defending resources important for female reproduction (i.e., food patches -Emlen and Oring 1977). Under these conditions, male-male competition may drive female mate choice or male access to reproductive partners (i.e., when male rank is directly related to reproductive success, Jack and Fedigan 2006). In other cases, males may act collectively, for example, during intergroup encounters, to defend reproductive access to fertile females, protect young infants, defend food patches, sleeping sites, their home range, or prevent a take-over by extragroup males (Pope 1990; Watts and Mitani 2001; Gibson 2008; Talebi et al. 2009; Garber and Kowalewski 2011). For example, Fashing (2001b) argued that adult male *Colobus guereza* engage in resource defense polygyny (food defense strategy), with resident males acting collectively to prevent males from neighboring groups and extragroup males from access to resources that attract receptive females (Emlen and Oring 1977). In a second study, Harris (2006) also argued that intergroup encounters in guerezas served an important role in resource defense and that higher ranked groups (defined as those who consistently defeated neighboring groups during intergroup encounters) had larger core areas with more food resources and access to higher quality foods (based on density, DBH, and basal area of preferred foods) than did groups of lower rank. Similarly, studies indicate that in howler monkey groups that contain multiple resident adult males, several males may act collectively to howl, chase, or defend the group against intruder males (Chivers 1969; Sekulic 1982a; Pope 1990; Kitchen 2004; Kowalewski 2007; Holzmann et al. 2012). Intergroup encounters in howler species can be relatively long [117.1 ± 94.4 min *A. caraya* (Kowalewski 2007)] and occur at variable rates [0.07 intergroup encounters per hour of observation, *A. palliata* (Chaput 2001) to 5.7 intergroup encounters per hour of observation, *A. caraya* (Kowalewski 2007)]. However, during these encounters not all males may participate, and therefore participating males may be subject to a CAP (Nunn 2000; Cooper et al. 2004). Garber and Kowalewski (2011), p 46) suggest that "…under conditions in which the benefits to free-riders are high (continued access to feeding sites and mating partners), and the costs are low (minimal social sanctions or retaliation), a collective action problem may arise resulting in a breakdown of cooperative behavior as additional individuals adopt a free-rider strategy…". When resources are not monopolizable, free riders may obtain benefits in reduced time and energy costs and reduced risk of injury by not joining in with others (van Schaik 1996; Nunn 2000; Nunn and Lewis 2001). Even when nonparticipation by free riders is easily detected, punishment may be difficult to apply or too costly to execute (Kitchen and Beehner 2007). However, if the absence of male joiners results in a group takeover by invading males, if the dominant male or joiner males aggressively attack or seek sanctions against non-participating males, and/or if females exercise mate choice and prefer to mate with males that act collectively, then the costs to non-joiners may be greater than the benefits of nonparticipation (Heinsohn and Packer 1995; Lazaro-Perea 2001; Kitchen 2004).

Finally, males who provide support to the dominant male or join in collective action may receive an immediate benefit if their participation helps to expel intruding males from the group and receive future benefits, if their actions result in collectively acting males being more tolerant of each other and/or interchange coalitionary support for access to limited resources such as fertile females during breeding periods (Johnstone 2000; Ostner et al. 2008; see also skew model discussion in Kutsukake and Nunn 2006). Thus, individual males in multimale groups must decide under what set of conditions they should act jointly in obtaining access to resources, reproductive partners, and in building social alliances and under what set of conditions to compete with other resident males over these same resources (Garber and Kowalewski 2011).

Kitchen and Beehner (2007) reviewed factors affecting male participation during intergroup encounters in nonhuman primates. These authors identified (see Table 20.1 in Kitchen and Beehner 2007) mate defense or indirect mate defense via protection of resources (Fashing 2001b), effects of rank, and access to resources (Nunn 2000); intergroup contact as a platform of information exchange: migration (Kitchen et al. 2004); and mating opportunities (Olupot and Waser 2001; Lazaro-Perea 2001; Henzi and Barrett 2003; Kowalewski 2007) as the most critical factors affecting the short-term costs and benefits and the long-term advantages of collective action vs. nonparticipation.

Primates of the subfamily Atelinae are characterized by considerable variation in the strength of male-male social bonds (Garber and Kowalewski 2011, 2013; Kowalewski and Garber 2010; Strier 1994; Strier et al. 2002). Field studies indicate that *Ateles* and *Brachyteles* exhibit strong long-term male intrasexual kin bonds, while *Lagothrix* is characterized by strong grooming relationships between adult and subadult males and male cooperation during intergroup encounters, but weaker male intrasexual social bonds than muriquis or spider monkeys (Di Fiore et al. 2011). *Alouatta*, which may reside in either one-male or multimale social groups, exhibits evidence of more context-dependent male-male kin and nonkin social bonds. Here, we use *Alouatta* as a model to test the hypothesis that male collective action, mate/group defense, and male-male affiliation are part of an ancestral atelin behavioral pattern. We assume that behaviors that are taxonomically widespread across the Atelinae are best considered as ancestral and were present in the common ancestor of the group. We also expect that traits associated with within-group male-male bonds such as embracing, grooming, or male-male proximity are directly linked to within-group male-male tolerance. Thus, males who are in greater spatial proximity or males who more frequently engage in grooming and embracing are likely to maintain a stronger social bond than males who infrequently or less frequently engage in these behaviors. In this regard, the existence of collective action in male howler monkeys may help to elucidate the costs, benefits, and function of cooperative behavior in Atelines. Thus, the goal of this chapter is to examine the CAP, the costs/benefits to free riders, the collective benefits to individuals that engage in joint actions, and possible solutions to the CAP during intergroup encounters in male black and gold howlers. We define cooperative behavior as any set of social interactions between two or more individuals in which at least one participant receives a potential benefit and the other participant(s) receives either a small immediate cost, an immediate benefit, or a potential delayed benefit. Following this definition we hypothesize that subordinate male participation in intergroup encounters provides a benefit to the central male, whereas the defection of one or more subordinate males results in a cost to the central male.

7.2 Evidence of Collective Action in Howler Monkeys

Despite the fact that all species of *Alouatta* commonly engage in prolonged bouts of howling, quantitative data on collective action are extremely limited. Below, we present data obtained from several studies to address the collective action framework in the genus.

*7.2.1 Mantled Howlers (***A. palliata***)*

In a 9-month study on Barro Colorado Island (BCI), Panama, Wang and Milton (2003) studied social interactions in a group of 6 adult male and 12 adult female *A. palliata*. These authors could not discern a clear set of dominance relationships that characterized male group members, although they were able to designate one male as the central male based on priority access to food resources, vocal coordination of group movement, and his degree of spatial centrality within the group. *Alouatta palliata* males in this group were characterized by an extremely low frequency of agonistic interactions (0.018 ± 0.02 events/h/male) and all 6 males were observed to copulate with resident females. This finding contrasts with the reverse age-graded linear hierarchy reported for male Costa Rican mantled howlers at La Pacifica (Glander 1980, 1992; Jones 1980). Shared reproductive access by males on BCI could imply either that the central male was tolerant of the mating access that other resident males had to receptive females and/or that female promiscuity and mate choice play an important role in male howler mating behavior. In this regard, Vehrencamp (1983) suggested that dominant individuals might concede some percentage of reproduction to a subordinate as an incentive to stay in the group and help to rear or protect the dominant's offspring. If a dominant male does not monopolize the mating activities of group females, scramble polygynandry and male egalitarian relationships may be expected to characterize male social interactions (van Hooff and van Schaik 1992).

Mantled howler males are well known for coordinated howling during intergroup encounters (Carpenter 1934, 1935; Chivers 1969; Milton 1980). Dias and Rodríguez-Luna (2006) studied patterns of male association in a translocated population of *A. palliata mexicana* from Agaltepec Island, Veracruz, Mexico (composed of 13 adult males, 21 adult females, 10 subadults, 9 juveniles, and 6 infants). Although these authors provide no quantitative information on coalitionary behavior during intergroup encounters, they report that males showed nonrandom patterns of association and subgrouping. These patterns varied based on season of the year, the presence and number of resident females in subgroups, and kinship. Specifically, during the dry season the presence of many receptive females resulted in reduced levels of male–male association. Moreover, when the number of females in subgroups increased, the number of males in subgroups also increased. Social tolerance among subgroup males was limited, however, suggesting an increase in reproductive competition. During the wet season, male–male associations were more common, and association preferences were largely kin-based. In addition, Dias et al. (2010) report differences in the social interactions of males residing in two groups of *A. p. mexicana*: one group that was recently taken over by a coalition of two males, and a second group that had a stable composition of two adult males and four adult females (plus juveniles and infants) for at least 9 months (both groups under study were similar in age/sex composition). They found that the social relationships of male mantled howlers were strongly influenced by familiarity within dyads, and in particular, that coalition partners in the more stable social group were highly affiliative, in close spatial proximity, and engaged in cooperative howling; in comparison to the group with newly immigrant males.

*7.2.2 Black Howlers (*Alouatta pigra*)*

In the case of *A. pigra*, Kitchen et al. (2004) found that males who were co-residents in the same group for over 4 years were more likely to engage in collective action when exposed to playbacks of howling from one or three adult males compared to resident males who were characterized by more short-term associations. These authors report that during simulated intergroup encounters (through playbacks) individual male participation in howling varied depending on their group of residence and the type of encounter. For example, subordinate males in long-term alpha-subordinate associations exhibited stronger howling and approach responses than did subordinate males in short-term alpha-subordinate associations (Kitchen 2000). In this later case, some subordinate males were never observed to participate in group defense (Kitchen 2000). Based on data from 112 howling bouts (in response to playbacks) subordinate males joined the central male in howling 58.9 % of the time. Additionally, some subordinate males cooperated more consistently than others. In one group a subordinate male joined the central male in more than 80 % of 22 natural inter-group encounters. In another group a subordinate male participated in 59 % of 22 encounters, and in a third group the resident subordinate male was never observed to join the displaying central male during 13 encounters. These studies on black howlers lack genetic data from which to examine the role of kin and nonkin bonds in male social interactions.

*7.2.3 Ursine Howlers (*Alouatta arctoidea*)*

In the 1980s Sekulic published a series of articles describing patterns of howling and social behavior in *A. arctoidea* (formerly *A. seniculus*) in Venezuela. Based on these studies, there is evidence that male participation in howling bouts was related to the nature and duration of the alpha-subordinate association (Sekulic 1982a). Sekulic (1982b, c) suggested that support by a younger adult male was critical for the central male's ability to maintain its position in the dominance hierarchy in four groups with 1–3 adult and subadult males. Male–male coalitions in this species functioned in maintaining within-group dominance relationships. Sekulic (1982b, c) reported subordinate males howl more frequently when there were fewer adult males in the group (Sekulic 1982a); however, the duration of howling bouts was not correlated with the total number of resident adult and subadult males. In ursine howler monkeys the presence of at least one additional simultaneously howling male appeared to offer significant benefits to the central male compared to residing in a one-male group.

Pope (1990, 1998) also studied Venezuelan red howlers (*A. arctoidea*). She reports that male coalition partners acted collectively to invade groups, evict resident males, remain together, and interact jointly to maintain their reproductive position in the group. These male coalitions consisted equally of related males ($N=14$) and non-related males (*N* = 18). Coalitions formed by relatives (50 % were formed by brothers or half brothers) lasted longer (8.2 years vs. 3.3 years) and were more stable than were coalitions composed of nonrelatives (Pope 2000a). Cooperation between males served to enhance the probability of successfully defending reproductive access to the limited number of currently receptive females (see also Crockett and Rudran 1987) from extragroup males. In this species (or at least for this site; see also Agoramoorthy and Hsu 2000), the group's central male was observed to monopolize access to fertile females. However, Agoramoorthy and Hsu (2000) did not collect genetic data from which to assess paternity. The advantages to subordinate males of collective howling could include inclusive fitness benefits, increased mating opportunities, alpha male tolerance associated with group membership, and/or future inheritance of the central and primary breeding position in the group.

7.3 Black and Gold Howlers as a Suitable Model for the Study of CAPs

Studies on black and gold howlers (*A. caraya*) offer another instructive model for exploring the costs and benefits to individuals and groups of cooperation through collective action. In this species groups are generally composed of 2–4 adult males, some of whom are related and others who are not related (Oklander et al. 2007, 2010). Regardless of kin relationships, males residing in the same group are highly tolerant of one another, form coalitions, and cooperate in territorial behavior and mate defense against males from neighboring groups (Kowalewski 2007; Garber and Kowalewski 2011). Although there is evidence of mate guarding and serial copulations by the groups' dominant male, all adult male group members mate with resident females during their fertile and non-fertile periods (Kowalewski and Garber 2010). Kowalewski (2007) has shown that during intergroup encounters individuals from neighboring groups may obtain information regarding potential coalitionary or migratory partners, female receptivity, and the possibility of a group takeover. However, given that both access to feeding sites and access to receptive females are shared in *A. caraya* (Kowalewski and Garber 2010) (females *A. caraya* solicit males and mate during all phases of their reproductive cycle, see also Van Belle et al. 2009 for a discussion of this in *A. pigra*), female social and reproductive strategies (ability to escape central male mate guarding, copulation with multiple nonresident males) are likely to influence male behavior and mating opportunities. In an 18-month study of four black and gold howler monkey groups, Kowalewski (2007) presents data indicating that males were often each other's nearest neighbor or preferred social partner. Males engaged in bouts of intrasexual grooming and embracing that appeared to play an important role in maintaining intrasexual alliances (Garber and Kowalewski 2011). In many cases, bonds between individual males persisted over periods of several years (Kowalewski 2007; Garber and Kowalewski 2011). Strong and persistent social bonds and shared mating opportunities within the group provide benefits to all resident males if their collective actions serve to discourage nonresident males from mating with resident females or taking over the group.

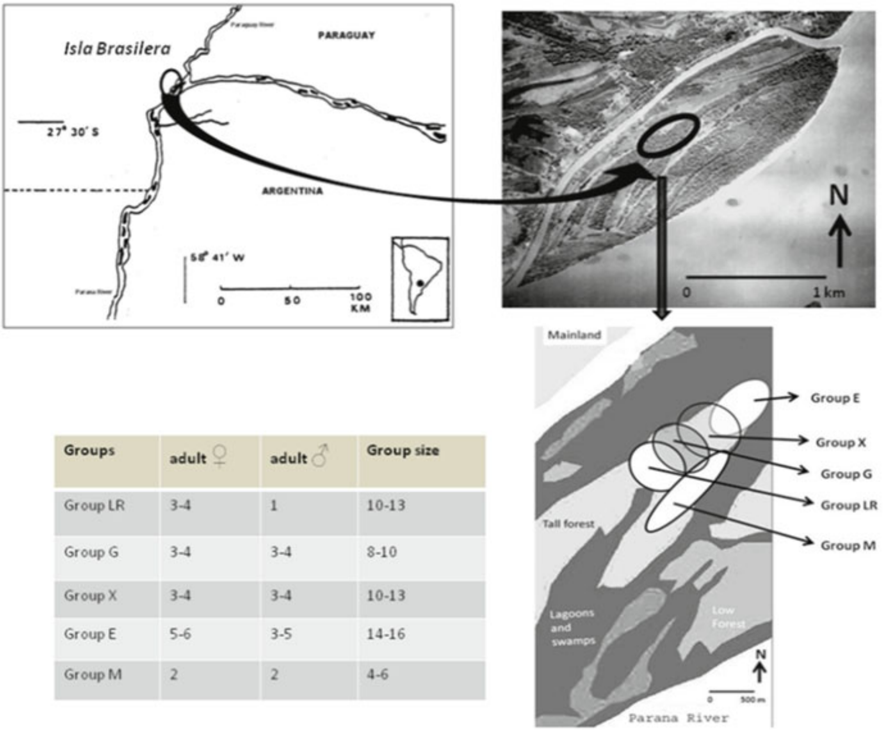
Below we present quantitative data on collective action, howling, and intergroup encounters in black and gold howler monkeys.

7.4 Study Site

Data were collected on the behavior and ecology of two groups of black and gold howlers over 12 months (December 2003–November 2004) on Isla Brasilera, in northern Argentina (27°20′S–58°40′W) (Fig. 7.1). The island represents an area of 292 ha without permanent human settlement and is covered by continuous flooded forest and temporary lagoons. The climate is subtropical with an average annual temperature of 21.6 °C and an average annual rainfall of 1,200 mm. A more complete description of the site is provided elsewhere (Kowalewski and Zunino 2004; Kowalewski 2007). Over 1,465 h of behavioral data were collected from the two study groups. Individuals in each group were followed from sunrise to dusk for 5 days a month. Group X contained nine members including three to four adult males and three to four adult females (group size changed during the study). Group G contained 11–12 individuals including four adult males and four adult females. Age-sex categories were based on criteria used by Rumiz (1990). All adults in our study groups were marked with anklets and ear tags (Kowalewski and Garber 2010) to ensure accurate identification. We recorded the behavior during intergroup encounters in our two study groups, as well as their interactions with three neighboring groups (Group E, Group M, and Group LR). Home range overlap between groups ranged from 60–80 % (Kowalewski 2007).

7.5 Intergroup Encounters

For this study we defined intergroup encounters when at least 50 % of the focal group visually contacted a neighboring group (0–40 m at our study site) and/or any individual initiated an extra group social interaction including moving towards the group, vocalizing, playing, or engaging in aggressive physical contact (Kowalewski 2007). Occasionally, the groups would separate by more than 30 m and then come back into contact. If no more than 30 min passed before the two groups moved towards each other (within a distance of 10 m), we treated the two (or more) episodes as the same encounter in our analyses. Each intergroup encounter was subdivided into 30 min intergroup encounter bouts (IEB), in order to better analyze individual male performance during the encounter. These IEB were subdivided in three subsets: (1) Vigilance: close spatial proximity and direct attention to the actions of another group, (2) Howling: close spatial proximity and at least one



Groups	adult ♀	adult ♂	Group size
Group LR	3-4	1	10-13
Group G	3-4	3-4	8-10
Group X	3-4	3-4	10-13
Group E	5-6	3-5	14-16
Group M	2	2	4-6

Fig. 7.1 Location of the study site in Northern Argentina, relative position of each study group within the island and group composition during the study (from Kowalewski and Garber 710, Figure 1)

resident male howling at the nearby group, and (3) Fighting: close spatial proximity and physical aggression among males from neighboring groups. Following Kitchen et al. (2004), we assumed that group defense by howling or visual contact represents a threat and signals the willingness to engage in aggressive behavior. Moreover, when two howler males engaged in fighting, we assumed that the potential for injury, even among individuals of the "winning" group, is high (Cheney 1987). Therefore, we argue that the cost of participation increases from vigilance to vocalizations to fighting.

7.6 History of the Study Groups

Group X. This group included four adult males (Gatti, Jesus, Primo, and Tobi), four females, plus juveniles, and infants. Gatti held the central male position for a period of 6–7 years until he was found dead in 2008 (Kowalewski 2007; Oklander 2007;

Garber and Kowalewski 2011; Pavé et al. 2012). Jesus was identified as an adult member of this group since 2001 but left the group in 2007. Primo disappeared in 2006. Toby emigrated in June 2004. In 2006 Group X was taken over by a neighboring group. Based on genetic data reported in Oklander (2007), Gatti and Jesus were identified as cousins or half sibs, and both were unrelated to Primo and Tobi. The genetic relationship between Primo and Tobi is unknown. In all figures and tables males other than central males are ordered by age from the oldest to the youngest.

Group G. This group was composed of four males (Jose, Hermoso, Ova, and Rocky), four females, juveniles, and infants. Jose became the central male in 2002 (Oklander 2007). At that time he was at least 7 years old. As a result of this change in his status, the previous central male transferred to the neighboring Group M where he became that group's central male. In October of 2004, a natal adult male Hermoso, who was 6–7 years of age and unrelated to Jose (Hermoso was the son of a male in Group G who died in 2001; Oklander 2007), began to act as the group's central male. During a 3–4-month period, Jose and Hermoso were co-dominant. Thereafter, Hermoso became the group's lone central male (V. Fernandez, pers. com) until 2010 when he was found dead. Thus, Hermoso spent over 6 years as the central male of Group G. Hermoso's ascension to the position as lone central male was not associated with any major social disruption in the group. Jose died while still a resident in Group G in June 2005. The remaining two adult males (Ova and Rocky) were residents of Group G for 5 years. They left together in 2005. Ova spent 1 year in LR group and then disappeared, while Rocky became the central male of a new group that remained together for almost 3 years. The group with Rocky as its central male was located two home ranges south of Group G and neighboring Group LR (Fig. 7.1). As previously stated Jose and Hermoso were unrelated and Ova and Rocky were half sibs, and both sons of Jose.

Neighboring groups. The composition and size of three neighboring groups were also recorded. Group X's range overlapped with groups E, M, and G. Group G's range overlapped with Groups X, M, and LR (Fig. 7.1). The composition of these groups during the study varied from multimale groups with 3–5 adult and subadult males to single adult male groups and 3–5 adult females.

7.7 Results

During the 12-month study we recorded a total of 284 intergroup encounters that involved Group X ($N=150$) and Group G ($N=134$) and at least three neighboring groups (see Fig. 7.1). Together, this comprised a total of 933 30-min IEBs for analysis. Seventy-six percent of IEBs involved vigilance, 20 % howling, and in only 4 % did adult males engage in direct physical combat (i.e., fighting). Intergroup encounters occurred on average twice per day and lasted an average of 2 h a day. Given that groups at our study site are active for an average of 12.2 h per day and resting accounted for 60–65 % of each groups' daytime activity budget, male black and gold howlers devoted 41–47 % of non-resting hours each day to group defense.

Table 7.1 Male participation across fighting, vocalizing, and vigilance IEBs in both Groups X and G

Groups/males	Central male	Jose/Hermoso	Ova	Rocky
G				
Fighting IEB	18 (100 %)	12 (67 %)	12 (67 %)	14 (78 %)
Vocalizing IEB	74 (100 %)	69 (93 %)	69 (93 %)	71 (96 %)
Vigilance IEB	291 (100 %)	261 (90 %)	261 (90 %)	251 (86 %)
	Central male[a]	Jesus	Primo	Toby[b]
X				
Fighting IEB	15 (100 %)	12 (80 %)	12 (80 %)	10 (67 %)
Vocalizing IEB	113 (100 %)	81 (72 %)	81 (72 %)	69 (61 %)
Vigilance IEB	422 (100 %)	354 (84 %)	354 (84 %)	259 (61 %)

[a] Gatti

[b] Toby left the group during the study

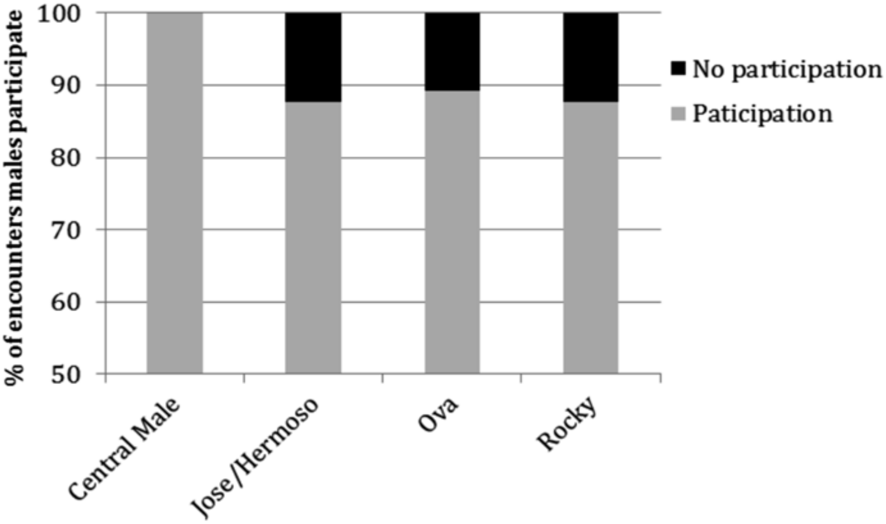


Fig. 7.2 Percentage of individual male participation and defection from intergroup encounters bouts in Group G. Jose and Hermoso switched central male position during the study. Their participation was controlled by the number of intergroup encounter bouts that they participated either as central male or secondary male

Given overall similarity in the pattern of intergroup encounters for both focal study groups, we pooled IEB data for further analysis. A correlation analysis between the number of males in each group and the number of males participating during intergroup encounters indicated a strong positive relationship ($r=0.74$, $N=933$, $P<0.05$). Central males participate during all IEBs and across all behavioral contexts (Table 7.1). Although the participation of at least one other resident adult male occurred 72–96 % of the time (considering all IEBs together), some individual males defected or failed to participate more than others (Figs. 7.2 and 7.3). In Group G, rates of defection were similar across all noncentral males (Gadj = 0.5,

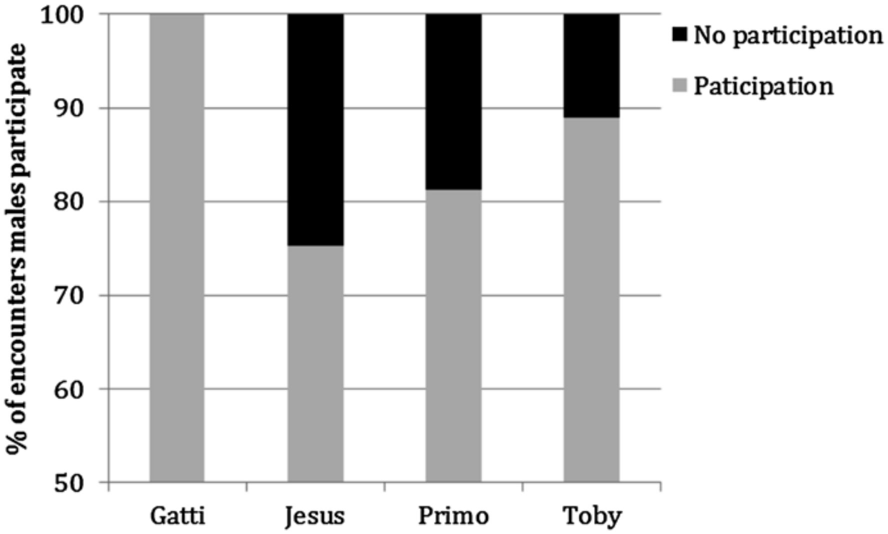


Fig. 7.3 Percentage of individual male participation and defection from intergroup encounters bouts in Group X. Toby left the group during the study. His participation was controlled by the number of intergroup encounter bouts that he participated in

df = 2; $P > 0.05$). In Group X patterns of individual male defection differed (Gadj = 28.7, df = 2; $P < 0.05$). In this group Jesus defected during 25 % of encounters, Primo 19 %, and Toby 11 %.

Using the pooled data, the relationship between the number of males present in each group and the number of males jointly howling during an intergroup encounter was weak ($r = 0.09$, $N = 933$, $P < 0.05$). The central male howled alone in 36 % of cases, and all resident males simultaneously howled in approximately 35 % of cases (Fig. 7.4). We next examined whether the number of adult males howling during an IEB correlated with the number of males participating in the encounter (in both groups the number of males participating ranged from one to four). As indicated in Fig. 7.5, during intergroup encounters when two resident males participated, both males howled simultaneously 50 % of the time. When three and four males participated in the encounter, each was observed to howl simultaneously during (65 %) and (53 %) of bouts, respectively.

We also analyzed individual male participation during vigilance, howling, and fighting IEBs in each group (Table 7.1). We recorded 33 IEBs in which at least one howler of the resident group was involved in aggressive interaction with howlers of the intruder group. In group G the central male participated in all of these encounters, whereas the participation of other males was relatively constant (67–78 %). A similar pattern was found in Group X where the central male participated in all bouts of fighting, while subordinate males joined the central male in fighting during 67–80 % of these encounters. The primary differences between groups involved Toby, a subordinate male in Group X. Toby emigrated from the group prior to the

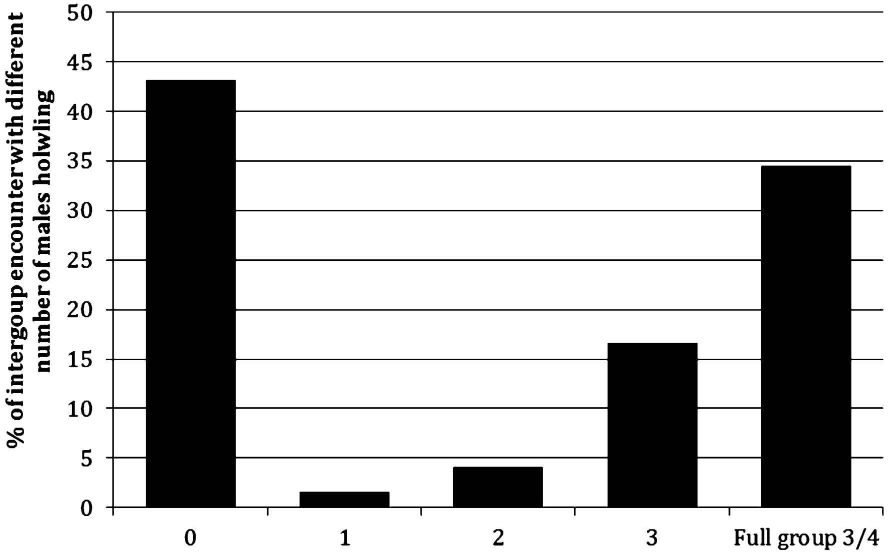


Fig. 7.4 Percentage of intergroup encounter bouts during which different number of joining males participated in coordinated howling

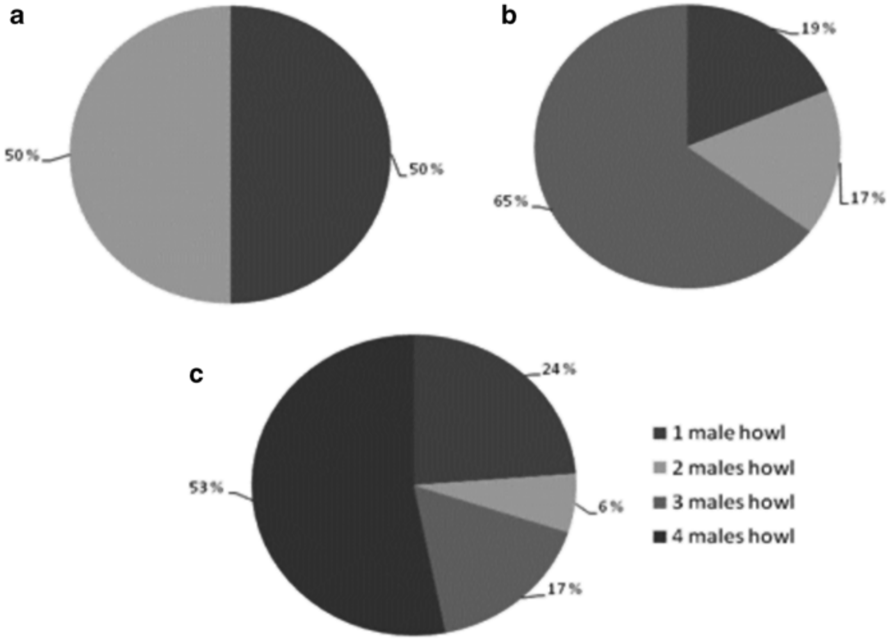


Fig. 7.5 Participation of males howling during intergroup encounters bouts depending on the number of males participating in the encounter (**a**) two males, (**b**) three males, and (**c**) four males

end of our study. However, while he was a resident of Group X, Toby engaged in only 61 % of vocalizing and vigilance IEBs and 67 % of fighting IEBs. Taken together these results suggest that although the central male assumes the primary role in group and mate defense, all other resident males also contributed and acted collectively in supporting the central male. Moreover, even during the highest risk encounters involving physical combat, noncentral males acted collectively with the central male 67–80 % of the time (Table 7.1). Finally, although we do not know the set of factors that resulted in Toby's emigration from Group X, he participated in collective action the least among resident male group members.

7.8 Discussion

Among New World primates, evidence of collective action and cooperative behavior has been reported across several taxa. This includes patrolling behavior in adult male spider monkeys (Fedigan and Baxter 1984; Symington 1988; Chapman 1990), male–female duetting in titi monkeys (which may play a role in both reinforcing socio-sexual bonds and excluding same-sex adults from entering their range (Müller and Anzenberger 2002), cooperative infant caregiving by adult helpers in tamarins and marmosets (Garber 1997; Digby et al. 2011), and coordinated howling and range defense among resident male howler monkeys (Horwich and Gebhard 1983; Pinto et al. 2003; Kitchen 2004; da Cunha and Jalles-Filho 2007; Gavazzi et al. 2008; Garber and Kowalewski 2011).

In general we have found that while resident adult male *A. caraya* participate collectively in encounters with neighboring groups, there was evidence of individual variation in the frequency and context of male cooperative behavior. While central males participated in 100 % of the encounters, other resident males varied in their participation: 61–96 % of howling bouts, 61–90 % of vigilance bouts, and 67–80 % of intergroup fighting. Several factors may have contributed to both the high frequency and limited variation in noncentral male participation. These include:(1) Hermoso, who was unrelated to the other resident males in his group, may have used participation in collective action during intergroup encounters to increase his dominance status; (2) Ova and Rocky, who were sons of and therefore had shared a long-term bond with the central male Jose, supported him during 86–96 % of IEBs; (3) males who participated in howling and fighting during intergroup encounters may have used these behaviors to signal their fitness or mate quality to resident adult females as well as to females in neighboring groups; and (4) individual subordinate males may have developed strong nonkin social bonds. For example Jesus and Primo were each other's most common social partner and tended to coordinate their activities during resting, traveling, and feeding (Kowalewski 2007; Garber and Kowalewski 2011). In 84 % of cases, when Jesus engaged in an IEB, Primo also engaged in that behavior. This could reflect a form of reciprocity (offering coalitionary support during an intergroup encounter for other cooperative acts reciprocated in the future) or mutualism (each benefits by their coordinated behavior in defending against extragroup males).

In both howler groups approximately 11–25 % of intergroup encounters were characterized by at least one male defector. Thus we ask the question, how do central males who participated in 100 % of intergroup encounters overcome the CAP posed by free-riders? Based on ecological data (e.g., census of all trees, shrubs, and vines and phenological data) collected over the course of 18 months in the home range of howler Groups X and G, there was no evidence that access to feeding sites was a primary factor driving within-group or between-group howler social interactions (Kowalewski 2007). Rather, given evidence that in black and gold howler females present and solicit copulations from males, even males from neighboring groups are receptive during both fertile and non fertile periods, mate defense appears to be the major benefit to males of collective action during intergroup encounters (Kowalewski and Garber 2010). Differential involvement in encounters, especially those involving fighting, may be a result of asymmetrical benefits due to reproductive skew favoring the central male (the central male engages in 63 % of group copulations and sires the vast majority of group offspring) (Oklander et al. 2014). Thus, it appears that the central male receives the greatest benefit of collective action when at least one male joins him in intergroup encounters. This clearly shifts the cost/benefit ratio in favor of the central male over free-riders as long as there are other cooperating adult males. However, is there evidence that noncentral males who engage in collective action with the central male received a benefit over free-rider males? In an attempt to answer this question we note that although the central male engages in mate guarding resident females, all noncentral males were observed to mate with resident females during periods when they were likely to be fertile (Kowalewski and Garber 2010). Moreover, in *A. caraya* 96 % of intergroup encounters involved low cost defensive behaviors such as vigilance and howling. Although these behaviors continued for an average of 2 h per day, vigilance (which accounts for 76 % of time engaged in intergroup encounters) is not incompatible with resting which is presumed to be a period during which howlers devote energy to digesting structural carbohydrates present in leaves, bark, and other plant parts (Garber et al. 2014). Thus, through a combination of central male tolerance, male-male friendships, and female mate choice and female mating promiscuity, noncentral males who engage in joint actions with the central male may have increased breeding access to fertile females ensuring that offspring born into the group are sired by resident males (collective mate defense). Male howlers may escape the CAP and reduce incentives for free-riders under conditions in which the joint actions of multiple individuals (1) enhance group stability, (2) reduce opportunities for extragroup male takeovers or infanticide (see Van Belle and Bicca-Marques 2014 for a more detailed discussion of the role of infanticide in understanding sexual selection and mating strategies in *Alouatta*), and (3) increase the likelihood that resident males sire most or all group offspring. In addition, as the *per capita* cost of collective action decreases (either as a function of the number of participants or due to the fact that behaviors associated with collective action such as howling and vigilance have limited costs), the cost/benefit curve shifts away from free-riding as an effective strategy. In our two howler study groups, all adult males participated in the majority of intergroup encounters (>75 %). Assuming that participation in intergroup encounters represents an honest signal for other group members and a measure of competitive ability (males—coalition or migrant partner—and females—mating partner) (Zahavi 1990) or is an indication of enhanced competitive ability (Nakamichi and Koyama 1997; Nowak and Sigmund 1998; Roberts and Sherratt 1998; Nunn and Lewis 2001), then a free-rider strategy is expected to result in reduced reproductive success compared to participating resident group members.

7.9 Comparison with Atelines and Embracing Behavior

In contrast to *Brachyteles* and *Ateles*, which represent taxa characterized by female biased dispersal and male philopatry, in *Lagothrix* and *Alouatta* both males and females are reported to migrate from their natal group and therefore established groups are composed, at least to some degree of unrelated adults (Glander 1980; Bonvicino 1989; Mendes 1989; Clarke 1990; Rumiz 1990; Kinzey 1997; Crockett 1998; Pope 2000a, b; Di Fiore et al. 2011). In *Brachyteles* and *Ateles*, males remain in their natal group building strong associative and cooperative relationships, especially during feeding and when engaged in patrolling behavior associated with mate defense (Di Fiore et al. 2011). For example, in *Ateles paniscus chamek* association indices and the exchange of grooming were higher and more intense between adult males than in male–female and female-female dyads (Symington 1990). In the case of *Ateles geofroyi*, Fedigan and Baxter (1984) found a similar pattern of males engaging in affiliative interactions more often with other males than with females. This suggests the existence of strong male kinship bonds, as well as reciprocity and mutualism as the bases for cooperative and coordinated behaviors. Fedigan and Baxter (1984) also report that adult males exhibit embracing behaviors more frequently than adult females (males: 0.52 embraces per hour vs. females: 0.21 embraces per hour) and that this behavior occurs in the context of intergroup encounters. Male intrasexual embraces in *Brachyteles* and *Lagothrix* similarly occurs principally during intergroup encounters (Kavanagh and Dresdale 1975; Ramirez 1988; Strier et al. 2002; Strier 1994). In the case of male muriquis, grooming interactions are rare (Strier 1994). However, males do engage in coordinated and cooperative behaviors similar to those reported in *Ateles* (Di Fiore et al. 2011), are in close spatial proximity 54.5 % the time (proximity is defined as <5 m), engage in embraces (average rate of 0.11 embraces per hour), and cooperatively defend group females from extragroup males (no rate provided, Strier 1994; Strier et al. 2002).

Ritual embracing by resident males during intergroup encounters also occurs in several species of howler monkeys [*A. arctoidea* no rate provided (Sekulic 1982b); *A. palliata* 0.022 embraces per hour (Wang and Milton 2003), 0.016 embraces per hour (Dias et al. 2008); *A. caraya* 0.02 embraces per hour (Kowalewski 2007)]. In the case of *A. palliata* in Costa Rica, the alpha male initiated the majority of howler male embrace greetings (Zucker and Clarke 1986, 1998). However, on BCI, evidence supporting a dominance-correlated pattern of initiator and recipient greeting was not apparent, suggesting that embracing may be a measure of the strength of the social relationship among male dyads rather than an indicator of social status. Moreover, male mantled howlers emit a persistent and highly stereotypic vocal signal called the embrace greeting (Dias et al. 2008) that may serve to reaffirm social relations among new and preferred partners. Thus, there exist several similarities in male-male social bonds, greeting gestures, spatial proximity, and collective action during intergroup encounters and patrolling behavior across all ateline genera, suggesting the possibility that male collective action and male social affiliation represent behavioral patterns present in the common ancestor of all atelines.

Although quantitative data on the costs and benefits of intrasexual cooperative behavior in male howler monkeys are extremely scarce, we suggest that male affiliation in howlers is best described in terms of mutualism (shared immediate benefits to all or most participants) with the possibility of some level of reciprocal exchange (immediate costs and delayed benefits among long-term partners). Reciprocity could take the form of coalitionary support against intruder males by sets of preferred partners, but data on this are extremely limited. Here, we suggest that behaviors associated with intergroup encounters such as border patrolling, vigilance, collective roaring, and joint fighting may result in mutually beneficial cooperative behavior (mutualism) favoring collective action. We strongly encourage researchers to develop methods to more precisely quantify the costs and benefits to noncentral males of collective action and defection, and the importance of negotiated social relationships in the exchange and interchange of resources and services in primates.

7.10 The Challenge to Primate Socioecology

In conclusion, this study of collective action during intergroup encounters in male black and gold howlers provides a framework for understanding the advantages to adult males of residing in multimale multifemale groups and the benefits that individuals receive as members of a functioning social unit. Whereas traditional models of primate socioecology (van Schaik 1989; Sterck et al. 1997) have tended to emphasize the costs of group living, we feel that models of collective action and cooperation provide a more balanced approach in evaluating the interactive role of competitive and affiliative behaviors in understanding primate social behavior (Sussman and Garber 2011). Our results and previous findings (Kowalewski and Garber 2010; Garber and Kowalewski 2011) suggest that individual howlers may adjust their participation during IEBs in order to reduce the costs and enhance the benefits of collective action in maintaining reproductive access to resident females. How howlers negotiate the cost/benefit ratio of collective action remains unclear. However, we suggest that intergroup encounters are platforms where CAPs may arise, are negotiated, and solved through joint actions by central males and noncentral males. Future studies should focus on comparing differences in individual male and female behaviors associated with mate defense, collective action, access to reproductive partners, female mate choice, and individual male reproductive success in howlers that reside in unimale and multimale groups. Finally, the application of the collective action framework to identify the benefits and costs to individuals of joint participation in group activities offers critical insight into the evolution and function of affiliative behavior and social cooperation in primates.

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Chapter 8
Howler Monkey Positional Behavior

Dionisios Youlatos and Denise Guillot

Abstract This chapter reviews the positional behavior and grasping tail use in *Alouatta* with the specific goal of exploring behavioral diversity among members of this genus. Despite long-term studies, data on positional behavior derive mainly from five species (*Alouatta arctoidea*, *A. macconnelli*, *A. seniculus*, *A. palliata*, *A. caraya*) and indicate consistent patterns. A diagonal gait, a deliberate quadrupedal walk along single branches, clambering on multiple branches, and vertical climbing are the major locomotor modes, accompanied by varying rates of tail-assisted suspensory locomotion. These modes occur more frequently on small and medium branches of mainly horizontal inclination. Regarding feeding postures, above branch sitting is dominant, with below branch tail–limb assisted postures variably representing one third of the postural repertoire. Postural behavior mainly takes place on small branches of horizontal and oblique inclinations in tree peripheries. Data on tail use derive from only three species (*A. macconnelli*, *A. seniculus*, *A. palliata*) and consistently indicate that tail-supported behaviors occur more frequently in the context of feeding. Tail-assisted postures appear to increase access to food resources, providing stability and freeing the hands when procuring and processing food items. In addition, the tail is frequently recruited during travel and the context in which it is used depends on both locomotor mode and substrate size. Despite some underlying differences, this positional profile provides evidence that *Alouatta* evolved into specific adaptive strategies related to social and ecological factors enabling it to exploit multiple habitats throughout central and southern America.

Resumen Este capítulo revisa el comportamiento posicional y el uso de la cola en *Alouatta*, con el objetivo específico explorar la diversidad conductual en los miembros del género. A pesar de existir estudios de largo plazo, los datos del comportamiento posicional derivan mayormente de 5 especies (*Alouatta arctoidea*,

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A. macconnelli, *A. seniculus*, *A. palliata*, *A. caraya*), todas indicando patrones consistentes. Las formas de locomoción más comunes en el género son el desplazamiento diagonal, un cuadrupedalismo deliberado a lo largo de ramas, el trepado en múltiples ramas y la escalada vertical; todas éstas acompañadas de locomoción suspensoria asistida por la cola en distinto grado. Estos modos suceden con mayor frecuencia sobre ramas pequeñas y medianas, en su mayoría de inclinación horizontal. En cuanto a las posturas durante la alimentación, el sentado sobre las ramas parece dominante, así como el colgado debajo de las ramas asistido por cola y patas/pies; lo que representa un tercio de su repertorio postural. Los comportamientos posturales tienden ocurren principalmente en pequeñas ramas horizontales y oblicuas de la periferia de los árboles. Los reportes de uso de cola derivan de sólo 3 especies (*A. macconnelli*, *A. seniculus*, *A. palliata*) e indican que las conductas apoyadas por la cola ocurren más frecuentemente en contextos de alimentación. Este tipo de posturas asistidas por la cola se incrementan durante el acceso a la comida, al proporcionar mayor estabilidad y libertad en las manos para procurar y procesar los alimentos. Además, la cola es frecuentemente retraída durante el desplazamiento y el contexto en el cual se usa depende tanto del modo de locomoción como del tamaño del sustrato. A pesar de diferencias subyacentes, los perfiles posicionales evidencian que *Alouatta* evolucionó estrategias adaptativas específicas relacionadas con factores sociales y ecológicos que le permite explotar múltiples hábitats a lo largo de Centro y Sudamérica.

Keywords Howler monkey • *Alouatta* • Locomotion • Postures • Prehensile tail

8.1 Introduction

The atelines form a unique group among platyrrhines as they are the largest and most widely distributed New World primates. This monophyletic group is composed of four (or five) genera: *Alouatta*, *Ateles*, *Lagothrix*, (*Oreonax*), and *Brachyteles* (Rosenberger and Strier 1989; Groves 2001; but see Rosenberger and Matthews 2008). In general, they all share a set of derived morpho-behavioral features, such as large body size (5–12 kg), a relatively long prehensile tail with a friction pad, a diet composed of leaves and fruit, increased rates of hind limb suspensory postures, and a tendency for forelimb suspensory locomotion, the latter exemplified in *Ateles* and *Brachyteles* (Rosenberger and Strier 1989; Strier 1992). Nevertheless, the group also exhibits a remarkable diversity in morphology and behavior, with *Alouatta* being the most distinctive form. In fact, *Alouatta* diverged early (~15.5 mya) from the other atelines and evolved remarkable adaptations to an energy-minimizing strategy, increased folivory, restricted home and day ranges, compact social systems, and increased vocal communication (Milton 1980; Rosenberger and Strier 1989; Strier 1992; Hartwig et al. 1996; Jones 2008; Halenar 2011). Related to these adaptations, *Alouatta* adopted a novel locomotor and postural strategy, characterized by increased rates of above-branch deliberate crouched quadrupedalism along and across substrates, cautious bridging between crowns and substantial proportions of tail-assisted hind limb suspended postures (see summaries in Jones 2008; Guillot 2009). This behavioral profile evolved early in *Alouatta* evolution and very likely contributed to its remarkable distributional expansion north towards Mesoamerica, and south, towards the southern cone, exploiting a wide variety of habitats and forest types.

Locomotion and postures (=positional behavior; Prost 1965) play a central role in primate evolution (Washburn 1951; Fleagle 1988; Garber 2011; Youlatos and Meldrum 2011), as they contribute to fitness by providing access and manipulation of food sources, increasing vigilance and enabling predator avoidance, allowing access to mates and enhancing social interactions (Bock and von Walhert 1965). Therefore the study of positional behavior is important not only for elucidating form–function relationships within evolutionary lineages but also for understanding their adaptive significance (Cant 1992). In this way, knowing the positional behavior of atelines is essential for interpreting the evolution of behavioral and ecological diversity within the clade. Ateline positional diversity is reflected by a gradient from the more quadrupedal *Alouatta* to the highly suspensory *Ateles* and *Brachyteles*, while the intermediate nature of *Lagothrix* has been increasingly recognized (Fleagle and Mittermeier 1980; Gebo 1992; Guillot 2009; Schön Ybarra 1984; Youlatos 1998; Cant et al. 2001, 2003; Jones 2008; Youlatos 2008; Youlatos and Meldrum 2011). This notable diversity is accompanied by an analogous morphological gradient in their postcranial skeleton, and by equally diversified social and ecological traits that denote morphological and socioecological convergence with early catarrhines, hominoids, and modern great apes (Erikson 1963; Cartmill and Milton 1977; Fleagle and Simons 1982; Temerin and Cant 1983; Rosenberger and Strier 1989; Strier 1992; Rose 1994; Larson 1998; DiFiore and Campbell 2007; Halenar 2011). This important convergence between Old World hominoids and atelines, along with their highly derived nature, promoted a series of positional studies of the members of the group and more particularly *Alouatta*, since the mid 70s.

This chapter reviews this evidence on the positional behavior of the different species of *Alouatta*. Although *Alouatta* was considered to exhibit the least versatile positional behavior compared to other atelines (e.g., Erikson 1963; Rosenberger and Strier 1989), the fact that it has the widest distribution of any other platyrrhine and has invaded very different habitats, lends support to the contrary. Therefore, our aim is to identify any similarities and/or differences across species and habitats by reviewing in detail the available data from mainly published material. We are confident, that this review will contribute to the understanding of the evolution of the unique positional behavior of the genus and its adaptive importance. For these purposes, initially, we will analyze the different locomotor and postural modes exhibited by *Alouatta*, and subsequently evaluate the profiles of the different species, by using uni- and multivariate analyses.

8.2 Locomotor Modes

This part describes briefly the different locomotor modes that have been observed in *Alouatta*. These patterns refer to howlers as a genus, despite the fact that they may derive from certain species that have been studied in detail in the field.

8.2.1 Quadrupedalism

Quadrupedalism is generally defined as pronograde progression involving all four limbs above and along a single horizontal or near-horizontal support (Hunt et al. 1996). Although quadrupedalism is the dominant locomotor mode exhibited by much of the Primate Order (Rose 1973), qualitative descriptions characterize howler quadrupedalism as unusual in that it is particularly crouched, slow, deliberate and cautious (Carpenter 1934; Richard 1970; Mendel 1976; Cartmill and Milton 1977; Fleagle and Mittermeier 1980; Cant 1986; Prates et al. 1990; Bicca-Marques and Calegaro-Marques 1995). Reliance on quadrupedalism also appears to vary across habitats, seasons and between species of howler monkeys. Observations of fast quadrupedal running appear to be limited to larger supports while slow, careful movements are common on the smaller peripheral branches and vines (Richard 1970).

Both qualitative and quantitative studies reveal several distinct kinematic features of howler quadrupedalism that appear unique to this genus. Stride lengths are particularly long, the stance phase comprises nearly two thirds of the gait cycle and some joint movements are delayed compared to those observed in other primates (Youlatos and Gasc 2011). These features contribute to the slow, deliberate appearance of howler quadrupedal progression. In addition, howlers exhibit considerable flexion of the elbow joint and protraction of the forelimb contributing to their crouch movements during compliant walking (Fig. 8.1a; Schmitt 1999; Youlatos and Gasc 2011). The supporting hind limb is externally rotated at the hip and bowed out at the knee (Grand 1968; Youlatos 1994) and the elbows are almost never fully extended during quadrupedal walking and standing (Gebo 1992). The combination of the externally rotated hip, bowed knee, and bent elbow contribute to the side-to-side swaying motion of the shoulders and hips (Gebo 1992).

Like other primates, howlers rely primarily on diagonal sequence gaits (91.9 % of observed strides examined by Youlatos and Gasc 2011) in which touchdown of the hind limb is followed by touchdown of the opposite forelimb but lateral sequence gaits, in which touchdown of the hind limb is followed by touchdown of the same side forelimb, is also observed.

8.2.2 Vertical Ascent and Descent

Howler ascents and descents along a single vertical or near vertical support (within roughly 22° of vertical) involve a variety of locomotor responses to the mechanical challenges of movement along steep supports (Fig. 8.1b, c). While clambering

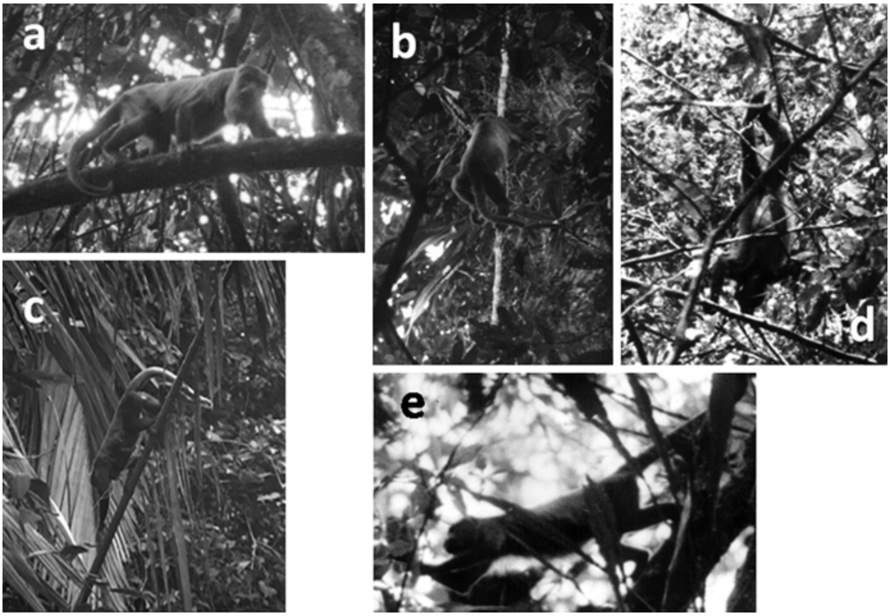

Fig. 8.1 Howler locomotor modes: quadrupedal walk (**a**), vertical ascent (**b**), oblique descent (**c**), downwards oblique clamber (**d**), and horizontal bridge (**e**)

behaviors are also used to move up or down through the canopy, vertical ascents and descents involve quicker, more direct routes on larger substrates. Drops would be the most rapid way to change height in the canopy, but howlers tend to avoid these behaviors and are significantly more likely to use descents (Guillot 2009). While flexed elbows and knees characterize most quadrupedal movements, this degree of flexion seems to deepen during steep ascents and descents. Descents are typically head-first (Guillot 2009) and may involve diagonal sequence quadrupedalism, but bounding descents, in which the forelimbs move forward simultaneously followed by the simultaneous movement of the hind limbs, also occur during head-first descents down particularly steep vertical supports (Youlatos and Gasc 1994). The tail plays a crucial role in slowing and controlling the animal's progression while bounding (Youlatos and Gasc 1994).

8.2.3 Clamber

This locomotor category, sometimes referred to as scramble or lumped into a broad "climbing" category, is distinguished from vertical ascents and descents by progression over multiple non-parallel substrates that may be oriented in numerous directions (Fleagle and Mittermeier 1980; Hunt et al. 1996; Cant et al. 2001). Clambering often involves irregular patterns of limb use and this mode occurs more frequently when moving among small terminal branches during feeding (Schön Ybarra 1984; Gebo 1992). It often involves agile movements requiring notable joint mobility where both shoulders and hips are habitually abducted (Fig. 8.1d; Gebo 1992; Youlatos 1994). Clambering occurs among smaller branches and twigs (e.g., Youlatos 1994) and due to the irregularity of support orientation and size, the animal tends to progress relatively slowly (Schön Ybarra 1984).

8.2.4 Bridge

Bridging refers to a gap crossing behavior in which the forelimbs reach out to grasp the destination supports while the hindlimbs and tail retain their grasp until a secure transition across the space can be made (Schön Ybarra 1984; Youlatos 1993; Hunt et al. 1996). Although quadrupedalism may be the dominant locomotor mode during the general behavioral contexts of feeding, foraging and travel, bridging is the dominant locomotor mode during movements between trees when negotiating these gaps (Prates et al. 1990; Bergeson 1998; Guillot 2009). Bridging also occurs significantly more often during the context of travel due to the necessity of moving between trees and usually from and to small supports (Youlatos 1993).

In howlers, bridging is often initiated by standing above a fairly stable support with the hindlimbs and tails attached while the forelimbs reach out to grasp the destination (Schön Ybarra 1984; Youlatos 1993). The animal may attempt to lunge across a gap or shift its body weight back and forth causing the supporting branch to sway towards the destination and, thus, shorten the gap (Schön Ybarra 1984; Youlatos 1993). Howlers bridge cautiously, frequently pausing before and during the movement and will often not relinquish the initial supports until they have grasped destination supports with multiple limbs (Fig. 8.1e; Cartmill and Milton 1977; Youlatos 1993). In most cases, the arms are raised either at or above the level of the shoulder (Youlatos 1993, 1994). Adult howlers use bridging behaviors to cross gaps more often than younger individuals who are more likely to leap (Bezanson 2006). Younger individuals are also often observed to manage the challenge of these arboreal discontinuities by running across the backs of bridging adults (Bernstein 1964; Richard 1970), or, more rarely, when mothers manipulate branches to create bridging distances (Koch and Bicca-Marques 2004).

8.2.5 Leap and Drop

Both leaps and drops have an airborne phase; however, leaps are produced by powerful propulsive action of the hindlimbs and have an appreciable horizontal trajectory, while drops involve a purposeful fall from a support (Hunt et al. 1996; Cant et al. 2001). In general, these airborne behaviors are not very frequent for howlers (Mendel 1976; Fleagle and Mittermeier 1980; Guillot 2009). These cautious animals tend to avoid leaps over long distances (Gebo 1992). While leaps of 3–4 m have been sometimes observed (Carpenter 1934), shorter leaps appear to represent the majority (e.g., Youlatos 1994). Leaps are usually initiated from a crouched position in which the limbs are deeply flexed (Schön Ybarra 1984; Youlatos 1994). The animal typically shifts its weight back and forth before forcefully and very rapidly extends its limbs (0.5 s; Youlatos 1994); the limbs will remain extended during the airborne phase (Schön Ybarra 1984; Youlatos 1994). More dynamic initiations, such as running or rapid clambering, have been also recorded albeit less often. The destination is often the flexible terminal branches of the adjacent tree where the animal tends to land forelimbs-first or on all four limbs nearly simultaneously (Schön Ybarra 1984; Youlatos 1994). Leaps, drops, and the bridging behaviors, described above, are all used to negotiate the discontinuities in arboreal pathways and these behaviors tend to increase when howlers are moving between trees (Guillot 2009).

8.2.6 Miscellaneous Modes

Arboreal bipedal locomotion and the tail-assisted forelimb suspensory locomotion that characterize other ateline primates are extremely rare or not observed in *Alouatta* (Richard 1970; Cartmill and Milton 1977; Gebo 1992; Bicca-Marques and Calegaro-Marques 1995; Guillot 2009). However, howlers may sometimes be observed progressing short distances in an *inverted quadrupedal* fashion. During this behavior, the animal is suspended supinograde below single middle-sized supports. All four limbs are under tension and the tail is frequently wrapped around the substrate. The individual moves a short distance using a diagonal sequence gait and typically ends the sequence by hoisting itself on top of the supporting branch. In more open habitats, howlers will descend to the ground where they occasionally incorporate bipedalism over short distances into bouts of quadrupedal galloping (Schön Ybarra 1984).

8.3 Postural Modes

This part describes briefly the different postures that have been observed in *Alouatta*. These patterns refer to howlers as a genus, despite the fact that they may derive from certain species that have been studied in detail in the field.

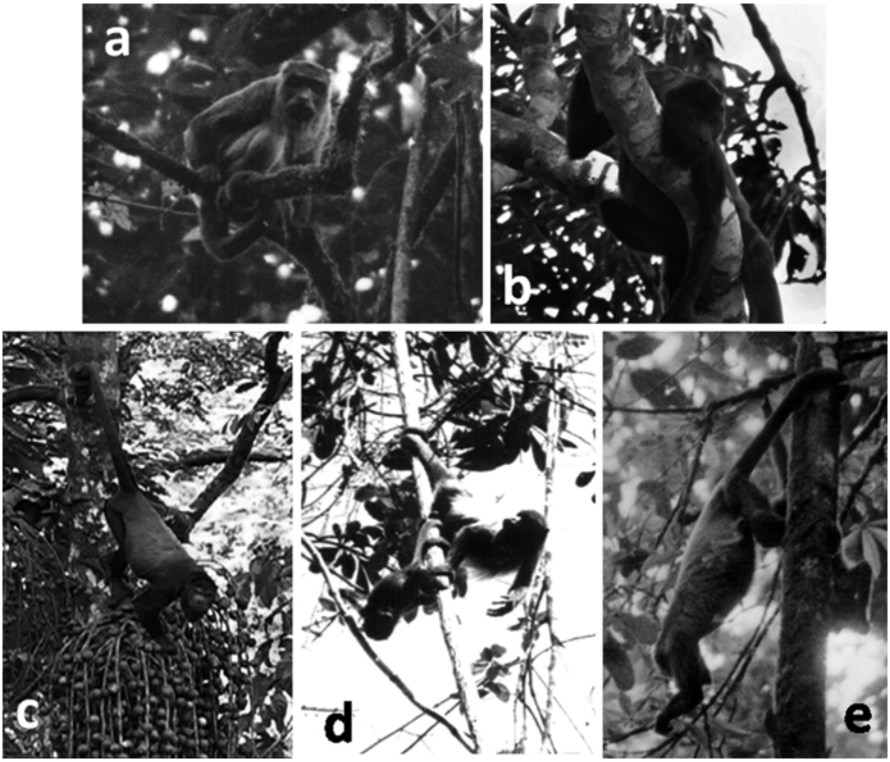

Fig. 8.2 Howler postures: Sitting (**a**), recline (**b**), tail and hind limbs hanging postures (**c–e**)

8.3.1 Supported Postures

This group of postures usually refers to stances, where the animal is positioned above substrates. The animal's weight is carried by a variety of limbs, or some other part of the body, and supported by the branch. In howlers, these postures correspond to sit, squat, stand, bipedal stand, and recline or lie.

Among anthropoids the seated posture is very frequent (Rose 1974), and usually involves two separate postures that differ significantly, not only biomechanically but also in the context in which they occur. *Sit or Ischial Sit* refers to the seated posture where the majority of body weight is borne by the rump, and the hind limbs may be either be flexed and resting upon the substrate or extended and hanging freely (Fig. 8.2a). This posture usually involves the use of the prehensile tail anchoring on the same branch or below (Rose 1974; Grand 1977; Youlatos 1994; Lawler and Stamps 2002; Bezanson 2009). Substrates used are frequently medium-to-large horizontal or subhorizontal branches that are usually located in or near the center of the tree crown (Mendel 1976; Prates et al. 1990; Youlatos 1994). It frequently occurs during long rests or sleeping as suggested by Urbani et al. (2011). In this way, the animal is well supported mechanically.

The other seated posture is *Squat or Nonischial Sit*. In this posture, the animal sits at right angles to the length of the substrate, while the hind limbs are usually particularly flexed and the hind feet firmly grasp the substrate (Hunt et al. 1996). In this case, no weight is borne by the rump. This posture occurs frequently on relatively small horizontal or subhorizontal substrates or twig entanglements in the periphery of tree crowns principally during feeding. As this posture is rather dynamic, extra stabilization is frequently provided by the prehensile tail, which usually grasps firmly on a different branch, generally located above the supporting substrates (Schön Ybarra 1984; Youlatos 1994; Lawler and Stamps 2002). Furthermore, the forelimb may also be frequently used, grasping above or at the same level with the animal securing balance.

Quadrupedal and Tripedal Stand are postures that are relatively common in howlers, especially during feeding behavior. In these postures, the body is held pronograde and basically parallel to the substrate. Limbs can be either partially flexed or particularly flexed presenting a crouched stance. Habitually, the elbows and knees are held abducted (Schön Ybarra 1984). Contact with the substrate is assured by the firm grasps of both hands and feet. However, when the supportive substrate is large the extremities are simply placed on it. When one forelimb is not in contact with the supportive substrate(s) the posture is referred to as tripedal. In this case, the nonsupported hand may be either free, manipulating food items, or providing additional support upon another substrate, usually in front of or above the animal. The tail is also considerably used, anchoring either above or below the supportive substrates (Prates et al. 1990; Lawler and Stamps 2002). Both postures are habitually used upon small and medium branches.

Bipedal Stand is a rather infrequent posture and is practically used during feeding (Youlatos 1998). The body is kept orthograde, but may frequently lean slightly forward. Support is assured by the hind limbs, which are extended at the hip, can be well flexed at the knee, while stability is assured by the powerful grasping of the hind feet (Schön Ybarra 1984). Additionally, the tail is often used and placed on the same supportive substrate or onto another above. During bipedal stand, at least one of the forelimbs provides support by grasping on nearby substrates.

Recline, *Lie*, or *Sprawl* represent a group of postures that are mainly used during rest and sleep on medium and large horizontal substrates (Youlatos 1994). In these postures contact with the supportive substrate is extensive and assured by the back, the belly or the flanks of the animal (Fig. 8.2b). Accordingly, the body may be either prono- or supinograde. The fore- or hind feet may or may not provide further support upon the main substrate and sometimes may hang freely. During these supported postures tail use is common, and seems to culminate when the animals are sprawling. This latter posture is particularly common during long resting bouts.

8.3.2 Suspended Postures

This group incorporates a variety of postures, where the animal hangs below a sub(super) strate by a combination of limbs, always involving the active grasp of the prehensile tail. Three postures have been thus far reported for howlers in the field and are, by order of frequency, tail-hind limb(s) hang, tail-only hang, and tail-hind limb(s)-forelimb hang (Schön Ybarra 1984; Gebo 1992; Youlatos 1994; Youlatos and Gasc 2001; Prates and Bicca-Marques 2008; contra Bezanson 2009). In these postures, the body is mainly held vertical or oblique and only seldom pronograde (Schön Ybarra 1984; Guillot 2009). Transitions between postures often involve very agile, flexible use of the limbs requiring a wide range of excursions particularly at the hips, knees, ankles, and tail. These agile movements enable the animal to maintain multiple secure holds on available supports.

Tail-Hind Limb(*s*) *Hang* (Fig. 8.2c–e) actually represents an array of suspended postures that always involve the tail and one or both hind limbs. In field studies, this posture is usually defined this way, although tripod may also be included in this category (Hunt et al. 1996). Tail hind limbs hang usually occurs below small branches in tree peripheries (Youlatos 1994). The tail always grasps with its curled extremity on a substrate and is always hyperextended and under tension (Youlatos 1994; Lawler and Stamps 2002). Usually both hind limbs are involved. Single hind limb grasp is much less common (Youlatos 1994). In all cases, the hind limbs are under tension and are usually extended at the hip and knee and the hind feet are plantar flexed and strongly inverted. Secure grasping is assured by the powerful grip of toes and hallux around either the same supportive substrate on which the tail is attached or nearby branches. The body is oriented vertically or oblique, and is actively moving in space reaching and manipulating food items below the animal. In many cases of "hind limb assisted hanging" postures, the hind limbs may be under pressure, maintained semi-extended at the hip and knee and pressed against the substrate, transferring part of the weight rearwards. In this case, the posture has been termed *Inverted Bipedal* (Bergeson 1998) or *Horizontal Tripod* (Hunt et al. 1996; Bezanson 2009) and the body is oriented horizontally or oblique downwards. In all cases, the body and hind limb positions in space usually depend on the arrangement of the available substrates and the location of the food item.

Tail-Only Hang is self-explanatory and involves the active and powerful grasp of the tail with no other limbs involved. In some studies, it has been also defined as Tail free (Schön Ybarra 1984; Schön Ybarra and Schön 1987). It is usually shared below small and medium sized branches (Youlatos 1994). The tail is under tension and hyperextended and grasps by the naked friction pad at its extremity. The body is usually held vertically and occasionally pronograde and moves in space by the action of pelvic and tail musculature, which seems to regulate body inclination and direction in space. The hind limbs hang freely while the forelimbs reach and manipulate food (Prates et al. 1990).

Tail-Hind Limb(*s*)*-Forelimb Hang* also represents a variety of postures that involve any combination of fore- and hind limbs along with the grasping tail. In a series of field studies, this mode is defined as (postural) *Bridge* (Bicca-Marques and Calegaro-Marques 1993; Kowalewski et al. 2002; Prates and Bicca-Marques 2008). The hyperextended tail grasps with its extremity and assures suspension, bearing the major part of body weight. Hind limbs are usually extended, knees usually abducted, and feet inverted and plantar flexed grasping powerfully the same or nearby substrates. The grasping forelimb is used in variable positions. It may be placed at the shoulder level or below and the elbow is frequently semi-extended and partially abducted. Forefoot grasping occurs via a zygodactylous or powerful grasp on a substrate well below the grasping tail and below or at level with the grasping hind feet. The body is habitually kept oblique and sometimes pronograde. As in the other hanging postures, body and hind limb position in space, and consequently joint movements, actually depend on the arrangement of the available substrates and the location of the food item.

8.4 Positional Behavior of *Alouatta* in the Wild

The locomotor and postural behaviors of *Alouatta* have been extensively studied across its distributional range since the 70s. This is partly due to its very wide geographical distribution and use of diverse habitats, from primary to secondary rain forests, as well as much drier environments and savanna-forest interfaces. Despite this fact, we only know a fraction of its positional behavior, because only seven out of the 14 species have been studied thus far. Below we review these field studies of locomotor and postural behavior in order to outline several general patterns for the genus and/or differences across species (Tables 8.1 and 8.2).

The locomotion of the Yucatán black howler monkey (*A. pigra*) is known only from a short study in the dry forests of Tikal in Guatemala (Cant 1986). In contrast, the mantled howler monkey (*A. palliata*) has been extensively studied in a riparian forest (La Pacifica: Gebo 1992), a dry forest in Santa Rosa National Park (Bergeson 1998), and premontane wet forests (La Selva: Bergeson 1998; La Suerte: Bezanson 2009) in Costa Rica, as well as in a wet forest in Barro Colorado Island, Panama (Richard 1970; Mendel 1976). The ursine howler monkey (*A. arctoidea*) has been studied in a mixture of shrub and tree patches in Hato Masaguaral, Venezuela (Schön Ybarra 1984; Schön Ybarra and Schön 1987). The positional behavior of the Colombian red howler monkey (*A. seniculus*) is known from two wet rainforest sites in Ecuador, the Tiputini Biodiversity Station (Guillot 2009) and the Proyecto Primates in Yasuní National Park (Youlatos 2004). The Guianan red howler monkey (*A. macconnelli*) has been studied in wet rainforests in Nouragues, French Guiana (Youlatos 1994, 1998; Youlatos and Gasc 2001) and in Raleighvallen-Voltzberg, Surinam (Fleagle and Mittermeier 1980). The black-and-gold howler monkey (*A. caraya*) has been studied in a semi-natural forest in Estância Casa Branca (Bicca-Marques and Calegaro-Marques 1995), an orchard forest in Estabelecimento Nossa Senhora da Conceição (Prates and Bicca-Marques 2008) in Rio Grande do Sul, Brazil, and in a flooded forest on Isla Brasilera, Paraná, in Northern Argentina

(Kowalewski et al. 2002). Finally, a single study concerns the southern brown howler monkey (*A. guariba clamitans*) in a seasonal temperate forest in Rio Grande do Sul in Brazil (Azevedo and Bicca-Marques 2007).

These studies have provided valuable information on the locomotor and postural behavior of the genus. Some species have been well studied (e.g., *A. palliata*) in many different locations, while the positional behavior of others (e.g., *A. pigra*, *A. guariba*, *A. arctoidea*) is known only from single reports and, therefore, these results should be considered with caution. On the other hand, all these studies differ between them in terms of data collection methods (bout, instantaneous sampling), forest structure (wet or dry, primary or secondary, savanna-woodland interface, premontane or lowland, etc.), study periods (wet or dry seasons, actual duration of field study), behavioral context of positional profiles (travel, feed, combined for locomotion, feed, rest or combined for postures), and positional mode definitions (specific or generalized definitions) that render comparisons particularly difficult. Despite this flaw, we attempt to provide some general lines based on the comparable available data. For these reasons, we used locomotor and postural profiles during travel and feed/foraging behaviors respectively, where available. Additionally, we tried to combine the available data in comparable grouped modes, based on the different definitions provided by the authors and eventually recalculating percentages, when feasible. These new percentages, available in Tables 8.1 and 8.2, were log-transformed and subsequently used for comparing the species between them through ANOVAs.

8.4.1 Locomotor Behavior

All studies of the positional behavior of *Alouatta* in the wild seem to emphasize the pronograde quadrupedal nature of howler locomotion. Whether quadrupedalism is defined only as quadrupedal walk and run or also involves vertical ascent/descent and pronograde clamber in all directions, it certainly represents the major locomotor mode of *Alouatta* (Table 8.1). When only walk and run are summed up, the available data show that the *A. guariba* and *A. palliata* are major walkers/runners, while *A. arctoidea* and *A. macconnelli* the least ($F = 1.04$, $p = 0.507$). Additionally, all studies show that walk is more frequent than run (Table 8.1; see also discussions in Cant 1986; Youlatos 1994; Youlatos and Gasc 2011), and this may partly support the overall energy conserving strategy of howlers. When walk, run, vertical movements, and clamber are considered together as quadrupedalism, they practically monopolize the locomotor behavior of *Alouatta* (70.8–96 %, Table 8.1). *A. pigra* appears to be the most quadrupedal species along with *A. macconnelli* and *A. palliata,* while *A. arctoidea* has scored the lowest rates ($F = 1.12$, $p = 0.444$).

When climbing, *sensu lat*o: i.e., vertical movements along single supports and clamber to all directions, is considered, it also represents a considerable proportion of howler locomotion, and *A. seniculus* and *A. arctoidea* scored the highest percentages (Table 8.1). For most species, the high rates are mainly due to clamber, as

Table 8.1 *Alouatta* locomotor behavior: percentages of recorded modes of the different species (where available, locomotor profiles are based on data for traveling; percentages have been recalculated based on mode definitions from the authors and recombined according to our grouped patterns)

Species	*pigra*	*palliata*			*arctoidea*	*seniculus*		*macconnelli*		*caraya*			*guariba clamitans*
Study site	Tikal	BCI	La Pacifica	La Suerte	Hato Masaguaral	Tiputini	Yasuní	Ralleighvallen Voltzberg	Nouragues	ECB	ENSC	Isla Brasileira	Barra de Ribeiro
Country	GUA	PAN	CR	CR	VEN	ECU	ECU	SUR	FRG	BRA	BRA	ARG	BRA
Study	1	2	3	4	5	6	7	8	9	10	11	12	13
Method	inst	inst	bout	inst	inst	inst	inst	bout	inst	inst	inst	inst	inst
Quadrupedal walk		70.0	47.0	80.9	25.4	30.9	50.9	80.0	37.3	66.4	37.9	59.2	65.0
Quadrupedal run	96.0	5.0		0.8	2.4					2.5	3.6	3.2	9.0
Climb up		9.0	37.0	7.9	45.1	14.5	5.2	16.0	5.5	19.0	15.3	21.2	9.0
Climb down		7.0				18.5					14.0		
Clamber						24.6	22.8		38.4				
Leap		12.3	4.0	2.4	12.3	1.5	2.5	4.0	2.3	2.7	16.8	1.6	14.0
Drop				0.8		0.2			0.5				
Bridge	4.0	3.3	10.0	4.8	3.3	9.3	16.0		13.5	9.9	12.5	14.8	3.0
Bimanual		9.8	1.0	2.4	9.8	0.1	2.4						
Quadrupedal suspensory			2.0			1.1			0.2				
Tail swing									0.3				

Countries: *ARG* Argentina, *BRA* Brazil, *CR* Costa Rica, *ECU* Ecuador, *FRG* French Guiana, *GUA* Guatemala, *PAN* Panama, *SUR* Suriname, *VEN* Venezuela

Method: bout; inst: instantaneous sampling

Studies: 1: Cant (1986); 2: Mendel (1976); 3: Gebo (1992); 4: Bezanson (2009); 5: Schön Ybarra (1984); 6: Guillot (2009); 7: Youlatos (2004, unpublished); 8: Fleagle and Mittermeier (1980); 9: Youlatos (1994); 10: Bicca-Marques and Calegaro-Marques (1995); 11: Prates and Bicca-Marques (2008); 12: Kowalewski et al. (2002); 13: Azevedo and Bicca-Marques (2007)

Table 8.2 *Alouatta* postural behavior: percentages of recorded postures of the different species (postural profiles are mainly based on data for feed/forage; percentages have been recalculated based on mode definitions from the authors and recombined according to our grouped patterns)

Species	*palliata*				*arctoidea*	*seniculus*		*macconnelli*	*caraya*			*guariba clamitans*
Study site	BCI	La Pacifica	Santa Rosa	La Suerte	Hato Masaguaral	Tiputini	Yasuní	Nouragues	ECB	ENSC	Isla Brasileira	Barra de Ribeiro
Country	PAN	CR	CR	CR	VEN	ECU	ECU	FRG	BRA	BRA	ARG	BRA
Study	1	2	3	4	5	6	7	8	9	10	11	12
Method	inst	bout	inst	inst	inst	inst	inst	bout	inst	inst	inst	inst
Sit	75.0	53.0	56.8	63.8	42.6	40.1	47.9	57.5	62.0	61.4	75.0	66.0
Squat				1.3								
Quadrupedal stand	3.0	20.0	13.5	1.8	10.1	28.7	11.4	13.2	5.5	9.4	4.0	7.0
Tripedal stand				1.7	4.0							
Crouch				1.5								
Bipedal		2.0		0.3	15.8			4.3				
Recline		12.0			3.4	0.8	1.3	0.1	1.0	0.6	13.0	
Tripod			8.6	6.0								
Tail suspensory	20.0		8.7	20.5	6.0	30.4	7.3	2.3	15.0	4.1	3.0	10.0
Tail HL suspensory		11.0	7.3		18.1		20.5	20.0				
Tail HL + FL suspensory	2.0	3.0	6.3	3.1			3.0	1.2	17.0[a]	24.4[a]	5.0	17.0[a]
Other			8.4									

Countries: *ARG* Argentina, *BRA* Brazil, *CR* Costa Rica, *ECU* Ecuador, *FRG* French Guiana, *PAN* Panama, *SUR* Suriname, *VEN* Venezuela

Method: bout; inst: instantaneous sampling

Studies: 1: Mendel (1976); 2: Gebo (1992); 3: Bergeson (1998); 4: Bezanson (2009); 5: Schön Ybarra (1984); 6: Guillot (2009); 7: Youlatos (2004, unpublished); 8: Youlatos (1994); 9: Bicca-Marques and Calegaro-Marques (1995); 10: Prates and Bicca-Marques (2008); 11: Kowalewski et al. (2002); 12: Azevedo and Bicca-Marques (2007)

[a] Termed as "bridging" by the authors

revealed by detailed mode descriptions (Schön Ybarra 1984; Schön Ybarra and Schön 1987; Gebo 1992) and available data, where clamber usually accounts for over 20 % of all locomotor observations (Youlatos 1994, 1998; Youlatos and Gasc 2001; Guillot 2009; Table 8.1). On the other hand, vertical climb is less used, with shared proportions of upward and downward movements (Table 8.1).

Leaping is not a common locomotor mode in *Alouatta*. This is depicted by the relatively low rates that are used across species (Table 8.1). *A. guariba* and *A. arctoidea* showed high rates of leaping, as well as *A. caraya*, but with a great variability across studies (Table 8.1). *A. seniculus* was the species that apparently leaps less ($F=0.85$, $p=0.581$).

On the other hand, bridging is more regularly but variably used across species. *A. caraya*, *A. seniculus*, and *A. macconnelli* have scored quite high rates showing that this mode is broadly used. In contrast, this was not the case for *A. guariba* and *A. arctoidea* which used it infrequently ($F=1.82$, $p=0.291$; Table 8.1). If bridge is included in a broader suspensory locomotor category involving bimanual suspension, hoist, inverted quadrupedalism or tail swinging, the same species, with a slightly different order, also rank first (*A. seniculus* and *A. macconnelli*, followed by *A. caraya*; Table 8.1). In contrast, *A. pigra* and *A. guariba* seem to be the less suspensory species ($F=1.69$, $p=0.0291$).

8.4.2 Postural Behavior

In terms of postural behavior, all studies demonstrate the relatively high frequency of sitting during feeding behavior in *Alouatta* (Table 8.2). In effect, sit (combining ischial sit and squat) seems to represent almost half of all postural events. More precisely, *A. caraya*, *A. palliata*, and *A. guariba* used sitting extremely frequently, while *A. seniculus*, *A. macconnelli*, and *A. arctoidea* sat much less (Table 8.2, $F=2.16$, $p=0.206$). An inverse pattern arises, when stand is considered (Table 8.2). *A. seniculus*, *A. macconnelli*, and *A. arctoidea* use quadrupedal and tripedal stand regularly, whereas this mode is not common in *A. caraya*, *A. palliata*, and *A. guariba* ($F=2.26$, $p=0.194$).

In contrast, suspensory postures are used in a more or less uniform way by all species, with *A. seniculus*, *A. macconnelli* scoring the higher rates (Table 8.2; $F=0.261$, $p=0.934$). A finer analysis of specific hanging postures is extremely difficult as most studies do not discern the limbs involved during suspension. However, the studies with available comparative data show that *A. palliata* and *A. seniculus* seem to frequently employ tail-only hang, *A. seniculus* and *A. macconnelli* use tail and hind limbs hang regularly, and *A. guariba* and *A. caraya* are the species, which engage their forelimbs more frequently during hanging (Table 8.2).

8.4.3 Habitat Use

Alouatta is a relatively large-bodied platyrrhine mainly exploiting the forest canopy and sharing its traveling and feeding activities between the middle and upper layers (Mendel 1976; Fleagle and Mittermeier 1980; Gebo 1992; Stevenson and Quiñones 1993; Youlatos 1994, 1998, 2004; Youlatos and Gasc 2001; Almeida-Silva et al. 2005; Garber and Jelinek 2006; Agostini et al. 2010). In few places, where different howler species are found syntopically (*A. guariba* and *A. caraya*), the two species tend to use different forest strata to avoid potential competition, but are still confined to the higher levels of the canopy (Agostini et al. 2010). All above studies have also shown that the higher canopy layers are used during both traveling and feeding. The high canopy layers are characterized by a rather uniform and relatively continuous structure of relatively large and stable branches in the centers and a dense network of intertwined smaller branches in the peripheries that provide a relatively even milieu for howlers to move securely either within or across tree crowns (Oldeman 1974; Grand 1984). During feeding, most howler species also use the high canopy layers, where most of the food items are located (*A. seniculus*: Stevenson and Quiñones 1993; *A. macconnelli*: Fleagle and Mittermeier 1980; Julliot and Sabatier 1993; Youlatos 1994; *A. palliata*: Urbani 2003; Garber and Jelinek 2006). Fruit and flush leaves that comprise the majority of howler diet are located in the higher forest strata and howlers tend to forage and consume these items there. A few species (*A. palliata* in Costa Rica: Gebo 1992) have been found to use lower layers. Feeding in lower canopy layers may also depend on food type. Thus in *A. seniculus*, feeding on fruit and leaves mainly occurs high in the canopy, whereas feeding on other items, such as soil or arthropods, may occur at the lower parts of the forest and even on the ground (Izawa 1993; Stevenson and Quiñones 1993; Blake et al. 2010). Ground use has been reported for howler species such as *A. seniculus* (Izawa 1993; Stevenson and Quiñones 1993; Blake et al. 2010), *A. caraya* (Prates and Bicca-Marques 2008), *A. arctoidea* (Schön Ybarra 1984), and *A. palliata* (Glander, in Gebo 1992), despite their primarily arboreal habits. The context of occasional terrestriality in howlers has been associated with the use mineral licks (*salados* or *saladeros*) to supplement their diet (Izawa 1993; Stevenson and Quiñones 1993; Blake et al. 2010), crossing open spaces in relatively sparsely forested areas, savanna-forest interfaces or highly fragmented forests (Schön Ybarra 1984; Prates and Bicca-Marques 2008) or as a result of interspecific competition (Simmen personal communication).

Data on tree crown use are relatively limited in most studies of positional behavior. In general, it appears that feeding and sleeping place trees tend to have larger crowns than trees used as traveling platforms (Garber and Jelinek 2006). However, the way that tree crowns are used by howlers has been seldom quantified, although the few published data show that activities are usually shared between peripheries and the central parts of tree crowns. More precisely, when traveling, *Alouatta* uses frequently the central and intermediate zones of tree crowns (Youlatos 1994; Guillot 2009). These parts are characterized by the presence of medium and relatively large substrates or various inclinations. In this microhabitat, *Alouatta* walk quadrupedally on horizontal, and ascend and descend on inclined substrates traveling in relative safety (Grand 1984; Prates et al. 1990; Guillot 2009). During travel, use of crown peripheries is restricted. Tree peripheries are composed of entanglements of small flexible branches, whereupon howlers usually clamber, when moving within the same tree, or employ bridging locomotion when crossing adjacent crowns (Youlatos 1993; Guillot 2009).

In contrast, an inverse pattern is observed during feeding activities. The majority of feeding postures are adopted in crown peripheries at rates ranging from 47 % in *A. seniculus* (Guillot 2009), 50 % (Bezanson 2009) to 81 % in *A. palliata* (Bergeson 1998) to as high as 89 % in *A. macconnelli* (Youlatos 1994, 1998). This increased use is directly related to the location of most food items, such as flush leaves and fruit, which are primarily found in tree peripheries. The larger and wider trees exploited during feeding activities provide expanded tree peripheries and probably supply an abundance of food sources within the same location in the forest (Garber and Jelinek 2006). In this way, access to food items is accomplished through extensive clambering on the small flexible substrates of the tree peripheries, and the different food items are acquired, manipulated, and ingested by a variable combination of dynamics above and below branch postures (Youlatos 1994; Guillot 2009). This combination of particular locomotor and postural modes occurs in specific places within single large feeding trees and assures faster rates of food intake while minimizing travel routes across assemblages of food items. This interaction between positional modes, tree zones, and canopy layers is further reflected on substrate use.

Substrate size use by howlers is relatively variable and depends on the species, branch size definition, the behavioral context, and definitely substrate availability (Table 8.3). Comparisons across studies are extremely difficult as the different substrate size classes have been defined by using dissimilar criteria and this may be related to a differential way of estimated diameters and orientations (e.g., see Bezanson et al. 2012). Tentatively, the available data show that very fine supports (generally <2 cm in diameter) are used variably during traveling locomotion (Table 8.3). Finer analysis shows that clamber is the primary locomotor mode occurring upon such fine substrates, along with bridging and landing from leaps, especially the longer ones (Fleagle and Mittermeier 1980; Schön Ybarra 1984; Youlatos 1994; Guillot 2009). In studies with broader size categories, it is evident that howlers largely use substrates <5 cm in diameter representing variably from one third (Gebo 1992) to over half of all substrates used (Kowalewski et al. 2002; Guillot 2009; Table 8.3). In a similar manner, the use of substrates of middle size categories (e.g., 5–10 cm in diameter) or middle to large categories (5–20 cm in diameter), also represents considerable proportions but varies across species (Table 8.3). *Alouatta palliata* and *A. caraya* generally use larger branches (Gebo 1992; Kowalewski et al. 2002; Bezanson 2009) than *A. arctoidea*, *A. macconnelli*, and *A. seniculus*, which use higher rates of smaller substrates (Schön Ybarra 1984; Youlatos and Gasc 2001; Youlatos 2004; Guillot 2009). These two clusters of species apparently show different patterns of habitat use, as with their locomotor and postural behaviors.

Table 8.3 *Alouatta* substrate size use: percentages of size categories for the different species during travel locomotion and feeding postures

Species	*palliata*				*arctoidea*	*seniculus*			*macconnelli*		*caraya*	
Study site	La Pacifica		Santa Rosa	La Suerte	Hato Masaguaral	Tiputini	Yasuní		Nouragues		Isla Brasileira	
Country	CR		CR	CR	VEN	ECU	ECU		FRG		ARG	
Study	1		2	3	4	5	6		7		8	
Method	bout		instant	instant	instant	instant	instant		instant bout		instant	
Context	Travel	Feed	Feed	Feed	Travel/feed	Travel	Travel	Feed	Travel	Feed	Travel	Feed
<2 cm	37.0	28.0	63.3	53.4	39.1	12.2	24.1	29.2	40.1	53.1	58.0	45
2–5 cm			27.3		59.5	48.9	58.0	70.3	39.7	37.6		
5–10 cm	42.0	43.0	8.4	44.8		22.3					18	24
10–20 cm			1.0		1.4	12.1	14.5	0.5	15.1	5.9	24	31
>20 cm						3.2	2.6	0.0	5.1	0.5		
>25 cm	21.0	29.0		0.7								

Countries: *ARG* Argentina, *BRA* Brazil, *CR* Costa Rica, *ECU* Ecuador, *FRG* French Guiana, *PAN* Panama, *SUR* Suriname, *VEN* Venezuela
Studies: 1: Gebo (1992); 2: Bergeson (1998); 3: Bezanson (2009); 4: Schön Ybarra (1984); 5: Guillot (2009); 6: Youlatos (2004, unpublished); 7: Youlatos and Gasc (2001); 8: Kowalewski et al. (2002)

Furthermore, when substrate size use during feeding activities is considered, these two groups also show different patterns, but not in a very clear manner (Table 8.3). *Alouatta seniculus* and *A. macconnelli* show a considerable increase of fine/small substrate use during feeding locomotion and postures (Fleagle and Mittermeier 1980; Youlatos and Gasc 2001; Youlatos unpublished data). In contrast, *A. palliata* and *A. caraya* exhibit a decrease in small substrate (<5 cm in diameter) use and an increase in the use of larger diameter branches (Gebo 1992; Kowalewski et al. 2002). Additional studies on the feeding postural behavior of *A. palliata*, show relatively high rates of fine and small supports (Bergeson 1998; Bezanson 2009), contrasting previous observations. These rates would accord with the frequent use of tree peripheries while feeding in order to collect leaves and fruits. However, similar patterns in substrate size use need to be interpreted with caution. Feeding patterns in most howler species differ significantly between seasons of fruit abundance and fruit scarcity and this is more pronounced in the forests found in the northern and southernmost borders of its distribution (DiFiore and Campbell 2007 for review). Additionally, although leaves may be found everywhere in a tree crown, flush leaves, flowers, and fruits are usually (but not always) located in tree peripheries, where fine flexible and fragile branches abound. These differences in microhabitat use may result in differences of positional behavior and substrate use (Youlatos 1998). However, exact correlations are difficult to assess precisely, especially when no particular connection between specific postural mode, substrate use, and food types have been yet identified (Youlatos 1994; Bergeson 1998).

8.4.4 Tail Prehension

The central role of the grasping tail in posture and locomotion is one of the defining characteristics of all members of subfamily Atelinae. Its adaptive relevance is revealed in part by unique anatomical features of the ateline tail including its relative elongation, larger sacral canal, greater dorsal and ventral muscle masses, and the presence of external tactile pads and other features of the caudal and sacral regions of the vertebral column (Ankel 1972; Rosenberger 1983; Lemelin 1995; Schmitt et al. 2005; Organ 2008). Behavioral studies of *Alouatta* reveal associations between tail use and behavioral context (feeding/foraging, travel, rest), tree crown location, substrate size, substrate orientation, dietary resources consumed and whether it was hyperextended, extended, flexed or wrapped with respect to the plane of the vertebral column. Despite differences in the data collected, these studies indicate that the prehensile tail plays a particular role in providing access to food resources and enhancing stability in the precarious arboreal environment (Grand 1972; Meldrum 1998).

The prehensile tail is very frequently used during feeding activities, when it is largely employed as the main weight-bearing limb (*Alouatta palliata*: Mendel 1976; Wheeler and Ungar 2001; Lawler and Stamps 2002; Russak 2005; Bezanson 2009, 2012; *A. macconnelli*: Youlatos 1994; *A. seniculus*: Guillot 2009). The tail may be also used at lower rates during travel, but it mainly wraps flexed-around supports without bearing significant parts of body weight. The role of the tail in the context of feeding in contrast to travel lends support to the idea that the grasping tail evolved as a feeding adaptation. The well-developed caudal muscles not only can support the full weight of the body but also assist in reorienting the body in space during bridging behaviors or suspended feeding postures effectively extending the range of the animal's reach, playing an important role in increasing its "feeding sphere" (Mittermeier and Fleagle 1976; Bicca-Marques and Calegaro-Marques 1993; Youlatos 1993).

The grasping tail may also serve as a "safety mechanism" (Mendel 1976). It is often held as if ready for action (Carpenter 1934) and frequently grasp supports other than the one bearing most of the animal's weight, either above or below (Mendel 1976; Youlatos 1994). Even during quadrupedal progression along relatively large and stable supports, the tail is frequently observed to trail along touching and briefly grasping surrounding branches as the animal moves (Youlatos 1994; Lawler and Stamps 2002). The tail is also observed to be wrapped around the support in almost half of all observations of above branch feeding postures (Youlatos 1994; Lawler and Stamps 2002; Bezanson 2006). Thus, in a variety of contexts, the tail serves to stabilize the animal and distribute its weight over multiple supports which may be particularly adaptive when moving and foraging on the unstable supports that characterize the crown periphery (Mendel 1976). In effect, most field studies have revealed that tail use, and particularly its weight-bearing role significantly increased when howlers moved or adopted postures on small and vertically oriented substrates (Wheeler and Ungar 2001; Lawler and Stamps 2002). On the other hand, there are no obvious relationship between body weight and tail use in howlers, because male and female mantled howlers (*A. palliata*), despite substantial size dimorphism, did not differ in tail use behaviors regardless of the behavioral context observed or the substrate size or orientation (Wheeler and Ungar 2001). Bezanson's (2006, 2009) study examined the ontogenetic development of tail use in *Alouatta palliata* revealed a counterintuitive pattern of tail use. Although both juveniles and adults increased rates of suspension in the context of feeding, juveniles exhibited higher rates of tail suspension during feeding than adults (Bezanson 2006, 2009, 2012; but see Russak 2005). Juveniles also adopted tail suspended behaviors during social activities such as play (Fontaine 1994; Russak 2005).

A limited number of studies have examined the orientation of tail use, i.e., whether it was attached above the tail base and hence hyperextended, attached level with the tail base and extended behind the animal or attached below and strongly flexed. Cant (1986) observed that *A. pigra*'s anchorages tended to be level or strongly flexed and attached to substrates below the animal. In contrast, Youlatos (1994) has observed in *A. macconnelli* that during locomotion, the tail mainly grasped in substrates above the animal, whereas there was a more shared use during feeding postural behavior. In summary, the grasping tail plays the most crucial role during feeding and foraging, especially on small and highly inclined substrates, of all age groups and is involved during the important development play interactions of younger howlers (Bezanson 2006, 2009, 2012). While it is engaged far less frequently during travel, it is actively recruited when bridging gaps and is thus an essential part of the howler strategy for traversing its arboreal environment.

8.5 Comparative Positional Behavior

The above account on the studies of the positional behavior of *Alouatta* reveals that howlers are more or less consistent in their way of moving and employing feeding postures in the wild. No particular pattern seemed to emerge from this preliminary analysis grouping or separating species. *Alouatta* seems to rely mainly on above-branch pronograde locomotion and sitting feeding postures (Rosenberger and Strier 1989; Jones 2008). More precisely, in terms of locomotor behavior, all species seem to be largely quadrupedal, using walk and pronograde clamber. Leaping is seldom used, while bridging is a habitual way to travel across trees within the canopy (Youlatos 1993; Guillot 2009). Regarding postures, howlers largely feed while seated, whereas stand is variably employed. Suspension is often used during feeding, where a variety of postures, always involving the tail and/or the hind limbs and forelimbs are employed in variable rates. In contrast, apart from bridging, suspended locomotion is rather rare and modes requiring elbow extension and raising the arm above the head are seldom used (Erikson 1963; Rosenberger and Strier 1989; Jones 2008).

The univariate comparisons were unable to significantly discriminate between species, and therefore we attempted to test whether multivariate analyses would reveal any tendencies that distinguish between species. For these purposes, we applied a Principal Components Analysis (PCA) combining major locomotor (quadrupedal, climb, leap, and suspended) and postural (sit, stand, and suspended) categories. The results of this analysis are illustrated in Fig. 8.3. The figure shows that the PCA managed to discern two clusters arranged mainly around PC 1, which describes 58.1 % of the explained variance. On the negative side of PC 1, a broad group involves *A. palliata* and *A. guariba*, along with *A. caraya* located close to the middle of the axis. This group was behaviorally related to increased rates of walk and sit. The limited positional data for *A. pigra*, the other Mesoamerican species, show that the Yucatán black howler also relies on walk for traveling (Cant 1986) and would very likely fit in this group, should enough positional data were available. This behavioral grouping is also partly supported by molecular and chromosomal data. *A. palliata*, along with *A. pigra*, which inhabit the northernmost range, form a basal group within *Alouatta* (Cortés-Ortiz et al. 2003; Villalobos et al. 2004) and seem to have adopted a more pronograde positional strategy with increased rates of quadrupedal walk and sit. Additionally, *A. guariba*, a taxon also having derived relatively early in *Alouatta* history in the southernmost range (Cortés-Ortiz et al. 2003; Martins et al. 2011), has also adopted a similar positional strategy. On the other hand, the more evolved *A. caraya*, a sister taxon to the seniculus group (Cortés-Ortiz et al. 2003; Villalobos et al. 2004) appeared to use intermediate rates of these modes.

On the other end of PC 1, the other group, composed of *A. arctoidea*, *A. seniculus*, and *A. macconnelli*, was behaviorally associated with climb, stand, and to a lesser degree, suspensory locomotion. They represent three closely related and recently derived species (Bonvicino et al. 2001; Oliveira et al. 1999; Cortés-Ortiz et al. 2003; Villalobos et al. 2004), located in the very core of *Alouatta*'s range, and seem to have evolved a less pronograde locomotion and more dynamic positional strategy during feeding, using more climb, stand, and suspension.

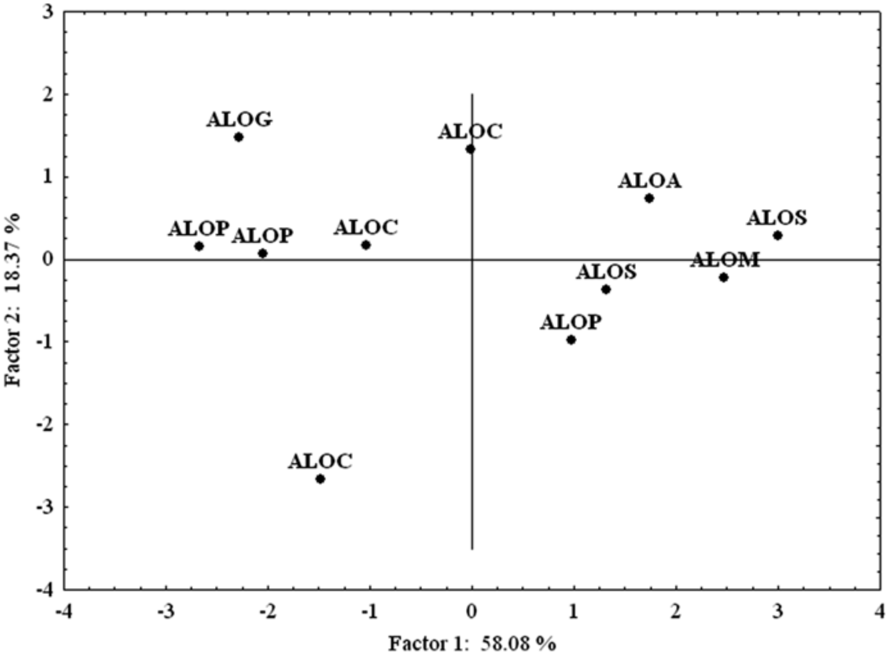

Fig. 8.3 Principal Components Analysis (PCA) of locomotor and postural behavior of howler monkeys (ALOA *A. arctoidea*, ALOC *A. caraya*, ALOG *A. guariba*, ALOM *A. macconnelli*, ALOP *A. palliatta*, ALOS *A. seniculus*)

Our multivariate analysis of positional data demonstrates that *Alouatta* may not be a very uniform group in terms of locomotion and postures. In contrast, it appears to exhibit a certain locomotor and postural variety, which was further associated with specific phylogenetic groups. Thus, the more primitive species seem to rely more on an above-branch-quadrupedal-pronograde positional strategy, whereas the more derived forms have adopted a more climbing/suspensory strategy. This complicates reconstructions of the positional behavior of the earliest atelines.

Recent analyses have shown that the ateline last common ancestor (LCA) was *Lagothrix*-like, incorporating a mixture of pronograde quadrupedal walk, clamber, and suspensory locomotion and postures (Jones 2004, 2008). Based on this interpretation, it is very likely that the alouattin ancestor may have inherited this particularly flexible positional behavior (Schön Ybarra and Schön 1987). To some extent, this is supported by the locomotor adaptations of *Protopithecus*, a primitive alouattin, which shows a mosaic of forelimb suspensory and quadrupedal (even semi-terrestrial) adaptations (Halenar 2011). A transition towards a more pronograde behavior, would have occurred relatively rapidly, as the earliest taxa (*palliata*, *pigra*) that diverged and migrated to the north, towards the southern forests of Mesoamerica (Cortés-Ortiz et al. 2003), would have already adopted the more restricted above-branch locomotion (Jones 2008). This positional strategy, accompanied by the evolution of a more energy-minimizing strategy and a tendency towards increased folivory and restricted group ranges, is also found in the subsequent diversification of species (*caraya*, *guariba*), currently inhabiting the more temperate forests of the southernmost part of *Alouatta*'s distribution (Cortés-Ortiz et al. 2003; DiFiore and Campbell 2007; Martins et al. 2011). Finally, the more recently derived taxa (*macconnelli*, *arctoidea*, *seniculus*) very likely reverted to the ancestral condition of a relatively more flexible positional behavior, incorporating comparably higher rates of clamber and suspended locomotion and postures (see also Jones 2004). Alternatively, if *Protopithecus* is not included in the alouattin group, then it is very likely that the whole howler lineage slightly modified its positional behavior towards less suspensory and climbing activities, as currently exhibited by the seniculus core group. In this way, the earliest branches (trans-Andean and later the southernmost expansion) would have independently adopted an even more quadrupedal/sitting positional strategy as an adaptation to the more seasonal conditions of the Mesoamerican and south-Brazilian and Argentinean forests. Both hypotheses need to be examined by further studies of these and other howler species in the wild.

8.6 Summary

Compared to other arboreal quadrupeds, which regularly integrate distinct locomotor modes into a single bout of travel, *Alouatta* locomotion is dominated by slow quadrupedal progression along relatively large horizontal supports. Despite the remarkable variability in postural behavior that the prehensile tail affords, their locomotor profile is quite restricted or conservative in contrast to many other primate genera and this lack of locomotor variability is particularly notable when contrasting *Alouatta* to other ateline genera (Guillot 2009; Youlatos and Gasc 2011). Although *Alouatta* diverged relatively early in ateline evolution, it is increasingly clear that they are a poor model of the ancestral state. Their overall positional behavior involves a suite of derived behavioral and morphological adaptations unique to this genus (Erikson 1963; Cant 1986; Schön Ybarra and Schön 1987; Rosenberger and Strier 1989; Kagaya 2007; Youlatos and Gasc 2011; Youlatos and Meldrum 2011).

Despite the dominance of slow quadrupedalism behaviors among all howler species, this review reveals subtle interspecific distinctions. The earliest derived groups, occupying the northernmost and southernmost extent of the howler geographic distribution, exhibit increased reliance on quadrupedalism. In contrast, more recently derived species, such as *A. seniculus*, exhibit higher frequencies of climbing, clambering, and bridging. Further evaluation of these patterns will benefit from additional studies, particularly of less well-known species including *A. pigra*, *A. arctoidea*, and *A. guariba*. In addition, it will be valuable to further explore the relationship between habitat differences and positional behavioral differences seen among species of *Alouatta*.

In terms of habitat use, howlers demonstrate a relative consistency. Almost all species use the high forest layers, the central tree zones during traveling and the tree peripheries during feeding. Lower forest layer or ground use is occasional and frequently related to the exploitation of particular food sources. This pattern of forest utilization is consistent with predictions related to body mass and feeding niche segregation among platyrrhines, where large bodied herbivores occupy and negotiate with no particular difficulty the higher and peripheral parts of tree crowns (Fleagle and Mittermeier 1980; Rosenberger 1992). This pattern is also related to substrate use, where howler species, especially the *seniculus* group, exhibit high rates of small branch utilization. This is further associated with the more flexible positional habits that allow them to use multiple and variable paths to travel between feeding sites and exploit them more efficiently. On the other hand, the use of larger substrates and inner parts of trees provide secure pathways whereupon howlers guide themselves safely in order to gain access to more unstable parts of crowns. However, associations between positional modes, used substrates, and tree crown parts have not yet been explored in detail. Further research in relation to travel patterns and spatial mapping would provide valuable information in order to understand any interrelations between cognition and morphology for an integrated understanding of their adaptive significance.

Apart from that, more studies are required in order to establish or clarify any interspecific similarities and differences, as reviewed in this chapter. First of all, we need additional data on the positional profiles of more *Alouatta* species, in order to test whether our suggested positional/phylogenetic grouping actually hold. Positional behavior can be a very fertile ground for research, especially if combined with more detailed and quantitative descriptions of how modes are actually performed, through intensive video recording and kinematic analysis in the field (e.g., Guillot 2009; Youlatos and Gasc 2011). This would provide more robust associations between behavior, function, and morphology towards a more evolutionary and adaptive context. Furthermore, more data are required regarding ontogenetic factors that determine behavioral profiles, related to the development of social interactions and habitat/resource exploitation (e.g., Bezanson 2006, 2009), as well as to the ontogeny and evolution of postcranial variability observed within the genus (Halenar 2011). These would necessitate long-term studies gathering data from different sites for same and different species in order to understand the evolutionary constraints that shaped the unique morpho-behavioral adaptations of howler monkeys.

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Chapter 9
Ranging Behavior and Spatial Cognition of Howler Monkeys

Vanessa Barbisan Fortes, Júlio César Bicca-Marques, Bernardo Urbani, Vanina Alejandra Fernández, and Thiago da Silva Pereira

Abstract Since the first long-term field study of mantled howler monkeys carried out by Clarence R. Carpenter on Barro Colorado Island about 80 years ago, howler movement patterns and range use have been studied in several species and study sites throughout Mexico, Central, and South America. Howler monkeys often use small home ranges (<30 ha) and travel short distances each day (<1,000 m) compared with other atelines. Home range size, day range length, and patterns of use of space may vary both within- and between-species in response to differences in forest structure, patterns of resource distribution and phenology, the area of habitat available, group size, and population density. Within-species variability has been shown to increase with increasing sample size. In addition, howlers present a pattern of repetitive use of a limited number of routes to travel between feeding and

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sleeping sites that has been related to a strategy aimed at reducing the distance travelled while allowing them to keep track of the phenology of important food sources. In this chapter we present the results of a comprehensive review of the literature on the ranging behavior of *Alouatta* (spp.). We used Generalized Linear Models (GLMs) to test whether home range is affected by (1a) fragment size, (1b) population density, (1c) group size, and (1d) group biomass, and whether day range is affected by (2a) fragment size, (2b) population density, (2c) group size, and the contribution of (2d) fruits and (2e) leaves to the diet. We also included species and method of estimating home range as factors in the models. We found that the size of the home range is negatively influenced by population density, and that there are differences between species (*A. palliata* uses significantly larger home ranges), and estimating methods. We also found that the length of the day range is negatively affected by population density, and the contribution of fruits and leaves to the diet, but positively affected by group size. Interspecific comparisons showed that *A. guariba clamitans* tends to travel farther daily than *A. palliata*. Cognitively, recent evidence supports the idea that howler monkeys are capable of encoding, processing, updating, and recalling a topological spatial representation of a set of landmarks (including major feeding and resting sites) as prominent beacons for navigating along commonly used routes within their home ranges.

Resumen Desde los primeros estudios a largo plazo que realizó Clarence R. Carpenter hace alrededor de 80 años en la Isla de Barro Colorado, los patrones de desplazamientos y el uso del hábitat de los monos aulladores han sido ampliamente estudiados en varias especies y sitios a lo largo de México, Centro y Suramérica. Los monos aulladores frecuentemente presentan pequeñas áreas de acción (<30 ha) y desplazamientos diarios cortos (<1.000 m) en comparación con otros atélidos. El tamaño del ámbito hogareño, longitud de los desplazamientos diarios y los patrones de uso del espacio pueden variar tanto dentro y entre las especies en respuesta a las diferencias en la estructura del bosque, los patrones de distribución de los recursos y fenología, el área del hábitat disponible, el tamaño del grupo, y la densidad de población. La variabilidad dentro de las especies se ha demostrado que aumenta con el aumento de tamaño de la muestra. Además, los aulladores presentan un patrón de uso repetitivo de un número limitado de rutas de viaje entre los sitios de alimentación y descanso, algo que se ha relacionado con una estrategia de reducción de la distancia que, al mismo tiempo, les permite monitorear la fenología de las potenciales fuentes de alimentación. En este capítulo se presentan los resultados de una revisión exhaustiva de la literatura sobre el comportamiento de desplazamiento y uso del espacio en *Alouatta* (spp.). Utilizamos modelos lineales generalizados (MLG) para someter a prueba si el ámbito hogareño se ve afectado por (1a) el tamaño del fragmento, (1b) la densidad poblacional, (1c) el tamaño del grupo, y (1d) biomasa proporcional de los grupos; y si los desplazamientos diarios se ven afectados por (2a) el tamaño del fragmento, (2b) la densidad poblacional, (2c) el tamaño del grupo, y la contribución de (2d) frutas y (2e) hojas en la dieta. También se incluyeron las especies y el método de estimación del ámbito hogareño como factores en los modelos. Se encontró que el tamaño del ámbito hogareño se ve influenciado negativamente por la densidad poblacional, y que existen diferencias entre especies (*A. palliata* utiliza ámbitos hogareños significativamente más grandes), y los métodos de estimación. También se encontró que la longitud del recorrido diario se ve afectada negativamente por la densidad poblacional y la contribución de frutas y hojas en la dieta; pero positivamente afectada por el tamaño del grupo. Comparaciones interespecíficas mostraron que *A. guariba clamitans* tiende a viajar más lejos que *A. palliata*. Cognitivamente, las evidencias recientes apoyan la idea de que los monos aulladores son capaces de codificar, procesar, actualizar y recordar la representación espacial topológica de un conjunto de puntos de referencia (incluyendo los más importantes sitios de alimentación y descanso) como elementos prominentes para navegar a lo largo de rutas comúnmente usadas dentro de su ámbito hogareño.

Keywords Day range • Habitat use • Home range • Memory • Movements

9.1 Ranging Behavior

Howler monkeys were the focus of the first systematic primate field study, carried out by Clarence Raymond Carpenter on Barro Colorado Island, Panama, between 1931 and 1932. Carpenter (1934) described the ranging behavior of mantled howler monkeys (*Alouatta palliata*) based on 22 consecutive days of observation. He argued that howler travel was characterized by the repeated use of familiar routes to navigate between feeding sites, a behavior that suggests that these monkeys may mentally represent spatial information as a route-based map in which a forager is expected to acquire, recall, and integrate a set of interconnected pathways or route segments that are linked by a set of landmarks or nodes (Bennet 1996; Urbani 2011). Despite Carpenter's limited period of observation, he identified key aspects of the ranging behavior of howler monkeys (Urbani 2011), that were confirmed by later and more extended field studies (Milton 1980; Garber and Jelinek 2006; Fernández 2008; Hopkins 2008; Pereira 2008).

The ranging behavior of nine species of howlers has been studied from Mexico to southern Brazil and northeastern Argentina, but most studies involved the observation of a single social group. Therefore, our knowledge of within-population variability is quite limited because only a few researchers have monitored more than a single group in the same forest (Larose 1996; Ostro et al. 1999a; Arrowood et al. 2003; Bridgett 2006; Kowalewski 2007; Hopkins 2008; Agostini 2009; Gómez-Posada and Londoño 2012). In this chapter we present the results of the most comprehensive review of the literature so far to analyze the ecological and demographic factors that affect the ranging behavior of howler monkeys. Like previous studies, we evaluate whether group size, population density, habitat availability, and food consumption are proximate causes of home range size and day range length. We also included species, home range estimation method, and group biomass as possible explanatory variables, whose potential influence was never assessed in a genus-wide comprehensive review. We used generalized linear models (GLMs) because they analyze all variables simultaneously while modeling their possible effects independently, and fit the model to alternative distributions (not necessarily linear). In the second part of the chapter we discuss the cognitive challenges faced by howler monkeys when navigating between feeding and resting sites, and present the major findings of recent research.

9.1.1 Factors Affecting Home Range Size

The home range used by a primate group is limited by several factors, including the availability of suitable habitat and food, the density and size of neighboring conspecific groups, and the risk of predation. Because most forests represent a mosaic of habitat types that vary in floristic composition, density and spatial distribution of plant species, and their phenology, the total area of forest available does not necessarily match the area of "suitable habitat." To perform this analysis requires data on species (resource) distribution at a fine spatial scale, a quite complex and time-consuming task that gets impractical with increasing potential habitat area. Therefore, there is an almost complete absence of such detailed evaluations in the literature (the exceptions are restricted to tiny habitat patches, e.g., Bicca-Marques 1994; Prates 2007). As a consequence, most studies have used the size of the study area as a proxy of habitat availability in regression analyses. A strong positive relationship between habitat availability and home range size was evidenced both at the genus level ($n=39$ groups in 29 study sites, Bicca-Marques 2003, based on nine howler species according to the taxonomy adopted by Cortés-Ortiz et al. 2014) and at the species level for *A. palliata* in Los Tuxtlas, Mexico ($n=21$ measures of 19 groups in 10 study sites, Cristóbal-Azkarate and Arroyo-Rodríguez 2007). However, in forest fragments below a given size threshold possibly represented by the size of the home range of groups living in continuous forests or large fragments (that is, in habitats where there are no spatial constraints, without taking into account the influence of neighboring groups) home range size may be limited.

The distance to neighboring habitat patches may also affect home range size by changing the costs of moving across unsuitable or highly disturbed environments and their associated risks (e.g., exposure to predation or parasite infections). Regular travel on the ground for distances of up to about 100 m to reach isolated food patches has been observed in systematic studies of groups inhabiting forest fragments and anthropogenic habitats (*A. guariba clamitans*: Fortes 2008; *A. caraya*: Muhle 2008; Prates and Bicca-Marques 2008; *A. palliata*: Pozo-Montuy and Serio-Silva 2007; Pozo-Montuy et al. 2013). For instance, the home range of a group of *A. g. clamitans* studied by Fortes (2008) in the Brazilian state of Rio Grande do Sul comprised 3 very small fragments (0.2, 0.5 and 1.1 ha) isolated by 35–50 m of grassland that were crossed by the howlers on a daily basis. Similarly, the home range of a group of *A. palliata* in Tabasco, Mexico, included several trees scattered in a pastureland, to which the howlers traveled regularly to feed on fruits (Pozo-Montuy et al. 2013). The costs of adopting this strategy are illustrated by 2 events of predation, 1 by a coyote (Pozo-Montuy and Serio-Silva 2007, 499 h of observation) and the other by a domestic dog (V.B. Fortes, unpublished data, 654 h of observation). Unfortunately, data on the energy spent and on rates of predation or parasitic contamination under varying landscape scenarios are missing to allow a long-term cost-benefit analysis of ground travel at both the individual and the population level.

The number and age-sex composition of individuals living together in a social unit may also influence home range size by affecting the overall amount of food required to satiate all group members. Studies of groups in interbreeding populations suggest the existence of such relationship (*A. pigra*: six groups ranging from four to ten individuals, Ostro et al. 1999a; *A. seniculus*: five groups ranging from five to ten individuals, Gómez-Posada et al. 2007). However, this pattern was not observed in within-species comparisons among different study sites (see Table 9.1). Groups of *A. g. clamitans* with 7–8 individuals used near 70 ha in Misiones, Argentina (Agostini et al. 2010), but only 4–8 ha in study sites in southeast (Mendes 1989; Gaspar 1997) and south Brazil (Cunha 1994; Fortes 1999; Fialho 2000; Marques 2001). There are also cases in which smaller groups range over wider areas than larger ones. For instance, whereas a group of *A. seniculus* composed of 8 individuals had a home range of 182 ha in a continuous rainforest in Colombia (Palacios and Rodríguez 2001), a group of 18 individuals used only 3.7 ha in a bamboo forest fragment in the Andes (Gómez-Posada and Londoño 2012). Here, again, the isolation of howlers in forest fragments (especially small ones) plays a critical role by hampering dispersal and promoting the establishment of larger groups. Therefore, analyses of multiple groups sharing a forest several times larger than the maximum home range recorded for the species are more appropriate to assess the effect of group size and composition on home range size. However, because nutritional requirements vary among age-sex classes and female reproductive state (Serio-Silva et al. 1999; Raguet-Schofield 2010; Amato 2013), group biomass might be a better measure to relate with home range size.

Unlike the effect of group size or biomass, howler monkey population density is reported to have an inverse relationship with home range (Crockett and Eisenberg 1987; Cristóbal-Azkarate and Arroyo-Rodríguez 2007). Studies carried out in large forest tracts (where there are no spatial constraints due to fragmentation) showed that the smallest home ranges are frequently found under the highest population densities (*A. g. clamitans*: Chiarello 1992; *A. caraya*: Kowalewski 2007; Bravo and Sallenave 2003; *A. seniculus*: Gómez-Posada and Londoño 2012), whereas the largest ones are found under very low densities (*A. g. clamitans*: Steinmetz 2000; Miranda 2004; Agostini 2009; *A. caraya*: Agostini 2009; *A. palliata*: Estrada 1984; Stoner 1996) (see Table 9.1). The largest home range ever reported for howlers (182 ha) was recorded in a continuous forest (>600,000 ha) where *A. seniculus* is found at a density of only 0.04 individuals per hectare (Palacios 2003).

Food availability and diet composition are probably the most assessed potential causes of howlers' use of space. The first studies addressing this issue proposed a negative relationship between the degree of folivory (contribution of leaves to the diet) and home range size based on the assumption that leaves are more abundant and evenly distributed than fruits (Milton 1981). This is clearly an oversimplification

Table 9.1 Variables describing use of space and the factors that may affect this use in different species of howler monkeys (*Alouatta* spp.)

References	Study length months (h)	Mean day range (m) ± SD	Day range min–max (m)	Home range (ha)	Method	Core area ha (%)	HR overlap ha (%)	Size study area (ha)	Group size	Howler density (ind/ha)	Fruits (%)	Leaves (%)	Forest type
A. guariba clamitans													
1, 2	7 (493)	523	197–1,100	7.9	GC (25 × 25 m)	–	–	570	7	1.17	16	71	Rainforest
3, 4, 5	12 (718)	467	241–808	4.1	GC (25 × 25 m)	–	1.38 (33)[a]	250	6	1.19–1.77	6.5	80.4	Subtropical
6	12	393	155–741	3.9	–	–	–	35	7–10	–	41.7	50.4	Semideciduous
7	–	–	–	8.5	–	–	–	234	7–9	–	14.9	61.9	Subtropical
8	12 (408)	494	–	12.5	GC (50 × 50 m)	–	–	165	3–4	0.10	>44.7	49.5	Semideciduous
9	12 (835)	790	376–1,564	7.2	MCP (afl)	–	–	~1,000	7–9	–	16.2	58.8	Semideciduous
10[1]	7 (454)	584	230–950	6.4	GC (10 × 10 m)	–	–	12	9	1.04	39.5	53.9	Semideciduous
10[2]	7 (415)	481	235–735	4	GC (10 × 10 m)	–	–	27	8	1.50	58.9	30.1	Semideciduous
11	12 (~700)	608	235–1,527	11.6	GC (25 × 25 m)	–	–	80	4	–	14.7	62.7	Semideciduous
12	12	–	–	4.5	GC (25 × 25 m)	–	–	7,900	8–10	–	15	55	Subtropical
13	–	546	50–1,280	33 (41.6)	GC (MCP)	–	–	120,000	5–6	–	23	74	Subtropical
14, 15[1]	12 (580)	958 ± 305	305–1,677	13.5	MCP	–	–	272	11	0.92–1.25[b]	16	55	Araucaria
15[2]	12 (484)	769 ± 103	274–1,451	8.6	MCP	–	–	5,533	8	0.65–0.85[c]	47	34	Semideciduous
16	12	567	–	6.5	GC (25 × 25 m)	–	–	120	6	0.93	26	62	Semideciduous

17^{1}	12	582 ± 168	252–1,210^{d}	19.5	GC (50 × 50 m)	1.8 (9)^{e}	–	700	10	0.38	–	–	Araucaria
17^{2}	12	495 ± 207	–	14	GC (50 × 50 m)	2 (14)^{e}	–	700	4.5	0.38	–	–	Araucaria
18	12 (560)	–	75–1,187	5	GC (25 × 25 m)	–	–	5	5–8	Max 1.60^{f}	39	52	Semideciduous
19^{1}	12 (577)	709 ± 207	324–1,193	4.9	MCP	–	–	~1,000	5	1.10	9	78	Semideciduous
19^{2}	12 (623)	679 ± 274	92–1,463	5	MCP (afl)	–	–	20.2	6	2.20	35	59	Semideciduous
19^{3}	12 (654)	734 ± 228	349–1,273	1.8	MCP (afl)	–	–	1.8	7	3.30^{f}	18	67	Semideciduous
20^{1}	12 (352)	759 ± 71	244–1,666	69.9 (70.3)	MCP (95% KDE)	7.4 (11)^{g}	(41)^{h}	165	7–8	0.10	24^{i}	62^{i}	Araucaria
20^{2}	12 (308)	744 ± 95	75–1,538	47.4 (31.6)	MCP (95% KDE)	2.1 (7)^{g}	(99)^{j}	165	4	0.10	–	–	Araucaria
21	12 (636)	520 ± 127	265–1,034	2.2	GC (20 × 20 m)	–	–	2.2	6	2.70^{f}	15	78	Araucaria
Mean ± SD		**620 ± 142**	**50–1,677**	**13.00 ± 15.9**			**58 ± 36%**		**6.9 ± 2.0**	**1.17 ± 0.91**	**25.9 ± 14.3**	**59.8 ± 13.0**	
A. belzebul													
22	–	450	350–650	9.5	–	–	–	271	6–8	–	59	13	Subtropical
23	6 (401)	1,474	861–2,409	13.8 (10.9)	GC (25 × 25 m) (MCP)	0.3^{k}	Low	33,100	7	2.0^{l}	70.8	28.6	Rainforest
24	10 (1,203)	684 ± 215	269–1,300	17.8	GC (25 × 25 m)	–	–	20,000	6	–	42.8/43.9^{m}	46.6/43.4^{m}	Rainforest
25	14	–	–	10.6	GC	–	–	266.53	16	–	–	66.3	Rainforest
Mean ± SD		**869 ± 537**	**269–2,409**	**12.6 ± 3.7**					**9.0 ± 4.7**	**2**	**57.7 ± 13.8**	**38.2 ± 22.8**	
A. discolor													
26	10	761	167–1,425	50.1 (63.2)	GC (MCP)	–	–	10,000	7–9	–	55	25	Rainforest

(continued)

Table 9.1 (continued)

References	Study length months (h)	Mean day range (*m*) ± SD	Day range min–max (m)	Home range (ha)	Method	Core area ha (%)	HR overlap ha (%)	Size study area (ha)	Group size	Howler density (ind/ha)	Fruits (%)	Leaves (%)	Forest type
Mean ± SD		**761**	**167–1,425**	**56.7**					**8**		**55**	**25**	
A. caraya													
27	–	345	130–1,200	5.5	–	–	–	12	6	–	–	–	Subtropical
27	–	–	–	6.3	–	–	–	12	6	–	–	–	Subtropical
28	–	341 ± 156	112–1,200	5.5	–	–	–	12	5.5	–	26.7	54.5	Subtropical
29, 30	12 (745)	454 ± 176	156–893	2	GC (20 × 20 m)	0.16[n]	–	2	15–17	Max 8.5[f]	29	61	Seminatural
31[1]	17 (1,680)	513 ± 253	Min 85	1.7	GC (20 × 20 m)	1.3[o]	0.4	141	16	4.25	18[p]	64[p]	Subtropical
31[2]	17 (1,680)	602 ± 350	Max 1,515	2.2	GC (20 × 20 m)	1.8[o]	0,4	141	21	4.25	–	–	Subtropical
32	12 (50)	–	–	6	–	1.5	–	170	5	0.82–1.02	–	–	Subtropical
32	(100)	280	120–500	5	–	1.6	–	170	3	0.82–1.02	–	–	Subtropical
33[1]	(306)	564 ± 245	154–1,065	5.0 (3.2)	GC (MCP)	1 (20)[q]	1.25 (25)	1,050	11–9	2	–	–	Semideciduous
33[2]	12 (288)	842 ± 364	416–1,638	18.8 (18.4)	GC (MCP)	Nule[q]	1.5 (8)	–	13–11	0.64	–	–	Semideciduous
34	12	684 ± 225	300–1,300	5.9 and 6.0	GC (20 × 20 m)	–	(70.5)[r]	400	10.5	3.48	24	46	Subtropical
35	12 (699)	371 ± 116	168–628	0.7	GC (15 × 15 m)	–	–	0.7	12–14	Max 20[f]	12.3	82.4	Seminatural
36	12 (830)	272 ± 99	113–540	1.3	Wfu	–	–	1.3	4–5	Max 3.85[f]	1.9	75.3	Seminatural
37[1]	12 (383)	840 ± 95	62–1,582	93.8 (111.9)	MCP (95% KDE)	27.03 (24)[s]	(46)[t]/(6)[u]	165	12–14	0.15	19[v]	64[v]	Araucaria

37^{2}	12 (351)	709 ± 59	228–1,308	17.8 (17.3)	MCP (95% KDE)	2.36 (14)[s]	(75)[w]/ (38)[x]	165	5–7	0.15	–	–	Araucaria
Mean ± SD		**524 ± 201**	**62–1,638**	**11.7 ± 23.3**			**38 ± 26%**		**9.8 ± 5.3**	**5.44 ± 6.38**	**18.7 ± 8.6**	**63.9 ± 11.3**	
A. seniculus													
38	10 (340)	706 ± 382	–	22	–	–	–	270	9–10	–	42	53	Rainforest
39	–	–	–	25	–	47.4–90.8	–	469	8	–	–	–	Rainforest
39	–	–	–	28.4	–	–	–	469	8	–	–	–	Rainforest
39	–	–	–	30	–	–	–	469	13	–	–	–	Rainforest
40, 41	10 (496)	1,150 ± 394	370–2,200	182	GC (100 × 100 m)	17[y]	0	–	8	0.04	52.3	35.3	Rainforest
42	–	–	–	14.5	–	–	–	–	9	–	–	–	Rainforest
42	–	–	–	21.5	–	–	–	–	10	–	–	–	Seminatural
43	6 (534)	–	469–878	21	–	–	–	–	–	–	–	–	Rainforest
44^{1}	18 (705)	–	–	2.1	MCP	–	0.9[z]	110.7	13	3.8	–	–	Dry
44^{2}	18 (556)	–	–	3.7	MCP	–	0.9[z]	110.7	18	3.8	–	–	Dry
44^{3}	12 (311)	–	–	4.8	MCP	–	0.9[z]	110.7	17	3.8	–	–	Dry
44^{4}	12 (260)	–	–	3.8	MCP	–	0.9[z]	110.7	13	3,8	–	–	Dry
Mean ± SD		**928 ± 313**	**370–2,200**	**29.9 ± 49.0**					**9.58 ± 1.86**	**0.04**	**47.2 ± 7.3**	**44.2 ± 12.5**	
A. juara													
45	12 (492)	320	–	7.5	–	–	–	1,240,000	8	–	47	46	Rainforest
46	–	–	–	6.7	–	–	–	–	5.5	–	–	–	Rainforest
Mean ± SD		**320**		**7.1 ± 0.6**					**6.8 ± 1.8**		**47**	**46**	

(continued)

Table 9.1 (continued)

References	Study length months (h)	Mean day range (*m*)±SD	Day range min–max (m)	Home range (ha)	Method	Core area ha (%)	HR overlap ha (%)	Size study area (ha)	Group size	Howler density (ind/ha)	Fruits (%)	Leaves (%)	Forest type
A. arctoidea													
47^{1}	14 (603)	–	Max 430	7.1	–	–	–	3,200	6–9	–	–	–	Dry
48	–	340	20–840	4–7	–	–	–	–	–	–	–	–	–
48	–	445	–	–	–	–	–	–	–	–	–	–	–
Mean±SD		**393±74**	**20–840**	**6.3±1.1**					**7.5**				
A. pigra													
49^{1}	10	520±185	–	10.4	DP	–	–	4,700	7	0.47	–	–	Semideciduous
49^{2}	10	648±230	–	15.8	DP	–	–	4,700	10	0.47	–	–	Semideciduous
49^{3}	10	441±176	–	9.3	DP	–	–	40,000	6	0.03	–	–	Rainforest
49^{4}	10	567±263	–	20.2	DP	–	–	40,000	4,5	0.03	–	–	Rainfores
50^{1}	6 (290)	246±108	0–383	2.2	DP	–	22.3	71	2	–	40[aa]	56[aa]	Semideciduous
50^{2}	–	485±190	128–716	4	DP	–	12.3	71	6	–	–	–	Semideciduous
50^{3}	–	476±180	180–814	4.1	DP	–	–	71	3	–	–	–	Semideciduous
50^{4}	–	576±182	182–856	2.8	DP	–	–	71	4	–	–	–	Semideciduous
51	12	–	–	14±5.1 (8–21)[bb]	GC (100×100 m)	–	(54±32)[bb]	385	–	0,39	–	–	Rainforest
Mean±SD		**491±129**	**0–1,015**	**9.2±6.4**			**30±22%**		**5.9±2.3**	**0.25±0.25**	**40**	**56**	
A. palliata													
52	14 (2071)	596	207–1,261	9.9	–	–	–	10	13	–	13	69	Rainforest
53, 54^{1}	10	488±152	104–792[d]	31.1	MCP	–	–	1,600	17	1.13	47	44	Rainforest
53, 54^{2}	10	392±127	–	31.7	MCP	–	–	1,600	17	1.13	37	53	Rainforest

55, 56^{1}	12	123 ± 101	11–503	60	GC (100 × 100 m)	–	–	700	16	0.22	51	49	Rainforest
57^{1}	60	148	10–893	–	–	–	–	700	16	–	–	–	Rainforest
58, 59	24 (394)	–	–	108	GC (120 × 120 m)	–	–	10,800	40	–	29	49	Dry deciduous
60^{1}	6 (324)	374/390[cc]	–	30.5[dd]	GC (10 × 10 m)	–	–	10,800	28	–	–	–	Dry deciduous
60^{2}	6 (304)	407	–	–	–	–	–	10,800	20–22	–	–	–	Dry deciduous
60^{3}	6 (241)	362/331[cc]	–	46[dd]	GC (10 × 10 m)	–	–	10,800	14–11	–	–	—	Dry deciduous
60^{4}	6 (291)	306	–	–	–	–	–	10,800	10	–	–	–	Dry deciduous
60^{5}	6 (275)	184/262[cc]	–	17.8[dd]	GC (10 × 10 m)	–	–	10,800	7–4	–	–	–	Dry deciduous
60^{6}	6 (302)	322	–	–	–	–	–	10,800	6	–	–	–	Dry deciduous
61^{1}	15 (140)	–	–	54	GC (100 × 100 m)	–	–	1,200	20–23	0.07–0.15	17	72	Rainforest
61^{2}	15 (208)	–	–	35	GC (100 × 100 m)	–	–	1,200	11–14	0.07–0.15	29	65	Rainforest
62	12	326	161–475	3.6	Wfu	–	–	3.6	7	1.94[f]	54.3	40.6	Rainforest
63^{1}	12 (1,300)	752 ± 292	–	21.9 (20.3)	MCP (DP)	–	(0)[ee]	125	25.9	0.56	34.8[ff]	55.8[ff]	Semideciduous
63^{2}	–	568 ± 256	–	15.8 (13.7)[gg]	MCP (DP)	–	(7)[ee]	125	15.3	0.56	–	–	Semideciduous
63^{3}	–	572 ± 301	–	21.3 (17.3)	MCP (DP)	–	(5)	125	20.2	0.56	–	–	Semideciduous
64^{1}	10 (1,010)	453 ± 189	109–958	26	95% MCP	–	22.61 ha	1,600	13.6 ± 2.8	–	41.3 ± 27.9[hh]	47.2 ± 22.1[hh]	Rainforest
64^{2}	10 (1,001)	771 ± 440	81–2,850	44	95% MCP	–	18.90 ha	1,600	23.4 ± 1.2	–	–	–	Rainforest

(continued)

Table 9.1 (continued)

References	Study length months (h)	Mean day range $(m) \pm$ SD	Day range min–max (m)	Home range (ha)	Method	Core area ha (%)	HR overlap ha (%)	Size study area (ha)	Group size	Howler density (ind/ha)	Fruits (%)	Leaves (%)	Forest type
64^3	6 (219)	474 ± 229	130–828	29	95% MCP	–	17.98 ha	1,600	16.8 ± 2.9	–	–	–	Rainforest
64^4	6 (416)	288 ± 233	0.05–974	18	95% MCP	–	9.01 ha	1,600	9.0 ± 2.1	–	–	–	Rainforest
Mean ± SD		**432 ± 172**	**0.05–2,850**	**33.3 ± 23.9**			**36 ± 33%**		**16.1 ± 8.6**	**0.70 ± 0.60**	**35.3 ± 13.7**	**54.5 ± 10.8**	

Only studies longer than 6 months are included

References and Study sites: (1, 2) Mendes (1985, 1989)—Caratinga Biological Station, Brazil; (3, 4, 5) Chiarello (1992, 1993, 1994)—Santa Genebra Municipal Reserve, Brazil; (6) Cunha (1994)—Itapuã State Park, Brazil; (7) Gaspar (1997)—Campinas, Brazil; (8) Martins (1997)—Rio Claro Farm, Lençóis Paulista, Brazil; (9) Fortes (1999)—Campo de Instrução de Santa Maria, Brazil; (10^1) Fialho (2000)—Morro da Extrema, Porto Alegre, Brazil (Encosta troop); (10^2) Fialho (2000)—Lami, Porto Alegre, Brazil (Restinga troop); (11) Limeira (1996)—Amazonas Farm, Rio de Janeiro, Brazil; (12) Lunardelli (2000)—Parque Estadual da Cantareira, São Paulo, Brasil; (13) Steinmetz (2000)—Intervales State Park, Brazil; (14, 15^1) Marques (1996, 2001)—Aracuri Ecological Station, Brazil; (15^2) Marques (2001)—Itapuã State Park, Brazil; (16) Oliveira (2003)—Água Branca Farm, SP, Brazil; (17^1) Miranda (2004)—Chácara Payquerê, Balsa Nova, PR, Brazil (Forninho troop); (17^2) Miranda (2004)—(Patropi troop); (18) Koch (2008)—Barra do Ribeiro, Rio Grande do Sul, Brasil; (19^1) Fortes (2008)—Campo de Instrução de Santa Maria, Brazil (G troop); (19^2) Fortes (2008)—(M troop); (19^3) Fortes (2008)—(P troop); (20^1) Agostini (2009)—El Piñalito Provincial Park, Misiones, Argentina (Cosacos troop); (20^2) Agostini (2009)—(Gitanos troop); (21) Guzzo (2009)—Ipê, Rio Grande do Sul, Brazil; (22) Bonvicino (1989)—Fazenda Pacatuba, Paraíba, Brazil; (23) Jardim (1997)—Estação Científica Ferreira Penna, Brazil; (24) Pinto et al. (2003)—Cauaxi Ranch, Paragominas, Brazil; (25) Porfírio de Souza (2005)—RPPN Pacatuba, Paraíba, Brazil; (26) Pinto (2002)—Paranaíta, MT, Brazil; (27) Zunino (1986)—Northeastern Argentina; (28) Zunino (1989)—Northeastern Argentina; (29, 30) Bicca-Marques (1993, 1994)—Estância Casa Branca, Rio Grande do Sul, Brazil; (31^1) Bravo and Sallenave (2003)—Brasilera Island, Argentina (Gringos troop); (31^2) Bravo and Sallenave (2003)—(Enfermitos troop); (32) Aguiar et al. (2003)—Balsa Nova, Paraná, Brazil; (33^1) Ludwig (2006)—Mutum Island, Paraná river, Brazil (GM troop); (33^2) Ludwig (2006)—Porto Rico, Paraná, Brazil (GP troop); (34) Kowalewski (2007)—Brasilera Island, Argentina; (35) Prates (2007)—Alegrete, Rio Grande do Sul, Brasil; (36) Muhle (2008)—Tupaciretã, Rio Grande do Sul, Brazil; (37^1) Agostini (2009)—El Piñalito Provincial Park, Misiones, Argentina (Orishas troop); (37^2) Agostini (2009)—(Reviro troop); (38) Gaulin and Gaulin (1982)—Finca Merenberg, Colombia; (39) Izawa and Nishimura (1988)—Serranía La Macarena, Colombia; (40, 41) Palacios and Rodríguez (2001), Palacios (2003)—Caparú Biological Station, Colombia; (42) Morales-Jimenez (2003)—Otun Quimbaya Sanctuary, Risaralda, Colombia; (43) Santamaría and Rylands (2003)—Biol. Dyn. Forest Frag. Proj., Amazonas, Brazil; (44^1) Gómez-Posada and Londoño (2012)—LMO forest fragment, Quindío, Colombia (Matapalo troop); (44^2) Gómez-Posada and Londoño (2012)—(Ocaso troop); (44^3) Gómez-Posada and Londoño (2012)—(troop 4); (44^4) Gómez-Posada and Londoño (2012)—(troop 5); (45) Queiroz (1995)—Mamirauá Ecological Station, Amazonas, Brazil; (46) Soini (1986)—Cahuana Field Station, Pacaya-Samiria N.R., Peru; (47^1) Neville (1972)—Hato Masaguaral ranch, Venezuela (troop 1); (48) Sekulic (1982)—Hato Masaguaral, Venezuela; (49^1) Ostro et al. (1999a)—Community Baboon Sanctuary, Belize (C1 troop); (49^2) Ostro et al. (1999a)—(C2 troop); (49^3) Ostro et al. (1999a)—(E1 troop); (49^4)

Ostro et al. (1999a, 1999b)—(E2 troop); (50^1) Bridgett (2006)—Monkey River, Belize (troop A); (50^2) Bridgett (2006)—(troop B); (50^3) Bridgett (2006)—(troop N); (50^4) Bridgett (2006)—(troop Q); (51) Gavazzi et al. (2008)—Lamanai, Belize; (52) Glander (1978)—Hacienda La Pacifica, Guanacaste, Costa Rica; (53, 54)^1 Milton (1977, 1980)—Barro Colorado Island, Panama (Lutz Ravine troop); (53,54)^2 Milton (1977, 1980)—(Old Forest troop); (55, 56)^1 Estrada (1982, 1984)—Los Tuxtlas Station, Mexico (troop S); (57^1) Estrada and Coates-Estrada (1984)—Los Tuxtlas Station, Mexico (troop S); (58, 59) Chapman (1987, 1988)—Santa Rosa National Park, Costa Rica; (60^1) Larose (1996)—Santa Rosa National Park, Costa Rica (SN troop, 1991); (60^2) Larose (1996)—(SN troop, 1992); (60^3) Larose (1996)—(EX troop, 1991); (60^4) Larose (1996)—(EX troop, 1992); (60^5) Larose (1996)—(SE troop, 1991); (60^6) Larose (1996)—(SE troop, 1992); information on population density in Santa Rosa National Park is from Fedigan et al. (1985); (61^1) Stoner (1996)—La Selva Biological Reserve, Costa Rica (troop 1); (61^2) Stoner (1996)—(troop 2); (62) Estrada et al. (1999)—Los Tuxtlas, Mexico; (63^1) Williams-Guilén 2003—Finca La Luz, Nicaragua (troop 1); (63^2) Williams-Guilén 2003—(troop 2); (63^3) Williams-Guilén 2003—(troop 3); (64^1) Hopkins (2008)—Barro Colorado Island, Panama (troop 8); (64^2) Hopkins (2008)—(troop 2); (64^3) Hopkins (2008)—(troop 6); (64^4) Hopkins (2008)—(troop 7)

Notes: [a]5 neighboring groups; [b]Schneider and Marques (1999); [c]Buss (2001); [d]both groups considered together; [e]quadrats used in more than 30% of daily routes; [f]only one group; [g]fixed kernel 50%; [h]with Orishas and Reviro (black howler groups); [i]both groups averaged (fruits include 7% consumption of Araucaria seeds); [j]with Orishas (black howler group);[k]quadrats used in more than 30% of observations; [l]Ferrari and Lopes (1996); [m]unlogged/logged forest; [n]quadrats used more than 70% of sampling days; [o]exclusive (actively defended) area; [p]both groups averaged; [q]quadrats used in ≥10% records; [r]3 neighbor groups; [s]fixed kernel 50%; [t]with Cosacos and Gitanos (brown howlers groups); [u]with Reviro; [v]both groups averaged; [w]with Cosacos (brown howlers group); [x]with Orishas; [y]30.8% time records; [z]Overlap index (Di Bitetti 2001); [aa]4 groups averaged; [bb]average for 22 groups; [cc]both years (1991/1992) averaged; [dd]for the whole study period; [ee]small tips of their home ranges overlapped with other (non-studied) groups; [ff]3 groups averaged; [gg]only 9 months; [hh]troops 8 and 2 averaged

Abbreviations: *HR* home range, *GC* grid cell counting, *MCP* minimum convex polygon, *afl* adjusted to forest limit, *wfu* whole fragment was used, *DP* digitized polygons, *KDE* kernel density estimates of food availability that does not take into account seasonal and habitat differences in plant species density, dispersion, phenology, crop productivity, and howler monkey dietary selectivity in terms of plant species and stage of development of preferred leaves and fruits (see chapters on diet, digestion and nutritional ecology in this volume). A study of *A. palliata* at Los Tuxtlas, Mexico, illustrates this point. A group composed of 14 individuals studied by Estrada (1984) used one of the largest home ranges ever reported for *Alouatta* spp. (ca. 60 ha, see Table 9.1) despite ingesting a diet rich in leaves (49% of feeding records). Estrada (1984) attributed this finding to a foraging pattern based on young leaves (39%) of patchily distributed tree species. According to him, the study group traveled extensively among scattered 1-ha quadrats during periods of high leaf consumption. Because the other three groups studied in the same site followed a similar pattern, Estrada (1984) could not evaluate how the exploitation of more clumped leaf sources would influence home range use. The scarcity of data on the distance among food patches in most studies carried out in the last four decades, with the exception of those recent ones focusing on the cognitive aspects of foraging, represents an additional limitation for testing the relationship between the degree of folivory and home range size.

9.1.2 Factors Affecting Day Range

Day range may also be influenced by factors such as group size, size, density and distribution of food sources, location of neighboring groups (territorial encounters) and, possibly, predation risk. Unlike the positive relationship found between fragment size and home range described above, fragment size was not a good predictor of the average length of the daily path in a genus-wide analysis carried out by Bicca-Marques (2003). His analysis showed that groups using small home ranges in forest fragments may travel as much as groups inhabiting larger habitat patches (Table 9.1). This finding seems to be related to a pattern of travel to scattered resources, the monitoring of the phenology of potential food sources distributed throughout the home range and/or the monitoring of home range boundaries.

Consistent with Bicca-Marques' (2003) results, Fortes (2008) observed similar day ranges in 3 study groups of *A. g. clamitans* that inhabited forest fragments of discrepant sizes: 1.8 ha (mean ± SD = 734 ± 228 m), 20 ha (679 ± 274 m), and ~1,000 ha (709 ± 207 m). The group inhabiting the smallest area moved back-and-forth on the ground between the 3 isolated small fragments 49 times in 59 sampling days. As a result, day ranges longer than 1,000 m were more common there (14%) than in the largest fragment (7%). In 23 complete days of observation the former group moved from one fragment to another. About half (43.5%) of these fragment changes occurred when diet richness started to stabilize (indicated by the species accumulation curve), whereas the remaining 56.5% happened before stabilization. This strategy allowed the group to include new items in the diet as indicated by the low values of Jaccard similarity index between the diet composition observed in fragments used in sequence (Fortes and Bicca-Marques 2012). Therefore, tracking the spatial availability of food resources and obtaining a balanced diet and/or avoiding the ingestion of an overload of the same secondary compounds appear to be critical factors in howler ranging behavior, irrespective of fragment size. The positive relationship found between mean day range and average number of plant species used as food sources per day by Bicca-Marques (2003) lends support to this hypothesis.

A positive relationship between group size and day range has been proposed for predominantly frugivorous species based on the assumption that larger groups deplete fruit patches faster than smaller ones (Chapman et al. 1995; Chapman and Chapman 2000; but see Sussman and Garber 2011 for a critique of the Ecological Constraints Model). Although howlers are better described as folivorous–frugivorous (Crockett and Eisenberg 1987), they may behave as predominantly frugivorous under certain circumstances, either during the year (*A. belzebul*: Jardim 1997) or certain seasons or months (*A. g. clamitans*: Koch 2008; *A. caraya*: Bicca-Marques and Calegaro-Marques 1994; A. *pigra*: Pavelka and Knopff 2004). In addition, their preferred leaf sources may also be depletable (Snaith and Chapman 2007). Therefore, it is also possible to predict that howler group size has a direct influence on day range, particularly when exploiting scattered and depletable food sources.

Again, contrasting results have been found. Studies that failed to demonstrate a positive relationship for howlers in general (among other folivorous primates) attributed this result to a weak or absent food competition and/or a reliance on alternative, fallback food items, such as mature leaves (Isbell 1991; Janson and Goldsmith 1995). A significant relationship was found in four out of seven studies that evaluated this aspect at the species level, particularly in *A. palliata* (Larose 1996; Williams-Guilén 2003; Hopkins 2011), the howler monkey that forms the largest groups and presents the wider variation in group size (see Di Fiore et al. 2011). The fourth study that found this relationship involved a population of *A. pigra* at the Community Baboon Sanctuary (Ostro et al. 1999a). However, studies on this species at the Cockscomb Basin Wildlife Sanctuary (Ostro et al. 1999a) and Lamanai (Arrowood et al. 2003) failed to find such relationship. At Lamanai day range was predicted by group spread, a relationship compatible with the occurrence of feeding competition (Arrowood et al. 2003). Therefore, it is possible that the strength of the relationship between group size and day range is context-specific, depending on site characteristics (e.g., size, spatial distribution, and productivity of nearby feeding patches; Chapman and Chapman 2000) and population density. Unfortunately, analyses integrating this information are rare in *Alouatta* studies (Bridgett 2006 is an exception). Bridgett (2006) mapped the location of 201 trees and collected phenological samples to evaluate fruit availability within the home ranges of 4 groups of *A. pigra* in Belize. He calculated a coefficient of dispersion of fruiting trees for each home range and related it to the groups' ranging patterns.

Milton (1980) states that howlers are travel minimizers because of energetic constraints imposed by a diet rich in leaves that are low in ready energy, an assumption that leads to the prediction that day range should be inversely related to the contribution of leaves to the diet. However, howlers have been observed to travel over longer distances during periods of both high frugivory (*A. g. clamitans*: Mendes 1989;

Martins 1997; Fortes 1999; Marques 2001; Oliveira 2003; *A. pigra*: Bridgett 2006; *A. caraya*: Agostini et al. 2010) and high folivory (*A. g. clamitans*: Limeira 1996; *A. palliata*: Estrada 1984). Zunino (1986) addresses the complexity of this relationship by proposing two main behavioral strategies related to the Optimal Foraging Hypothesis: high cost-high reward and low cost-low reward (Zunino 1986).

The adoption of a high cost-high reward strategy would be expected during periods when howlers are feeding on fruit, a food item richer in ready energy than leaves. This strategy was observed by Pavelka and Knopff (2004) in *A. pigra*, in which time moving increased from 5.4% in the season of low fruit consumption (14%) to 9.4% in the season of high fruit consumption (67%). Similarly, a group of *A. g. clamitans* inhabiting an Araucaria forest (Aracuri Ecological Station) in southern Brazil showed the longest day ranges (mean ± SD = 1,200 ± 182 m, maximum = 1,512 m, $n = 11$ days) when traveling between scattered Brazilian pine trees (*Araucaria angustifolia*) to consume their seeds (Marques 2001). These displacements occurred during the Fall, when the howlers could be expected to save energy to cope with the low ambient temperatures (mean minimum temperature = 11 °C) and the needs of thermoregulation (Bicca-Marques and Azevedo 2004). However, in accordance with the high cost-high reward strategy, the seeds of *A. angustifolia* are fourfold richer in carbohydrates (total carbohydrates = $38.7 \text{ g} \times 100 \text{ g}^{-1}$; Cordenunsi et al. 2004) than the most consumed fruit by the study group (*Campomanesia xanthocarpa*, Myrtaceae; total carbohydrates = $8.9 \text{ g} \times 100 \text{ g}^{-1}$; Vallilo et al. 2008), thereby possibly offsetting an increase in travel costs.

On the other hand, a low cost-low reward strategy would be expected when howlers rely mostly on leaves (particularly mature ones), a food item containing less readily available energy (Milton 1979). This strategy was observed by Limeira (1996), who reports a negative correlation between the consumption of mature leaves and day range in *A. g. clamitans*. However, her study group also presented a positive correlation between day range and the consumption of young leaves from an important source, *Apuleia leiocarpa* (Fabaceae), a pattern similar to that previously reported by Estrada (1984) for *A. palliata*.

Again, it is important to consider that these strategies were proposed based on the oversimplified idea that fruits would be more sparsely distributed than leaves in time and space. For instance, other studies have shown that when fruit sources are clumped or hyperabundant in the environment, howlers may travel over shorter distances while "camping" at productive sites and feeding intensively on fruit for several days (Fialho 2000; Palacios and Rodríguez 2001; Oliveira 2003; Miranda 2004; Kowalewski 2007); that is, adopting a strategy of low energy expenditure even with a high energy intake.

Finally, some studies found no relationship between diet composition and day range. This result was observed in groups showing a low level of fruit consumption throughout the year (*A. palliata*: Chapman 1988; *A. g. clamitans*: Chiarello 1993) and in a group of the latter species that fed heavily on highly abundant fruit species that fruit asynchronously (*Syagrus romanzoffiana*, Arecaceae, and *Ficus* spp., Moraceae) throughout the year in a seasonal forest (Itapuã State Park) in south Brazil (Marques 2001). These studies highlight that day range may vary among habitats and times of the year in response to spatiotemporal chances in the availability of particular food items.

9.1.3 Hypotheses

Given the lack of consistent trends and the complexity of the relationships between ecological and demographic factors and the patterns of ranging behavior in *Alouatta* spp. discussed above, we tested whether home range size is affected by (1a) fragment size, (1b) population density, (1c) group size, and (1d) group biomass, and whether day range length is affected by (2a) fragment size, (2b) population density, (2c) group size, and the contribution of (2d) fruits and (2e) leaves to the diet. We also included species and method of estimating home range as factors, due to evidence showing that home range size differs among howler species (Bicca-Marques 2003) and that estimates may vary widely among methods (Grueter et al. 2009; Gula and Theuerkauf 2013) as discussed below.

9.1.4 Methods

We compiled data on the ranging behavior of nine howler monkey species from 56 studies that provided information on home range size and/or day range length and a set of potential predictive demographic and ecological variables (Table 9.1). We limited the review to studies lasting at least 6 six months and that covered more than 1 season to reduce the potential influence of seasonality on the results. We used GLMs to assess whether group size and biomass, population density, fragment size, and the contribution of fruits and leaves to the diet were good predictors of home range size or day range length. We also included species identity and home range estimating method as factors in the models. Group biomass was calculated multiplying the relative contribution of each age-sex class for the group size by the mean biomass of that class according to the literature (Glander 1980; Ford and Davis 1992; Smith and Jungers 1997; Glander 2005; Di Fiore et al. 2011). When there was no information on body mass for a given species we used data from its closest congener for which this information is available.

We began by adjusting the complete model (including all possible explanatory variables) for each of the dependent variables (home range size or day range length) based on the lower values of AIC (Matthiopoulos 2010). For the analysis of home range we also tested a model excluding the variable fragment size because its effect was negligible in the first model. Although there is a high correlation ($r_S = 0.89$) between time invested consuming fruits and leaves, we decided to test a model for day range including both variables because they are not perfectly complementary and each item has its own suspected influence on howler movement (energy balance vs. nutrient mixing or toxin avoidance). The significance of the fitted terms and their interactions was assessed using the Wald statistic (McCullagh and Nelder 1989).

Traditionally, home range size was estimated either by the Minimum Convex Polygon (MCP; e.g., Milton 1980) or the Grid Cell (GC; e.g., Estrada 1982) method. The MCP method is calculated by measuring the area inside the convex polygon that results from the connection of the extreme locations of the group's range. This method is highly sensitive to the number of recorded locations and to the occurrence of outliers (group excursions to areas rarely visited) and, therefore, tends to overestimate the area of the home range, especially if it has an irregular shape (Grueter et al. 2009; Fieberg and Börger 2012). The GC method is calculated by overlaying a grid of cells of a particular area on a field map of the study site and counting the number of cells visited by the group. The method tends to overestimate the area of the home range when cell size is large and to underestimate it when cell size is small (Kool and Croft 1992; Grueter et al. 2009). The definition of an optimal grid size should take group spread into account, a parameter that increases with increasing group size and that may be affected by the productivity and dispersion of feeding patches. Therefore, although 10 × 10 m cells as used by Larose (1996) are likely to be small, 25 × 25 (Chiarello 1993), 50 × 50 (Pinto et al. 2003), 100 × 100 (Palacios and Rodríguez 2001), or 120 × 120 m (Chapman 1987) cells may be adequate under different circumstances. We suggest the use of the maximum reliable group spread (calculated as the maximum reliable perpendicular distance of the line transect census technique, see NRC 1981) to determine cell size in each study.

Digitized Polygons (DP) are created by mapping day range paths with a strip buffer zone at each side of the path. The polygon is traced using an MCP and all lacunae (areas outside the paths) inside this polygon are excluded. Similar to the other methods, the estimated area of the home range increases with increasing sample size. However, this method appears to generate more realistic estimates because it does not include areas inside the polygon based on mathematical assumptions (as the 95% MCP does), excludes areas not visited by the animals, and takes into account group spread for calculating the width of the buffer zone. The remaining subjectivity concerns the definition of the width of the buffer zone and the size of the lacunae to exclude, a decision that is made by the researcher (Ostro et al. 1999b).

The use of probabilistic techniques, such as kernel density estimates (KDE), is more recent and restricted to fewer studies (Hopkins 2008; Agostini 2009). This method provides the probability of finding a group at a particular location on a plane (probability density function), but has the limitation of increasing the probability of excluding areas used by the howlers (such as corridors between habitat patches) by splitting the home range into multiple small polygons (Fieberg 2007; Fieberg and Börger 2012). Despite these limitations, the use of different methods to calculate the home range of study groups of three howler species produced quite similar estimates (*A. pigra*: Williams-Guilén 2003; *A. g. clamitans*: Ludwig 2006; Agostini 2009; *A. caraya*: Agostini 2009).

We used the Kruskal-Wallis analysis of variance to compare home range and day range among species because of missing data in the data sets included in both models. We analyzed the relationship between pairs of variables (frugivory vs. folivory and intraspecific home range variance vs. sample size) via Spearman rank correlation test. All tests were performed using Statistica 10.0 (Statsoft 2011) and considered a level of significance of 0.05.

9.1.5 Testing the Hypotheses

The home range of study groups varied from 0.7 to 182 ha (median = 10 ha, mean ± SD = 19 ± 27 ha, $n = 85$ groups). Thus, a more than 200-fold difference in size separates the smallest (0.7 ha in *A. caraya*, Prates and Bicca-Marques 2008) from the largest (182 ha in *A. seniculus*, Palacios and Rodríguez 2001) home range. This difference is explained by the area of habitat available for the *A. caraya* group and possibly by the presence of competing primate species and a lower howler population density in the study site of *A. seniculus*. Home range size differed significantly among howler species ($H = 25.94$, $p < 0.0005$, $\phi = 7$, $n = 85$, *A. discolor* was excluded from the analysis because of small sample size), being significantly larger in *A. palliata* (33 ± 24 ha; Dunn *post-hoc* test, $Z_{\text{crit}} = 3.1$, $p < 0.05$). Within-species variance was large (Fig. 9.1) and directly influenced by sample size (Spearman rank correlation $r_s = 0.78$, $p = 0.02$, $n = 8$ species).

The model excluded *A. belzebul*, *A. discolor*, and *A. juara* because their data sets were limited to only one or two study groups each and because there are missing data for some variables. For the remaining six species, fragment size (1a), group size (1c), and group biomass (1d) did not show a consistent effect on home range size, whereas population density (1b) showed a negative relationship with this variable (Table 9.2). According to this model, the home range of *A. seniculus* was significantly smaller than those of the other howlers, independent of other factors. However, this occurred because only two studies fulfilled the data requirements to be included in the model, and one of them (Gómez-Posada and Londoño 2012) involved four groups with quite small home ranges in a bamboo forest fragment. In fact, the median home range for *A. seniculus* (considering all data) is 21 ha, only inferior to that of *A. palliata* (30 ha) and the single estimate available for *A. discolor* (57 ha).

The inverse relationship between population density (1b) and home range size and the results for *A. seniculus* are maintained after excluding fragment size from the model. However, this new model shows that the method used to estimate home range has a significant effect on the results. Whereas the Grid Cell method with smaller quadrats (≤50 × 50 m) tends to result in lower home range estimates, the use of larger quadrats (≥100 × 100 m) tends to produce higher values, independent of other factors. There was also a significant interaction between species and method, with studies on *A. palliata* using the Grid Cell method (either ≤50 × 50 or ≥100 × 100 m) estimating larger home ranges, and studies on *A. caraya* using the MCP method (adjusted to the borders of the fragment) estimating smaller ones. This model showed that *A. g. clamitans* uses larger home ranges, independent of other factors, a result that probably derives from the restricted *A. palliata* data set included in the model.

Day range varied from 0 m in *A. pigra* to 2,850 m in *A. palliata* (median = 494 m, mean ± SD = 506 ± 190 m, $n = 72$ groups; Table 9.1). Mean day range at the species level ranged from 320 m in *A. juara* in the Mamirauá Sustainable Development Reserve (only 1 study group; Queiroz 1995) to 928 m (SD = 314 m, $n = 2$ groups) in *A. seniculus* (Fig. 9.2), and it varied among species ($H = 18.84$, $p = 0.004$, $\phi = 6$, $n = 70$; *A. juara* and *A. discolor* were excluded from the analysis because of small sample sizes). A *post-hoc* Dunn test showed that the average day range of *A. g.*

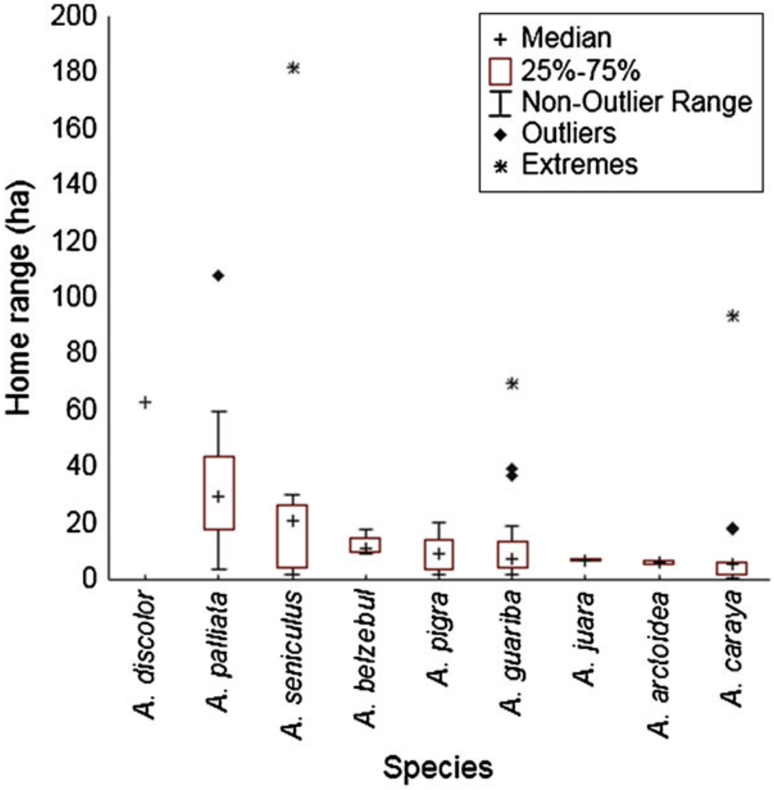

Fig. 9.1 Home range of howler monkey species (data set from Table 22.1)

clamitans (mean ± SD = 620 ± 142 m) is significantly longer than that of *A. palliata* (432 ± 172 m; $Z_{\text{calc}} = 3.34$, $Z_{\text{crit}} = 3.04$, $p < 0.05$).

The model for day range considered only three howler species—*A. g. clamitans*, *A. palliata*, and *A. caraya*—due to missing data for the others. Fragment area (2a) did not show a significant effect on day range, but both population density (2b) and group size (2c) did, independent of other factors. Whereas the first showed a negative relationship with day range, the latter showed a positive relationship. Finally, the degrees of frugivory (2d) and folivory (2e) showed negative relationships with day range, although the first was stronger (Table 9.3). Species identity also had a significant influence on day range: *A. g. clamitans* showed longer day ranges than *A. palliata*, irrespective of other factors, thereby corroborating the results of the nonparametric tests presented above.

Table 9.2 Summary of the effects included in the generalized linear model explaining home range size in howlers (distribution: gamma, link function: log, $n = 51$)

Effect	Level of effect	Estimate ± SE	Wald statistics	p
Complete model (AIC = 348.84; ϕ = 33)				
Intercept		1.91344 ± 1.931702	0.98119	0.321906
Fragment size		0 ± 0.000014	0.10850	0.741860
Population density		**−0.15924 ± 0.029479**	**27.17776**	**0.000000**
Group size		−0.06458 ± 0.063438	1.03646	0.308645
Group biomass		0.10893 ± 0.083227	1.71316	0.190576
Species	*A. g. clamitans*	0.86996 ± 0.459839	3.57924	0.058506
	A. palliata	0.88412 ± 1.828717	0.23374	0.628767
	A. pigra	−2.01215 ± 2.105268	0.91349	0.339189
	A. seniculus	**−1.00607 ± 0.472254**	**4.53845**	**0.033142**
	A. arctoidea	0.23217 ± 0.502308	0.21364	0.643928
Method	GC1	−0.04576 ± 2.026468	0.04414	0.833590
	GC2	1.41431 ± 6.228192	0.05157	0.820360
	MCP	0.62634 ± 2.065563	0.09195	0.761716
	DP	−0.01407 ± 0.331608	0.00180	0.966151
Model excluding fragment size (AIC = 346.95; ϕ = 34)				
Intercept		**2.53658 ± 0.400594**	**40.09465**	**0.000000**
Population density		**−0.15939 ± 0.029498**	**29.19520**	**0.000000**
Group size		−0.06211 ± 0.062795	0.97834	0.322609
Group biomass		0.010385 ± 0.081541	1.62220	0.202786
Species	***A. g. clamitans***	**0.93322 ± 0.417365**	**4.99957**	**0.025354**
	A. palliata	0.29521 ± 0.350976	0.70745	0.400291
	A. pigra	−2.38405 ± 1.794564	1.76487	0.184019
	A. seniculus	**−0.92651 ± 0.411093**	**5.07952**	**0.024210**
	A. arctoidea	0.30007 ± 0.460813	0.42403	0.514931
Method	**GC1**	**−1.08896 ± 0.218783**	**24.77422**	**0.000001**
	GC2	**3.45885 ± 0.447073**	**59.85576**	**0.000000**
	MCP	−0.05084 ± 0.196393	0.06701	0.795743
	DP	−0.02969 ± 0.327449	0.00822	0.927765
Species*Method	***A. palliata* × *A. caraya*/ GC1 x MCP ad**	**1.36880 ± 0.258815**	**27.97049**	**0.000000**
	***A. palliata* × *A. caraya*/ GC2 x MCP ad**	**−2.75546 ± 0.522078**	**27.85587**	**0.000000**

Significant effects are in bold

GC1 grid cell (≤50 × 50 m), *GC2* grid cell (≥100 × 100 m), *MCP* minimum convex polygon, *MCP ad* minimum convex polygon adjusted to fragment borders, *DP* digitized polygon

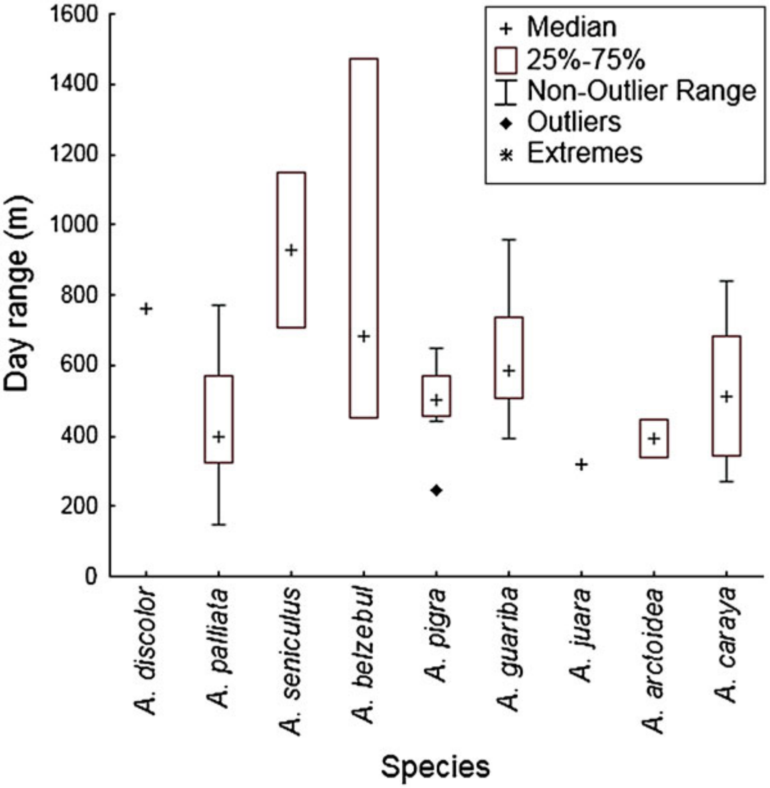

Fig. 9.2 Day range of howler monkey species (data set from Table 22.1)

Table 9.3 Summary of the effects included in the generalized linear model explaining day range length in howlers (distribution: normal, link function: log, $n=24$, $\phi=16$, AIC = 312.1)

Effect	Level of effect	Estimate ± SD	Wald statistics	*p*
Intercept		**6.9990 ± 0.57898**	**146.1329**	**0.000000**
Fragment size		0 ± 0.00003	0.3107	0.577281
Population density		**−0.0505 ± 0.01896**	**7.1047**	**0.007688**
Group size		**0.0414 ± 0.01551**	**7.1119**	**0.007657**
% Frugivory		**−0.0142 ± 0.00588**	**5.8128**	**0.015910**
% Folivory		**−0.0123 ± 0.00625**	**3.8861**	**0.048687**
Species	***A. g. clamitans***	**0.3508 ± 0.09040**	**15.0560**	**0.000104**
	A. palliata	**−0.5385 ± 0.14922**	**13.0226**	**0.000308**

Significant effects are in bold

9.1.6 Understanding the Ranging Behavior of Howler Monkeys

Howler population density is an important factor influencing howlers' use of space. In the presence of a high density of conspecific groups howler home ranges are usually smaller (Bravo and Sallenave 2003; Kowalewski 2007; Gómez-Posada and Londoño 2012) than those observed in study sites where howler density is lower (Estrada 1984; Steinmetz 2000; Palacios and Rodríguez 2001; Miranda 2004; Agostini 2009). However, the lack of detailed data on resource availability and distribution at most study sites does not allow to determine whether population density is the proximate cause or just a consequence of habitat carrying capacity and/or shrinking (see the chapter by Behie and Pavelka 2014). In any case, social groups need to use home ranges large enough to fulfill their nutritional requirements for enabling their long-term survival.

On the other hand, the area of forest is not a critical factor, despite the predictable effects of habitat loss at one extreme of the range of habitat availability. The influence of the area of potential habitat available on home range is relaxed because at the other extreme of the range, continuous forests or large forest tracts may be inhabited by groups using either large (Steinmetz 2000; Palacios and Rodríguez 2001; Agostini 2009) or small home ranges (Queiroz 1995; Ostro et al. 1999a; Ludwig 2006; Fortes 2008). The latter situation is often found under high population densities as discussed above. The fact that stable howler groups have been observed occupying small home ranges in fragments smaller than 10 ha (Estrada et al. 1999; Fortes 2008; Guzzo 2009; Muhle 2008), sometimes during many years (Bicca-Marques 1994; Prates 2007; Zunino et al. 2007), highlights their adaptation to conditions of constrained space.

Howlers do not use their home ranges homogeneously by concentrating their activities in core areas; that is, those portions of the home range exploited at a higher frequency than expected by chance. This pattern has been observed irrespective of habitat availability or home range size. For instance, the group of *A. seniculus* studied by Palacios and Rodríguez (2001) that ranged over 182 ha used a core area of ca. 8–9%, a similar proportion to that reported for *A. caraya* in a 2-ha home range by Bicca-Marques (1994). However, the criteria used to define core areas have differed widely among studies (quadrats used ≥10% time records: Ludwig 2006; ≥30% time records: Jardim 1997; Palacios and Rodríguez 2001; quadrats visited in ≥30% of daily routes: Miranda 2004; ≥70% of daily routes: Bicca-Marques 1994; ≥50% kernel density: Agostini 2009). More critical than the actual size of the core area, a description of howlers' use of space shall integrate information on the activities performed at highly used sectors of the home range, the number and spatial arrangement of these areas, the causes of the avoidance or reduced use of others, and the potential costs (including travel) of each ranging strategy.

Core areas may be associated to preferred sleeping sites, as suggested by Chivers (1969) based on a 3-month study of *A. palliata* on Barro Colorado Island, Panama (a single core area of night positions located in the center of the home range), and

Jardim (1997) in her study of *A. belzebul* in the Caxiuanã Biological Station, state of Pará, Brazil (multiple clusters of sleeping trees distributed mainly at the periphery of the home range). Few studies have quantitatively analyzed the spatial distribution of sleeping sites (e.g., Bicca-Marques 1994; Jardim 1997; Bravo 2009). While both groups of *A. caraya* studied by Bravo and Sallenave (2003) used a single sleeping tree in about 50% of the nights, no sleeping site of the group of *A. g. clamitans* studied by Fortes (1999) was used for more than 8% of nights (21 out of 51 sleeping trees were used just once), suggesting contrasting strategies of sleeping site use. The scarcity of the database on sleeping site selection, spatial distribution and use compromises testing hypotheses on the influence of the proximity to feeding sites, parasite or predator avoidance, thermoregulation, or social contact (see Anderson 1998).

Our model showed that population density has an inverse relationship with day range. This is a surprising finding because the need of defending/advertising the home range and its valuable resources against neighboring groups via border patrolling should be expected to increase as the population grows. However, this outcome is compatible with a low level of between-group contest competition for food among howlers (Isbell 1991). Therefore, the positive correlations found between day range and the frequency of group confrontations in *A. caraya* (Bravo and Sallenave 2003; Kowalewski 2007) and *A. palliata* (Hopkins 2008) might be related to contexts of mate monitoring instead of food competition or "territory" defense as stated by Kowalewski and Garber (2010) and Fernández et al. (2013). Comparative studies of the vocal communication, especially the frequency and spatial distribution (core area vs. periphery of the home range) of loud calling sessions, among species and varying contexts of population density, group size and resource availability and distribution, might be particularly insightful for understanding how howler groups cope with the social and ecological pressures of an increasing population density.

The influence of group size on day range is compatible with the contention that larger groups demand more food to satiate their group members and, therefore, may need to travel farther to fulfill their nutritional requirements. There is certainly a trade-off between the benefits of a larger group (e.g., predator protection and information-sharing) and the costs of additional travel or increased within-group competition (Chapman et al. 1995; Chapman and Chapman 2000) for food and/or mating opportunities. In the context of mating competition it is possible that between-group competition plays a critical role in the relationship between group size and day range. According to Kowalewski (2007), adult males cooperate to defend their mating partners during intergroup encounters. Therefore, larger groups may be expected to engage in group confrontations and seek contact with females from neighboring groups more frequently than smaller groups containing fewer males.

The negative relationship between day range and the contribution of fruit to the diet may be a consequence of a preference for exploiting highly productive and/or clumped fruiting sources, in whose vicinity howlers may "camp", a foraging strategy that challenges the high cost-high reward strategy proposed by Zunino (1986). On the other hand, the negative relationship between folivory and day range corroborates Milton's (1998) findings that howlers cope well with plant toxins and that they do not need to travel much to avoid an overload of the same secondary metabolites. However, according to Bicca-Marques (2003), there is a positive relationship between day range and diet diversity. Additionally, Fernández et al. (2012) show that the percentage of time (or feeding records) devoted to the consumption of a food item is not a good proxy for the biomass, energy, and nutrients ingested. Consequently, the use of broad categories, such as fruit and leaves, instead of the analysis of the nutritional and energy contents of ingested food items may compromise our interpretation of the actual foraging strategies adopted by howlers.

Finally, home range overlap is an important aspect of howler use of space that has been partially neglected because of logistical difficulties. The collection of accurate data on this variable requires a long-term monitoring of several habituated neighboring groups. However, because most studies have focused on a single social group, overlap has been estimated based on eventual sightings of neighboring groups inside the focal group's home range. Estimates of home range overlap are available in less than one third of the publications listed in Table 9.1 (*A. g. clamitans*: Chiarello 1993; Agostini 2009; *A. palliata*: Williams-Guilén 2003; Hopkins 2008; *A. belzebul*: Jardim 1997; *A. pigra*: Bridgett 2006; Gavazzi et al. 2008; *A. seniculus*: Palacios and Rodríguez 2001; Gómez-Posada and Londoño 2012; *A. caraya*: Bravo and Sallenave 2003; Ludwig 2006; Kowalewski 2007; Agostini 2009). Whereas overlap is nil in forest fragments inhabited by a single group or extremely low or absent in areas with low population densities (e.g., *A. seniculus,* Eastern Colombia: Palacios and Rodríguez 2001), it may be quite high (70%) under high population densities (e.g., *A. caraya*, Brasilera Island, Argentina: Kowalewski 2007).

9.2 Spatial Cognition

Alouatta is one of the most studied Neotropical primate genera in the wild, and the first to have its patterns of use of space described (ca. 80 years ago by C.R. Carpenter). Despite many tens of thousands of observation hours throughout its distribution since the classical monograph published by Carpenter (1934), only a handful of studies have addressed the cognitive challenges that howler monkeys face in navigating within their home ranges. Their small home ranges (often <30 ha), short day ranges (rarely >1,000 m), and cohesive foraging may have contributed to this situation by suggesting that they should face simpler spatial challenges than species ranging over larger areas (Clutton-Brock and Harvey 1977; Milton 1981). However, howlers are constantly challenged by the need to find appropriate food items to compose a nutritionally balanced diet (Righini and Garber 2012), a physiological need that shall be a critical selective force for the evolution of their spatial skills. These challenges exist even when the targeted resources are not fruits or seeds, but new leaves (Estrada 1984; Limeira 1996) or flowers (Fortes 1999; Marques 2001) of important food species, since in most cases these food sources do not present an uniform spatial distribution and their availability varies temporally, requiring howlers to be able to track their occurrence in the forest.

Although it is still unknown the kind of spatial information that howlers perceive, encode, and recall for guiding their movements within the tridimensional canopy milieu and the strategies that they adopt to increase their foraging efficiency, the importance of spatial knowledge to howler navigation can also be assessed by observing the travel patterns of groups confronted with unfamiliar areas, such as translocated groups. In this sense, groups of *A. pigra* showed a more exploratory travel pattern soon after release in a new site by shifting the location of their monthly ranges and exploring a larger number of new areas each month than did established groups (Ostro et al. 1999a, 2000).

Milton (1981) reports that howlers use a goal-directed travel pattern when moving between feeding trees by using specific routes at a higher frequency than expected by chance. She suggests that they rely on (1) "pivotal trees," a small number of trees that are visited regularly during consecutive days or in the same day, and (2) "arboreal pathways," travel routes (>100 m in length) that are repeatedly used to travel between "pivotal trees." These "arboreal pathways" connect food patches and appear to be part of a strategy aimed at minimizing travel, which also allows them to monitor the phenological status of potential feeding trees (Milton 1981, 2000). She also suggests that the small set of "pivotal trees" (often feeding sources) used by mantled howlers during several days "[…] seemed to give the monkeys a base from which they could move out in various directions and search for other resources" (Milton 1980: 103), and that they seem to know when to visit these trees to find the necessary resources (Milton 2000).

Despite Carpenter's and Milton's reports, the first studies specifically designed to address the cognitive bases of howler monkey navigation only began to be conducted more than two decades after the publication of Milton's seminal papers (Milton and May 1976; Milton 1980, 1981, 1993). These studies tested predictions such as (1) howlers minimize ("optimize") the distance traveled by using straight-line movements to the nearest available tree of a few target species; (2) they monitor the availability of large and/or preferred food sources, and exploit the most productive trees available; (3) they repeatedly use travel pathways that include large trees that provide more food and from where they enjoy enhanced visibility of the surroundings, thereby reducing the need for memory load; and (4) they use these tall (high-visibility) trees where different routes intersect as nodes or decision points, an indication of a topological mental representation (*A. caraya*: Ventura 2004, 2005; Fernández 2008; *A. palliata*: Garber and Jelinek 2006; Hopkins 2008, 2011; *A. g. clamitans*: Pereira 2008).

The use of straight-line routes to the nearest target (feeding or sleeping) tree was partially supported by these studies as discussed below. The circuit index (CI: actual distance traveled/most efficient route distance; Garber and Hannon 1993) is a good proxy for path directedness, and offers a measure of the frequency of use of the shortest route to the next target (Garber and Jelinek 2006; Hopkins 2008; Fernández 2008). The indices recorded by Garber and Jelinek (2006) during 15 days of observation show routes close to linearity, at most 9% longer than the possible most efficient route (CI = 1.05). Possibly because ranging patterns vary temporally in response to changes in food availability, Hopkins (2011) recorded a higher circuit index (CI = 1.37–2.66) for the same species at a different site, whereas the highest amplitude was found for *A. caraya* (CI = 1.05–11.93) in Argentina (Ventura 2004, 2005).

In southern Brazil, brown howlers visited the nearest tree of target food species in 41% of the observations (*n* = 160 trees, 20 days of data collection). However, they used "less-direct" routes (traveled longer distances) when feeding on fruit of *Ficus organensis* by selecting the most productive trees and bypassing less-productive sources of the same species (Pereira 2008). This strategy might be related to a preference for foraging in areas with higher resource availability (trees with larger diameter at breast height), or to the selection of routes crossing areas with higher canopy connectivity (Hopkins 2011). This strategy can also be interpreted as evidence of spatial knowledge because these trees were usually outside the monkeys' potential field of view (Garber 1989; Janson 1998; Cunningham and Janson 2007). Additional evidence of spatial knowledge comes from the ability of howlers to reach the same target feeding and resting sites ("pivotal trees," sensu Milton 1980) from different directions and distances (Garber and Jelinek 2006; Pereira 2008).

Studies have also confirmed that howlers adopt strategies compatible with an efficient monitoring of preferred and most important food sources (Milton 1981, 2000; Garber and Jelinek 2006; Hopkins 2008, 2011; Pereira 2008). Brown howlers traveled farther and visited more trees when feeding on unripe than on ripe fruit of *F. organensis* (Pereira 2008), suggesting that they were keeping track of unripe fruit availability as a way of predicting future ripe fruit production, as suggested by Di Fiore (2003) for woolly monkeys (*Lagothrix lagotricha poeppigii*), and Janmaat et al. (2006) for sooty mangabeys (*Cercocebus atys atys*) and grey-cheeked mangabeys (*Lophocebus albigena johnstoni*). Howlers also usually travel along the same, highly predictable routes (*A. caraya*: Bicca-Marques and Calegaro-Marques 1995; Pereira 2004; Fernández 2008; *A. discolor*: Pinto 2002; *A. g. clamitans*: Limeira 1996; Fortes 1999; Marques 2001; Pereira 2008; *A. palliata*: Garber and Jelinek 2006; Hopkins 2008), an evidence of travel optimization using the available spatial knowledge (route-based spatial representation), that may, on the other hand, increase their vulnerability to some kinds of predators (Quintino and Bicca-Marques 2013). According to Garber and Jelinek (2006), howlers travel significantly shorter distances when reusing the same tree sequences than when selecting new tree sequences and directions.

The more frequent use of a few larger trees that provide wider visibility, especially in the low- and middle-canopy levels (Garber and Jelinek 2006; Pereira 2008), supports the idea that howlers use these trees as decision (or detection) nodes. Current evidence supports the idea that howlers do not need to remember neither the positions of a large number of trees in their home range, nor the availability of food. Remembering a limited number of route segments that lead to nodes, and their distances, is sufficient to allow howlers to monitor a series of potential feeding places. This task requires less cognitive processing than a continuous updating of a mental map that includes several landscape features and their current relationships (Barton 2000; Di Fiore and Suarez 2007). These findings are consistent with the idea of a topological, or route-based, mental representation (sensu Dyer 1991). It is also important to highlight that patterns of howler monkey spatial exploration were very consistent across these studies, despite the fact that they were conducted in areas varying in habitat availability and floristic and structural characteristics (from tropical evergreen to subtropical deciduous forests, and from continuous to gallery forests and forest fragments).

Finally, a recent study examined how age, sex, reproductive status, and dominance rank influence leadership of progressions in two groups of *A. caraya*. According to Fernández et al. (2013), leadership is based on age. Adult black-and-gold howler monkeys lead group progressions. This pattern agrees with previous studies on *A. caraya* (Bicca-Marques and Calegaro-Marques 1997), *A. palliata* (Costello 1991), and other primates (Boinski 1991; Janson and Di Bitetti 1997; Fashing 2001; Barelli et al. 2008), and is believed to be associated with a deficient knowledge of the home range by immature individuals (Janson and van Schaik 1993). However, the observation that *A. caraya* males lead the group in intergroup encounters is also consistent with a male mate defense hypothesis (Fernández et al. 2013). Studies on the ontogeny of ranging behavior and analyses of individual movement patterns across behavioral contexts (e.g., feeding, resting and intergroup encounters) are particularly useful for testing these hypotheses.

9.3 Conclusions and Prospects

Studies on the ranging behavior of howler monkeys are highly biased toward a few taxa (*A. palliata*, *A. pigra*, *A. seniculus*, *A. caraya* and *A. g. clamitans*) and have shown that some patterns are highly conservative among species (such as the short, often <1,000-m long day ranges), whereas others are more variable both within- and between-species (such as the size of the home range). Research on howler spatial cognition is new and has been restricted to three taxa (*A. palliata*, *A. caraya*, and *A. g. clamitans*), thereby limiting our ability to evaluate the influence of species, foraging syndrome, habitat structure, and resource availability among other factors on the strategy adopted by howler groups to navigate within their home range.

Our modeling allowed us to confirm that population density is an important factor influencing howlers' use of space, showing a negative relationship with both home range size and day range length, and that *A. palliata* groups tend to use larger home ranges than the other howlers. Although within-study comparisons of methods for estimating home range have produced similar results as reported above, our model identified significant differences derived from the size of the quadrats chosen for the Grid Cell method as well as significant species*method interactions. These differences in the sensitivity of the methods compromise comparisons and highlight the need of standardization.

Despite the natural increase in sample size from the time of Bicca-Marques's (2003) review to the present study, the difference found in the effect of habitat availability (fragment size) on home range size may have resulted from differences in the statistical methods applied. Whereas the linear regression analysis ran by

Bicca-Marques (2003) may have been driven by the spatial limitation imposed to howlers at the lower extreme of the range of habitat availability, our modeling appears to have been influenced by the fact that howler groups rarely use home ranges >50 ha (indeed, they are often <30 ha) irrespective of the area of habitat available. Therefore, instead of contradictory, these analyses may be highlighting distinct characteristics of the data set.

The expected positive effect of group size on day range was also supported by our model, but the proximate causes of this relationship remain unknown. This finding is compatible with both within- and between-group competition for food or mates, respectively. A detailed mapping of the spatial distribution of potential food sources, including an assessment of the distances between actual feeding and resting sites, together with an accurate monitoring of their phenology within the home ranges of several groups of the same population would be insightful to better interpret the ranging behavior of howler monkeys living under varying scenarios of group size, population density, food availability, and habitat carrying capacity.

The unexpected negative relationships between both the degree of folivory and frugivory with day range found in our model suggest that interpretations based on general assumptions of temporal and spatial availability and quality of gross categories of food (e.g., fruit vs. leaves) are too simplistic. Data on the number of sources of fruit, leaves, flowers, and other food items exploited on a daily basis, and their respective contributions to the diet, are needed to evaluate whether energy balance, nutrient mixing, and/or toxin avoidance play a significant role in the pattern of daily ranging behavior. Unfortunately, only a handful of studies report this kind of data, whose integration with recent approaches of nutritional ecology (Raubenheimer et al. 2009, 2012; Felton et al. 2009) shall be particularly enlightening. It is possible that these negative relationships resulted from the frequently high foraging investment (e.g., >50% of feeding time) of howlers on a few top species (see Bicca-Marques 2003; Chaves and Bicca-Marques 2013). This hypothesis would be supported by data showing that, on a daily basis, diet species richness is inversely related to the difference in the contribution of leaves and fruits, an open issue for future research. Evidence from studies on spatial cognition confirming that howlers present a high degree of fidelity to particular routes, feeding and resting trees and that they tend to favor more productive trees to visit is compatible with this hypothesis.

In sum, despite tens of thousands of observation hours of howler monkeys and the large amount of data amassed on their ecology and behavior as evidenced in our comprehensive review, there are still many gaps in our knowledge of basic aspects of their natural history that compromise our understanding of their pattern of use of space and information on some species and study regions is virtually nill. Future studies focusing on any aspect of the ranging behavior discussed in this chapter that, in addition to the potential causal variables that we have evaluated, also integrate detailed analyses of resource availability (via fine-scale assessments of habitat floristic composition, species density and spatial distribution, phenology, and crop productivity), daily diet species richness, the amount of biomass ingested of each food item and its energy and nutritional value among others will be better equipped to appropriately test hypotheses about the ecological and social causes of the patterns of range use and the cognitive challenges faced by howler monkeys for navigating within their home ranges in order to get access to a balanced diet. A study with this approach conducted simultaneously on multiple neighboring groups in the same interbreeding population will be particularly welcome.

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Part III
Conservation and Management

Chapter 10
The Ethnoprimatology of the Howler Monkeys (*Alouatta* spp.): From Past to Present

Bernardo Urbani and Loretta A. Cormier

Abstract This chapter reviews the interface between humans and howler monkeys based on evidence from the archaeological record and the ethnography of contemporary indigenous societies. The record of howler monkeys interconnections with humans may be traced back to the Pre-Hispanic period. Data suggest that Mesoamerican civilizations such as the Mayans and Aztecs interacted with howlers. Also, members of societies from northern South America established relationships with howler monkeys before the Contact period. Among current indigenous societies, howlers are not only eaten, but also figure in mythic, sacred, and social symbologies. As large-sized atelines, howler monkeys are among the preferred primate prey for a number of cultures in the tropical Americas. However, some groups avoid them as prey. Cultural taboos on howlers as food are often linked to magical contagion whereby ingestion of howlers is believed to pass on their undesirable traits, such as lethargy. In addition, due to other behavioral features, such as vocalizations and ideas of human similarity, howler monkeys are common characters in the cosmologies of contemporary indigenous societies. For example, in native mythologies of lowland South America, the creation of howlers is often related to human body transformation. Thus, it can be argued that howler monkeys are/were subjects of different social representations among the native societies of the Neotropics.

Resumen Este capítulo revisa la interface entre humanos y monos aulladores basado en la evidencia arqueológica y la etnografía sobre sociedades indígenas contemporáneas. La evidencia de interconexiones entre monos aulladores y humanos puede retrotraerse hasta el período prehispánico. Los datos sugieren que civilizaciones mesoamericanas como los Mayas y Aztecas interactuaron con araguatos. Igualmente miembros de sociedades del norte de Suramérica establecieron relaciones con

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monos aulladores antes del período de contacto. En las sociedades indígenas actuales, los aulladores no son sólo consumidos, sino también aparecen en simbologías míticas, sagradas y sociales. Al ser primates de gran tamaño, los araguatos están entre los primates preferidos como presas por parte de varias culturas en la América tropical. Sin embargo, algunos grupos humanos los evitan como presas de cacería, en tanto que se considera tabú cultural la ingesta de monos aulladores como alimento, al asociarse regularmente con el contagio mágico de atributos no deseados como el letargo. Adicionalmente, debido a sus características comportamentales como la vocalización, así como las ideas en torno a su similitud con los humanos, los monos aulladores son personajes comunes en las cosmologías contemporáneas de las sociedades indígenas. En este sentido, por ejemplo, en mitologías de las tierras bajas de Suramérica, la creación del araguato habitualmente se relaciona con la transformación del cuerpo humano. En resumen, se puede sugerir que los monos aulladores son y fueron sujetos para ser representados socialmente de forma diferencial por las sociedades originarias del Neotrópico.

Keywords Human-nonhuman primate interaction • Platyrrhine • Mesoamerica • Lowland South America • Neotropics

10.1 Introduction

In 1998, L. Sponsel introduced the term “ethnoprimatology” as an intersection between the biological and cultural subfields of anthropology. Sponsel (1997) made a strong case that nonhuman primates could be studied using a multidisciplinary approach combining methods and theory of ethnography and primatology. In doing so, he introduced a number of new lines of research in ethnoprimatology. Among them, predation on primates was highlighted as a kind of human-nonhuman primate interaction that must be studied in detail, since it has been long neglected in the anthropological literature. In addition, Sponsel (1997) advocated the idea that humans and nonhuman primates are symbiotically linked in occupying the same ecological niche. In this sense, humans and nonhuman primates are closely related because they compete for resources, share successional landscapes, and exchange and allocate similar diseases (Sponsel 1997). This integrative view of nature and primates in general—including humans—serves to broaden our views on nature conservation, and nature as a part of the human realm.

Understanding the natural world through a folk biological perspective presents a challenging task today (Medin and Atran 1999). Such comprehensive study not only helps to elucidate how our world—including its plants and animals—is constructed, but also shows its repercussions in policy-making and public concerns (Medin and Atran 1999). In this dichotomous dialogue, values about nature and current discourse about the use of nature are in constant movement (Atran and Medin 2008). As summarized by Sanga (2004), the knowledge and use of nature is dynamic. For instance, in South America, the Amazon landscape appears to be a construction of natural events and anthropogenic use of the space based on political and sociocultural decisions (Rival 2006). However, for example, cultural anthropologists often lump all nonhuman primates into the category of "monkey," failing to understand differences in indigenous perceptions of primate species and also failing to recognize significant differences in wild primate social behavior and ecological adaptation (Cormier and Urbani 2008). As in the case of spider monkeys, which we addressed in a previous chapter, the availability of data on perceptions and interactions with howlers and other Neotropical primates by various societies is lacking or is limited in the literature (Cormier and Urbani 2008). As both authors stressed, ethnoprimatology is intended to improve understanding of the dynamic interactions between different cultures and different primate taxa. Thus, here we suggest that the relevance of ethnoprimatological research lies in the possibility of understanding how primates are culturally constructed, the dynamics of such social constructions, and the "universals" and variations in the dyadic interface between human and nonhuman primates in time and space.

This chapter parallels a previous review on the ethnoprimatology of spider monkeys (*Ateles* spp.) presented by Cormier and Urbani (2008). In the chapter presented here, we focus on the ethnoprimatology of howler monkeys (*Alouatta* spp.). Both taxa, spider and howler monkeys, are among the most widely distributed of the Neotropical primates, and consequently, interact with various indigenous societies in Mesoamerica and South America, from past to present. We concentrate and integrate three ethnoprimatological issues: the use and perception on howlers during the Pre-Columbian period, the procurement of howlers as food—and avoidance as food taboos—and the role of howlers in the symbologies, cosmologies, and mythologies of Amerindian societies.

10.2 Howler Monkeys in the Pre-Columbian Period: Looking at the Archaeological Record

As found for spider monkeys, evidence of atelines, and Neotropical primates in general, is relatively rare in the archeological record (Cormier and Urbani 2008). As we discussed previously, there are a number of reasons why so few wild primate remains have been found. One possible explanation is that wild primates may have been disarticulated where they were hunted, and only later brought to the indigenous villages. Another possibility is that terrestrial mammals may have been preferred over primates, and consequently, monkeys do not appear at the same frequency as other vertebrates such as ungulates. Bruner and Cucina (2005) also proposed that the low representation of howlers in the archaeological record could have been due to their loud vocalizations, which may have led to negative attitudes and taboos in Pre-contact human populations. Further, they suggest this may offer a possible explanation for their limited iconographic depiction in the past. In addition, it has been argued that the current distribution of Neotropical primates, and howler monkeys in particular, may have been induced in part by the interaction with humans during the Pre-Hispanic period (Hershkovitz 1984; Baker 1992; Sponsel 1997; Urbani 2005). In this section, we provide information on how howler monkeys were perceived and used before European contact.

One line of biological evidence that may suggest a long history of close interaction between humans and howler monkeys is that howlers are the only reported natural host of lice in the Neotropics. *Pediculus humanus* is a parasite of *Homo sapiens* globally. Two other louse species, *P. schaeffi* infects chimpanzees in tropical Africa and *P. mjoebergi* howler monkeys, and possibly other primates, in the New World (Hopkins 1949; Kowalewski and Gillespie 2009). This may be suggestive of a long and extensive human–howler interaction with lice (*Pediculus* sp.), probably dating from the earliest times of human colonization in the tropical Americas (M. Kowalewski, personal communication).

Among the Aztecs of central Mexico, a tooth of *Alouatta palliata* has been found in the Neighborhood of the Merchants of the Pre-Hispanic city of Teotihuacán (Valadez-Azúa and Childs-Rattray 1993). This zooarchaeological remain dated from the Xolalpan Period, 400–650 years AD was recovered in a rubbish dump. Inhabitants of eastern coastal origin in the Gulf of Mexico occupied this part of the city. Valadez-Azúa and Childs-Rattray (1993) suggested that primates and other animals were trafficked from this region (today Veracruz State) to the central valley of Mexico. Also in Mesoamerica, *Hun Batz*, the howler monkey god in the Mayan book *Popul Vuh*, is frequently represented in sacred pottery (Coe 1977, 1978; Anonymous 1994; Bruner and Cucina 2005). As described by Braakhuis (1987), *Hun Batz* has multiple roles. This deity is represented in Mayan vases as a diviner with a pivotal role in the Mayan calendar. In addition, *Hun Batz* has other sacred functions. In conjunction with the god *Hun Chuen* (the spider monkey deity), they create humankind and serve as artisan creators (Braakhuis 1987; Anonymous 1994).

Preuss (1901) provided the earliest work that covered the role of primates and primate representation in pre-Hispanic Mesoamerica material culture (for El Salvador, see also Felten 1961 and Haberland 1961). However, it was not until the research of South (2005) when a review of the representation of primates in Pre-Columbian Maya material culture was summarized. Using the Maya Vase Database, she identified a series of physical attributes in the iconography of Mesoamerican primates in order to interpret which monkey corresponded to each representation. Key attributes used were limb proportions, skull and face configuration, tail features and uses, positional repertoire, hand use through opposable thumb, and pelage colors and patterns. It was found that the majority of the primates depicted were spider monkeys, followed by howler monkeys (South 2005). In most cases when howlers were represented, they were shown in scribal postures, while spider monkeys appeared more like performers of rituals.

In South America, Urbani and Gil (2001) presented information about howler monkey remains in a speleological location in northeastern Venezuela. The formation consisted of dislocated bones associated with stone tools. Possible interpretations on how these howlers were used are still an open question since the bones were not burned and no evidence of fire was found. Thus, the howler monkeys may have been used not only as food, but possibly as pets, or have had a cosmological meaning for the people that inhabited this area. Urbani and Gil (2001) delineated ethnohistorical information that seems to point out the cosmological significance of primates among indigenous societies in this part of Venezuela; however, no final conclusion can be determined. In a work in progress about the interaction of Pre-Hispanic societies of northern Venezuela with nonhuman primates, B. Urbani (unpublished information) found that howler monkeys were deposited in archaeological sites. In Los Roques Archipelago, north of the central Venezuelan mainland, a howler monkey cranium was found in an archaeological site associated with other mammals (Antczak and Antczak 2006). Certainly this primate was brought from the continent since these monkeys are not part of the insular fauna. In all cases, howler remains belonged to *Alouatta arctoidea*, and are associated with deposits of Pre-Hispanic societies (B. Urbani, unpublished information).

10.3 Howler Monkeys as Food: An Ethnographic Exploration

Accounts on the use of howlers and other monkeys were recorded in Spanish documents from the earliest time of the Contact period. For example, the son of Cristóbal Colón, Hernando Colón (1488–1539), provided a description of his father's arrival to the island of Trinidad, 4 days before his first landing in continental South America in Venezuela:

> "en una punta que llamó de la Galea… Allí encontraron también muchas huellas de animales que parecían ser cabras, y también los huesos de uno; pero, como la cabeza no tenía cuernos, creyeron que sería algún gato paúl, o mono; después supieron que lo era, por los muchos gato paúles que vieron en Paria. Aquel mismo día, que fue el primero de Agosto, navegando entre cabo de la Galea y el de la Playa, sobre la mano derecha, hacia el Sur, vieron la tierra firme…" [in the point he named Galea (currently known as Galeota Point, southeastern Trinidad)… They found many animal footprints that looked like goats, and also bones from one, but, since the head did not have horns, they believed it was a *gato paúl*, or monkey, later they knew that it was, since they saw many *gatos paúles* in Paria (Peninsula in Venezuela). That same day, August first (1498), sealing between Cape Galea and Cape Playa, at the right hand, to the South, they saw *terra firme*…] (H. Colón 1932:132).

This report not only represents the first account of a Neotropical primate, but also appears to specifically refer to howlers, since the term *gatos paúles* tended to be used for this primate taxon in early accounts of Neotropical monkeys (Urbani 1999, 2011). Moreover, it also likely represents the first report on the use of this primate genus (*Alouatta macconelli*) by Amerindians. Close to the Island of Trinidad, in 1759, the Franciscan priest Antonio Caulín (1719–1802) wrote his *Historia Choro-Graphica*, *Natural y Evangelica de la Nueva Andalucía*, where he referred to the local use of howler monkeys in northeastern Venezuela. In his chapter about the animals of the region and their "properties," he wrote,

> Araguáto. En los montes fértiles y frondosos habitan comúnmente estos animales, que se pueden contar en la clase de Monos, de color roxo, y la magnitud de un Perro podenco;

> tiene barba crecida como los Machos de Cabrío; y sus buches son muy medicinales para los que adolecen de asma, y otros afectos del pecho, bebiendo el agua, que ha estado en infusión dentro de ellos [Howlers. In the fertile and exuberant forests is where commonly these animals inhabit, they may be counted as kind of monkeys, of reddish color, and the size of a Dog (referring to a greyhound-like dog); they have a grown beard as in Male Goats; and their throats (referring to the hyoids) are of very medicinal value for those that suffer from asthma and other illnesses of the chest, by drinking the water, that remains inside it, as an infusion] (Caulín 1966:75–76)

Despite these early reports, there is currently limited ethnographic research on Amerindian perception and uses of howler monkeys. In this section, we present data on the use of howlers as food, as well as food taboos.

Souza-Mazurek et al. (2000) reported that among the Waimiri-Atroari in northern Brazil, *Alouatta macconnelli* is the second preferred primate species. The authors calculated that from 99 hunted howlers recorded in their study, they provide 611.8 kg of meat. In addition, they found that the sex ratio of howler corpses indicated that males were preferred over females. The Waimiri-Atroari organize hunting parties on boat along the rivers of the *igapó* areas of their indigenous territory during the wet season for the sole purpose of hunting howler monkeys. This area is the primary part of the forest the howlers inhabit, where they can also be easily observed during hunting. Similarly, the Brazilian Yanomami rank howler monkeys as the second preferred primate prey in both "traditional" and "acculturated" villages (Saffirio and Scaglion 1982). In Venezuela, Hames (1979) found that the Yanomami also have howlers as the second preferred primate prey, while it ranked fourth, among the Ye'kuana during a 216-day study. Actually, howlers occupied the twelfth position among all mammalian prey of the Ye'kuana, providing 87.45 kg of meat (Hames 1979).

In Suriname, Mittermeier (1991) reported that Caribs and Tirio largely selected primates as their game source. For the Tirio, howler monkeys ranked first as both the most hunted monkey and the most hunted mammal. The same pattern was found in the Tirio, where howlers represented 65 % of primate remains in their kitchen. Among Carib-speakers in Suriname, capuchins were the most preferred primate species with howlers and spider monkeys ranking after. *Alouatta macconnelli* and *Chiropotes satanas* were both reported to be consumed by all interviewees that had eaten monkeys. However, howlers were not considered their favorite primate species, positioned after *Sapajus apella*, *Pithecia pithecia*, and *Ateles paniscus*. Mittermeier (1991) reported that howler infestation with botflies and their strong smell may serve as a deterrent to howler consumption. In addition, the use of hyoids was reported to have medicinal value.

Among the Murui (Witoto) of the Amazon of Colombia, Townsend and Ramírez (1995) indicated that red howlers (*Alouatta seniculus*) are folivorous/frugivorous and are known to feed on *achiote* (*Bixa* sp.) plants as well as earth. The Murui also reported that howlers prefer to travel in liana forests. Also in the Colombian Amazon, Parathian and Maldonado (2010) found that in the villages of San Martín and Mocagua, inhabited by a majority of Tikuna Amerindians, howlers ranked as the second most harvested primate species, after *Aotus* spp., a primate used mainly as pet. In relation to the consumption of primate meat, large-bodied monkeys were preferred. In this category, howlers appeared to be harvested more than woolly monkeys.

The Achuar of Ecuador hunt howler monkeys with shotguns and dogs (Descola 1996). Likewise, the Ecuadorian Siona-Secoya also hunt howlers (Vickers 1980). Vickers calculated an estimated harvest rate of 56 howler monkeys per year, ranking them as sixth in vertebrate game meat. The author also predicted that the probability of finding a howler monkey in a single hunting day is only ~3.7 % during a 6-year period, resulting in among the lowest time effort for all mammalian game. Similarly, according to Harner (1973), howler monkeys are a significant game source for the "Jívaro," and are found by hunting parties that use blowguns with poisoned darts.

In the market of Iquitos in the Peruvian Amazon, Castro et al. (1975) found that, during a period of 7 months, howlers represented the second most sold primate meat. Male howlers appeared to be preferred, most likely due to their larger size. Total weight of howler meat distributed per month reached up to 200 kg, with an estimate of 1.1 tons during the 7-month study period. Also in Peru, Eakin et al. (1980) indicated that for the Shipibo-Conibo, atelids, including howlers, are highly valued prey. Once the adults are hunted, they tend to keep the offspring as pets. According to Campos (1977), among the Shipibo, howlers and other monkeys are hunted with shotguns, and occasionally with blowguns and arrows. Similarly, in the Amahuaca of the Peruvian Amazon howlers are the second ranked mammal game, after spider monkeys, providing the majority of primate meat (Carneiro 1970). Amahuaca hunt primates and other mammals solitary with bow and arrows. Finally, howlers ranked fourth in terms of mammal prey, among the Huambisa of Peru (Berlin and Berlin 1983).

For the Piro and Machiguenga of Peru, Alvard (1993) indicated that howler monkeys are found by hunting parties, and rank as the fourth most searched prey, having a high return value in term of calories per hour of pursuit. During the study, howlers were spotted nine times, and at all instances, they were pursued with shotguns, accounting for an estimated time of 3.8 h per hunt. Assuming a total of 1,300 cal/kg of howler meat, then a total of 85,020 cal from howler meat may have been consumed during the study period. Alvard and Kaplan (1991) pointed out that during hunting, howlers are located by their loud vocalizations. These authors found a marked bias towards male individuals over females and adults over juveniles (Alvard and Kaplan 1991).

Shepard (2002) reported that *Alouatta* is the most abundant primate in the Matsigenka land. However, it is not the preferred one, since woolly and spider monkeys were selected in a 10:1 higher ratio than howlers, and capuchins twice as much as howlers. Howlers are not considered as tasty as the other frugivorous atelines (Shepard 2002). Additionally, the Matsigenka perceive howlers as carriers of spirits since they are considered shamans (*seripigari*) due to their conspicuous vocalization. Voss and Fleck (2011) indicated that the Peruvian Matses identify the phenotypically different *Alouatta juara*, which mainly inhabit the primary forests and swamps with *Mauritia* palms. In the majority of cases, howlers are located by their vocalizations, but the Matses do not imitate their howling. Once found, howlers tend to stay quiet, and hunters may climb the trees and use shotguns or bows and arrows to hunt them. On a few occasions, howlers are spotted and hunted in mineral licks.

In Brazil, the Araweté's hunting for howlers involves ritual behavior, and shamans consider themselves as relatives of the monkeys (Viveiros de Castro 1992). Thus, howlers should be hunted by those shamans, who also kill the spirits (*ha'o we*) of the monkeys prior to consumption. Subsequently, the monkeys are mounted in a rack and smoked, and then sliced and boiled at home. Only then may members of the community eat pieces of howler meat. Setz (1991) reported the consumption of two species of howler monkeys among the Nambiquará of Brazilian border with Bolivia. However, in the Nambiquara villages, a domesticated young adult howler was kept as a pet during the study period, and consequently not killed. When the Sirionó of eastern Bolivia hunt howlers (*téndi*), a single member of the hunting party locates a male individual as the initial target (Holmberg 1985 [1950]). Subsequently, females tend to rush together and then are killed one by one by the same hunter or group of hunters.

The Kalapalo of the Upper Xingu Basin (Brazil) are not habitual hunters and practice it in parallel to the performance of other activities such as fishing (Basso 1973). However, they do organize hunting activities specifically for howler monkeys as part of a ceremony. They use bow and arrows to obtain avian prey as well as *Alouatta* (Basso 1973), but shotguns have also been introduced to the area. The Ka'apor, in the eastern Pre-Amazonian region, also hunt howlers (Baleé 1985). Howler monkeys ranked tenth among vertebrates that were obtained in two sites along the Turiaçu River in Brazil, and fifth in term of weight of all obtained prey (Baleé 1985). Interestingly, howler monkeys ranked first among mammals, with respect to allocated hunting time (an average of 73 min). In the same region, among the Guajá, de Queiroz and Kipnis (1997) found that in the osteological dump of the studied settlement, howler monkeys ranked as the first primate species, in both the outer and excavated parts of the dump. Cormier (2003) also supports these findings, with howlers being the most utilized animal prey during the wet season.

The Lacandón of Chiapas in Mexico used to hunt howler monkeys with a special type of barbed edged arrow (*flecha barbada*) until shotguns were introduced (Baer and Merrifield 1972). During hunting, the Lacandon located howlers by their vocalizations. Thompson (1930) indicated that howler monkeys (*baaɔ*) are hunted by the Maya in Belize. Shotgun hunting was practiced after working in the plantations. In southern Mesoamerica, the Teribe of Panama include howlers (*Alouatta palliata*) as one of their preferred prey (Reverte 1967). They organize hunting rounds; however, they normally engage in opportunistic shotgun hunting while gardening in their fields. Among the Guaymi of Costa Rica, *Alouatta palliata* is the least hunted primate species, since its meat is not highly valued (González-Kirchner and Sainz de la Maza 1998). In addition, half of the Guaymi (54 %) perceived howlers as bad omen. In order to avoid bad luck, they are killed when they are found near a household. However, this Amerindian group also considers this primate to have medicinal value, as reported by 93 % of the interviewees. González-Kirchner and Sainz de la Maza 1998) indicated that the Guaymi use howler fat as skin "cream," and when diluted with hot water, as a beverage serves to cure diseases. In addition, howlers rarely raid crops and *Alouatta palliata* is not used as pet, because of its proclivity to die in captivity.

Urbani (2005) has compiled a wide range of ethnographic data from 56 Amerindian societies that hunt Neotropical primates. Howlers were reported to be hunted in 55 % (31/56) of these indigenous groups (Table 10.1). Considering this dataset, the results indicate that this primate taxon ranks as the most commonly hunted primate in the Neotropics. In addition, howlers were chosen as part of the top five preferred game in 71 % (10/14) of the cases where the total number of prey was reported. In geographical terms, hunting *Alouatta* was found to be distributed evenly, with 45 % (14/31) of the study sites, where howlers were reported to be hunted, located in Mesoamerica, the Pantanal and the Guianan forests, and the remaining 55 % being Amazonian.

Howler monkeys are subject to a wide range of food restrictions and preferences that vary considerably among cultures. Explanations for food choices and taboos range from foraging theory (e.g., Alvard et al. 1995) to "primitive" environmental conservation (McDonald 1977; Ross 1978). However, ecologically deterministic models are not sufficient to explain hunting behavior towards primates. One illustrative example is that howler monkeys are the most abundant mammal in Manu National Park, but the Matsigenka take the similar-sized woolly and spider monkeys at ten times the rate of howler monkeys (Shepard 2002). Broadly, primates cannot be considered to be merely a source of food. Cross-culturally, the physical and behavioral similarities between humans and wild primates often attribute them a special role in the symbolic life of a culture. On the other hand, howlers are not always described as preferred mammal game. In multiple Amerindian societies, howler meat is avoided for reasons including magical contagion, ritual couvade, or simply due to taste preferences. For instance, the Barí of Venezuela view red howler monkeys as similar to three-toed sloths (*Bradypus variegatus*) in terms of lethargy and lack of cleverness, and so avoid these primates to prevent acquiring their negative qualities (Lizarralde 2002). If hunted, the Barí locate them by listening to their calls, and then tend to kill the entire group. Howler heads are severed in the forest, since it is believed that their brains may produce sickness, and more specifically madness. In addition, howlers are not kept as pets by the Barí (Lizarralde 2002). Taboos on howlers are relatively common, and they are often considered as bad omens. It is believed that they may transmit diseases and lethargy. Also in the Amazon, Shepard (2002) reported that the Peruvian Matsigenka have taboos on children eating howlers, since it is believed that these monkeys may transmit their lethargy.

Several South American groups avoid all species of monkeys. For example, among the Kagwahív (Parintintin), monkeys are kept as pets, but are avoided as food, due to their similarity to human beings (Kracke 1978). On the other hand, the Kalapalo, who consider most land animals disgusting, do eat monkeys, because they are classified as "like-human-beings" (Basso 1973:14–15). A recent review of the literature on primate taboos, among indigenous Amazonian peoples, identified *Alouatta* as the most frequently prohibited taxon (Cormier 2006). Such taboos are not uniform, meaning that in some societies howlers are food items. Among the Parakanã, howlers are the only primate genus that is considered to be edible (Fausto 2012). The Guajá also prefer howler monkeys over the six other primate species in

Table 10.1 Indigenous societies that hunt howler monkeys (*Alouatta* spp.) for subsistence

Human society	*Alouatta*[1,2]	Indigenous name	Study site	References
Aché	5/16 years; 17th	NA	Mbaracayu Reserve, Paraguay	Hill and Padwe (2000)
Aguaruna	NA/10 months; NA	NA	Cenepa-Santiago Rivers, Amazonas, Peru	Berlin and Berlin (1983)
Amahuca	NA/“years”; second	NA	Ucayali, Amazonas, Peru	Carneiro (1970)
Ashuar	NA/“years”; NA	NA	Pastaza River, Amazonas, Ecuador	Descola (1996)
Awareté	NA/1 year; NA	*ačiči*	Ipixuna River, Amazonas, Brazil	Viveiros de Castros (1992)
Colombian Barí	8/4 months; NA	NA	Southwestern Sierra de Perijá, Colombia	Beckerman (1980)
Venezuelan Barí	36/12 months; NA	*borou*, *kamas-kougda*	Southeastern Sierra de Perijá, Venezuela	Lizarralde (2002)
Guajá	NA/15 months; NA	*wari*	Maranhão, Amazonas, Brazil	Cormier (2003)
Guaymi	NA/11 months; second	NA	Costa Rica	González-Kirchner and Sainz de la Maza (1998)
Huambisa	NA/10 months; NA	*yakúm*	Cenepa-Santiago Rivers, Amazonia, Peru	Berlin and Berlin (1983)
Huaorani	85/11 months; fourth	NA	Quehueiri-ono, Shiripuno River, Napo, Ecuador	Mena et al. (2000)
Ka’apor	7/105 days; tenth	NA	Turiaçu River, Maranhão, Amazonas, Brazil	Baleé (1985)
Lacandón	NA/15 months; NA	*ba’ts*	Norte del Najá, Chiapas, Mexico	Baer and Merrifield (1972)
Matsigenka	1/1 year; NA	NA	Manu Biosphere Reserve, Peru	Shepard (2002)
Belizean Maya	1/“years; NA	NA	San Antonio, Toledo District, Belize	Thompson (1930)
Mayangna	1/34 days; fifth	NA	Amak, Bosawas Reserve, Nicaragua	Merriam (1998)
Nambiquará	NA/148 days; NA	*elhu*, *ilho*	Guapore-Chapada Parecis, Matto Grosso, Brazil	Setz (1991)
Paaca Nova	NA/NA; NA	NA	Guaporé River, Rondônia, Brazil	von Graeve (1989)
Piro	13/10 months; fifth	NA	Manu River, Peru	Alvard and Kaplan (1991), /Alvard (1993, 1995)

(continued)

Table 10.1 (continued)

Human society	*Alouatta*[1,2]	Indigenous name	Study site	References
Shipibo	NA/16 months; NA	NA	Pisqui River, Amazonas, Peru	Campos (1977)
Shipibo-Conibo	NA/>5 years; NA	*roó*	Ucayali River, Amazonas, Peru	Eakin et al. (1980)
Siona-Secoya	56/1 years; sixth	NA	San Pablo de Shushufindi, Aguarico, Amazonas, Ecuador	Vickers (1980)
Surinam's Carib	2/15 months; fiurth	NA	Bigi Poika, Surinam	Mittermeier (1991)
Suya	NA/2 years; NA	*kupüdü*	Suya-Missu Rivers, Mato Grosso, Brazil	Seeger (1981)
Teribe	NA/NA; NA	*bip*	Teribe River, Bocas del Toro, Panama	Reverte (1967)
Tirio	56/15 months; second	NA	Sipaliwini-Pouso Tirio area, Surinam	Mittermeier (1991)
Waimiri-Atroari	99/13 months; fifth	*arawyta*	Alalau River-BR 174, Roraima-Amazonas., Brazil	Souza-Mazurek et al. (2000)
Brazilian Yanomamö	5/5 months; fourth	*iro*	Catrimani River, Roraima-Amazonas, Brazil	Saffirio and Scaglion (1982)
Venezuelan Yanomamö	2/217 days; second	NA	Toropo-teri, Padamo River, Amazonas, Venezuela	Hames (1979)
Ye'kwana	11/216 days; sixth	NA	Toki, Padamo River, Amazonas, Venezuela	Hames (1979)

NA Not available

[1] Number of *Ateles* hunted/length of the ethnographic study

[2] Rank number of this primate species in relation to all game mammal species hunted by each of the listed indigenous societies

their area (Cormier 2003). The Matsigenka like howlers the least of the primates in their area, reporting that they do not taste as good as other monkeys (Shepard 2002). The Cashinahua consider howlers, as well as owl monkeys and squirrel monkeys, to be inedible, but hunt capuchins and spider monkeys (Kensinger et al. 1975).

Most avoidances or taboos of howler monkeys, and primates in general, are associated with the social or ritual status of the group members, including their age/sex and reproductive status. Age/sex related restrictions can be found among the Matses and the Desana. Among the Mayoruna, children eat howler monkeys, but adults do not (Milton 1991). The Matses believe that eating howlers may cause young people to become lazy, and it is only allowed to older persons (Voss and Fleck 2011); however, they are generally avoided as prey. For the Desana, howler and owl monkeys are prohibited to pre-adolescent boys (Milton 1991). Among the Kayapó, all monkeys are taboo for all women (McDonald 1977). The most frequent primate taboos relate to reproductive status. A number of Amazonian groups practice the couvade, which involve restrictions, often dietary, that apply to both the mother and father during pregnancy (Rivière 1974). The couvade is often linked with what is known as plural paternity or partible paternity in a number of Amazonian groups, where fetuses are created from the build-up of their father(s) semen during pregnancy; thus a child may be believed to have more than one "biological" father (see Beckerman and Valentine 2002). The purpose of the dietary restrictions is to protect the fetus and sometimes neonates and young from plant and animal foods that could potentially pass on unfavorable characteristics to the child (Metraux 1949).

In some cases, all monkeys are prohibited to parents during pregnancy, as in the Yanomami (McDonald 1977), and the Tukano (Reichel-Dolmatoff 1971, 1989). Howler monkeys are restricted specifically to several groups with the couvade. Among the Tukano of Colombia, Reichel-Dolmatoff (1971) reported that howlers are taboo as food. They are reported to "weep" and not to howl, as well as to provoke bad luck since they are considered capable of witchcraft. For the Tapirapé, capuchins may be eaten by anyone, but howlers are prohibited for women, adolescents, and the fathers of children less than 2 years old (Wagley 1977). The Sirionó have a similar restriction; howlers and owl monkeys are taboo for pregnant women, all children, and both the father and mother of a child for the first 3 days after birth (Holmberg 1985 [1950]). In the Huaorani couvade, only the heads of howler monkeys—and woolly monkeys—are prohibited (Rival 1998). In other groups, howler monkeys are hunted, but the couvade applies to other species. For example, the Wapishana hunt eight species of monkeys, including howlers, but the couvade applies only to spider monkeys (Henfrey 2002).

A few other ritual restrictions on howler monkeys have also been reported. Among the "Jivaro," howler monkeys are not to be eaten by either males or females for 2 months after crops are sown (McDonald 1977). The Sirionó believe that if one eats a young howler monkey, one's lips will turn white and anemic (Priest 1966), though, the consumption of howler meat is a taboo for pregnant women, children, and parents of recently born babies (Holmberg 1985 [1950]). The Suyá classify howlers differently from other monkeys because they are considered to have a pungent odor and are frequently forbidden to individuals undergoing any type of dietary restriction (Seeger 1981). Even so, the Suyá classify howler monkeys as edible vertebrates, but they are prohibited as food after childbirth.

10.4 Howler Monkeys in Mythology and Cosmology

Animal myths and metaphors may involve not only symbologies and cosmologies, but a culture's view of the social relationships of humans to wild primates and other species and the relationships among non-human species. Among the Yagua, monkey species are seen as related to each other, not through a Linnaean-like taxonomy, but through kinship (Chaumeil and Chaumeil 2005). The howler monkey is considered to be the grandfather of all monkey species, with particularly strong bonds of friendship with the spider monkey and woolly monkey. The squirrel monkey is considered to be the uncle of the capuchin monkey. Among the Guajá, howler monkeys are considered to be in a patrilineal sibling relationship with both humans and bearded sakis, but bearded sakis and humans do not share the same close relationship (Cormier 2003). Cultural views of kinship may also involve non-primate species. The Guajá consider the owl monkey to be a patrilineal sibling of the kinkajou (*Potus flavus*) because both are nocturnal and both bear long, similar looking tails.

10.4.1 Transformation

In a previous work, on the ethnoprimatology of the spider monkey, we stressed contagion and transformation as two important themes that occur in the symbolic systems of Neotropical peoples and their relationship to plants and animals (Cormier and Urbani 2008). In the Amazon, Viveiros de Castro (1998, 1999) described that a frequent theme in the cosmologies of indigenous peoples is to view animals as former human beings. South American cultures, which have myths involving the transformation of various monkey species into a human being, include the Aguaruna (Brown 1984), the Barí (Lizarralde 2002), the Bororo (Wilbert and Simoneau 1983), the Desana (Reichel-Dolmatoff 1976), the Kayapo (Wilbert 1978), the Yanomaö (Wilbert and Simoneau 1990), and the Xikrin (Wilbert and Simoneau 1984). The Guajá (Cormier 2003) and the Matsigenka (Shepard 2002) also have myths involving the transformation of howler monkeys into human beings.

Transformation may link to what Viveiros de Castro (1998) has termed "perspectival multinaturalism." He describes a common Amazonian animistic view of plants and animals as sharing a common spiritual and social nature, but due to differences in bodily forms, have differing subjective perceptions. Put more simply, he describes a peccary wallowing in the mud as seeing itself as a human swinging in a hammock or a jaguar drinking blood seeing himself or herself as a human drinking manioc beer. Both transformation and perspectival multinaturalism can be seen in a Lokono (Arawak) myth involving a howler monkey (Drummond 1977). A hunter shoots a female howler monkey, roasts her, but eats only her tail. When he returns home, the howler carcass is missing and a woman is in his hammock. She becomes his wife. The wife hears other howlers in the forest and her new husband tells her that they are her uncles, drinking cassava beer. They climb a tree and drink with the "uncles," but when the uncles realize that the true identity of the wife is a howler, they abandon the husband in a tree.

A similar myth is narrated by the Munducuru (Murphy 1958). Here, a Munducuru man marries a howler monkey who has taken the form of a woman. She asks her husband to visit her howler relatives, but makes him promise not to laugh at them. When the howlers begin to sing, he laughs and is abandoned on a tree. When he escapes, he kills all the howler monkeys except his wife. She later has a son, with whom she will have an incestuous relationship that will give rise to the current population of howler monkeys.

A number of myths involving transformation also serve as cautionary tales. Rival (1996) has made that argument specifically for monkeys among the Huaorani of Ecuador. Thus, many myths involve social catastrophes created when monkeys try to behave either too much like human beings or too differently from human beings. In a Matsigenka myth, the behavior of a howler monkey and a spider monkey are contrasted. *Yaniri*, the howler was once a lazy shaman who spent all his time taking ayahuasca (see below) and singing. Instead of raising his own crops, he borrowed beans from his brother-in-law *Osheto*, the spider monkey. But because he was lazy, he ate the beans rather than planting them and returned to ask *Osheto* for more beans. In anger, *Osheto* punched *Yaniri* in the throat, creating the howler's enlarged larynx.

The Sirionó also explain the howler's enlarged larynx by means of a cautionary tale (Holmberg 1985 [1950]). Here the jaguar kills the son of *Yási*, the moon and creator divinity. As *Yási* searches for the killer of his son, he comes upon *Tendí*, the howler monkey, *Erubát*, the spider monkey, and *Seáči*, the coati, who are all drinking. *Yási* was angry at them for being drunk and grabbed the howler by the neck, causing him to howl and pulling it into the shape it is today.

10.4.2 Contagion

The widespread cross-cultural belief in contagious magic has been documented since the days of the late nineteenth century cultural evolutionists in anthropology (Frazer 1911). Contagious magic suggests that once in contact with a substance, it continues to exert an effect. In a similar way, contact with a monkey is believed to be able to confer either desirable or undesirable traits, in a number of South American cultures.

The Bororo believe that eating monkeys, in general, can confer their attributes of speed and grace (Crocker 1985). The Matsigenka make a contrast between contagion with howler monkeys and capuchins (Shepard 2002). As indicated before, eating howlers can cause one to become lazy and eating capuchins can cause one to become a thief, consistent with their mythology. Somewhat similarly, the Barí make a contrast with potential contagion with howler monkeys and spider monkeys (Lizarralde 2002). The Barí value the manual dexterity of spider monkeys. They keep them as pets and wear spider monkey tooth necklaces to confer their traits. However, howler monkeys are believed to be both slow and of low intelligence. The Barí neither keep them as pets nor do they wear howler monkey tooth necklaces.

The "howling" of howler monkeys can also evoke a kind of magical contagion or associative symbolism. The Sirionó believe in a magical contagion related to the loud territorial calls of howler monkeys (Priest 1966). If a male howler monkey is eaten, it may lead to bad dreams causing one to howl at night. The Yagua also link howlers to altered states of consciousness (Chaumeil and Chaumeil 2005). Howlers are called *ramanuji* “ayahuasca” where their loud roaring calls serve as a metonym for the hallucinations produced by the Malpighiacea vine, *Banisteriopsis caapi* (the base hallocinogenic compound of the “ayahuasca”). Somewhat similarly, howler monkeys are considered to be shamans in Matsigenka folklore and to pose spiritual hazards (Shepard 2002). Among the Parakanã, the percussive sound of bamboo striking the ground is associated with howler calls (Fausto 2012).

The Bororo believe that supernatural contact with a howler monkey involves a kind of contagion that can also transform (Crocker 1985). Thus, they have a principle of transformation that manifests in natural phenomena called *bope*. Howler monkeys are often spirit familiars for *bope*. Becoming a shaman involves being surprised in the forest by a howler monkey, which questions the individual and demands that he smokes a cigarette. The sight of a *bope* resembling a howler may also mean the imminent death of the witness or a relative.

10.4.3 Reflexivity

Reflexivity in anthropology is a means for interpreting the ways in which a group’s cultural values are projected onto others. Ohnuki-Tierney (1984) defines reflexivity as the sense of distancing from the self in order that the self becomes an object of study itself. In her own work, she uses reflexivity as a means of understanding the changing use of the monkey as a metaphor in Japanese history (Ohnuki-Tierney 1984, 1987, 1990). A similar treatment can be found of the Monkey King in China (Burton 2002) and in Haraway’s (1989) critique of primatologists. Such projections can occur with any number of nonhuman species, such as roosters in the Balinese cockfights (Geertz 1973) or the multi-layered symbolism of cattle among African pastoralists (Evans-Pritchard 1940; Comoroff and Comoroff 1990). However, primates are particularly amenable to reflexivity due to their similarities to humans. The Yagua use howlers as a reflexive symbol to designate both self and other (Chaumeil and Chaumeil 2005). One of the Yagua clans is called *kandaria*, “howler monkeys.” However, they refer to their neighbors, the Mayoruna, with the more pejorative *kandamunuñu* “wild howler monkeys.”

Howlers and other monkeys sometimes appear as dream symbols. The Ese Eja of Peru have a story of a woman who associated a dream she had of a howler monkey with her new-born child with a lump on the side of his neck (Peluso 2004). Among the Achuar, dreaming of a man with a red beard means that one will be successful in hunting a howler; if one dreams of a man with a pale face, it will be a successful capuchin hunt (Descola 1989). These signs are based on homologies of the pelt colors of the howler and capuchin species of the area. In Juruna cosmology, howlers have a dream-like quality (Lima 2000). They are said to appear like phantoms and the Juruna have no desire to hunt or eat them.

The Guajá hunter-gatherers have one of the most complex symbolic systems associated with howler monkeys (Cormier 2003). Howler monkeys are the preferred game over the other six primate species in the area. Orphaned infant howlers are raised as pets and considered to be quasi-human beings. Howler monkeys are considered to be "true" patrilineal siblings to the Guajá people, with other plants and animals considered to be matrilineal siblings. At a meta-level, the shared consanguinity of the Guajá to howler monkeys is explained by their creation myth. Howler monkeys were once human beings who were transformed into monkeys so that other humans would be able to eat and survive. Howlers are said to be like humans because they "sing," which is intrinsically the way the Guajá travel into the spirit world. Also in Guajá cosmology, the divinity *Yu* is the master hunter and controller of all howler monkeys. *Yu* is a spiritual sibling with the *yu* palm (*Astrocaryum gynacanthum*) which the Guajá identify as an important howler food. Thus, *Yu* eats howlers and howlers eat *yu*, just as humans eat former humans (howlers) in a system of symbolic cannibalism.

10.5 Discussion

Broadly speaking, far more research is available on the role of nonhuman primates as a food source than their role in the social and symbolic domains of the lives of indigenous peoples with whom they share space. In part, this is a consequence of disciplinary specialization. In anthropology, ethnographers and primatologists typically deal with quite different primary subjects of research interests. While ethnographers tend to specialize in a specific culture or linguistically-related cultures (the language family), primatologists tend to specialize in a specific species or biologically related taxon (the genus).

Consequentially, it is not uncommon to find no more specificity among ethnographers in communicating information about wild primates than terms such as "monkey," "mono," or "macaco." These terms have little scientific value to primatologists, for the Western folk category of "monkey" does not even entail differentiation between New World and Old World species. Primatological orientation towards research that seeks to expand understanding of a particular genus or species can be equally uninformative for ethnographers who are attempting holistic understandings from a particular culture's point of view. Cultural experiences are locally based and locally informed. Broad categories of inquiry such as "*Alouatta*" include meanings and interpretations from cultures as diverse as the ancient Mesoamerican Mayan state, societies in the Brazilian grassy lands, and Amazonian hunter-gatherers. M. Lizarralde (personal communication) has suggested that even within the subdiscipline of "ethnoprimatology" that has emerged over the last 15 years, research still tends to be oriented towards *ethno*-primatology, prioritizing culture and related cultures, and ethno-*primatology*, prioritizing primate species and their related genus.

In the case of howler monkeys, the ways in which they were perceived by Pre-Hispanic societies are still little known. Nevertheless, it can be argued that since humans initiated the early colonization of the tropical Americas, probable parasite exchange appeared to link *Homo* and *Alouatta* populations. Before contact, there is limited archaeological evidence in terms of osteological remains and representations of howlers. In Mesoamerican civilizations and indigenous of South America, howlers not only appeared to play a relevant role in their cosmologies but also as food sources, and possibly, as pets.

Howlers often have a symbolic role in indigenous mythologies and cosmologies, especially among the cultures of lowland South America where the taxon is widespread. Two commonly occurring themes are magical contagion and transformation. Magical contagion influences dietary practices, particularly the ritual couvade. Monkey to human transformation is a common theme in mythology, not only with howlers, but with wild primates in general and to a lesser extent, other animals and plants. One characteristic that sets howlers apart from other wild primates are its territorial vocalizations, which link the howler with shamanistic abilities in between the material and spiritual worlds.

The contemporary ethnographical literature of Central and South American indigenous societies presents selected information on how primates, in general, and howlers in particular, are used and perceived. In the case of hunting and meat consumption, howlers rank as one of the preferred primates consumed as food. Their large size seems to be one rationale for why they are preferentially selected as game. In addition, the territorial calls of the howlers make them somewhat easier to locate in the forest, where they are hunted not only by using bows and arrows but also shotguns. On the other hand, due to its predominant resting behavior, howlers are sometimes tabooed or avoided among different Amerindian societies. Here, it is believed that the negative attribute of lethargy may be transmitted if howlers are eaten. Certain classes of persons in indigenous communities, such as elders and shamans, are in some cases the only persons allowed to consume howlers. This human–nonhuman primate relationship reveals an intricate set of values and beliefs around phenotypically similar howlers that permit them to be represented differently by various societies across their wide distributional range in the tropical Americas.

As indicated by Cormier and Urbani (2008), the role of Neotropical primates, and atelines, as pets needs to be further studied. The limited information that refers to howlers as pets tends to indicate that they are infrequently kept in Amerindian villages. This may not so much represent a preference, but may reflect the difficulty of keeping these primates in captivity because of their highly folivorous diet. In addition, as noted by Cormier and Urbani (2008), Amerindians possess an extremely broad understanding of the ecology and behavior of primates. However, relatively few ethnographic reports provide information on the ethnoecology of Neotropical primates, or the knowledge of indigenous societies on the biology and behavioral ecology of the primates with whom they share their spaces (but see Voss and Fleck 2011; Cormier 2002, 2003; Lizarralde 2002). Even though, despite of these limitations, Neotropical ethnoprimatology is a cultural and biological cross-disciplinary area with continued potential for growth (e.g., Parathian and Maldonado 2010).

Finally, as indicated by Ford (2001), at the turn of the new millennium, ethnobiological research is at a "crossroad." In this sense, ethnobiology is confronting multiple challenges in a fast changing world. Ethnoprimatology is not exempt to those challenges, in which biological, ecological, cultural, philosophical, sociopolitical, historical, religious, and even linguistic realms as well as global, national, regional, community, and family economies impact on multinational and domestic realities that modulate contemporaneous indigenous uses, interactions and perceptions of nonhuman primates.

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Chapter 11
Anthropogenic Habitat Modification, Tourist Interactions and Crop-Raiding in Howler Monkeys

Tracie McKinney, Jessica L. Westin, and Juan Carlos Serio-Silva

Abstract In this chapter, we review how anthropogenic disturbance specifically impacts members of the genus *Alouatta*, one of the most geographically expansive and ecologically flexible of platyrrhine groups. This report initiates with a brief discussion of the use of matrix landscapes, the effects of ecotourism, and the potential for crop-raiding by howler monkeys. We then present three case studies of howler monkey responses to these challenges. We found that tourism in Suriname leads to greater travel and foraging time and poorer health for *A. macconnelli. A. palliata* in Costa Rica living in an agricultural matrix respond to habitat modification through active crop-raiding, and *A. pigra* in Mexico provide an illustration of how to evaluate remnant monkey populations for potential ecotourism. The chapter concludes with recommendations for encouraging shared landscapes with howler monkeys, including ways to minimize crop damage by monkeys and ways to encourage sustainable, conservation-based ecotourism.

Resumen En este capítulo, revisamos cómo los disturbios antropogénicos impactan de manera directa a los miembros del género *Alouatta*, los cuales son platirrinos con una amplia distribución geográfica y notable plasticidad ecológica para adaptarse a su entorno. Iniciamos con una breve discusión sobre el uso de la matriz del paisaje, un análisis de los efectos del ecoturismo y el papel de los monos aulladores en el uso de los recursos que contienen los agrosistemas. Presentamos tres casos de estudio en los que se muestra la respuesta de los monos aulladores a estos desafíos. Encontramos que el turismo en Surinam promueve un mayor tiempo de viaje y

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forrajeo en *A. macconnelli*, además de provocar deficiencias en la salud de los individuos. Por otra parte, individuos de *A. palliata* que habitan en una matriz de bosque mezclado con tierras dedicadas a la agricultura en Costa Rica, responden a la modificación del hábitat a través del consumo activo de frutos cultivados. Poblaciones de *A. pigra* en México nos permiten ilustrar cómo evaluar el estado de conservación de las poblaciones de monos remanentes y su uso potencial en ecoturismo. El capítulo concluye con recomendaciones para promover paisajes antropogénicos compartidos con los monos aulladores, incluyendo estrategias para minimizar el daño en las cosechas por estos primates, así como acciones para favorecer el ecoturismo sostenible.

Keywords Anthropogenic change • Crop-raiding • Ecotourism • Matrix habitat

11.1 Introduction

Anthropogenic habitat modification creates complex challenges for all wildlife, but this issue is particularly relevant for the widely dispersed and ecologically variable order Primates. Primates may take advantage of anthropogenic habitats through provisioning (Altmann and Muruthi 1988; Grossberg et al. 2003) or crop-raiding (Naughton-Treves et al. 1998; Hill 2005; Baker and Schutt 2005; De Freitas et al. 2008), but pay with the added risks of poor habitat quality (Cowlishaw and Dunbar 2000; Riley 2008), harassment from domestic dogs (De Oliveira et al. 2008), and persecution by land-owners (Newmark et al. 1994; Chism 2005). The ways in which a primate species responds to these challenges are an extension of the ways in which it responds to any long-term environmental factor, such as habitat changes caused by storms, herbivore activities, or tree falls (Isabirye-Basuta and Lwanga 2008). Some primate populations have been influenced by anthropogenic factors for so long that any behavioral or ecological responses can now be viewed as part of their natural patterns (Fuentes and Hockings 2010; Lee 2010). Rather than viewing anthropogenic change as a completely separate issue from environmental change, it may be best to examine these challenges as differences in degree, not in kind.

While traditional primate field research has attempted to avoid anthropogenic modification in favor of troops living under more “natural” conditions, all primate communities deal with some form of habitat change as a result of human activities (Struhsaker 1999; Pavelka 2002). The effects of anthropogenic change have therefore become an increasingly important area of interest for primatologists, and are the focus of the sub-disciplinary field of ethnoprimatology (Sponsel 1997; Strier 2003; Riley 2006; Fuentes 2006; Wolfe and Fuentes 2007; Lee 2010). Across their global distribution, many primate species have populations living in transitional habitats, where the effects of human intervention impact their ecology and behavior. When studied, these interactions have primarily been viewed through a conflict paradigm, emphasizing disease transmission, human-primate conflict, and crop-damage (Fuentes and Hockings 2010; Lee 2010). However, some modified landscapes are well suited for use by nonhuman primates, and it is possible to conceive of sustainable use of shared landscapes by both humans and our neighbor primates (Lee 2010). As the field of ethnoprimatology grows, interdemic comparisons are vital. Such studies help determine which species are at higher risk of population decline because of endogenous factors, and which are simply dealing with unsustainable levels of anthropogenic disturbance (Silver and Marsh 2003; Reader and McDonald 2003; Cowlishaw et al. 2009; Chapman and Rothman 2009).

In this chapter, we focus on the ways the genus *Alouatta* shares space with humans in modified landscapes. The chapter first outlines the mixed results of research into the effects of anthropogenic habitat modification, and highlights what few patterns have been demonstrated to date. We then review human–monkey interactions in two situations in which howler monkeys are likely to find themselves: as inhabitants of ecotourism sites, and as agricultural crop raiders. After this brief literature review, we will consider three case study examples of how different howler monkey populations are responding to the challenges of close human contact. We begin with *A. macconnelli*, and report how one population is affected by growing ecotourism in Suriname. Then we describe how *A. palliata* in Costa Rica deals with tourist encounters and exploits crops in an agricultural matrix. Finally, we consider *A. pigra* in forest fragments in Mexico, and explore ways to evaluate these populations for potential ecotourism as a tool for conservation.

11.2 Anthropogenic Habitat Modification

The term "anthropogenic change" is incredibly vague, and can apply to a number of exogenous pressures on primate survival. Proximate causes of anthropogenic habitat change include urban land development, agriculture, timber extraction, mining or hydroelectric operations, and climate change (Cowlishaw and Dunbar 2000; Chapman and Peres 2001; Strier 2007). Each of these very different types of habitat modification has their own effects on primate populations, which in turn vary by the species involved, local community interactions, and the manner and degree in which the modification is conducted. Because of the diverse forms of modification and the widely variable organisms that comprise the order Primates, the wide array of studies concerning the issue have yielded relatively few generalized patterns (Arroyo-Rodríguez and Dias 2010). At its extreme, anthropogenic change causes extirpation of primate populations, but may also impact the animals in more subtle ways, through the alteration of community interactions, breeding patterns, foraging behaviors, and social systems that occur with any form of habitat change (Sterck 1998; Martínez-Mota et al. 2007; Fischer and Lindenmayer 2007).

Anthropogenic modification naturally deals with the loss of contiguous habitat, and many studies have been conducted that examine the effects of fragment size, patch shape, distance to next fragment, and distance to nearest water source (Estrada et al. 2002; Anderson et al. 2007; Arroyo-Rodríguez et al. 2008; Arroyo-Rodríguez and Dias 2010). Primate populations that do survive in fragments face reduced habitat size, isolation from other forest fragments, and a landscape dominated by secondary vegetation (Fahrig 2003; Fischer and Lindenmayer 2007; Arroyo-Rodríguez and Dias 2010). While such studies have been immensely useful for understanding the challenges to primates in reduced and modified habitats, the simple distinction of "fragmented" versus "non-fragmented" forest is becoming less valuable; many projects have been critiqued for design flaws, since they fail to discuss the degree of fragmentation, to consider confounding variables at different study sites, or to account for useful landscapes in the surrounding matrix (Fahrig 2003; Arroyo-Rodríguez and Dias 2010). These variable landscapes engulfing more pristine habitat fragments were traditionally viewed as a relatively uniform sea of less desirable landscapes (McArthur and Wilson 1967). The modified areas surrounding forest fragments, or "matrix" habitats (Cowlishaw and Dunbar 2000; Anderson et al. 2007), are in fact used by many wildlife species, and today are an important topic of study for primate behavior, ecology, and conservation. Therefore, a more practical description of primate habitat considers landscapes along a continuum of modification ranging through intact, variegated, fragmented, and relictual forests (McIntyre and Hobbes 1999). Instead of viewing these areas as a barrier between useful habitats, this mosaic of landscapes may be better seen as a "selective filter" (Gascon et al. 1999; Ricketts 2001; Bowne and Bowers 2004) through which more tolerant species will travel and forage more freely, while less flexible species will be confined to fragments or remain near forest edges. One study of *A. pigra* in forest fragments, for example, reports that the monkeys feed and rest in all matrix elements with arboreal cover (Pozo-Montuy et al. 2011); another investigation notes that five of eight Mesoamerican primate species are well known to forage or live in agroecosystems (Estrada 2006). Some matrix areas are clearly well suited for primate use, and this use of intermediate landscapes might be a key strategy ensuring the survival of certain primates in anthropogenic habitats (Williams-Guillén et al. 2006; Estrada 2006; Anderson et al. 2007; Asensio et al. 2009; Fuentes and Hockings 2010).

Endogenous factors—those determined by species biology, such as social organization, species interactions, or responses to stress—direct the ways in which a species may respond to exogenous processes such as habitat modification or changes in food availability (Fischer and Lindenmayer 2007). Folivorous, behaviorally flexible taxa may be particularly adept at surviving in fragmented or altered habitats (Sorensen and Fedigan 2000; Vásquez and Simberloff 2002; Silver and Marsh 2003; Kamilar and Paciulli 2008), and primate species that are frequently found in secondary habitats in nature may be better suited to survival in human-modified environments (Cowlishaw and Dunbar 2000). The most common factors that allow primates to survive in fragments are dietary flexibility and sufficient patch size, but these are poorly understood; survival might be based in part on factors in the surrounding matrix (Isabirye-Basuta and Lwanga 2008). Primates with low ecological flexibility, slow reproductive rates, and large home range requirements are the least flexible in terms of responding to habitat change or destruction (Rylands and Keuroghlian 1988; Onderdonk and Chapman 2000; Fisher and Owens 2004; Michalski and Peres 2005; Cowlishaw et al. 2009). Specifically, the atelines are particularly susceptible to anthropogenic disturbance because of their large body size, longevity, low reproductive rates, and dependency on a continuous canopy for locomotion (Di Fiore and Campbell 2007; Wiederholt et al. 2010; Pozo-Montuy et al. 2011).

Despite these endogenous factors that would suggest susceptibility to habitat disturbance, *Alouatta* may be an exception among the atelines. As the widest-spread genus in the Neotropics, ranging from southeastern Mexico to northern Argentina (Crockett 1998; Di Fiore and Campbell 2007), it is no surprise that *Alouatta* populations are found in matrix habitats throughout their range, and are often present in patches where no other neotropical primate can persist (Garber et al. 1999; Fedigan and Jack 2001; Williams-Guillén 2003; Arroyo-Rodríguez and Mandujano 2006; Arroyo-Rodríguez and Dias 2010). One study, for example, found no difference in *A. macconnelli* population density between logged and unlogged forest, even though the density of other endemic primates (*Ateles paniscus* and *Cebus olivaceus*) was significantly reduced (Bicknell and Peres 2010). This "colonizing" taxon is found in primary evergreen and semi-evergreen forests, riparian forest, dry deciduous forests, rain forests, and secondary or disturbed forests (Crockett 1998; Horwich 1998). The variation in habitat reflects the plasticity in home range sizes and diet characteristic of howler monkeys. Home range size is more variable within *Alouatta* species than between them (Crockett and Eisenberg 1987), and this taxon—while the most folivorous of the New World monkeys—lacks the complex physiological adaptations that would restrict them to folivory, allowing for a dietary shift to ripe fruits whenever they are available (Milton 1998; Pavelka and Knopff 2004). Ultimately, the howler monkeys' dietary flexibility, small home range sizes, and energy-saving strategy are keys in their persistence despite extreme habitat modification (Crockett 1998; Arroyo-Rodríguez and Dias 2010; Bicknell and Peres 2010).

11.3 Tourist Interactions

The potential for primate–human interactions is increasing with the growing interest in ecotourism. The term ecotourism is used loosely, but usually includes any nature-based tourism that incorporates an educational or environmentally sustainable mission (Björk 2000; Blangy and Mehta 2006; Horton 2009). As ecotourism grows, primates are among the most sought-after groups of wildlife—they are active, gregarious, and eerily reminiscent of us. Nature-based tourism has the potential to be a great tool for primate conservation, especially in impoverished areas where wildlife must compete with economic development (Grossberg et al. 2003; Jha and Bawa 2006). As one of the most threatened of all mammal taxa, the dynamic primates are an ideal flagship group for general biological conservation as well (Cowlishaw et al. 2009; IUCN 2012).

Primate tourism remains a fairly understudied area, but the discrepancy between the goals of ecotourism and its potentially damaging effects has become a cause for concern (Björk 2000; Blangy and Mehta 2006; Horton 2009; Timm et al. 2009).

Preliminary studies suggest that increasing interactions with humans elevates primate cortisol levels (Behie et al. 2010), reduces the frequency of social interactions (O'Leary and Fa 1993; De la Torre et al. 2000), alters ranging behaviors and substrate use (De la Torre et al. 2000; Grossberg et al. 2003) and increases the potential for cross-species disease transmission (O'Leary and Fa 1993; Chapman et al. 2005; Hsu et al. 2009; Muehlenbein et al. 2010). Most tourists are unaware of the potential impact of their behaviors on wildlife (Grossberg et al. 2003), and the majority of human–primate interactions are initiated by tourists (O'Leary and Fa 1993; Sabbatini et al. 2006; Hsu et al. 2009; McCarthy et al. 2009). This creates a difficult ethical position for primatologists, who recognize the challenges of balancing the economic needs of a region with the well-being of the wildlife involved (Fedigan 2010; Lee 2010).

11.4 Crop-Raiding by Primates

As a group, primates are generally considered eclectic omnivores, due to their dietary selectivity and intraspecific dietary flexibility (Chapman and Chapman 1990; Altmann 2009). One key factor in this flexibility is their ability to exploit alternative food resources. Recent examinations of primates in habitat fragments find that many supplement available food with resources from the surrounding matrix (Estrada 2006; De Freitas et al. 2008; Asensio et al. 2009). This ability to shift resources when something highly palatable or profitable is found (Altmann 2009), coupled with their intelligence and curiosity, predisposes many primate species to crop-raiding.

One of the most reliable predictors of crop-raiding is the type of crops grown; primates prefer easy-to-pick crops high in calories or simple sugars (Nijman and Nekaris 2010). It is generally believed that primate crop-raiders supplement their natural foraging behaviors, rather than fully replacing wild food with raided crops (Naughton-Treves et al. 1998; De Freitas et al. 2008). This "landscape supplementation" (Asensio et al. 2009) enhancing natural foraging behaviors has become part of many species' subsistence strategies, allowing them to persist within highly modified environments. However, as is the case with any drastic environmental change, crop-raiding by primates has its consequences. The addition of raided crops to a wild-foraged diet has been associated with higher population densities (Moore 1999; Singh et al. 2006), larger troop sizes (Biquand et al. 1992), and altered activity budgets (Altmann and Muruthi 1988; Saj et al. 1999) and ranging patterns (Saj et al. 1999; Kogenezawa and Imaki 1999; Sabbatini et al. 2006).

The best known crop-raiding primates are the catarrhines, particularly *Papio* (Chism 2005; Hill 2005), *Macaca* (Richard et al. 1989; Southwick et al. 2005), and *Cercopithecus* (Saj et al. 1999; Hill 2005). Crop-raiding is less prevalent in the Americas, likely due in part to increased arboreality of platyrrhine primates. To date, this behavior has been reported for the neotropical genera *Ateles* (Waters and Ulloa 2007), *Cebus* (Galetti and Pedroni 1994; Baker and Schutt 2005; De Oliveira and Fialho 2007), *Saimiri* (Boinski et al. 1998; Daily et al. 2003), and *Alouatta* (McKinney 2010). The ability of howler monkeys to survive in matrix habitats throughout their range is attributed in part to their ability to shift to a more frugivorous diet whenever possible, and to become more folivorous if necessary (Silver and Marsh 2003; Arroyo-Rodríguez and Dias 2010). The variability of howler monkey diets should not be underestimated—their fruit intake has been reported at anywhere from 5 % (*A. guariba*: Chiarello 1994) to nearly 50 % (*A. palliata*: Estrada 1984) of their total annual diet. *A. caraya* has even been reported consuming wild and domestic birds' eggs (Bicca-Marques et al. 2009). Howler monkeys appear to choose travel pathways with higher resource availability than comparable straight-line paths (Hopkins 2011), and those living in forest fragments have been known to gather as much as 20 % of their total annual diet from outside their home patch (Asensio et al. 2009). Therefore, while the only howler monkey species currently recognized as a crop-raider is *A. palliata* (McKinney 2010), the wide distribution and dietary flexibility of the genus suggests that the prevalence of crop-raiding in this group is likely to be much higher.

11.5 Case Studies

11.5.1 Alouatta macconnelli *in Suriname*

Suriname is located on the northeastern coast of South America, north of Brazil, between Guyana and French Guiana (Fig. 11.1). The country is 163,820 km^2 in area and has an estimated population of 492,000 people (World 2011), with a population density of three persons per square kilometer (World Resources 2008). More than

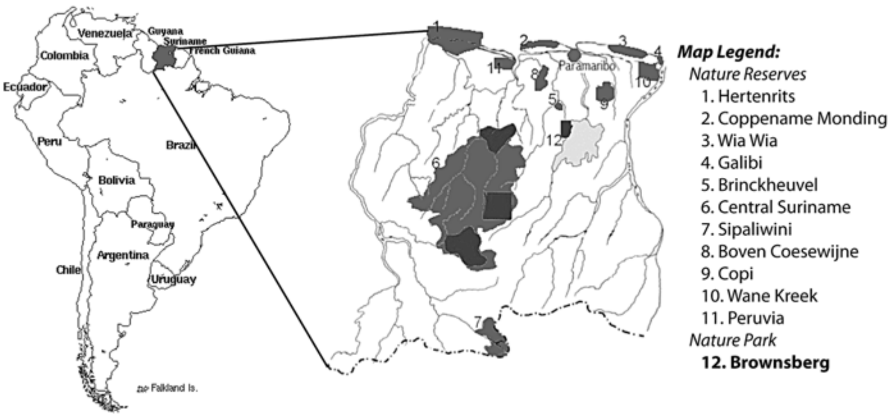

Fig. 11.1 Protected areas in Suriname, northern South America (Sources: www.antor.org/suriname/ and www.surinameinfo.com)

90 % of the Surinamese people live along the coast (McCarry 2000) while the interior of the country is mainly populated by small villages of indigenous tribes and non-indigenous tribal people known as Maroons (Heemskerk 2002).

Approximately 82 % of the land area of Suriname is covered by natural vegetation consisting of tropical rainforests, savannas, mangrove forests, and swamp forests (Fitzgerald 2003). Suriname has four distinguishable seasons: two rainy seasons and two dry seasons, and the average annual rainfall is 2,200 mm per year (The Encyclopedia of Earth 2008). Much of Suriname's land area is protected in 11 nature reserves and one nature park (Fig. 11.1). The Brownsberg Nature Park (BNP) was established in 1970 and is managed by the Foundation for Nature Conservation in Suriname (STINASU) as part of a long-term lease granted by the government of Suriname (Werkhoven and Baal 1995; Fitzgerald et al. 2002; Fitzgerald 2003; STINASU 2008). STINASU, a semi-governmental organization, conducts research projects, nature education programs, and tourist excursions in BNP (STINASU 2008). The park consists of 12,200 ha of both disturbed and undisturbed evergreen rainforest. Because of its location only 130 km south of the capital city of Paramaribo, BNP can be reached within three hours by car or bus, and is a popular destination for both domestic and international tourists (STINASU 2008). The park is equipped with infrastructure for both day and overnight guests, exhibits high biodiversity including all of Suriname's eight primate species, and contains beautiful scenery and waterfalls. Tourists and researchers alike visit BNP and the park hosts an average of 20,000 guests annually (Westin 2007).

The main facilities of BNP lie atop a 500-m lateritic plateau where tourist lodges are situated near an overlook of the nearby lake, and trails extend from the lodging area to various waterfalls and scenic views. Within this area, seven of Suriname's eight primate species can be spotted. The eighth species, the squirrel monkey (*Saimiri sciureus*), is also found in the park but does not range into the main tourist area (Fitzgerald 2003).

In recent years, Brownsberg has experienced illegal gold mining activities along its borders and has seen an increase in tourism (Westin 2007). In the early 2000s concerns were raised about the impact of both of these activities on the health of the park's ecosystems. In response, research projects were undertaken to study the effects of both gold mining and tourism. This case study will highlight the impact of tourism on the park's red howler monkey (*A. macconnelli*) population.

Westin (2007) compared the behavior patterns and health parameters of howler monkeys living in areas with high tourist presence with those of monkeys living in areas of low tourist presence, alternating observations of the two areas every other week. Activity budgets of the two groups were monitored as well as monkey responses to individual human disturbances, to address the behavioral impacts of tourism. Ecological parameters, including rainfall, temperature, fruit availability, and forest structure, were also monitored in the two study areas and were found not to differ substantially (for more details see Westin 2007). Indicators of health, including the presence of wounds, scars, and botfly lesions, as well as fecal analyses for intestinal parasites addressed the impacts of tourism on health. Results indicated that monkeys in the two areas exhibited different behavior patterns, specifically that

Table 11.1 Behavioral patterns by area (Non-Tourist vs. Tourist) at Brownsberg Nature Park

Behavior category	Non-tourist area monkeys (%)	Tourist area monkeys (%)
Remain stationary	76.53	61.65
Forage	12.73	20.41
Travel	6.90	14.17
Vocalize	2.69	2.34
Eliminate waste	0.67	1.07
Interact with others	0.48	0.36

Percentages represent the behavioral scans in which monkeys were observed to engage in each behavior out of the total number of behavioral scans. Behavioral scans were recorded every 5 min. The first three behavioral categories were found to be significantly associated with area type (Rao-Scott Adjusted χ^2 test: $\chi^2=51.65$, $df=5$, $p<0.0001$)

remaining stationary, foraging, and traveling were significantly associated with the area (Rao-Scott Adjusted χ^2 test: $\chi^2=51.65$, $df=5$, $p<0.0001$) (Rao and Scott 1992). Monkeys in the tourist area rested less, and both foraged and traveled more, than monkeys in the non-tourist area (Table 11.1). These behavioral alterations may have long-term impacts on fitness if the trade-off between increased activity and decreased resting results in energy imbalances, especially if the increases in energetic costs of travel are not compensated for by equivalent increases in calorie consumption. Tourist area monkeys also altered their behavior patterns in response to changes in weather and fruit availability seasons, while non-tourist area monkeys did not. For example, tourist area monkeys rested significantly more and traveled significantly less during the dry season, while non-tourist area monkeys traveled and rested similar amounts on average throughout all seasons, but altered their food types consumed in response to what was seasonally available. The difference in behavior patterns between the two areas may indicate a behavioral plasticity found in the tourist area monkeys due to tourist presence that is not seen in the less disturbed, non-tourist area monkeys, which are more in tune with natural fluctuations in food availability.

In response to individual human disturbances, monkeys in areas of low tourist presence responded to disturbances of all levels more often than monkeys in areas of high tourist presence, and this discrepancy holds when considering the sex of the monkeys (Table 11.2). Disturbances were ranked by noise level: the presence of a researcher was a Level 1 disturbance; quiet disturbances such as tourists walking by or low volume music were Level 2 disturbances; and the loudest disturbances such as trucks or buses were Level 3 disturbances (Rao-Scott Adjusted χ^2 tests: non-tourist versus tourist area females: disturbance level 1: $\chi^2=10.16$, $df=3$, $p=0.02$; disturbance level 2: $\chi^2=23.87$, $df=3$, $p<0.0001$; disturbance level 3: $\chi^2=8.63$, $df=3$, $p=0.03$; non-tourist versus tourist area males: disturbance level 1: $\chi^2=19.28$,

Table 11.2 Frequency of monkey response to human disturbance by area, sex, and disturbance rank at Brownsberg Nature Park

Disturbance	NT female (%)	T female (%)	NT male (%)	T male (%)	NT average (%)	T average (%)
Level 1	6.6	2.7	8.7	3.0	7.7	2.9
Level 2	8.4	1.8	11.5	2.8	10.0	2.8
Level 3	17.4	4.7	40.0	8.3	30.2	6.5

Percentages represent the number of responses by female or male monkeys in each area to disturbances of each level out of the total number of disturbances to which the monkeys were exposed

In all comparisons, non-tourist (NT) area monkeys responded more often than tourist (T) area monkeys

All comparisons were significant at $\alpha = 0.05$

$df = 3$, $p = 0.0002$; disturbance level 2: $\chi^2 = 19.91$, $df = 3$, $p = 0.0002$; disturbance level 3: $\chi^2 = 17.37$, $df = 3$, $p = 0.0006$) (Westin 2007). Tourist area monkeys uniformly responded less often to human disturbances, perhaps because constant exposure to tourist activities has resulted in habituation to tourist presence. In both areas, presence of a researcher consistently prompted responses, and males responded more often than females to human disturbance (Westin 2007).

Westin (2007) concluded that the monkeys in the two areas exhibited different behavioral profiles, both for everyday behavior patterns and for responses to human disturbance. Tourist area monkeys altered their behaviors in response to seasonal change and over the long term by changing activity patterns, which represented long-term tourism influence and coping mechanisms for dealing with tourist presence. Tourist area monkeys were also less likely to respond to individual human disturbances because of their repeated exposure and habituation to them. Non-tourist area monkeys altered their behaviors in the short term by responding to individual disturbances, rather than altering behavior patterns in the long term. Human disturbances were much less frequent in the non-tourist area, thus monkeys were not habituated to them, and in fact responded more consistently to them.

This study also compared the health of monkeys in high and low tourist areas to determine whether tourist activities negatively impacted health. The health of the tourist area monkeys, as measured by the presence of wounds, scars, or botfly lesions, was poorer than that of the non-tourist area monkeys, with more groups and individuals in the tourist area exhibiting indicators of poor health, though few health comparisons were statistically significant (Westin 2007). Results of intestinal parasite infection comparisons between the two areas were mixed and nonsignificant, but with a general trend for worse health in the tourist area (Table 11.3). These health impacts could be due to tourism and the stress caused by tourist presence resulting in compromised immune function.

The impact of tourism on monkey health and behavior at BNP is measurable, but does not appear to be extreme or dangerous at this time. However, there could be future implications for the viability of tourist area monkeys if tourism at BNP continues at the current level or increases, and follow-up investigations are warranted

Table 11.3 Intestinal parasite infection by area at Brownsberg Nature Park

	Non-tourist	Tourist
Number of fecal samples analyzed	147	157
Number of analyzed samples w/parasites	9 (6.12 %)	11 (7.01 %)
Average Number of eggs per sample	1.33	1.45
Number of troops sampled	~15	~11
Number of sampled troops w/parasites	12 (80.00 %)	10 (90.91 %)
Number of parasite species found	3	2
Number of non-pinworm infections	5	2
Total Number of parasites	50	62

Comparisons of intestinal parasite infections show tourist area monkeys exhibiting a higher percentage of fecal samples with parasites, more eggs per sample (independent samples t test: $t=-0.26$, $df=18$, $p=0.79$), proportionately more troops with parasites (Fisher's Exact test: $p=0.61$), and more total parasites, but non-tourist area monkeys harbored more species of parasite (higher richness), and more non-pinworm infections (Fisher's Exact test: $p=0.44$)

(Westin 2007). As for the direct impacts of tourism on monkey behavior, monkeys within the tourist area appear to be habituated to the constant human presence within their home ranges. This may benefit both the tourism program at BNP, because visitors who have a better chance of seeing wild primates will be happier with their visit to the park, and the conservation status of the monkeys, because park visitors in turn could become interested in their protection. Alternatively, habituated monkeys may be less likely to flee from hunters should they be encountered. While hunting inside the park is technically illegal, a recent decrease in the number of game wardens may make enforcement of hunting laws difficult and may put habituated monkeys at increased risk of death or injury.

It should be noted that any effects suffered by the monkeys in response to tourism must be considered in the face of the gold mining pressures at the park boundaries. Specifically, tourism at BNP may be the only thing preventing miners, loggers, and hunters from overrunning the park. Small-scale gold mining and the logging associated with it are devastating to the environment and to howler monkey habitat (Fig. 11.2). At minimum, gold mining in Suriname affects waterways, which are diverted and polluted with mercury during the process. At maximum, large areas of forest are completely cleared to provide access to the gold-rich soils below them (Peterson and Heemskert 2001). Decades will be required for anything passing as monkey habitat to regenerate naturally. No studies have yet been undertaken to assess the impacts of mining on the monkeys, but due to the severe deforestation required, it stands to reason that local extinctions could occur. Additionally, a deforested, species-depauperate park would not have the same attraction for tourists. STINASU regularly intervenes to remove miners from within the park's boundaries due to the economic incentive provided by the park's visiting tourists, who incidentally do not want to hear or see miners during their visit. Without the income from tourism, STINASU would have little reason to keep the park free from mining; hence, the situation could be much worse for the monkeys if the park was closed to

Fig. 11.2 Impacts of BNP mining: destruction of creeks and surrounding watershed areas (*left*, photo by A.U. Vreedzaam); deforestation in the mining area (*right*, photo by J.L. Westin)

tourists (Westin 2007). Without tourist presence, which can be safely considered as the lesser of the two evils, there is nothing to stop the spread of gold mining and the subsequent negative impacts it will have on existing primate populations in the Brownsberg Nature Park.

11.5.2 Alouatta palliata *in Costa Rica*

Costa Rica stands out as an example of the potential for economic development to coincide with biological conservation. This tiny Central American nation maintains approximately 25 % of its total territory as protected wildlife areas (Baker and Schutt 2005; Van Hulle and Vaughan 2009). The nation is known for its ecotourism, and over one-half of all international tourists visit at least one protected area during their stay (Horton 2009). The possibility of seeing wildlife such as monkeys, macaws, sloths, and big cats brings visitors from all over the world.

Curú Wildlife Refuge (Fig. 11.3) is one of the smaller and lesser-known reserves in the country, but is recognized as one of the best locations in the region for viewing wildlife such as scarlet macaws and white-faced capuchins. Located in the southern tip of the Nicoya Peninsula, Curú is both a privately owned working hacienda and a designated wildlife refuge. The region is characterized by tropical dry/transitional moist forest, one of the most endangered forest types in the world (Herzog and Vaughan 1998; Timm et al. 2009). Like most transitional moist and tropical dry forests in Costa Rica, Curú experiences two distinct annual seasons (Gillespie et al. 2000), with rainy season running from May through October, and dry season from November through April. Many indigenous tree species flower and fruit asynchronously as a result of this sharp seasonal change (Céspedes and Lindquist 2007). Temperatures in the region range from 20 to 35 °C, with an annual mean of 28 °C, and rainfall averages 1,260 mm/year (Instituto Meteorológico Nacional 2008).

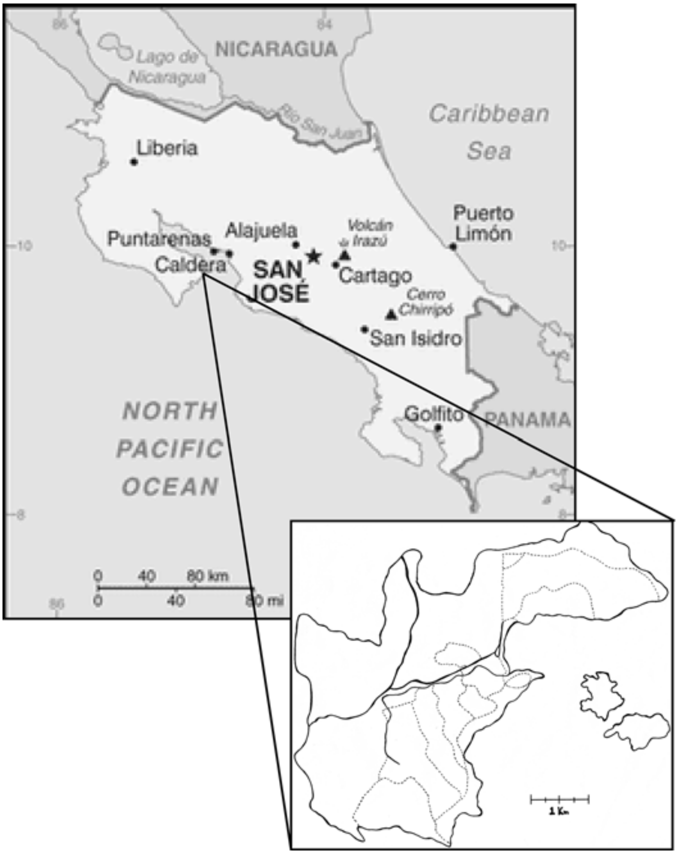

Fig. 11.3 Curú Wildlife Refuge in Costa Rica, Central America (Costa Rica map © US CIA 2008)

The refuge ranges in elevation from sea level to approximately 155 m. Of the 1,492 ha property, roughly two-thirds remain forested, mostly in the hilly areas of the property that are less suitable for agriculture. The remaining 500 ha of the refuge have been modified for human use. These anthropogenic landscapes include pasture for zebu cattle (*Bos indica*), small plantations of mango (*Mangifera indica*), banana (*Musa acuminata*), oil palm (*Elaeis guineensis*), soursop (*Annona muricata*), and guava (*Psidium guajava*), and secondary growth dominated by invasive coconut palms (*Cocos nucifera*). In addition to the anthropogenic landscapes, the sea level microhabitats of Curú include beach, mangrove swamp, and riparian forests. One well-maintained unpaved road bisects the property for a distance of roughly 3 km, bringing regular vehicular and foot traffic into the refuge.

This highly biodiverse area has been involved in conservation projects for many years. To date, 79 mammal species, at least 230 species of birds, and some 500 species of plants have been identified within the refuge (Baker and Schutt 2005).

Curú has served as a sanctuary for nesting sea turtles, and participated in a reef restoration project that significantly increased biodiversity in the bay (Federico Schutt, personal communication). The refuge also participates in ongoing rehabilitation projects for scarlet macaws (*Ara macao*) and for the black-handed spider monkey (*Ateles geoffroyi*) (Brightsmith et al. 2004; Baker and Schutt 2005). Because the small refuge is adjacent to the Nicoya Peninsula Biological Corridor, such projects have great potential to increase biodiversity in the region. A more complete description of the research site and its history may be found in Baker and Schutt (2005) or McKinney (2010).

Curú is an ideal location for ethnoprimatological research. The refuge includes both relatively undisturbed and highly modified landscapes, boasts a high monkey population density, and provides an opportunity to investigate monkey encounters with ecotourists and domestic crops. McKinney (2010) examined the effects of human interactions on mantled howler monkeys (*A. palliata*) at this site over a two-year period (January 2006 through December 2007). The human-commensal troop interest ranged in size from 27 to 30 animals during the course of the investigation, and averaged 4–5 adult males and 12–16 adult females. This group composition yielded a male to female ratio of 0.42 and an immature to adult female ratio of 1.08. A second, undisturbed troop was included in the project to serve as a study control. This troop was demographically comparable to the human-commensal troop, ranging from 25 to 28 individuals during the course of the study. The control troop maintained a male to female ratio of 0.33 and an infant to adult female ratio of 0.83. This troop ranged within a relatively uniform environment of primary and advanced secondary tropical forest, with no overt anthropogenic disturbance. The study described here reviews the effects of ecotourism and crop-raiding on *A. palliata* at Curú Wildlife Refuge.

Ecotourism is an increasingly important component of the landowners' livelihood, comprising over one-half of their income each year (Baker and Schutt 2005). Curú's roughly 10,000 annual visitors (Schutt, personal communication) come to relax on the beach, hike along one of the trails that wind through the forest, or to embark on a kayak or snorkeling trip to nearby Islas Tortugas. While the refuge does offer six rustic cabins, most tourists are day visitors and stay for only a few hours.

The range of the human-commensal troop encompassed several hiking trails, pasture land, small plantations, and the road into the refuge. While the human-commensal troop was selected based on their proximity to tourists and their use of anthropogenic landscapes, they had limited interactions with humans. In fact, the relative infrequency of tourist encounters by the commensal troop (1.98/h) were comparable to the encounter rate between the control troop and researchers (2.44/h) (Kruskal-Wallis $H=0.14$, $p=0.708$, $n=45$). However, both the duration and the types of interactions differed between the two groups. The human-commensal group had a mean interaction length of 461.3 s, while the control group's interactions with researchers were much shorter, at a mean of 103.5 s (Kruskal-Wallis $H=3.90$, $p=0.048$, $n=2{,}304$). Most human interactions recorded for both study troops were minor, involving vocalization or vigilance. Even among the human-commensal troop, the animals were never observed taking food from people or having any physical contact with visitors. However, monkeys were approached more closely by humans, and their interactions were more intense. These animals were regularly harassed by tourists and guides who "howled" at the monkeys in an attempt to elicit a vocal response. An attempt at physical contact was witnessed only once, when a child vigorously shook a small tree in which a monkey was resting.

The majority of interactions involved adult male monkeys; they were the primary actors in 66.12 % of the commensal troop interactions and in 54.75 % of control troop interactions. Participation by sex differed significantly ($\chi^2 = 17.641$, $df = 1$, $p = 0.000$), but participation by age class was comparable ($\chi^2 = 2.090$, $df = 1$, $p = 0.148$). Because the monkeys most commonly responded to disturbance through vocalization, this high representation of adult males in the interactions is understandable. Human–monkey interactions observed in the control troop were primarily monkey-initiated (69.96 %), and were mostly vigilance of observers and vocal responses to researcher movements. The majority of interactions in the commensal troop (68.09 %) were human-initiated; this difference in initiators between the two groups is significant ($\chi^2 = 83.788$, $df = 1$, $p = 0.000$).

The rate of human–monkey interactions observed was clearly associated with the average number of people encountered by the human-commensal troop (Pearson's $r = 0.670$, $p = 0.000$); an increase in human–monkey interaction rates was observed during the tourism peaks in the months of March and August. However, there was no relationship between the two for the control troop, which was contacted only by researchers (Pearson's $r = 0.273$, $p = 0.866$). This discrepancy, and that of whether monkeys or humans initiated interactions, reflects the qualitative differences in the types of interactions between the monkeys and tourists (commensal troop) and the monkeys and researchers (control troop). No researchers fed or approached the animals, and both the commensal and control troops were fully habituated to the researchers' presence. The monkeys were irritated by noise, and responded vocally to motors, talkative hikers, and noisy nature guides. Upon eliciting a response from the monkeys, tourists often carried on with disruptive behaviors.

In addition to tourist areas, the human-commensal mantled howler monkey troop at Curú ranged through a fragmented landscape (McIntyre and Hobbes 1999) encompassing small plantations of mango (*Mangifera indica*), banana (*Musa acuminata*), soursop (*Annona muricata*), and guava (*Psidium guajava*). Curú management considers the loss of some fruit crop to be an acceptable cost of tropical farming, and makes no effort to prevent crop-raiding by wildlife. While the monkey troop was never observed feeding from the banana, soursop, or guava crops, they made frequent use of the mango plantations whenever the fruits were in season (Fig. 11.4). Despite the presence of these small monospecific plantations, the commensal troop's range as a whole was only slightly less diverse that that used by the control troop. The commensal troop's range had a tree species richness of 55 and a Shannon-Weiner Index of 3.09; the control troop's range had a tree species richness of 45 and a Shannon-Weiner Index of 3.47. The two territories had about one-third of tree species in common, and ten dietary items were consumed by both study troops.

Both troops had a relatively conservative diet, with the majority of feeding concentrated on a limited sample of resources (Estrada et al. 1999). Each troop used a

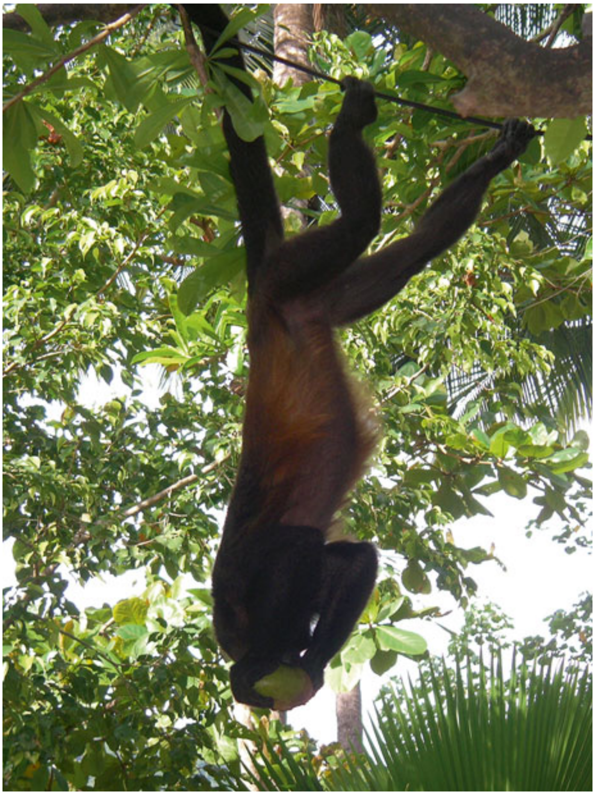

Fig. 11.4 Mantled howler monkey (*Alouatta palliata*) consuming mangos (photo by B. Binnington)

tree species with large, sugary fruits as their most frequently used resource; these and other commonly used foods are listed in Table 11.4. Due to the wide availability of and easy access to domestic mangos, the commensal troop had a significantly higher consumption of fruit, at 34.19 % of their annual diet versus 26.3 % of the annual diet in the control troop (Kruskal-Wallis $H = 9.23$, $p = 0.002$, $n = 48$). The use of fruit changed seasonally for the control troop ($H = 16.32$, $p = 0.012$, $n = 48$), but was not significantly different across seasons for the commensal troop ($H = 1.45$, $p = 0.225$, $n = 48$).

The combined effects of human interaction and crop-raiding have led to some noticeable modifications made by the human-commensal troop. The commensal troop maintained a much larger range than the relatively undisturbed control troop (41.6 and 20.4 ha, respectively), likely in response to the heavily fragmented landscape used by the commensal troop. The range of the commensal troop followed living fence rows and riparian forests, and encompassed some matrix habitats, such as pastures and road, that were not fully useable by the monkeys. With plantations, mangroves, and secondary forest, trees less than 10 m in height dominated the commensal troop's range. Therefore, they spent significantly more time on mid-and lower-level substrates than did the control troop (low, <10 m: $H = 16.02$, $p = 0.000$,

Table 11.4 Key resources for mantled Howlers at Curú Wildlife Refuge

Species	Common name	Commensal		Control		Parts eaten
		%	Rank	%	Rank	
Ficus sp.	Fig	8.65	2	16.77	2	Fr, Lv
Spondias mombin	Jobo	5.08	7	20.14	1	Fr
Mangifera indica	Mango	18.2	1	–	–	Fr
Anacardium excelsum	Espavel	7.37	4	3.44	6	Fl, Fr, Lv
Samanea saman	Cenízaro	8.56	3	0.88	14	Fl, Fr, Lv
Inga multijuga	Guabo d'estero	6.67	5	0.95	13	Fl, Fr, Lv
Trophis racemosa	Ojoche negro	1.05	15	6.24	3	Fl, Fr, Lv
Bursera simaruba	Indio desnudo	0.22	30	5.76	4	Lv
Andira inermis	Almendro de rio	5.84	6	–	–	Fl, Lv
Brosimum alicastrum	Ojoche	–	–	5.28	5	Lv
Enterolobium cyclocarpum	Guanacaste	0.67	19	2.48	7	Lv
Cecropia peltata	Guarumo	1.60	11	1.20	11	Fr, Lv
Bombacopsis quinata	Pochote	0.13	37	0.40	19	Lv

Principal foods of the two mantled howler monkey troops, including those which comprise over 5 % of total diet and foods eaten by both study troops. Foods are ranked by the overall percentage of the total diet during the two-year study period

$n=38$; mid-level, 10–20 m: $H=15.44$, $p=0.000$, $n=38$; canopy, >20 m: $H=19.09$, $p=0.000$, $n=38$). The commensal troop had fewer direct pathways between food patches, resulting in an increase in travel time ($H=7.37$, $p=0.007$, $n=45$) and foraging effort ($H=7.34$, $p=0.007$, $n=45$). Time at rest and time spent in social interaction did not significantly differ between the two troops. Overall, the human-commensal monkeys appear to be responding to their situation primarily through dietary change and energetic accommodations, making moderate behavioral adjustments in order to maintain a large range of heterogeneous landscapes.

11.5.3 Alouatta pigra *in Mexico*

The natural distribution of black howler monkeys (*A. pigra*) in southeastern Mexico is declining as a result of the expansion of cattle ranching, agriculture, and human population growth (Estrada et al. 2006). In recent years, cattle ranching has drastically modified the natural environment and put many tropical forest species in danger, including *A. pigra* (SEMARNAT 2008). Playas de Catazajá, in the north of the state of Chiapas, Mexico, is a municipality immersed in a large complex of lagoons (approx. 12,937 ha) which, via the Usumacinta River, are in direct contact with a system of wetlands in the Pantanos de Centla Biosphere Reserve (INIREB 1998). These wetlands house notable biological diversity, and in many cases offer critical habitat for seriously endangered species such as the black howler monkey. For these reasons, this site was recently decreed a State Natural Protected Area (Gobierno de Chiapas 2006).

Despite their current endangered status, black howler monkeys exhibit great behavioral and feeding flexibility, which allows them to adapt to different environmental conditions (Marsh 2003, Pozo-Montuy and Serio-Silva 2006, 2007). However, the long-term presence of howler monkey populations at disturbed sites is uncertain because they are vulnerable to hunting, disease, predation, food scarcity, and species trafficking (Estrada et al. 2006). This situation makes it necessary to carry out studies on howler monkey populations to monitor their continued existence over time. Unfortunately, information on the population characteristics of *A. pigra* in fragmented sites of Mexico remains limited to Palenque, Chiapas, and the Yucatan Peninsula (Estrada et al. 2002, Serio-Silva et al. 2006; Estrada and Van Belle 2006). Our research team is conducting large-scale population studies at several sites in the state of Tabasco and in northern Chiapas. One of our study sites, Catazajá, is a good example of a site with a large population of black howler monkeys for which there is no available information. In this case study, we evaluate the remnant population of *A. pigra* in Catazajá and their potential for ecotourism.

Between October 2004 and March 2006, we conducted periodic visits to forest fragments in the Playas de Catazajá area. During each visit, we collected ecological, behavioral, and demographic data on the howler monkey population and its habitat in an area corresponding to 75 % ($n=39$) of the *ejidos* (communal lands under the stewardship of rural inhabitants for agricultural activities) of the municipality. Once a howler monkey troop was located, we observed it for a minimum of 30 min and recorded sex and age class of each group member (following Rosales-Meda 2003 age-sex categories). Each *ejido* had 1–6 fragments, and the frequency of visits to a given *ejido* depended upon the number of fragments it contained. In each *ejido*, sampling was done on consecutive days until a census was completed for all fragments. *Ejidos* with 1–3 fragments were sampled in a single day, those with 4–5 required two days of field work, and those with six fragments required up to three continuous days of observation. Each troop was carefully identified and physical data (e.g., age, sex, size, scars) were recorded for each animal in the troop to ensure that individuals were not double counted in neighbor fragments.

In order to evaluate primate presence in the fragments, to make distribution maps for the monkeys, and to identify habitats that could be used for the conservation of *A. pigra* in Playas de Catazajá, we used GIS (ArcView) and orthophotographs on a scale of 1:20,000 (2003) with ground tracking (Fig. 11.5). We generated a database that included vegetation type (riparian, disturbed, and primary forest), fragment size (ha), distance to the nearest fragment (m), distance to the nearest human settlement (m), distance to the nearest body of water (m), and general demographic information on the primate group living in each fragment. These variables were selected because they have been identified as important by previous studies on howler monkeys in fragmented habitat (Estrada and Coates-Estrada 1995; Marsh 2003; Rodríguez-Toledo et al.2003; Anzures-Dadda and Manson 2007). The age-sex ratio of howler monkeys in each fragment was used as a proxy for population health and to calculate an Ecotourism Population Potential Index (EpPI).

To evaluate the potential for ecotourism of each population of howler monkeys, we adapted the Ecotourism Potential Index, after Berovides-Álvarez (2001). This

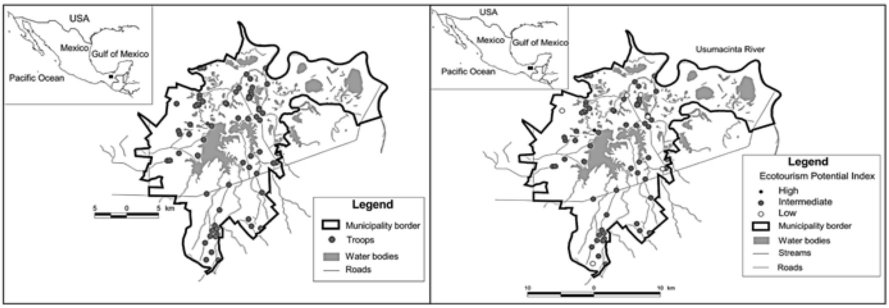

Fig. 11.5 Playas de Catazajá, Chiapas, México: distribution of *Alouatta pigra* troops (*left*); potential sites for ecotourism focusing on *Alouatta pigra* (*right*)

index evaluates four demographic parameters—the proportion of adult females/adult males, the proportion of infants/adult females, the proportion of juvenile females/juvenile males, and the proportion of infant females/infant males—and considers their variation to assess the levels of interest for ecotourism. Specific values assigned to each demographic parameter are shown in Table 11.5. With this information we could establish that the populations with high potential value for ecotourism are those that have a higher proportion of immature individuals (juveniles and infants), which are charismatic and more attractive to visitors. This biological information is useful for evaluating the conservation status of the habitat and the *A. pigra* populations, and for the implementation of sustainable conservation strategies for southeastern Mexican wildlife.

A total of 115 vegetation fragments across 39 sites at Playas de Catazajá, Chiapas, were surveyed (Fig. 11.5). In the 6.39 km^2 of remnant vegetation of the municipality, 659 individuals of *A. pigra* were recorded; 11 of these were solitary individuals, and the rest comprised 118 troops. Ecological density was 103.1 ind/km^2. There were 435 adults, 137 juveniles, and 87 infants. Of the howler monkeys recorded, 28 % ($n=184$) were adult males, 38 % ($n=251$) adult females, 10 % ($n=67$) juvenile males, 11 % ($n=70$) juvenile females, and 13 % ($n=87$) were infants. Mean troop size was 5.0 ± 2.6 (SE) individuals (range: 2–13). The most common social unit was unimale-multifemale (50 troops; 42 %), followed by multimale-multifemale (39 troops; 33 %), unimale-unifemale (16 troops; 14 %), unifemale-multimale (10 troops; 8 %); the remaining groups were same sex pairs (3 troops; 3 %). The mean number of adult males per group was 1.4 ± 0.7 (SE). There were 2.0 ± 0.1 adult females, 0.6 ± 0.1 juvenile males, 0.6 ± 0.1 juvenile females, 0.4 ± 0.6 infant males, and 0.3 ± 0.04 infant females. There were no adult males in two of the troops recorded, one troop had no adult females, and 13 troops had no immature individuals. The adult male to female ratio was 1:1.4; the adult female to juvenile ratio was 1:0.55, and the adult female to immature ratio was 1:0.87. These demographic data—particularly the presence of young howler monkeys—are vital for identifying troops that would be most attractive to tourists.

Table 11.5 Evaluation of Potential Sites for *A. pigra* Conservation and Ecotourism in Playas de Catazajá, Chiapas

Parameter	Range/description	Value
Ecotourism Habitat Potential Index (*EhPI*)		
Most abundant vegetation type	Riverine	3
	Primary forest	2
	Secondary forest	1
Fragment size	1.1–5 ha	3
	>5 ha	2
	0.06–1 ha	1
Distance to nearest fragment	1–200 m	3
	201–500 m	2
	>500 m	1
Distance to nearest human settlement	0–1,000 m	3
	1,001–5,000 m	2
	>5,000 m	1
Access to the site	Lake or river	3
	Paved road	2
	Unpaved road	1
Distance to the site	0–10 km	3
	10.1–20 km	2
	>20 km	1
Comfort of access	Comfortable	3
	Not comfortable	1
Ecotourism Population Potential Index (*EpPI*)		
Adult females per adult male	>2	3
	1–2	2
	<1	1
Juvenile females per juvenile male	>2	3
	1–2	2
	<1	1
Infants per adult female	>1	3
	1	2
	<1	1
Infant females per infant male	>2	3
	1–2	2
	<1	1

Values assigned to a variety of ecological and demographic parameters used in determining the Ecotourism-Habitat Potential Index (EhPI) and the Ecotourism Population Potential Index (EpPI) Using this scale, populations are ranked as high (10–12), medium (7–9), or low (4–6) on the EpPI index, and habitats as high (17–21), medium (12–16), and low (7–11) on the EhPI index. The two indices were combined to determine overall ecotourism potential for each site, as shown in Fig. 25.5 (after Berovides-Álvarez 2000)

The distribution of the black howler monkeys in the municipality of Catazajá is limited to the lowlands, riverine environments, and to low and mid-height rainforests close to the municipality of Palenque, Chiapas. Of all the *A. pigra* individuals recorded, 46.7 % ($n=308$) were located in riparian vegetation, 34.6 % in secondary vegetation ($n=228$), and 18.7 % ($n=123$) in the primary rainforest. The cumulative area of riparian vegetation surveyed was 259.65 ha, of secondary vegetation 157.77 ha, and of rainforest 222.03 ha. At Catazajá, 47.1 % of the fragments inhabited by howler monkeys had an area larger than 5 ha (mean ± SE: 9.1 ± 1.8 ha), 78.6 % of the fragments were less than 200 m away from the nearest fragment (mean ± SE: 131.3 ± 12.0 m), and 71.4 % of the fragments were less than 1,000 m away from the nearest town (mean ± SE: 909.5 ± 143.0 m). Seventy-five percent of the fragments were less than 500 m from a body of water (mean ± SE: 395 ± 804 m), 100 % of the fragments were within 500 m from a road or highway (mean ± SE: 5.6 ± 5.7 m), and 100 % of the fragments studied were associated with the presence of cattle and the illegal removal of flora and fauna. Applying the population data from the howler monkeys in each fragment to the EpPI scale described above, we found no fragment to have a high Ecotourism-Population Potential (see Table 11.5). Some fragments (11.4 %) were designated medium value according to this index. The remaining fragments (88.6 %) were classified as having low potential for ecotourism in terms of group composition. All fragments from the 39 localities were evaluated for Ecotourism-Habitat Potential, and 54.3 % were considered to have a high potential for ecotourism activities. The remaining fragments (45.7 %) had a medium EhPI index (Fig. 11.5).

The ecological density of howler monkeys at Catazajá is high, compared to other protected and fragmented sites in Mesoamerica (Van Belle and Estrada 2005). However, high densities in fragmented sites could be the result of howler monkeys crowding together in small fragments, the method used to estimate density, or insufficient sampling effort (Clarke et al. 2002; Estrada et al. 2002). For our study, the high density results from the monkeys crowding into the limited remaining areas of vegetation in the municipality. The howler monkey population at Catazajá is significantly denser than that of northern Balancán, which has large fragments of remnant vegetation and few howler monkeys. According to Pozo-Montuy et al. (2008), the probability of finding howler monkeys in northern Balancán is very low compared to similar riparian areas in Catazajá, where a 4 ha fragment has four or five troops (Bonilla-Sánchez 2006). Ostro et al. (2001) suggest that high howler monkey density can favor multimale-multifemale social units; however, this was not the case at Catazajá or in the fragmented landscape of Palenque studied by Estrada et al. (2002), where unimale-multifemale social units predominate. Perhaps the unimale-multifemale social unit is characteristic of this species in fragmented landscapes (Van Belle and Estrada 2005). However, this cannot yet be generalized given that differences have been found at other fragmented sites, such as Monkey River (52 ha) and in northern Balancán, where the majority of the troops are multimale-multifemale, with 2.3 and 2.4 adult males per troop, respectively (Pavelka et al. 2003; Pozo-Montuy and Serio-Silva 2006). We suggest that this demographic characteristic of *A. pigra* is quite variable and requires long-term study.

The population of black howler monkeys at Catazajá confirms the prediction that larger areas have a higher abundance of howler monkeys, as reported for *A. palliata* in Los Tuxtlas, Veracruz, and in Chiapas (Estrada and Coates-Estrada 1996; Anzures-Dadda and Manson 2007). For *A. pigra*, this same pattern has been found in a fragmented landscape of Balancán, Tabasco (Pozo-Montuy et al. 2008). However, our analyses indicate that, in addition to fragment size, the interaction of variables—specifically vegetation type, distance to roads and distance to bodies of water—better explain the variation in howler monkey abundance. These variables incorporate anthropogenic and ecological effects since the probability of finding howler monkeys depends on vegetation type, and a nearby body of water increases the probability of a fragment as howler monkey habitat (Bonilla-Sánchez 2006). The effect of the distance to the nearest roadway can be negative since a fragment that is accessible is more likely to disappear or to be less suitable for howler monkeys because of logging, firewood collection, and hunting (Bynum 1999; Bonilla-Sánchez 2006). The habitat evaluation and estimated group densities indicate that *A. pigra* has a high risk of local extinction in Playas de Catazajá. There is an urgent need to implement a conservation strategy for the region. While none of these study troops were found to have high ecotourism potential, we suggest that implementing some ecotourism strategies, especially for the medium potential troops, could be one important component of conservation efforts for howler monkeys in this region.

11.6 Discussion

Alouatta maintains its distinction as the most widely dispersed neotropical taxon due in part to its ability to thrive in modified landscapes. This success in habitat fragments and in anthropogenic environments appears to be a result of their dietary flexibility (Crockett 1998; Pavelka and Knopff 2004), small home ranges and energy-saving behavioral adaptations (Milton 1998; Korstjens et al. 2010), and the absence of big predators in modified habitats (Arroyo-Rodríguez and Dias 2010; Cristóbal-Azkarate et al. 2014).

Further study is necessary to understand the full impact of anthropogenic modification on these animals, and to determine whether survival in matrix habitats is sustainable over the long term. Howler monkeys generally live in parapatric distributions because of their high level of niche overlap; living in forest fragments may lead to high population densities, unnatural closeness of different howler monkey species, and ultimately hybridization (Aguiar et al. 2008; Bonilla-Sánchez et al. 2010; Agostini et al. 2010). In other cases, fragmentation can reduce dispersal rates, leading to dangerous inbreeding depression (Oklander et al. 2010). Howler monkeys in these modified landscapes also face a potential increase in mid-level and domestic predators (Arroyo-Rodríguez and Dias 2010). In addition to these environmental features, howler monkeys with high interaction rates with tourists show elevated cortisol levels which, over the long term, can reduce fecundity and increase morbidity (Behie et al. 2010). They also show increased diversity and loads of internal parasites (Cristóbal-Azkarate et al. 2010), and face a heightened possibility of transmitting disease between the monkeys and humans or domestic animals (Chapman et al. 2005; Valdespino et al. 2010; Kowalewski et al. 2011).

Despite these challenges, matrix landscapes may prove to be an invaluable tool for the cause of primate conservation. Maintaining a biodiverse matrix with pathways for travel between habitat patches is a growing focus for local conservation efforts (Daily et al. 2003; Timm et al. 2009), and is of increasing academic interest as well. It is possible for matrix habitat to become a mutually useful "shared space" (Lee 2010) between humans and nonhuman primates. Some studies indicate that the economic loss associated with crop-raiding is considerably less than that perceived by land owners (Siex and Struhsaker 1999; Williams-Guillén et al. 2006; Riley 2007), and others report primate use of agricultural lands with no crop damage at all (Muñoz et al. 2006; Nasi et al. 2008). Farmers can often reduce the impact of crop-raiding by planting less desirable crops, such as coffee or tea, as a buffer zone between highly favored crops and forested areas (Nijman and Nekaris 2010). Landowners may also use plants species that are useful to both livestock and wildlife as part of the agricultural matrix, such as in living fences or windbreaks (Asensio et al. 2009).

Primate tourism offers both an economic incentive to conserve wildlife populations and an opportunity to educate the public about endangered wildlife. The effects of tourist interactions on primate health, behavior, and diet can be substantially reduced with a few simple modifications to ecotourism sites. Behavioral guidance for visitors is an ideal starting point. Group size and frequency should be regulated, and visitors kept to a reasonable viewing distance (Klailova et al. 2010). Tourists may be screened for health concerns or—for particularly sensitive species—provided with gloves, face masks, or other items to minimize the risk of disease transmission (Muehlenbein et al. 2010). Behie et al. (2010) suggest that elevated stress hormones in *A. pigra* may be a factor of predictability; the monkeys do not know what visitors will do or when they will turn up, causing a marked increase in stress. McKinney's (2010) findings with *A. palliata* support this idea, as the type of interactions appeared more important than their frequency. Primate tourism is challenging for landowners, as they try to maintain accessibility of the animals through provisioning or other actions (Knight 2010). However, even with provisioned animals, predictability may be the key. If tourists are led to monkey viewing areas by guides, who then instruct visitors in monkey-viewing etiquette, the animals will learn what to expect with tourists and will likely become more tolerant of their presence. Provisioning may be replaced or supplemented with the maintenance of indigenous fruiting trees to attract the primates to viewing areas. Ecotourism projects should be linked with academic institutions, so that the effects of these activities may be monitored. Finally, ecotourism must be perceived as a way for local communities to regain their role as administrators of their lands and natural resources.

The behavioral and ecological plasticity characteristic of the howler monkeys makes them a prime candidate for survival in highly modified landscapes. With some effort on the part of land-owners, howler monkeys can live and forage in agroecosystems and other matrix habitats with minimal economic loss. Howler monkeys appear relatively tolerant of tourist activities, and developing well-conceived ecotourism venues in howler monkey habitat may be a viable tool for their conservation. Further research into the sustainability of howler monkey populations in such environments is certain to be a key element in the future of Neotropical primatology.

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Chapter 12
Health and Welfare of Howler Monkeys in Captivity

Rosalía Pastor-Nieto

Abstract Among platyrrhines, howler monkeys are commonly traded illegally as pets in Central and South America, resulting in the high mortality of specimens. Many of these animals end up in long-term captive situations in zoos and rehabilitation centers, where adaptation may be difficult. Careful husbandry planning, taking into account the animals' behavioral, anatomical, and evolutionary characteristics, can greatly improve survivability. This chapter aims to provide information on howler monkey welfare in captivity, including enclosure design, environmental enrichment, feeding and nutrition, and diseases, based upon the biology and ecology of the species. Digestive physiology, behavioral ecology, and the social system of howler monkeys are major factors to take into account to provide adequate captive conditions. Aspects such as social integration, controlled temperature, indoor and outdoor enclosures, and hiding places should be met. The provision of foraging plants within the enclosure is ideal to stimulate natural feeding behavior. Behavioral enrichment measures need to be devised to prevent behavioral disorders. For successfully maintaining howler monkeys in captivity, animals should be trained to consume a wide variety of natural fiber sources. Special attention should be placed on quantities of food sources rich in gluten and other allergenic proteins. Acute and chronic syndromes such as gastric dilatation, howler monkey wasting disease, and metabolic bone disease can be prevented when provided adequate diets. Many diseases may be acquired in the wild. However, other infectious diseases (viral, bacterial, and parasitic) are concomitant to stress and improper management. Very few studies have been carried out in captive howler populations to fully understand the husbandry and care requirements. Although howlers are very adaptive in nature and although it is a genus widely distributed throughout Central and South America, they are susceptible to many diseases that might threaten their population in the wild. Achieving a better knowledge of these factors in captivity may contribute to the development of healthy captive populations for future reintroductions to the wild.

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Resumen Entre los platirrhinos, los monos aulladores son comúnmente comercializados ilegalmente en Centro y Sudamérica, dando como resultado una alta mortalidad de ejemplares. Muchos de estos monos terminan en confinamiento por largos períodos de tiempo en zoológicos y centros de rehabilitación, donde su adaptación suele ser complicada. Para proveer de condiciones de vida adecuadas que permitan mayor sobrevivencia de individuos en cautiverio, se requiere de una planeación en el manejo que considere las características evolutivas, anatómicas y conductuales de la especie. El objetivo de este capítulo es proporcionar información para promover el bienestar a los monos aulladores en cautiverio, incluyendo el diseño de recintos, enriquecimiento ambiental, nutrición y sistema alimenticio, necesidades sociales y enfermedades reportadas en el género *Alouatta.* Aspectos tales como la integración social, locomoción elevada en tres dimensiones, el control de temperatura, instalaciones internas y al aire libre, así como sitios de resguardo, son aspectos importantes que se deben tomar en cuenta para el diseño de recintos. Se debe promover consumo de fuentes de fibra natural o forrajes naturales no tóxicos, los cuales favorecen una correcta digestión, salud de la microbiota y tránsito intestinal. Al igual que para otras especies de primates cautivos, se debe proveer de elementos de enriquecimiento ambiental para prevenir desórdenes conductuales. Es necesario evitar el consumo de proteínas alergénicas y azúcares simples para evitar trastornos gastroentéricos agudos y crónicos como la dilatación gástrica y el síndrome desgastante del mono aullador; así como dietas balanceadas en calcio, fósforo y suplementadas con vitamina D_3 para prevenir la enfermedad metabólica de los huesos. Muchas enfermedades de los monos aulladores pueden ser adquiridas en vida libre. Sin embargo, otras enfermedades infecciosas (virales, bacterianas y parasitarias) son concomitantes al estrés y a malas condiciones de cautiverio. Muy pocos estudios se han llevado a cabo en poblaciones cautivas de monos aulladores para comprender de manera completa sus necesidades de manejo y cuidado. Aunque los monos aulladores se adaptan fácilmente a distintas condiciones ambientales y constituyen un género ampliamente distribuido en Centro y Sudamérica, son susceptibles a muchos factores que pueden deteriorar su salud y amenazar a sus poblaciones silvestres. A través de un mejor entendimiento sobre los factores que afectan a los monos aulladores y a su manejo, salud y bienestar en cautiverio, se puede contribuir al desarrollo de poblaciones cautivas sanas que constituyan una opción para futuras reintroducciones y/o reforzamientos de poblaciones en vida libre.

Keywords *Alouatta* • Captive management • Health • Welfare

12.1 Introduction

There are numerous factors involved in the decline of wild populations of primates in Central and South America, two of the most important being habitat destruction and illegal pet trade. Forest clearing is still a serious threat because tropical forests are being fragmented and destroyed, due to agricultural encroachment, cattle ranching, road building, and installation of electric power lines (Mittermeier 1991; Vickers 1991; Pastor-Nieto 2007). All these activities allow poachers easy access into primate habitats.

Illegal trade of live monkeys continues to be a great threat to primates because it generally goes on undetected. Poachers chase and harass small groups of monkeys in forest fragments until the animals are forced to descend from trees. Then, the females carrying babies are killed, and surviving infants are sold to tourists at the edge of roads, or to animal dealers who will deliver the infants to specific customers (Cuaron 1991). For example, in Mexico, the trade of live monkeys is a very profitable activity for intermediate and final dealers, because a baby howler or spider monkey may sell for more than the national monthly minimum wage. In addition, local poachers may consume the meat of adult animals or use the carcasses for other purposes, such as fishing bait (Mittermeier 1991; Vickers 1991; Pastor-Nieto 2007).

Hunting and trade not only reduces the size of wild populations, it also modifies the demographic structure (age/sex structure) of the population, which is highly detrimental to large-bodied primates such as spider monkeys or howler monkeys, due to their low fecundity rates. By targeting females, the most sensitive reproductive unit, natural populations are placed in a risky situation (Cuaron 1991).

Unfortunately, information on the impact of illegal trade of primates in Central and South America is very scarce, and there are very few quantitative field studies that evaluate the effect of hunting of primates in rural communities. For example, in Mexico between 1995 and 2011, a total of 1,063 live, wild-caught spider monkey and howler monkey specimens were confiscated by the Procuraduría Federal de Protección al Ambiente (PROFEPA). Most of these specimens were transferred to zoological collections.

Within the ISIS-ZIMS databases, 70 zoological institutions worldwide hold howler specimens in their animal collections. Most of these specimens have been captive-bred. The geographic origin of breeding specimens is not always certain. Most of these zoological institutions are located in Europe and North America, where *Alouatta caraya* (black howler monkey) is overrepresented with a total of 58 institutions, followed by *A. arctoidea* (Venezuelan red howler monkey) with 9 institutions. The least represented species in captivity are the Guatemalan Black Howler monkeys (*A. pigra*) with two institutions and the Mantled Howler monkey (*A. palliata*) in only one registered zoological institution (ISIS 2012). There is a lack of information on captive numbers of howler monkeys in zoos of Central and South America.

To be able to provide improved management of captive howler monkeys, there are a number of fundamental considerations to take into account. These include nutritional needs healthy microbiota and digestion, prevention of behavioral pathologies such as infanticide and aggressive encounters, achievement of adequate social structures and group sizes, enriched environments and disease prevention. Other factors to consider, when first receiving wild howlers into captivity, include age and the psychological and health status of the particular individuals.

The purpose of this chapter is to summarize the factors related to adequate captive management of *Alouatta.* Proper management designed to promote welfare is essential for ex situ conservation of howlers in zoos and rehabilitation centers.

By meeting the most important welfare needs, these institutions may contribute to perform quality research and broaden our knowledge of this species.

To obtain adequate management, enclosure design, captive enrichment, nutrition, and major health concerns of these primates in captivity, it is essential to understand the link with their ecological adaptations. Howler monkeys are known to be a difficult species to maintain in captivity due to their specialized nutritional and social requirements (Lindbergh 1976; Edwards et al. 1989; Edwards and Ullrey 1999). Very few studies have been conducted in captivity due to the difficulty of keeping these primates outside of their natural environment.

12.2 Behavior in Captivity

Captivity may force primate species to behave in a totally different manner than their conspecifics in the wild. There are various reasons for this. On one hand, food is provisioned in abundance and therefore animals do not compete for resources, predation pressure is nonexistent and, in most cases, monkeys live in environments with controlled conditions. On the other hand, captivity prevents animals from dispersing to avoid conflict; therefore, they need to find alternative mechanisms to cope with group living (Cubas 1996; Mallapur and Choudhury 2003).

The genus *Alouatta* is one of the most extensively studied primates in the wild. The main reason for this is their wide distribution range in the Americas, and their lethargic nature (almost 70–80 % of time is spent resting). This allows observers to keep track of the behaviors of individuals, collect detailed data related to use of habitat resources, and monitor changes in population densities. Captive studies of howler monkeys are extremely scarce, although they could provide further information on specific behaviors, physiology and medical aspects.

Concerning captive behavior, the few studies conducted in captivity suggest that males are dominant over females. In many instances males act as control animals, by settling fights between females (Benton 1976). On the other hand, females tend to be more sociable and less competitive. Interestingly, females are observed to be more frequently involved in grooming bouts than males (Shoemaker 1978). Adults tend to spend a great proportion of their time resting; however, they have been observed playing early in the morning or late in the afternoon (Benton 1976). Food competition has been observed between females, especially over novel or scarce food items. Juveniles are commonly devoted to play (Benton 1976). A recent captive study was performed to evaluate the association of social behaviors and reproductive success of female *Alouatta caraya* in European Zoos. This study revealed that more offspring were born and survived from females held in family groups than from those in pairs. Moreover, regular hearing of howls of familiar conspecifics also increased reproductive success of females. Therefore, maintaining familiar groups seems to favor successful breeding in captivity (Farmer et al. 2011).

As many howler monkeys come into zoos and sanctuaries as confiscations and as ex-pets one sees a number of behavioral problems related to their unnatural upbringing and deficient health and psychological care. It is very well known that social interactions with conspecifics during infancy have been shown to affect the formation of affiliative and sexual preferences (Watts and Meder 1996). When animals have been hand-raised imprinting to the caretaker might seriously interfere with integration to a conspecific group. Planning for social integration is critical in these cases. Orphan infants should have visual, auditory, and/or olfactory contact with conspecifics as soon as possible. Integration process should be planned into different stages, and security for the introduced individual should be always a priority (Watts and Meder 1996). In such cases, nutritional transition has to be considered from the inappropriate foods provided as a pet to suitable foods for howler monkeys.

In captive howler monkeys, female rank is linked to reproductive condition, just as in the wild. High-ranking females reach sexual maturity and breed earlier than low ranking females. Passive infanticide appears to be a common feature of captive *Alouatta*, sometimes observed when females allow infants to fall from perches (Shoemaker 1982). Therefore during social integration juveniles should be closely monitored. In addition, males may benefit from infanticide by killing infants likely to be sired by a non-kin male, and hence shortening female's interbirth interval through the cessation of lactation and subsequent return to ovarian cycling. Infanticidal males are thought to gain reproductive advantage by impregnating the dead infant's mother (Sugiyama 1967; Hausfater and Hydy 1984; Crockett and Janson 2000).

Studies of *A. caraya* suggest the absence of reproductive seasonality in captivity (Shoemaker 1982; 1978), although controversial results have been obtained in the wild (Calegaro-Marques and Bicca-Marques 1993; Zunino 1996).

12.3 Management of Baby Orphans

When considering hand-rearing baby howler monkeys, there are several life stage factors to consider; these are age, weight, and dentition. Other features include anatomical differences among species, for example, descent of testes in scrotum. Newborns and infants of *Alouatta palliata*, have undescended testicles, compared to *A. pigra* and other howler species, in which, testicles are present in the scrotum from birth (Kinzey 1997). Infants are considered at 0–14 months of age, juveniles at 14–29 months of age, subadults at 28–35 months of age, and adults at 40–48 months of age. These age categories take into account dependence to mother, as well as size and type of diet (Balcells and Veá- Baró 2009).

Routine health examinations are essential. Basic criteria for hand rearing infant primates can also apply to baby howlers. Hypoglycemia is common in undernourished orphans. Hypoglycemia is treated by administering a 5 % glucose solution for the first 24 h (Summers et al. 2002). If the animal is alert and responding to external stimuli, it is ideal to administer this solution orally. Commercial brands of puppy bottle feeders are appropriate to provide oral fluids and milk formula. If the infant is lethargic or unwilling to eat, a size 8–12 French polyethylene nasogastric feeding tube can be used. The feeding tube can be maintained for several days if properly secured in place with tape (Moreland 1970; Bohm et al. 2012). Before fully introducing infant milk formula, a transitional option is mixing the formula with electrolytes, starting with 25 % formula-75 % electrolytes, then later providing 50 % to 100 % infant milk formula (Fig. 12.1). This process may take a few days, depending on how infants tolerate each stage (Barnes and Cronin 2010). Primilac (Bioserve Laboratories) infant primate formula is readily available. However, commercial infant human formulas have been used successfully in many primate species: an abandoned baby muriqui (*Brachyteles arachnoides*) was successfully bottle fed with human baby formula such as NAN (Nestlé Company) or SMA (SMA Nutrition) and returned to his mother in the wild (Nogeira et al. 1994). The opening of the nipple should allow an easy flow of the formula; excessive flow may choke the baby. Initially, one ounce may be offered every 2–3 h. Volume requirements and frequency of feeding are adapted according to demand. After the first week of bottle feeding it is advisable to verify an intake of 100–120 kcal/day (Swenson 1999; Summers et al. 2002).

Body weights of infants should be recorded on a daily basis. No weight gain or weight loss is an unequivocal sign of inadequate nutrition or early illness. The amount of weight gain is less important than a steady increase in weight.

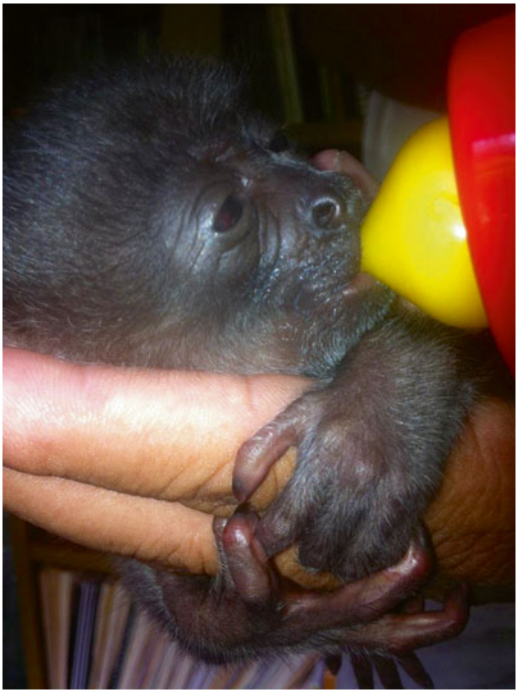

Fig. 12.1 Bottle-feeding a male newborn howler monkey (photo courtesy of Antonio Pastrana Martino)

The proper ambient temperature should be ranging from 27 to 32 ° C. Considering the high cost of an incubator, an infrared light situated at an adequate distance can provide a proper source of heat. Handling practices during the neonatal and infancy periods are essential for later development, as primates are characterized by an extended infancy period. During development, mother–infant contact is crucial to learn social skills (Harlow and Suomi 1971; Mason 1991; Joffe 1997; Pavé et al. 2010). Considering this, it is important to provide the infant with a "surrogate mother" to avoid imprinting with humans and promote gripping reflex. In this case, a cloth toy (i.e., a teddy bear) may be useful. For sanitation purposes, it is advisable to cover the cloth toy with an extra washable layer or have many available so they can be rotated and washed.

As soon as the babies feed by themselves, social integration with other conspecifics is important. Adoption of orphaned infants has been reported among howler monkeys in the wild. These adoptions have been observed in adult females. Therefore, adoptions would be a recommended husbandry alternative to promote social integration whenever possible, always taking into consideration the risk of infanticide (Agoramoorthy and Rudran 1992).

In natural conditions, baby howler monkeys suckle for 6 months to 1 year of age on average. If baby howlers are hand-raised, in addition to a baby formula, small amounts of solid foods can be offered, such as vegetables and greens (i.e., celery, spinach, watercress, zucchini, and green beans) (Fig. 12.2). A wide variety of leafy vegetables and mixed greens are vital for promoting natural foraging behavior.

Fig. 12.2 Female infant howler monkey *Alouatta pigra* feeding from elevated feeding tray (photo by Rosalia Pastor-Nieto)

If rearing facilities are located in or near natural habitats of wild troops of *Alouatta*, it is important to include the consumption of young shoots, buds and fruits of typical browse plant species. Inclusion of these natural foods is usually overlooked, even if they are readily available.

Orphan neonates or infants usually suffer from hypothermia. Predisposing factors include sudden temperature changes, wet and windy weather, improper housing conditions, low social rank and maternal neglect, disease (diarrhea), trauma, and stress. Animals suffering from hypothermia often appear cold, weak, and unresponsive, and may have stiff muscles, bradycardia, weak pulses, cardiac arrhythmias, and pale or cyanotic membranes. The most effective treatment consists of placing them in a shallow warm water bath (30 °C). Other effective measures include the use of hair dryers or a massage. As mentioned in other sections, the use of heat-lamps is also effective, but should be used with extreme caution to prevent thermal wounds. Hypothermia in infant primates is usually associated with hypoglycemia, therefore it is essential to initially provide a 25 % warm dextrose solution intravenously at 2–2.5 g/kg/day or 6–8 mg/kg/min. Care must be taken to not let this solution become extravasated, as it is hypertonic and may cause severe tissue damage. Oral administration of a 50 % dextrose solution may also be effective.

Finally, the social environment in captivity surrounding natural mother rearing should be closely monitored to prevent infanticide. In zoological collections, the risk of infanticide may be increased due to the presence of more than one male in a social group (Crockett and Janson 2000; van Belle et al. 2010).

12.4 Management of Subadults and Adults

Despite the difficulties in keeping infant and juvenile howlers in captivity, the proper captive management of adults also requires the consideration of specific important factors. Species-specific nutritional, behavioral, and housing requirements should be considered for successful captive management. Early detection of potential competitive behaviors and aggression of adults towards juveniles is also very important for establishing viable captive populations.

12.4.1 Nutrition

Proper nutrition of howler monkeys in captivity requires feeding formulation criteria that should be based on the behavioral and ecological demands of the genus. Howler monkeys are mainly folivorous, but supplement their diet with ripe and unripe fruits in the wild. Several studies on optimal foraging of howler monkeys reveal that their natural diets are high in fiber, derived from leaves, buds and shoots (20–80 % fiber), as well as fibrous fruits (20–70 % fiber). Wild howler monkeys are considered folivores-frugivores, based on selection of different plant parts, such as leaf shoots and buds, stems, flowers and fruits of a great variety of plant species, including epiphytic, and in different phenological stages (Coelho et al. 1976; Estrada 1984; Silva-López 1993; de Thoisy and Richard-Hansen 1997; Estrada et al. 1999; Silver et al. 2000; Serio-Silva and Rico-Gray 2002; Fuentes et al. 2003; Pavelka and Knopff 2004; Estrada et al. 2005; Pozo-Montuy and Serio-Silva 2006). To digest highly fibrous foods items, howler monkeys possess an elongated caecum for fiber fermentation, complex gut microbiota, and have a very slow gut transit time (Chivers 1994; Anapol and Lee 1994). The health of the intestinal microbiota of howler monkeys is essential to maintain adequate digestion. Only a few studies have examined the impact of captivity on the primate intestinal microbiota (Benno et al. 1987; Uenishi et al. 2007; Fujita and Kageyama 2007), all of which showed clear differences between wild and captive populations. Recent research has also shown that there is an impact of captivity on the hydrogenotrophic microbiota of howler monkeys, which has important implications for howler monkey health (Nakamura et al. 2010).

Because of these anatomical and physiological adaptations, it is assumed that howlers require a low protein intake. However, various studies suggest that they obtain great amounts of protein from young leaves, shoots and buds (Milton 1980; Silver et al. 2000; Serio-Silva and Rico-Gray 2002). Moreover, various authors have demonstrated that howler monkeys are very selective about the kinds of leaf buds they consume, favoring those that are rich in digestible proteins, amino acids, minerals, and different types of fiber (Milton 1980; Milton 1982; Silver et al. 2000). Many browse plant species provided in zoos are usually protein rich (Clauss and Dierenfeld 2008).

A basic aspect of diet formulation to meet the needs of captive New World monkeys includes proper protein-fiber ratio (da Rocha e Silva 2001). Properly formulated captive diets frequently consist of both a variety of leafy greens and vegetables, fresh browse, as well as a properly formulated commercial diet for folivorous primates, and an alternative protein source. Commercially available primate diets are highly recommended because they are balanced and contain adequate amounts of fiber (14 %) and crude protein (23 %) (Allen 1990). There are many commercial brands of primate diets available including Mazuri Leaf-Eater Primate diet (PMI Nutrition International), ZuPreem diet with 20 % protein, canned or dry (Premium Nutritional Products, Inc.), and Animal Spectrum Primate Diet's dry biscuits (18 % protein) (Animal Spectrum Laboratories). Additionally, when supplementation is necessary, Complan (H. J. Heinz Company) can be included in the diet (strawberry or vanilla flavors are very well accepted), especially if animals are undernourished. Special attention is focused on types of diets provided. Howler monkeys fed with legumes and cereals may suffer from changes in blood counts and chemistry profiles, such as an increase in alanine transaminase (ALT) and lymphocytosis. On the other hand, higher levels of albumin and bilirubin have been observed in captive howlers fed with diary products (Johnson et al. 2001).

When the leafy vegetable portion of the diet is provided at midday, it can increase activity and encourage natural foraging behaviors. As mentioned above, the inclusion of natural browse plant species is very important for the species' proper feeding ecology. Examples of nontoxic plant species cultivated in zoos and included as foraging source for herbivore primates are: *Bischofia javanica, Coprosma repens, Catalpa speciosa, Eugenia cumini, Eugenia jambos, Eugenia paniculata, Ficus benjamina, Ficus macrophylla, Ficus microcarpa nítida, Ficus microcarpa retusa, Ficus religiosa, Ficus thonningii, Hibiscus, Morus alba, Tecomaria capensis,* and *Tipuana tipu.* Some of these plant species have been successfully fed to primates in North American zoo collections. A more extensive list of nontoxic browse fed to primates in zoos is also provided by Tresz (2003) (Table 12.1, Fig. 12.3).

Table 12.1 List of browse species generally considered safe for primates (adapted from Tresz 2003)

Common name (English)	Scientific name
Acacia	*Acacia* spp.
Queen Palm	*Arecastrum romanzoffianum*
Desert Broom	*Baccharis sarothroides*
Bamboo	*Bambusa* spp.
Carob Tree	*Ceratonia siliqua*
Palo Verde	*Cercidium* spp.
Lemon Grass	*Cymbopogon citrates*
Umbrella Grass	*Cyperus alternifolius*
Ficus	*Ficus* spp.
Hibiscus	*Hibiscus* spp.
Desert Fern	*Lysiloma microphylla*
Mint	*Mentha* spp.
Banana	*Musa* spp.
Cat Nip	*Nepeta cataria*
Cat Mint	*Nepeta faassenii*
Basil	*Ocimum basilicum*
Oregano	*Origanum vulgare*
Jerusalem Thorn	*Parkinsonia* spp.
Fountain Grass	*Pennisetum setaceum*
Date Palm	*Phoenix dactylifera*
Pine	*Pinus* spp.
Cottonwood	*Populas fremontii*
Mesquite	*Prosopis* spp.
Pumpkin	*Pumpkin*
Pomegranate	*Punica granatum*
Rose	*Rosa* spp.
Palmetto	*Sabal* spp.
Sugar Cane	*Saccharum* spp.
Gooding's Willow	*Salix goodingii*
Bulrush	*Scirpus* spp.
Tamarisk	*Tamarix* spp.
Yellow Bells	*Tecoma stans (flowers)*
Cape Honeysuckle	*Tecomaria capensis (flowers)*
Tipu Tree	*Tipuana tipu*
Cat-tails	*Typha* spp.
California Fan Palm	*Washingtonia filifera*
Mexican Fan Palm	*Washingtonia robusta*

Fig. 12.3 Female infant howler monkey *Alouatta pigra* feeding freshly cut *Ficus* sp. (photo by Rosalia Pastor-Nieto)

In general terms, the total daily amount of food is divided into two or more portions. This is to keep the animals busy by prolonging feeding times and simulating wild conditions. Although each portion may be balanced to meet the nutritional needs of all animals in a group, high-ranking individuals tend to achieve preferential access to high quality foods (Wolfensohn and Honess 2005). Hierarchy sometimes deters subordinates from climbing to feeding platforms (pers obs); therefore, it is crucial to verify that low-ranking individuals are also provided with a balanced portion of the diet. Mixed exhibits with two or more species of howler monkeys are not recommended. Size differences, such as those seen between *Alouatta pigra* and *A. palliata* may result in intimidation of the smaller *A. palliata,* forcing them to climb to less optimal feeding stations (pers obs).

12.4.2 Housing and Behavioral Enrichment

Captivity provides a very static environment compared to wild habitats, often resulting in reduction in animal attention, propensity to seek, problem solving, and reduced interests in novel items. *Environmental poverty*, defined as *"inappropriate social and physical environments in relation to the basic needs of primates"* (Hosey et al. 2009), may trigger a series of nonadaptive responses, such as increased aggressiveness, abnormal behaviors (such as coprophagy, lethargy, auto-mutilation), stereotypic behaviors, inappropriate sexual behaviors (inappropriate mounts, hyper-sexuality or abnormal postures), inadequate immune response, disease, parasitism, and poor reproductive performance (Meyer-Holtzapfel 1968; Harlow and Suomi 1971; Mason 1991; Sapolsky 1993; Boere 2001; Hosey et al. 2009; Behie et al. 2010). Insufficient space and isolation are the most important characteristics of an impoverished environment (Hosey et al. 2009).

Conversely, *environmental enrichment* consists of a series of measures to modify these impoverished environments, with the goal of improving the physical and social potential of the animals, and therefore improving their quality of life by meeting their ethological needs (Hosey et al. 2009). Basic aspects of behavioral enrichment include minimal clinical interventions, minimizing and/or eradicating animal suffering, providing proper nutrition, adequate enclosure design and dimensions, promoting proper social conditions, and shaping novel and interesting environments by creating occupational therapies. Some examples of occupational therapies are food seeking on substrate, foraging plant species within the enclosure, nest-boxes, perches and refuges, promoting three-dimensional locomotion with ropes, tree trunks and/or branches, elevated feeding trays, and group housing (Novak and Suomi 1988; Woolverton et al. 1989; Boere 2001).

Moreover, enclosure design is not only linked to psychological well being but also to health. Considering that howler monkeys are tropical primates, housing has to take into account ambient temperature (optimal room temperature should be between 20 and 26 ° C), or an additional heat source should be provided. Another relevant, yet commonly overlooked, enclosure design is the position and location of feeding trays. Howler monkeys are arboreal primates adapted to feed and move on trees, and for this reason it is highly likely that they lack natural immunity to many terrestrial pathogens. Placing feeding trays on elevated platforms can aid in preventing further stress and disease. Enclosures for captive howlers should be designed to meet the needs of arboreal primates. Most zoos that hold howler monkeys include perches, nests, hammocks, and natural foraging vegetation within their facilities. Howler monkeys should be able to move in an elevated, three-dimensional environment (Hosey et al. 2009) (Fig. 12.4). In captivity, there is a tendency towards inactivity and a lack of use of the prehensile tail. Promoting natural feeding behaviors through enrichment activities, by varying the presentation of the diet encourages activity and use of the tail. Finally, enclosures should be designed with external and indoor sections and a heat source when low temperatures are expected to occur.

Aberrant behaviors are sometimes observed, like in *Alouatta clamitans* as described by Dada (2009). Among the most common pathologic behaviors are circle locomotion, head and body swinging, back hitting with tail, tongue flicking to observers, self-mutilation, flexing and stretching limbs, sexually directed behaviors, and aberrant eating. In this study, singled housed animals showed higher rates of stereotypic behaviors, among which locomotion in circles was observed in highest frequencies, especially before feeding hours, suggesting increased anxiety levels before feeding. Dividing the diet into a number of smaller portions and hiding them in different parts of the enclosure are good strategies to reduce levels of anxiety.

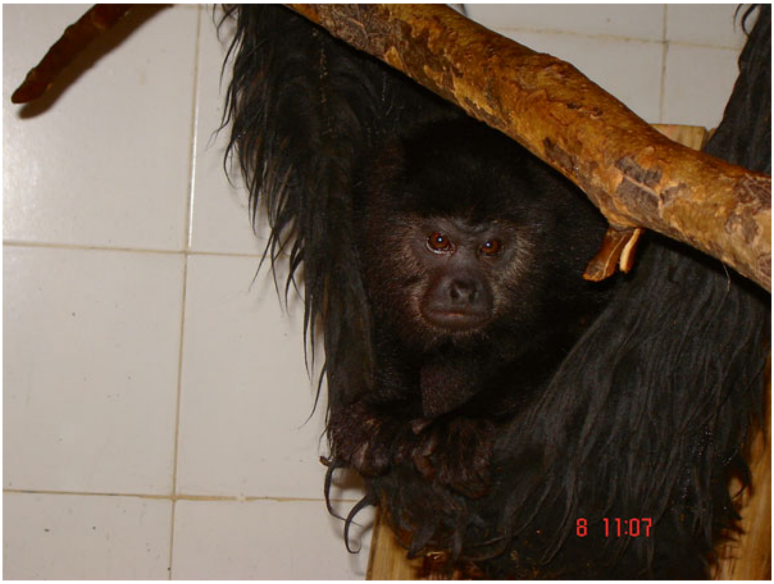

Fig. 12.4 Infant male *Alouatta pigra* resting on a hammock (photo by Rosalia Pastor-Nieto)

Social interactions with familiar conspecifics are essential for howler monkeys in captivity (Farmer et al. 2011). Other social events such as separation from the mother, a sibling or nursery peer, a cage partner, or a roommate are detrimental for howlers and may result in chronic stress and illness (pers obs). Another factor, possibly associated with captivity stress in some primate species is the visitor effect (Hosey et al. 2009), but its responses have not been yet evaluated in howler monkeys in captivity.

12.4.3 Injuries Associated with Improper Management

Conditions associated with overcrowding, lack of behavioral enrichment, and improper enclosure design may lead to otherwise avoidable animal injuries. In many cases, an increase in aggression is observed in overcrowded conditions, when a male sex-biased group is housed together, and when animals are maintained in improper facilities. The most common injuries include lacerations of ears, face, and fingers as a consequence of fighting. It is worthwhile mentioning that good knowledge of the behavioral characteristics of howler monkeys is essential to prevent injuries caused by fights, aggression, and infanticide (Crockett and Janson 2000). Captive howler managers should consider specific behavioral traits, such as signs of psychological well being. Factors such as group structure, hierarchy, and age are important factors to take into account to prevent aggressive behavior (Hosey et al. 2009).

12.5 Physical Examination and Restraint

General physical examination in howler monkeys includes dental examination, weighing, blood and stool samples, and rectal swabs for bacteriological cultures. It is also important to evaluate systolic arterial pressure and cardiac frequency, and to check for their coordination (Chagas et al. 2010). The pulse can be monitored at the lateral metatarsal area or at the femoral-inguinal region. The recorded clinical parameters are heart rate at 151–194 (bounce/min.), respiratory frequency of 19–25 breaths/min, systolic blood pressure at 154–163 mmHg, and rectal temperature ranging between 37.5 and 39 ° C. Oral and dental examinations are essential to discover oral lesions and dentition problems. The fur and skin of newly acquired howler monkeys should be checked for external parasites, miasis and bacterial infections, especially if suspected to be wild caught. Abdominal palpation is important for checking liver and kidney size, as well as the consistency of intestines and bladder palpation. Flexion and extension of the limbs to check for range of motion and articular flexibility can be crucial in cases of contracture and arthritis due to captive conditions. Venipuncture for blood samples is in the femoral vein, located in the femoral triangle. The use of a vacutainer is usually recommended to avoid excessive handling of primate blood. Reference hematological values for *Alouatta* are reported elsewhere (Canales et al. this volume).

To perform a thorough medical examination, improved immobilization techniques have made the restraint of monkeys much safer. Before manually restraining a howler monkey, there are several factors to consider, such as the animals' physical and health condition, temperament, duration of restraint, and the handler's experience (Ølberg 2007). Other important factors involved in successful animal handling are enclosure design and careful planning. It is very important that captive howler monkeys are housed under conditions that allow for safe handling without anesthesia. This may be accomplished by a combination of properly designed facilities and management practices allowing selective movement of animals (Bush 1996). The common capture and restraint techniques for howler monkeys are netting and holding the arms and neck while wearing leather gloves.

If chemical restraint is used, ketamine hydrochloride is generally a safe drug that has been widely used with excellent results (Ølberg 2007; Sainsbury et al. 1989). It can be used alone or in combination with other agents. Ketamine can be administrated within a wide range of doses, depending on the effect and duration desired. Ketamine is not recommended for painful or surgical procedures. Occasionally, hyperthermia might be observed in howler monkeys recovering from ketamine anesthesia. This condition is associated with increase of muscular activity, resistance to handling and abnormal respiratory function, which in turn promotes lactic acid accumulation. Therefore it is always important to monitor body temperature during anesthesia (Mosley and Gunkel 2007).

Other dissociative combinations such as tiletamine and zolazepam may be used for anesthesia induction and are highly recommended because of their short induction period and good muscle relaxation (Glander et al. 1991; Agoramoorthy and Rudran 1994; Karesh et al. 1998). Other induction and immobilization combinations used in primates are ketamine and midazolam, and ketamine and medetomidine (medetomidine reversed with atipamezole) (Vie et al. 1998; Ølberg 2007; Chagas et al. 2010). Inhalational general anesthetics such as isoflurane, halothane, or sevoflurane are ideal for long and painful procedures such as surgery.

12.6 Infectious Diseases

Captive howler monkeys are exposed to two main sources of disease: those that are naturally acquired while they are in the wild, and those that are related to captivity (Woodruffe 1999; Karesh et al. 2005). A broad summary of diseases acquired both in the wild and/or in captivity is provided in Table 12.2. Of particular concern are monkeys going through a captive rehabilitation process being potential carriers

Table 12.2 Reported infectious diseases of howler monkeys acquired in the wild and in captivity (viral, bacterial, and parasitic)

Disease	Etiological agent	References
Viral		
Dengue	Flavivirus	de Thoisy et al. (2000)
Yellow fever	Flavivirus	de Thoisy et al. (2000), De Rodaniche and Galindo (1957), Collias and Southwick (1952)
St. Louis Encephalitis	Flavivirus	de Thoisy et al. (2000), Holzmann et al. (2010)
Mayaro	Alphavirus	de Thoisy et al. (2000), Talarmin et al. (1998)
Papiloma	Papillomavirus	Sá et al. (2000)
Bacterial		
Ricketsiosis	*Haemobartonella*	de Thoisy et al. (2000)
Oportunistic/septicemia	*Chromobacterium violaceum*	Baldi et al. (2010)
Shigellosis	*Shigella flexeneri, S. sonnei*	Catao-Dias (2001)
Campylobacteriosis, Salmonellosis, Yersiniosis, Colibacilosis	*Campylobacter* sp.	de Souza Júnior et al. (2008)
	Salmonella sp., *Escherichia coli*	Banish et al. (1990), Juan-Sallés and Valls (1999), Joslin (2003), Oftedal (1991),
	Yersinia sp.	Kourany and Rossan (1971)
Mycosis	*Paracoccocidioides brasilensis*	Corte et al. (2007)
	Candida sp.	Gross et al. (2009)
Parasitic		
Protozoan parasites		
Babesiosis	*Babesia* sp.	de Thoisy et al. (2000)
Malaria	*Plasmodium* (*P. brasilianum, P. vivax, P. falciparum, malarie*)	Fandeur et al. (2000), de Thoisy et al. (2000), Duarte et al. (2006)

(continued)

Table 12.2 (continued)

Disease	Etiological agent	References
Chagas	*Trypanosoma*	de Thoisy et al. (2000)
Amibiasis	*Entamoeba* (*E. hystolytica, E. coli, E. polecki*)	de Thoisy et al. (2000), Stoner (1996), Stuart et al. (1990), Cristóbal-Azkarate et al. (2010), Stoner and González-Di Pierro (2006)
Toxoplasmosis	*Toxoplasma*	Bouer et al. (1999), Pena et al. (2011)
Enteromoniasis	*Enteromonas*	de Thoisy et al. (2000)
Tricomoniasis	*Trichomonas*	Carmona et al. (2005)
Parasitic enteritis	*Chilomastix*	Stoner (1996)
	Giardia	Stoner (1996)
	Isospora	Stoner (1996)
	Retortomonas	Stoner (1996)
	Balantidium	Stoner (1996)
	Giardia	Kowalewski et al. (2011)
	Criptosporidium	Kowalewski et al. (2011)
	Entamoeba coli	Eckert et al. (2006)
	Iodamoeba butschlii.	Eckert et al. (2006)
Pleuricellular parasites		
Gastrointestinal Nematodes	*Trypanoxyuris*	Pastor-Nieto (1991), Stoner (1996), Stuart et al. (1990), Cristóbal-Azkarate et al. (2010)
	Ascaris	Stoner (1996), Stuart et al. (1990), Cristóbal-Azkarate et al. (2010)
	Tricostrongylus	
	Ancylostoma	Stoner (1996)
	Parabronema	Pastor-Nieto (1991), Cristóbal-Azkarate et al. (2010)
	Enterobius	Stoner and González-Di Pierro (2006)
	Controrchis	Pastor-Nieto (1991), Stuart et al. (1990), Cristóbal-Azkarate et al. (2010), Kowalzik et al. (2010)
Cestodes	*Railletina*	Stoner (1996)
Filaria	*Dipetalonema*	de Thoisy et al. (2000), Notarnicola et al. (2007)

of diseases acquired in the wild. In the following sections, reported and potential diseases of howler monkeys are summarized. This information is very useful for captive managers in order to prevent disease transmission from newly acquired monkeys, especially in zoos and institutions located in endemic areas of disease to which howler monkeys are susceptible.

12.6.1 Viral Diseases

Recent studies have demonstrated that *Alouatta* are wild hosts/carriers of a variety of arboviruses. Howler monkeys appear to be particularly susceptible to yellow fever (YF) (Holzmann et al. 2010; Monath 1988; Galindo 1973), with extensive populations suspected to having been decimated in the 50s (Collias and Southwick 1952; Koontz et al. 1994; Pope 1966). Field research has shown that howler monkeys may be hosts to vector-borne infections, such as dengue, yellow fever, St. Louis encephalitis, and Mayaro fever (Talarmin et al. 1998; Fandeur et al. 2000; de Thoisy et al. 2000; Duarte et al. 2006). All of these diseases have been reported in wild specimens, and there are no reports for captive populations. Although it has been established that *Alouatta* is highly susceptible to arbovirus infections, such as yellow fever (de Rodaniche and Galindo 1957), this disease as a population regulating factor of howler monkeys is subject to controversy (Milton 1996). Recent field studies show a high seroprevalence of yellow fever titers in howler monkeys in South America, demonstrating that the virus is still circulating among wild primate hosts in endemic regions (de Thoisy et al. 2000; Holzmann et al. 2010). Recently, an outbreak of sylvatic yellow fever in Rio Grande do Sul, Brazil, caused the death of 2,013 howler monkeys (de Almeida et al. 2012). Yellow fever is a vector-borne disease, transmitted by various genera of mosquitoes. However, the main vectors, in Central and South America, are *Haemagogus* and *Sabethes*. Yellow fever is considered a re-emergent hemorrhagic fever. The lesions produced include icterus, renal and hepatic necrosis, and hepatic fatty change. The pathognomonic lesion is a peculiar hyaline change in necrotic hepatocytes or Councilman bodies (King 1976). It is important to consider that the re-emergence of yellow fever in wild howler monkeys is a stochastic epidemic that may pose a threat to their conservation.

Other serologic surveys have recently revealed that arboviral diseases such as dengue and St. Louis encephalitis are also present in wild individuals of *Alouatta* in South America (de Thoisy et al. 2000). The information generated by this recent research is most useful for captive howler monkey managers in endemic areas of these diseases of Central and South America, to prevent transmission and infections in zoos. Other viruses include one case of papillomavirus (confirmed by immunohistochemistry), which produced papular stomatitis (Sá et al. 2000), and seroprevalence of cytomegalovirus in free-ranging *Alouatta caraya* (Ferreyra et al. 2012).

12.6.2 Enterobacterial Diseases

Gastrointestinal bacterial infections are among the most common causes of death in confined *Alouatta*. However, most bacterial infections are difficult to assess mainly because they are caused by opportunistic normal flora, and are concomitant to captivity stress (King 1976). There are five enterobacteria of major concern in captive primates. These are *Shigella* (*S. flexeneri* and *S. sonnei*), *Salmonella* (*S. typhimurium*), *Campylobacter jejunii*, *Yersinia*, and *Escherichia coli.* All are causal agents of enteritis of varying degrees of severity, and all are considered zoonoses and anthropozoonoses. In all of them, transmission occurs by indirect routes, by contact with carriers and contaminated objects and foods (de Souza Júnior et al. 2008; Catao-Dias 2001). Clinical signs include blood and mucus in feces. Fecal cultures and antibiograms are essential for effective treatment, although a negative fecal culture may not exclude infection. Examination of Giemsa-stained smears for the presence of leucocytes, and general coprologic exams with Gram stained smears, have proven to be reliable methods to detect invasive bacterial or enteric infections (Benjamin 1988). During antibiotherapy, diarrhea, and probiotic ministration, the hydrogenotrophic microbiota is dramatically affected (Nakamura et al. 2011), and should consider this side-effect. These infections should be treated swiftly, as they can potentially derivate into septicemia (Zanotti-Cavazzoni and Goldfarb 2009). Bacteriological cultures and antibiograms are essential for adequate antibiotherapy to treat these infections.

Captive howler monkeys can be potentially infected with *Salmonella* and *Shigella* (de Souza Júnior et al. 2008), and there was one case report of a subcutaneous abscess associated with *Salmonella typhimurium* in *Alouatta* (Kourany and Rossan 1971). Reports also indicate that *Shigella* continues to be a significant and frequent cause of diarrhea (McClure 1980; Paul-Murphy and Wolff 1993; Banish et al. 1990). Interestingly, *Shigella* has been identified in normal and dysenteric stools of *Ateles* shortly after capture (García 1976). Monkeys infected with *Shigella* might remain as chronic asymptomatic carriers. It is also suspected that acute clinical disease may be precipitated in *Shigella* carriers by a variety of stressful situations. Gastroenteritis outbreaks in captive primates are commonly associated with substandard housing conditions and inadequate food management. Shigellosis has been characterized clinically and pathologically, and the main lesions observed include enteritis, gastritis, and colitis (Banish et al. 1990; Oftedal 1991; Juan-Sallés and Valls 1999; Duarte and Estrada 2003; Joslin 2003).

Salmonella is also known to produce subclinical to acute enteritis in New World primates (Brack 1987; Joslin 2003). *Salmonella* is a classical zoonosis, with food contamination being the main transmission route, and is commonly associated with enterocolitis under stressful situations (McClure 1980; Scott 1992; Ketz-Riley 2003).

Bacteriological diagnosis through routine techniques is very important to provide adequate treatment (Joslin 2003), although modern molecular techniques are currently used (Muldrew 2009).

12.6.2.1 Management of Diarrhea

Water is the single most important nutrient necessary for the proper functioning of cells. Electrolytes present in bodily water are essential for organic function, and vary in concentration depending on age and physiological state. Fluid therapy, in conjunction with antimicrobial agents, is imperative for the treatment of severe diarrhea in nonhuman primates. Infants and young howler monkeys are prone to developing dehydration and may become comatose within a few hours of the start of severe diarrhea, making fluid therapy critical. Lactated Ringers and 5 % dextrose solutions are isotonic and may be used for intravenous or subcutaneous fluid replacement. Accessible sites for venoclysis include the saphenous, antecubital, femoral, and jugular veins. Subcutaneous and intravenous rehydration is also possible. In severely dehydrated animals, a cut down procedure to access the femoral vein may be necessary. Standard fluid therapy in primates consists in administrating intravenous solutions at a rate of 100 mL/kg/24 h.

Oral or subcutaneous fluids are recommended in mild or moderate cases. After initial parenteral rehydration, oral electrolytes (oral electrolyte rehydration solution recommended by World Health Organization) should be provided for 2 or 3 days, followed by glucose containing preparations such as apple or grape juice. In very young animals the provision of a highly caloric diet is also important. Complete dietary preparations such as Ensure or PediaSure (Abbot Laboratories) or Complan (Complan Nutritional Products) are indicated when animals are undernourished or in critical health. Prevention incorporates hygienic measures in diet preparation.

12.6.3 Bacterial Diseases of the Respiratory Tract

Chronic and untreated respiratory diseases, in howler monkeys and other primates, may derivate as airsacculitis when mucus and inflammatory debris are accumulated in the guttural sac (Fig. 12.5). Cough, halitosis, and nasal discharge are the most frequently observed clinical signs of airsacculitis. Approaches to the management of airsacculitis include combinations of medical and surgical therapies (Jones 1997; Hill et al. 2001; Lowenstine 2003; Lawson et al. 2006). These therapies often require the drainage of exudate from the air sac, antibiotherapy, mucolytics, and nebulization (with mucolytics and antibiotics). It is important to perform bacterial cultures for proper diagnosis.

Respiratory diseases of bacterial origin are extremely common in newly acquired animals, especially when they are debilitated and/or parasitized. Most acute outbreaks of respiratory disease are multifactorial, produced by the combined action of two or more bacterial agents, and/or bacteria-virus associations (McClure 1980; Wallach and Boever 1983; Butler et al. 1996; Osborn and Lowenstine 1998; Petit and Gosi 2002; Joslin 2003). The most common agents of respiratory disease identified in New World monkeys are *Staphylococcus* (*S. aureus, S xylosus*)*, Streptococcus zooepidemicus, Klebsiella pneumoniae, Pasteurella haemolyitica, Haemophilus* sp.*, Pneumococus* sp.*, Proteus mirabilis,* and *Citrobacter freundii* (Osborn and Lowenstine 1998). However, most of these bacteria may also affect other organ systems, as well as generating systemic illness. For instance, *Staphylococcus* and *Streptococcus* infections tend to be localized in the upper respiratory tract, and are a major cause of pyogenic otitis, tonsillitis, and airsaculitis. Pneumonia produced by *Streptococcus* is characterized by the observation of polymorphs, fibrin-purulent exudates in alveoli, pleura, and pericardium (Catao-Dias 2001).

Fig. 12.5 Airsaculitis in a male howler monkey *Alouatta pigra*. Note the accumulation of purulent exudate in guttural sac (photo by Rosalia Pastor-Nieto)

Other lesions produced by *Streptococcus* are concomitant to septicemia and the most serious presentation involves suppurative meningitis and hydrocephalus (Scott 1992). *Staphylococcus* infections rarely turn systemic; however, when they do, they may cause acute myocarditis, characterized by multiple micro abscesses with hemorrhagic borders. Basic preventive measures include proper housing and management conditions. Preventive measures for respiratory disease include adequate nutrition, meeting caloric and protein, and vitamin requirements, and control of ambient temperature.

There is a recent report of a case of opportunistic bacterial infection by *Chromobacterium violaceum* in a wild howler monkey (*Alouatta palliata*) in Costa Rica (Baldi et al. 2010). Although *C. violaceum* has been characterized as a saprobe, it is also well known for its ability to act as an infectious agent in humans. The disease is systemic with the development of septicemia, skin ulcers, pulmonary and liver abscesses. Septic shock and multiple organ failure commonly result in the death of infected individuals.

There are no reports of tuberculosis in captive *Alouatta*. However, Scott (1992) describes a few cases of tuberculosis in captive *Ateles*. Tuberculosis screening is not recommended in captive howler monkeys unless a colony is suspected of having a possible outbreak or has been in contact with an infected person or animal. Apparently, the route of extension of the bacilli varies among primate species. It is suspected that the main spread route is the lymphatic system, and New World primates possess no thoracic duct. Therefore, the spread of infection and distribution of lesions are different between Catharrhines and Platyrrhines (Fiennes 1967).

Signs of tuberculosis include rough coat, weight loss, weakness, cough, enlarged lymph nodes and diarrhea, and animals may remain asymptomatic until late in the course of the disease. Because of the zoonotic risk of this disease, treatment is not recommended in primates and euthanasia of infected animals is considered.

12.6.4 Parasitic Diseases

A wide variety of parasitic infestations have been reported in Neotropical primates. Intensity of social interactions and high population density facilitates parasitic infections (Stoner and González-Di Pierro 2006). Therefore, overcrowding in captivity might be a predisposing factor associated with parasite infections. For captive howlers, provision on elevated feeding trays, perches, and locomotion in a three-dimensional environment may serve as essential preventative measures for parasitic infections, as, in the wild, they tend to move down the trees to defecate in specific sites, presumably as a parasite avoidance strategy (Gilbert 1997; Kowalewski and Zunino 2005).

12.6.4.1 Endoparasites

There are reports on amoebiasis and giardiasis in captive *Alouatta* indicating that *Alouatta* could be an asymptomatic carrier (Stoner and González-Di Pierro 2006; de Thoisy et al. 2000; King 1976). In many cases, the development of heavy parasitic loads is concomitant to captivity stress, chronic illnesses, undernutrition, and lack of hygiene. Signs of amoebiasis may range from mild or intermittent diarrhea, to acute dysentery with blood and mucus. *E. histolytica* cysts can be found in wet smears from colonic contents, but may also be identified in histologic examinations. Shedding is intermittent so repeated examinations are necessary. Fluid therapy is an essential part of treatment in acute cases (see Sect. 12.6.2.1). It is also important to treat both cyst and trophozoite presentations. Prevention incorporates hygienic measures in diet preparation to cut fecal-oral infection (Fig. 12.6).

Cases of intestinal *Tricomonas* infection have been reported in captive howler monkeys and other primate species (Brady et al. 1988; Brack et al. 1995; Carmona et al. 2005). In many cases, animals are asymptomatic. Enteritis caused by trichomonads is usually an opportunistic infection. The trichomonads inhabit the cecum, and have a tendency to penetrate the mucosal epithelial layer, causing desquamation of entire crypts.

Giardiasis is an enteric infection very commonly observed in captive primates with close contact to humans (Volotão et al. 2008; Kowalewski et al. 2011). Ingestion of contaminated food and/or water is the most common transmission route. *Giardia* thrives in the upper gastrointestinal tract (duodenum and jejunum), where it attaches to the intestinal mucosa. As a consequence, it damages microvilli, producing malabsorption of fats and carbohydrates. Clinical signs include diarrhea with

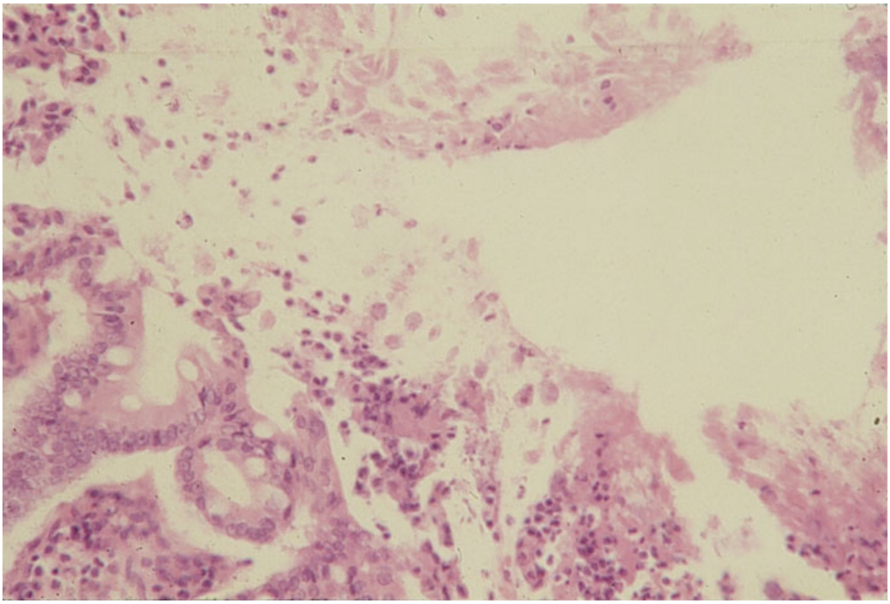

Fig. 12.6 Photomicrograph of a colon section of a howler monkey *Alouatta palliata,* with caliciform hyperplasia, inflammatory infiltration, and necrosis. Note some parasitic structures at lumen, which are compatible with *Entamoeba* (Hematoxylin-Eosin stain) (photo by Rosalia Pastor-Nieto)

mucus, cramps, gas, anorexia, vomiting, and fever. Cases of *Balantidium coli* have also been reported in captive *Alouatta* (Scott 1992). Monkeys infected with *Balantidium* may suffer from acute diarrhea or remain asymptomatic for years (King 1976; Catao-Dias 2001).

Other parasitic infections of medical importance are toxoplasmosis, malaria, and Chagas disease (Bouer et al. 1999; de Thoisy et al. 2000; Pena et al. 2011). In general, toxoplasmosis is acquired by primates in captivity mainly through contact with cat feces and uncooked red meats that are contaminated with oocysts and/or cysts. Signs of illness include decreased appetite, sluggishness, anorexia, and depression. Once animals are infected, the course of the disease tends to be acute and fatal, causing hepatomegaly, lung edema, liver multifocal necrosis, splenomegaly, and mesenteric fibrinohemorrhagic lymphadenitis (Scott 1992). Pulmonary disease ranging from congestion to pneumonia seems to be a consistent finding (Potkay 1992). Chagas disease is caused by *Trypanosoma* spp. It is a vector-borne parasitosis, in which triatomid bugs are the main vectors. The main lesions identified in trypanosomiasis are endocarditis and hyperplasia of reticulo-endothelial cells of liver and spleen. Trypanosomiasis is diagnosed in blood and/or organ smears or sections and through serological tests.

Malaria is a vector-borne re-emergent disease, transmitted by mosquitoes from the genus *Anopheles* (Deane 1976; Fandeur et al. 2000). Endemic areas in the

Americas are Panamá, Colombia, Venezuela, Peru, and Brazil. Howler monkeys infected with malaria may remain asymptomatic. Infected animals may suffer from anemia and a 72-h fever cycle (Quartan malaria). Special attention should be placed in preventing howler malaria cases in captivity in endemic regions, and vector control is the main recommended preventive measure.

In captivity, it is very common to observe positive coproparasitoscopic examinations on newly acquired howler monkeys, and treatment should always be aimed as a preventive measure. Reports on helminth parasites in *Alouatta* include *Trypanoxyuris minutus, Controrchis biliophilus, Parabronema bonnei, Mansonella* spp., and *Dipetalonema gracile* (Dunn 1968; Pastor-Nieto 1991; Castillejo-Allard 1993; Aceves Rivera 1995; Hermida-Lagunes et al. 1996; Bouer et al. 1999; de Thoisy et al. 2000; Bonilla-Boheno 2002; Abogado-Reyes 2005; Vitazkova and Wade 2006; Stoner and González-Di Pierro 2006; Trejo-Macías et al. 2007; Aguilar-Cucurachi et al. 2007; de Souza Júnior et al. 2008; Notarnicola et al. 2007; Valdespino et al. 2010; Cristóbal-Azkarate et al. 2010; Alvarado-Villalobos 2010; Pena et al. 2011).

Trypanoxyuris is located in the caecum, colon, and rectum of hosts, and, depending on the degree of infestation, may remain nonpathogenic. Typical manifestations of oxyuriasis are perianal pruritus, produced by female ovoposition in anal mucosa. Lacerations, and bacterial and mycotic infections around the anus, might be consequences of continuous scratching. However, in severe *Trypanoxyuris* infestations, colitis and/or hemorrhagic enteritis may occur (Fig. 12.7).

Fig. 12.7 Photomicrograph adult female nematode *Trypanoxyuris minutus* found in feces of a troop of wild howler monkeys at the Agaltepec Island, Catemaco, Veracruz, Mexico. Note the characteristic swollen cephalic vesicle of females (×10, photo by Rosalía Pastor-Nieto)

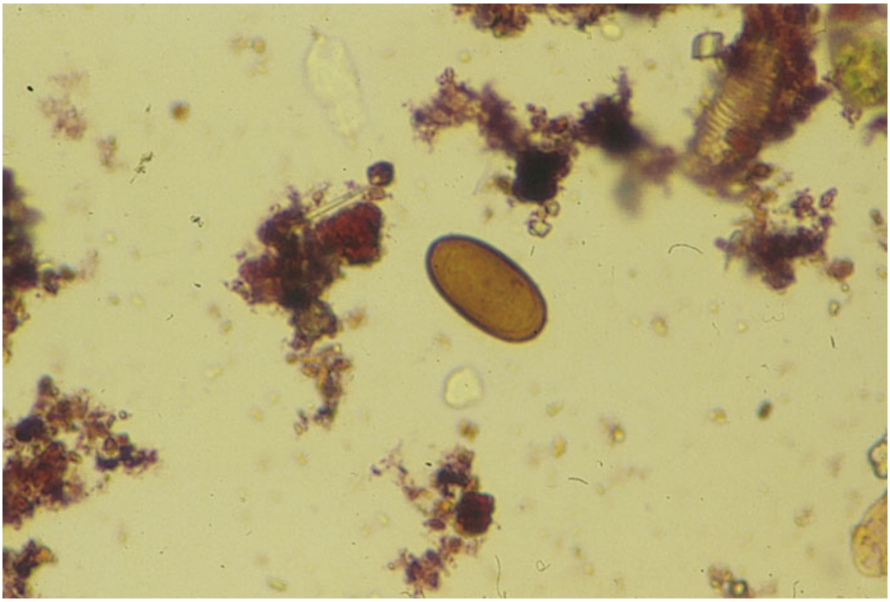

Fig. 12.8 Photomicrograph of the trematode egg of *Controrchis biliophilus*. This is an operculated egg found in a fecal sample of adult female howler monkeys at Chapultepec Zoo (×40, Photo by Rosalia Pastor-Nieto)

Although trematodiasis is only reported as incidental, it is worthwhile mentioning. *Controrchis biliophilus* inhabits the biliary passages of wild *Alouatta* and may remain for many years. The cycle of *Controrchis* requires two very different intermediate hosts: a snail and an ant (Kowalzik et al. 2010) (Fig. 12.8). Health implications are similar to other severe biliary trematodiasis: distension and irritation of biliary ducts, colecistitis, and cirrhosis in severe cases. *Parabronema bonnei* has been identified in howler monkeys (Pastor-Nieto 1991; Cristóbal-Azkarate et al. 2010). *Parabronema* is commonly located in the stomach. There are no reports on the health impact of this parasite in *Alouatta*; however it is possible that massive infestations might produce gastritis (Fig. 12.9).

12.6.4.2 Ectoparasites

Infestations with ectoparasites in howler monkeys are restricted to wild specimens and there are no reports in captivity. Myiasis or botfly infestations by *Alouattamya baeri* (King 1976: Milton 1996; de Thoisy et al. 2000; Pissinatti 2001) and *Cocliomya hominivorax* (cattle screwworm) have been reported in wild animals. Myiasis produces dermal cysts and secondary infections. Therapy consists of surgical extirpation of larvae.

Fig. 12.9 Adult male nematode *Parabronema bonnei* found in feces of a troop of wild howler monkeys at the Agaltepec Island, Catemaco, Veracruz, Mexico. Note the ventro-dorsal shields or plates (×40, photo by Rosalia Pastor-Nieto)

Pediculosis in Neotropical primates is commonly caused by lice of the order Anoplura. *Pediculus mjöbergi* is most commonly identified in wild *Alouatta* and *Ateles* (Pope 1966; King 1976; Karesh et al. 1998). Infestations by lice in captive howler monkeys have not yet been reported; however newly acquired animals need to be checked for parasite infection.

12.6.5 Mycotic Diseases

Mycotic diseases may develop in stressed and undernourished howlers. *Candida krusei* has been isolated from skin cultures of *Alouatta* (Gross et al. 2009). Mycotic cultures and identification of the agent are essential in order to provide proper antimycotic treatment. Other types of systemic mycosis are uncommon in captive howler monkeys. However, wild specimens are exposed to other infective fungi, such as *Paracoccidiodes* (Corte et al. 2007). In general, lesions induced by these agents are pyogranulomatous or granulomatous, and might be found in most internal organs such as lungs, brain, myocardium, mesenteric lymph nodes, liver, and spleen.

12.7 Noninfectious Diseases

Common nutritional and metabolic disorders in howler monkeys include metabolic bone disease, secondary hyperparathyroidism, howler monkey wasting disease, acute gastric dilatation, and arteriosclerosis.

12.7.1 Metabolic Bone Disease

Primates in captivity, including howler monkeys, are susceptible to and suffer from metabolic bone disease mainly deriving from secondary hyperparathyroidism. Metabolic bone disease should be considered as a consequence of husbandry mismanagement. Apparently, New World primates are more susceptible, due to a higher vitamin D requirement and/or a limited ability to use vitamin D_2, as there is evidence that vitamin D_2 is less active than vitamin D_3 in platyrrhines (Hunt et al. 1969). A possible explanation for this is the presence of a binding protein that acts as an interceptor when high levels of vitamin D are present in the blood (Meehan et al. 1996). Free-ranging howler monkeys possess higher circulating vitamin D metabolites compared to other captive New World monkeys (Crissey et al. 2003).

The main causes of metabolic bone disease are absolute calcium deficiency, calcium:phosphorus imbalance, vitamin D deficiency, and little or no exposure to UV light. In most cases, primates are provided with diets low in calcium or low in vitamin D_3, resulting in the excessive secretion of parathyroid hormone responsible of osteoclasia. A common manifestation is nutritional secondary hyperparathyroidism in howler and other New World monkeys and is characterized by chronic calcium reabsorption from bone, which may result in bowed and broken bones, lax appendicular joints, cupping of metaphyses, widening of epiphyseal plates, and thinning of the cortices, scoliosis, kyphosis, lordosis, and collapsed pelvis (Fowler 1978). Affected monkeys suffer from enlarged facial and mandibular bones (Ullrey et al. 1999). Most affected animals are unable to masticate solid foods or close their jaws. This enlargement of mandibular and maxillary bones is a compensating mechanism for osteoporosis, in which bone calcium is substituted by fibrous tissue. Dyspnea follows from occluded passageways and anorexia is common and associated with difficulties in mastication. Loss of *lamina dura dentes* causes loosening of the teeth (Swenson 1999; Paul-Murphy and Wolff 1993; Fowler 1978). Teeth may erupt in a haphazard fashion or fail to erupt. Elevated levels of serum alkaline phosphatase might also be observed due to osteoclasia (129 ± 28 UL as a range value in *Alouatta*, de Thoisy et al. 2000). Commercial diets vary widely in their vitamin D concentrations. Products balanced for New World primates provide higher levels than those designed for Old World species. However, it is necessary to verify vitamin D_3 concentrations in diets provided to captive *Alouatta*. In addition, exposure to sunlight and/or a UVB light source can be used as preventive measures. Depending on severity, oral or intramuscular cholecalciferol (D_3) together with a balanced calcium:phosphorus diet (1.5–2:1 respectively) should be provided for affected animals. A total amount of 250 UI/day of cholecalciferol (D_3) meet the daily requirements and UVB transparent skylights in enclosures should be installed, if animals have restricted access to sunlight (Carpenter 2005.

12.7.2 *Howler Monkey Wasting Disease*

A retrospective report on captive howler monkey mortality revealed that 40 % of the animals died from chronic renal failure associated with wasting disease (Fontenot et al. 2004). Clinical signs of howler monkeys suffering from wasting disease include unresponsive diarrhea, hyporexia, cachexia, and rough hair coat, very similar to the ones observed in callitrichid primates suffering from wasting disease. Howler monkeys presenting these clinical signs have a very high mortality rate. At necropsy, renal and intestinal lesions include lymphoplasmocytic infiltrate, interstitial fibrosis, and kidney glomerular sclerosis, suggesting an autoimmune response.

The study of wasting syndrome in callitrichids indicates a central role of inflammatory intestinal alterations during pathogenesis (Gore et al. 2001). A multifactorial etiology in the development of enteritis is assumed, whereas immunopathological processes seem to be of major importance. Inflammatory lesions in intestines, kidney, and liver, as lymphoplasmocytic infiltrates have been described in callitrichids suffering from wasting disease (Araújo de Moraes et al. 2007). There is evidence that the inclusion of soy products, cereals, and milk products, in primate diets may trigger an immune response, which has been confirmed in intestinal biopsies (Gore et al. 2001). Dietary protein and energy concentrations are very important in preventing protein/calory malnutrition, which might also be associated with wasting syndrome in callitrichids (Crissey et al. 2003).

Wasting disease may have an important impact in captive howler monkey mortality, although detailed studies lack a retrospective analysis of postmortem findings on eleven deaths of mantled and Guatemalan black howler monkeys recorded between 2007 and 2008 at Chapultepec and San Juan de Aragón Zoo in Mexico City, revealed that in six cases there were signs of enteritis, appetite loss, diarrhea, and emaciation. Postmortem microhistology revealed inflammatory infiltrate is present in several organs, mainly in the kidney and intestines (Figs. 12.10 and 12.11). The type of inflammatory infiltrate described in all cases was confirmed as lymphoplasmocytic and was detected in intestines and/or kidneys in 50 % of all cases evaluated. The lymphoplasmocytic infiltrate described was similar to the one reported by Fontenot et al. (2004). Taking into consideration that in Chapultepec and San Juan de Aragón Zoos, ingredients included in diets incorporated baby cereals, an allergic reaction to gluten and other cereals proteins had to be ruled out as a potential cause of enteric malabsorption. These diets were also poor in alternative protein sources (Table 12.3). Therefore, antibodies for celiac disease were evaluated from deceased specimens kept in a serum bank. Initial findings revealed the presence of anti-gliadine, anti-endomisial, and anti-transglutaminase

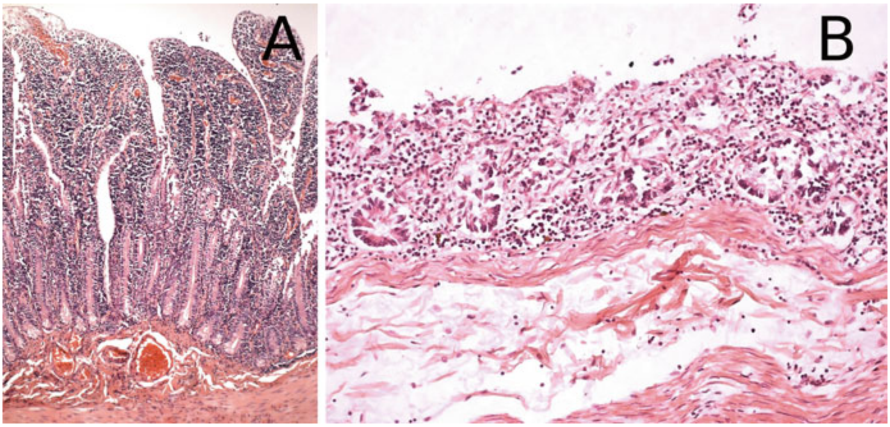

Fig. 12.10 Photomicrographs of atrophic intestinal mucosa with lymphoplasmocytic inflammatory infiltration in a howler monkey suffering from wasting disease: (**a**) widening of intestinal lamina propria caused by lymphoplasmocytic inflammatory infiltrate with moderate intestinal villi atrophy; (**b**) chronic lymphoplasmocytic enteritis with severe intestinal mucosa atrophy (photo by Rosaura Ruth Hernández Mote)

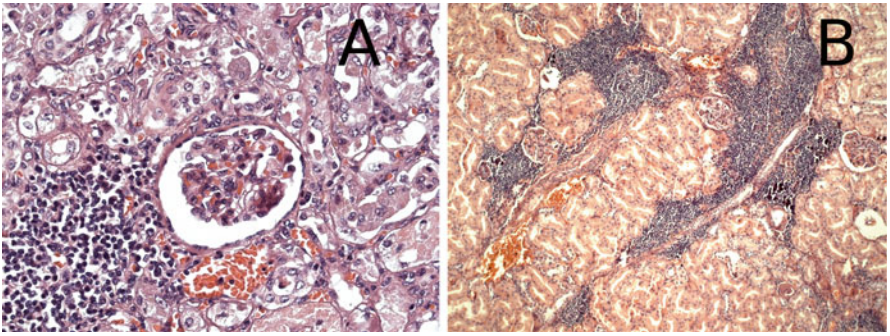

Fig. 12.11 Photomicrographs of different degrees of kidney inflammatory infiltration of lymphoplasmocytic cells in kidneys of howler monkey suffering from wasting disease: (**a**) lymphoplasmocytic nephritis with glomerular congestion; (**b**) severe lymphoplasmocytic infiltrate in kidney suggesting activation of the kidney as an immune compartment (photo by Rosaura Ruth Hernández Mote)

antibodies in 66.7 % of the cases (Table 12.4). More research on potential sensitivity to allergenic proteins and the activation of organs as immune compartments (Gluhovschi et al. 2010) is certainly warranted in *Alouatta*. Presumably, howler monkey wasting disease is a condition in which the lining of the small intestine is damaged by an allergic reaction to gluten and other allergenic proteins. By reducing ingestion of these allergenic proteins, a reduction in cases of howler monkey wasting disease is expected (Table 12.5). In similar cases, gluten-free diets in captive callithricids had positive effects by reducing cases of wasting disease in European zoos (Berndt et al. 2013).

Table 12.3 Howler monkey diet of Chapultepec Zoo rich in allergenic proteins

Ingredient (serves 1 monkey)	Description	Amount offered morning	Amount offered afternoon
Leaf eater primate biscuits[a]	Ground	150 g	150 g
Alfalfa	Fresh	1,000 g	
Romaine lettuce	Cut in 5 cm pieces	125 g	125 g
Ensure[b]	Fresh	100 g	50 g
Orange	Cut in 5 cm pieces	100 g	50 g
Papaya	Cut in 5 cm pieces	150 g	
Apple	Cut in 5 cm pieces	215 g	215 g
Banana	Cut in 5 cm pieces	100 g	100 g
Watermelon	Cut in 5 cm pieces	100 g	100 g
Sarabola[c]	Piece	100 g	100 g
Tecomaria and/or *Ficus* sp.	Freshly cut	Optional	

[a] Mazuri Primate Leaf Eater (PMI Nutrition International)
[b] Nutritional supplement (Abbot Laboratories)
[c] Baby cereals (wheat, oats, soy, barley) (Nestlé Company) mixed with sweetened yogurt, vitamins and probiotics

12.7.3 Acute Gastric Dilatation

Acute gastric dilatation occurs in many zoo primates, and howler monkeys are no exception. Gastric dilatation is caused by a variety of reasons such as chronic drug administration, food restriction, accidental overfeeding, and sugary diets. Monkeys may be found dead or may have clinical signs of colic, abdominal distention, and dyspnea. Death in untreated cases is due to impaired venous return and cardiopulmonary failure. Gastric distention with fermented gaseous ingesta and congestion of the abdominal viscera are the predominant lesions, and are related to intragastric fermentation associated with *Clostridium perfringens* and abnormal gastric function (Joslin 2003). Howler monkeys fed with excessive sugary diets, excessive amounts of fruit (such as mango), as well as prolonged antibiotherapy may cause gastric distention (Fig. 12.12a, b). For this reason, antibiotherapy should be administered with caution as it is one of the most common causes of gastric dilatation. Common antibiotics that cause this condition are penicillins (amoxicillin and ampicillin), lincosamides (lincomycin and clindamycin), aminoglycosides (gentamicin, amikacin), macrolides (erythromycin), and sometimes tetracyclines and cephalosporins (cephalexin) (Montali and Bush 1999).

Treatment consists of passing a stomach tube to relieve gastric gas and excess fluid buildup. Supportive therapy, including fluid therapy, antibiotics, analgesics, and corticosteroids for shock should also be initiated. The occurrence of bloat can be decreased by limiting food intake after fasting and anesthesia, changing diets gradually, feeding animals multiple times during the day, and the judicious use of broad-spectrum antibiotics that affect the gut flora (Montali and Bush 1999). It has been shown that antibiotic treatment can cause a pervasive disturbance in the microbial community composition, which requires more than 4 weeks to recover to the pretreatment state (Dethlefsen et al. 2008).

Table 12.4 Cases of howler monkey wasting disease evaluated at Chapultepec and San Juan de Aragón Zoos, Mexico City (2007–2008)

ID	Sex	Age at death (years)	Clinical signs before death	Microhistological lesions	Antibodies
Sacbé	Female	6	Appetite loss, diarrhea	Interstitial nephritis	Within range
			Emaciation	Glomerulonephritis	
			Blood and mucus in stools		
Sasil-Ha	Female	4	Appetite loss, diarrhea	Interstitial nephritis	Endomysial IgA 01:40
			Emaciation	Glomerulonephritis	Transglutaminase IgG 22
					Transglutaminase IgA15
Moncho	Male	12	Appetite loss, diarrhea	Tubular nephrosis	Within range
			Emaciation	Lymphocytic interstitial nephritis	
				Lymphoplasmocytic enteritis	
Je-Lipe	Male	4	Appetite loss, diarrhea	Tubular dilatation and atrophy	Gliadin IgG 25
			Emaciation	Lymphocytic interstitial nephritis	Gliadin IgA 23
				Lymphocytic enteritis	
Gelasio	Male	5	Appetite loss, diarrhea	Tubular nephrosis	Endomisial IgA 01:40
			Emaciation	Lymphocytic interstitial nephritis	Transglutaminase IgG 22
				Lymphoplasmocytic enteritis	Transglutaminase IgA 15
Willy	Male	7	Appetite loss, diarrhea	Membranous proliferative glomerulonephritis	Endomisial IgA 01:40
			Emaciation	Interstitial nephritis	Transglutaminasa IgG 22
				Lymphoplasmocytic enteritis	Transglutaminasa IgA15

Table 12.5 Modified howler monkey diets for adults and juveniles at Chapultepec Zoo Mexico, high in fiber and low in allergenic proteins

Adult diet				
Ingredient (serves 1 monkey)	Description	Amount offered morning	Amount offered midday	Amount offered afternoon
Leaf eater primate biscuits[a] + Ensure[b]	Mini biscuit soaked in nutritional supplement	200 g + 60 mL		
Vegetable mix (zucchini, green peas, green beans and carrots)	Cut in 5 cm pieces	400 g		
Mix of leafy greens (romaine lettuce, cabbage, celery, spinach)	Cut in 5 cm pieces	500 g		
Fruit (orange, apple, papaya, banana)	Cut in 5 cm pieces, only 1 fruit in rotation			150 g
Egg	Boiled, cut in halves	1 piece	Ad libitum	
Browse *Tecomaria, Ficus* sp.	Freshly cut			
Juvenile diet				
Leaf eater primate biscuits[a]	Mini biscuit	20 g	20 g	
Vegetable mix (zucchini, green peas Green beans and carrots)	Cut in 1 cm pieces	500 g	500 g	500 g
PediaSure[b]	Reconstituted	30 mL		30 mL
Chicken breast	Cut in 1 cm pieces	20 g		10 g
Browse *Tecomaria, Ficus* sp.	Freshly cut	Ad libitum		

[a] Mazuri Primate Leaf Eater (PMI Nutrition International)

[b] Nutritional supplements (Abbot Laboratories)

Fig. 12.12 Macroscopic lesions observed in a semi-captive specimen of howler monkey found dead at Parque Zoológico La Venta, Tabasco suffering from acute gastric dilatation: (**a**) gastric distention due to gas accumulation observed at necropsy; (**b**) distended intestines due to gas accumulation; serosal congestion and multifocal equimosis (photo courtesy of Parque Museo La Venta)

12.7.4 Arteriosclerosis

Arteriosclerosis is the accumulation of lipids in large and medium-sized arteries. Spontaneous arteriosclerosis has been reported in several New World species, including *Alouatta* (Manilow and Maruffo 1968). Differences between species include the location of coronary lesions, and may present congestive heart failure secondary to aortic valve lesions. In squirrel monkeys, whole egg supplementation has been associated with this condition (Paul-Murphy and Wolff 1993), but there are no relevant data for howlers.

12.8 Vaccination

Many species of primates are vaccinated for vaccine-preventable diseases of human childhood. The most common diseases vaccinated for are poliomyelitis, measles, mumps, rubella, tetanus, diphtheria, and pertussis. However, there are no reports of howler monkeys being infected by these diseases. However, several considerations should be taken into account before developing vaccination programs for captive howler monkeys, such as risk of developing the disease, efficacy of vaccine, and adverse reactions to the vaccination. Various studies have revealed a general low susceptibility of nonhuman primates to diphtheria, pertussis, mumps, and rubella (Loomis 1990). However, as mentioned before, vaccination should be considered depending on the prevalence of disease in human populations that are in contact with monkeys. In general terms, vaccination recommendations for Neotropical primates include vaccination against tetanus and measles. Vaccine trials on a variety of nonhuman primates have shown measles vaccine to be effective in producing titers with very few vaccine reactions. Nonhuman primates are susceptible to tetanus. Due to the ubiquitous nature of *Clostridium tetanae*, risk of exposure to spores should always be considered high, especially in captivity. *Clostridium tetanae* require penetrating wounds to produce disease, and these wounds are commonly a result of fighting. Tetanus vaccine has been proven to be safe and effective in most primate species including howlers. Additionally, vaccine schedules should be adapted from human schedules (i.e., tetanus at 2, 4, and 6 months of age; measles at 15 months and revaccination at 10–12 years of age).

12.9 General Conclusions for Howler Monkey Welfare in Captivity

Howler monkey care and husbandry in captivity have to take into consideration the ecological and behavioral adaptations of the genus. To be able to provide proper management, there are basic aspects to be considered such as digestive physiology and foraging and behavioral ecology. Orphaned infants requiring hand rearing should be provided with a surrogate mother and proper milk formulas before ablactation. Infants and juveniles should be socially integrated with other conspecifics, whenever possible. Infanticide risk should be taken into consideration in captive groups. Adequate diet is one of the key factors associated with husbandry success. Zoos should offer a wide variety of fiber sources, such as leafy greens and natural browse, to promote healthy natural gut microbiota and digestion, and to prevent nutritional and metabolic disorders. Diets should be attractive, varied, and carefully balanced in fiber, protein, and low in starch, sugars, and allergenic proteins.

Adequate captive conditions need to be provided to allow three-dimensional movement, a proper space, indoor enclosures, controlled temperature, and hiding places. Enclosure design should consider the arboreal habits and use of the prehensile tail. The provision of foraging species within the enclosure is ideal to stimulate natural feeding behavior. Food should never be provided at floor level, and this is to prevent the contamination with terrestrial pathogens to which *Alouatta* lacks natural immunity. Behavioral and environmental enrichment measures need to be devised to prevent behavioral disorders. Psychological well-being of captive howlers is of paramount importance and social deprivation should be avoided. Monkeys should be provided with the opportunity to develop natural behaviors, such as socializing with conspecifics, seeking and selecting food items, and living within a dynamic and enriched environment.

Complete physical examination is achieved by chemical immobilization. Routine medical examination includes morphometry and physical and dental examination, blood sampling and weighing. Biological sampling using fecal and rectal swabs should also be included in the medical examination. Newly acquired howler monkeys should be checked for external parasites, miasis, bacterial and viral infections. Venipuncture for blood samples can be done in the femoral vein, located in the femoral triangle.

Most infectious diseases (bacterial and parasitic) are concomitant to stress, improper management, and inadequate captive conditions. Viral diseases of howler monkeys are of serious concern as most of them are zoonotic and transmitted by vectors. Among reported viral infections of howler monkeys are dengue, yellow fever, St. Louis encephalitis, and Mayaro fever. It is very important that zoos located in endemic areas of these diseases within Central and South America take the adequate preventive measures to protect howler monkeys and personnel. Enterobacterial diseases such as salmonellosis and shigellosis are a significant health risk for captive howler monkeys. Most enteric diseases are the main cause of dehydration, and as a result, antibiotics in combination with fluid therapy are necessary. However, using antibiotics can be detrimental, because it can eliminate the normal intestinal flora and allow pathogenic bacteria to flourish in its place, resulting in gastric dilatation. During antibiotic treatment, fecal transfaunation may be advisable obtaining healthy gastrointestinal microbiota from one healthy captive howler monkey.

Good husbandry practices incorporate hygienic measures in diet preparation, hygiene and disinfection of enclosures, and rodent control. Various bacterial agents are associated to respiratory disease in New World primates. Many of these agents are cause of airsacculitis, septicemia, and meningitis. To prevent respiratory disease it is important to provide adequate nutrition, meeting caloric and protein, and vitamin requirements, and control of ambient temperature. Amoebiasis, giardiasis, and balantidiasis are common parasitic diseases of captive colonies of primates, and *Alouatta* is highly susceptible to these diseases. Prevention of gastrointestinal parasitism includes disinfection of fruits and vegetables and controlling water quality in zoos. Other parasites of medical relevance isolated from *Alouatta* are *Trichomonas, Toxoplasma, Plasmodium*, and *Trypanosoma.* To prevent these diseases, vector control and food hygiene within zoos are essential. A wide variety of helminth parasites have been identified in *Alouatta*, many of which are acquired in the wild. Ectoparasites such as botflies and lice have also been identified and should be checked in newly arrived specimens.

Other health concerns of captive *Alouatta* are preventable nutritional and metabolic diseases, such as metabolic bone disease, howler monkey wasting disease, acute gastric dilatation, and arteriosclerosis. These pathologies are commonly associated with poor nutrition and inadequate management, and are easy to prevent. Metabolic bone disease may be easily prevented with adequate intake of calcium:phosphorus ratio and vitamin D_3, as well as regular exposure to direct sunlight. Recent data indicate that wasting disease in howlers is associated with diets containing allergenic proteins. More research on potential sensitivity to allergenic proteins and the development of howler monkey wasting disease is certainly required. Meanwhile, special attention should be placed on avoiding food sources rich in gluten and allergenic proteins. Acute gastric dilatation in howler monkeys is related to sudden changes in gut microbiota. Diets rich in simple carbohydrates and prolonged antibiotherapy are predisposing factors. It has been shown that antibiotic treatment can cause a pervasive disturbance in the microbial community composition. Therefore, whenever antibiotherapy is necessary, careful selection of antibiotics and probiotic supplementation and/or fecal transfaunation are essential to recovery healthy gut microflora after treatment.

Vaccination recommendations are based upon whether captive colonies are located in endemic areas of specific diseases. Other factors to be evaluated are severity and risk of developing the disease, efficacy of vaccines, and adverse reactions. A basic vaccination scheme for New World primates and howler monkeys should also include immunoprophylaxis against tetanus.

All these issues provide the necessary background for establishing a rich and healthy environment for captive howler monkeys and create stable populations in captivity. Although howlers are very adaptive in nature, and even though it is a genus widely distributed throughout Central and South America, they are susceptible to many diseases that can easily deteriorate their health and threaten their wild populations. Given the alarming rate of destruction and fragmentation of howler habitats, wild populations are being seriously affected. If we ever need to recuperate wild populations we need to breed and correctly manage captive populations and meta-populations of these monkeys. For this, it is necessary to maintain healthy and robust captive populations. Joint efforts and collaboration between zoological institutions are also necessary. Moreover, research performed in captivity under controlled conditions will provide relevant information for any action plans designed to protect and conserve howler monkeys in the wild.

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Chapter 13
Fruit as a Key Factor in Howler Monkey Population Density: Conservation Implications

Alison M. Behie and Mary S.M. Pavelka

Abstract Howler monkeys (*Alouatta*) are widely regarded as the most folivorous of the neotropical monkeys and the ability of howlers to live in a wide range of environments including highly disturbed forests has been linked to this ability. Generally categorized as energy minimizing folivores leaves comprise at least half and as much as 90 % of annual feeding time. All howler species also consume fruit; however, this amount is quite variable both within and between species, and across different months of the year. Seasonality in fruit consumption in *Alouatta* appears to be directly tied to its availability, suggesting that for all species fruit is a preferred food item. A study of population density and diet in *A. pigra* following a severe hurricane suggests that frugivory may be more crucial to population stability and growth than previously thought. This chapter considers the effects of this hurricane on *A. pigra* in relation to what is known about frugivory in the Mesoamerican clade of *Alouatta* (*A. palliata* and *A. pigra*), focusing on relationships between diet, population density, group size, behavior, ranging, and reproduction. These data suggest that frugivory is an important part of the feeding ecology of these species and that periods of prolonged fruit shortage may have significant impacts on their population dynamics and survival. Given that both natural and anthropogenic habitat disturbance generally have a negative effect on fruit production, this could have important conservation implications for this primate genus.

Resumen Los monos aulladores (*Alouatta*) son generalmente considerados como los más folívoros de los monos neotropicales y su habilidad para vivir en una amplia variedad de ambientes, incluyendo bosques altamente perturbados, ha sido relacionada con esta característica. Generalmente clasificados como folívoros minimizadores de energía, las hojas comprenden desdeel 50 % hasta un máximo del 90 %

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de su tiempo de alimentación anual. Todas las especies de aulladores consumen también fruta, pero la cantidad de ésta es variable tanto dentro de cada especie como entre diferentes especies, y a lo largo de los diferentes meses del año. La estacionalidad en el consumo de fruta en *Alouatta* parece estar directamente relacionada con su disponibilidad, sugiriendo que la fruta es un elemento preferido en la dieta de todas las especies. Un estudio sobre la densidad poblacional y la dieta de *A. pigra* tras el impacto de un fuerte huracán sugiere que la frugivoría podría ser más crucial para la estabilidad y crecimientode la población de lo que se pensaba. Este artículo considera los efectos de este huracán en*A. pigra* en relación a lo que se conoce sobre la frugivoría en el clado Mesoamericano de *Alouatta* (*A. palliata* y *A. pigra*), centrándose en las relaciones entre dieta, densidad de población, tamaño del grupo, comportamiento, campeo y reproducción. Los datos sugieren que la frugivoría es una parte importante de la ecología alimentaria de estas especies y que periodos de prolongada escasez de fruta pueden tener un impacto significativo sobre la supervivencia y las dinámicas de la población. Dado que las perturbaciones del hábitat, tanto naturales como antropogénicas, tienen un efecto negativo en la producción de fruta, esto puede tener importantes implicaciones para la conservación de este género de primates.

Keywords Fruit consumption • Population density • Reproduction

13.1 Introduction

Howler monkeys (genus: *Alouatta*) have the largest distribution of any New World monkey, ranging from Southern Mexico, through Central and South America to Argentina. Characterized as the most folivorous neotropical primate, howler monkeys ingest a diet similar to that of Old World colobines relying heavily on leafy matter. Also similar to colobines, howlers are energy minimizers, generally employing behavioral strategies that are designed to conserve energy in order to cope with this highly folivorous diet (Milton 1980; Stanford 1991; DaSilva 1992; Milton 1998; Fashing et al. 2007; Bicca-Marques 2003; Pavelka and Knopff 2004). Such behaviors include direct and efficient foraging (Milton 1980; 1981), highly selective feeding (Milton 1981; 1979; Glander 1982; Crockett 1987; Lopez et al. 2005; Behie and Pavelka 2012), and spending between 60 and 80 % of their day inactive (DaSilva 1992; Silver et al. 1998; Pavelka and Knopff 2004; Prates and Bicca-Marques 2008; Dias et al. 2011). Despite these dietary and behavioral similarities with Old World colobines, howler monkeys lack the specialized stomach and foregut fermentation of colobines, instead relying on hindgut fermentation that takes place in the cecum and proximal colon (Milton and McBee 1983). However, as these organs are located past the small intestine, where mammals most efficiently absorb nutrients (Stevens 1988) the amount of energy and protein extracted from leafy foods during hindgut fermentation is potentially quite low. As a result, howlers may need to be selective about food choice, select foods that offer higher nutritional rewards per gram consumed, and to increase the use of energy minimizing strategies during lean times of the year (Milton 1998).

The key determinant of leaf selection for folivorous primates is argued to be the protein-to-fiber ratio (P:F) of leaves (Milton 1980; Silver et al. 1998; Chapman et al. 2002; Fashing et al. 2007; Ganas et al. 2009). The P:F of a leaf is a good general indicator of its quality because leaves that are higher in protein and lower in indigestible fiber are better sources of both protein and energy compared to those with a lower P:F. In the diets of primarily folivorous primates (based on greater than 50 % of time spent consuming leaves), protein (found in relatively high quantities in leaves) should be an abundant nutrient while sugar (found in relatively low quantities in leaves) should be a rare and potentially limiting resource (Felton et al. 2009). Therefore, howlers may be expected to adopt a food selection strategy designed to maintain a constant intake of protein, while attempting to boost their intake of sugar (Felton et al. 2009). This has been reported in wild spider monkeys (*Ateles chamek*) in Bolivia (Felton et al. 2009, and see Garber et al. 2014). This makes the ingestion of non-leafy food matter of particular importance for meeting howler physiological demands and may explain the fact that the diet of all howlers generally contains flowers, seeds, bark, and fruits. Of these items, easily digested sugar from ripe fruit is a particularly important resource and the amount of fruit ingested (based on feeding time) varies among howler species with average fruit consumption ranging from 2 % annual fruit consumption in *A. macconnelli* (Lopez et al. 2005), 7.5 % in *A. guariba* (Chiarello 1994; Galetti et al. 1994), 42 % in *A. seniculus* (Gaulin and Gaulin 1982) to 52.3 % in *A. belzebul* (de Souza et al. 2002; Pinto et al. 2003; Pinto and Setz 2004).

This variation also occurs in the minimum and maximum monthly fruit intake with some populations ingesting no fruit during certain months of the year (Estrada 1984; Chapman 1987; Julliot and Sabatier 1993; Chiarello 1994; Julliot 1996; Martins 2009; Agostini et al. 2010; see Garber et al. 2014) and others devoting at least 20 % of monthly feeding time to fruit consumption throughout the year (Pinto and Setz 2004). Despite these differences in the absolute percentages of time devoted to fruit ingestion, many howler groups show a preference for fruit, selecting it over other food items when available (*A. caraya*: Bravo and Sallenave 2003; *A. guariba*: Galetti et al. 1994; *A. palliata*: Glander 1981; Estrada 1984; Stoner 1996; Estrada et al. 1999; Asensio et al. 2007; Dunn et al. 2009; *A. pigra*: Silver et al. 1998; Pavelka and Knopff 2004). This suggests that much of the existing interspecies and intraspecies variation in fruit consumption may be due to the differing ecological conditions at each study site that results in variation in fruit availability.

Despite what appears to be evidence of the importance of fruit in the howler diet, the impact of fruit on howler population dynamics and behavior is not well understood. For example, mantled howler (*A. palliata*) population density is reported to be positively associated with forest age and the number of large trees in a forest patch (Degama-Blanchet and Fedigan 2006) while the density of black and gold howlers (*A. caraya*) is positively correlated with the density of fruit trees rather than large trees (Zunino et al. 2001). Further, while it is expected that howlers engage in energy minimizing behaviors, a review of the literature found that variation in fruit ingestion did not result in any consistent or predictable changes in activity pattern. For example, during periods of fruit scarcity a population of *A. pigra* in southern Belize decreased travel time from 9.52 to 5.45 % (Pavelka and Knopff 2004) whereas a population in northern Belize did not significantly change the proportion of time spent resting, traveling, or feeding (Silver et al. 1998). Finally, it has been suggested that populations of howlers that show seasonal birth peaks may time these peaks such that weaning occurs during months of peak fruit production, allowing for infants to maximize nutritional intake from a high energy resource (Crockett and Rudran 1987; DiBitetti and Janson 2000). Birth seasonality, however, has only been reported in approximately half of the studies that document birth patterns in the genus (Glander 1980; Milton 1982; Fedigan and Rose 1995; Brockett et al. 2000; Kowalewski and Zunino 2004).

One of the best ways to understand factors that influence population density and adaptive behavior is to study a population before and after a catastrophic event (Davies 1994). On October 2001, a category four hurricane (Iris) made landfall in Belize carrying sustained winds of 233 km/h and gusts of up to 282 km/h. Hurricane Iris resulted in substantial damage to a 96 km^2 riverine forest which was previously known for its high density of black howler monkeys. Thirty five percent of howler food trees died in the storm, as did 52 % of trees more specifically relied on for fruits (Behie and Pavelka 2005). Surviving trees did not produce any fruit for a full 18 months as trees predictably invested energy in leaf regrowth rather than reproduction (Boose et al. 1994; Grant et al. 1997; Behie and Pavelka 2012). A small number of individual trees flowered in the 6 months after the hurricane, all of which subsequently died (Pavelka, unpubl. data). After this 18-month period, fruit production and consumption resumed, although it did not reach pre-hurricane levels for just over 3 years. The dramatic changes in the food supply and population density after Hurricane Iris presented us with a natural experiment in which we could investigate how drastic and prolonged shortages in fruit production affected the demography of this population.

In this chapter we examine the effect of the prolonged fruit shortage caused by Hurricane Iris on this population of black howlers in Belize by investigating post-hurricane population density, activity budget, and reproduction in relation to changes in fruit availability and consumption. We then put this case study in the context of what is known about frugivory in other populations of *Alouatta pigra* as well as *A. palliata*. We compare habitat variables (seasonality, forest size), frugivory, population density and group size between the two species, and the effect that seasonal changes in frugivory have on their demography, activity budget, and reproduction (Table 13.1).

Table 13.1 Comparison on mean values for *Alouatta pigra* and *Alouatta palliata* demographic, habitat, and seasonal variables obtained from published studies

	Alouatta pigra	*Alouatta palliata*
Minimum monthly frugivory	1.65–10.5 (=6.35; CV=68.71)	0–17.5 (=5.7; CV=105.06)
Maximum monthly frugivory	23.0–84.6 (=57.3; CV=54.75)	38.0–90.58 (=68.4; CV=40.41)
Mean frugivory	16.41–41.38 (=30.3 CV=33.55)	1.9–71.8 (=36.6; CV=33.98)
Group size[a]	5.9–9 (=6.83; CV=19.55)	4–59 (=15.37; CV=79.78)
Forest size	32–40,000 (=11,196; CV=172.63)	1.3–10,800 (=645; CV=282.51)
Home range	0.16–18.7 (=6.67; CV=104)	3.6–108 (=28.48; CV=113.13)
AF:AM ratio	0.67–1.5 (=1.28; CV=24.39)	0.67–8 (=2.52; CV=91.59)
AF:Immature ratio	0.88–1.11 (=1.00; CV=8.83)	0.67–8 (=1.47; CV=112.65)
Minimum monthly rainfall	20.72–59 (=69.80; CV=67.91)	0–60.97 (=43.93; CV=84.89)
Maximum monthly rainfall	360–485 (=422.5; CV=20.92)	400–700 (=520; CV=34.71)
Total annual rainfall	1,906–4,570 (=2,430.2; CV=46.43)	1,490–4,900 (=3,260.81; CV=199.49)
Minimum monthly temperature	17.4–25 (=20.75; CV=22.83)	11–22 (=17.94; CV=24.39)
Maximum monthly temperature	22.4–39 (=27.2; CV=15.18)	28.5–38 (=32.05; CV=34.26)
Mean monthly temperature	26.6–28 (=35.07; CV=2.62)	24–27 (=25.51; CV=64.02)

[a] Significant difference found using a Mann–Whitney U test

13.2 Methods

13.2.1 Hurricane Study at Monkey River

Behavioral and demographic data on the effect of Hurricane Iris on a population of *A. pigra* in Belize were collected from four study groups living in an 86 ha study area that is part of the 9,600 ha Monkey River watershed forest fragment [16°21′N, 88°29′W] (see Pavelka et al. 2007; 2003 for full description and map). Population characteristics within the study area have been shown to be representative of the larger Monkey River forest (Pavelka et al. 2007).

Both pre- and post-hurricane population density were measured by way of true counts of all monkey groups within the study area. In May of 2001 we spent 3 weeks with 20 people in the 52 ha area intensively monitoring the monkeys and establishing group size and composition of the 8 social groups with a very high level of certainty. In October, just days before the storm, two researchers returned to the site and were able to locate and confirm no changes to the May group compositions. After the hurricane, and once trails were reopened, we spent a minimum of 3 days per week, from 2001 to 2008, locating each known group and monitoring changes to group size and composition. Births and disappearances were thus closely monitored.

Behavioral data were collected from four groups of monkeys from 2002 to 2006. Each monkey group was observed for 3 days per month and data were collected following a systematic rotation among all group members using 10-min focal animal samples (Altmann 1974). When feeding, the plant part and species ingested were recorded. This information was then used to calculate diet budgets by plant part and plant species.

To determine monthly fruit availability, we calculated the relative density (number of stems/trunks of species A divided by the total number of stems of all species) of each fruit tree from vegetation plots for that year and multiplied it by the fruit coverage on that species each month (adapted from Silver et al. 1998). Phenology surveys were completed twice per month on a sample of 212 feeding trees wherein the percent coverage of fruit on each tree was scored as either having 0, 25, 50, 75, or 100 % coverage (Snaith and Chapman 2008). For example, if there were 10 *Spondias mombin* trees out of a total of 100 trees, *Spondias mombin* would receive a relative density score of 0.1. This would then be multiplied by 0, 25, 50, 75, or 100 based on the average fruit coverage on *Spondias mombin* that month. Thus we obtained a reliable index of relative change in fruit available in the study area from month to month. Spearman rank correlations were used to investigate the relationship between fruit availability and both population density and infant survival.

To investigate the relationship between fruit scarcity and activity budget, we grouped together the months in the study before fruit returned to pre-hurricane levels (January 2002–April 2004; $N = 26$) and the months after fruit returned to pre-hurricane levels (April 2004–June 2007; $N = 32$) and used independent sample t-tests to test for significant differences between these two dietary periods and the time spent in each activity budget category (feed, inactive, locomote, and social).

Using spearman rank correlations, we also compared fruit consumption with the month of birth, the month of conception (calculated from subtracting 6 months from the month of birth), and the month of weaning (calculated as 8 months following the month of birth). This allowed us to investigate the relationship between the timing of birth, conception, and weaning with fruit consumption in the post-hurricane environment. All statistics were done in SPPS 20 and significance was set at $p < 0.05$.

13.2.2 Comparison of **A. pigra** *and* **A. palliata**

While past reviews have included studies of a minimum duration of 9 months (Bicca-Marques 2003; Cristobal-Azkarate and Arroyo-Rodriguez 2007), we found that following this standard would have eliminated almost all studies of *A. pigra*. Thus, for inclusion here studies had to be at least 6 months in duration and include information from both the wet and dry seasons. Additionally, studies were required to have calculated percent frugivory either on a month-to-month or an overall annual basis. When other variables such as population density or group size were not included in the chapter, an attempt was made to obtain these data from other published accounts from the same research site (see Appendix I for all included studies). Where frugivory data were only provided in graph format, Get Data Graph Digitizer was used to determine minimum and maximum monthly values. This resulted in the inclusion of 23 groups from 22 studies of *A. palliata* and four groups from four studies of *A. pigra*. To compare *A. palliata* to *A. pigra*, species-specific differences in fragment size, group size, population density, minimum monthly frugivory, maximum monthly frugivory, mean frugivory, and adult female to immature ratio were compared using Mann–Whitney U tests. When no differences were found between species, data were pooled to investigate the effect that frugivory (minimum, maximum, and mean) had on population density, group size, and adult female to immature ratio using a regression analysis. To remove the effect of fragment size or seasonality, we first performed a regression analysis to determine the relationship between forest size, rainfall, and frugivory variables. Due to limited sample size, no statistical analyses could be performed on birth seasonality or behavioral changes associated with seasonal fruit scarcity; however, these data were compared qualitatively. All statistics were done in SPSS 20 and significance was set at $p < 0.05$.

13.3 Results

13.3.1 Effect of Fruit Scarcity after Hurricane Iris on Population Density and Infant Survival in **A. pigra**

Figure 13.1 shows the change in population density and group size in the *A. pigra* population at Monkey River in relation to fruit consumption following Hurricane Iris (2001–2008). The sudden drop from 2001 to 2002 represents the losses measured in the first 6 months after the storm (see Pavelka et al. 2003). The population in the study area continued to fall to 25 individuals/km^2 in 2004, where it stabilized before starting a slow recovery in 2006. In terms of actual numbers of animals in the original 52 ha study area, the population fell from 53 individuals in 2001 to 31 individuals in 2002 to a low of 11 individuals in 2004. Based on these data, we predicted a local extinction (Pavelka et al. 2007). Changes in average group size shadowed changes in population density, falling to a low of 3.77 in 2004. Since that time, there

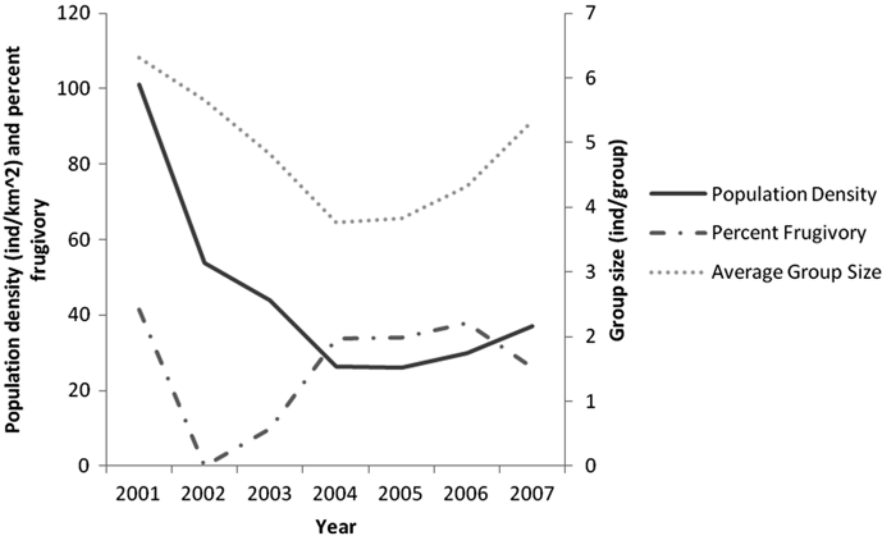

Fig. 13.1 Monkey River black howler monkey population density, group size, and fruit consumption before (2001) and following Hurricane Iris (2002–2007). Population density and group size scores were obtained from true counts of the Monkey River study site every year in May and frugivory is based on data collected year round from four study groups. The reduction in the 2007 frugivory value is due to the fact that behavioral data was only collected in the dry season that year when fruit production is lower than the rainy season. Significant positive correlations were found between fruit consumption and both population density ($r_{sp}=0.635$; $p=0.002$) and group size ($r_{sp}=0.572$; $p=0.004$)

has been a steady increase with an average group size of 5.73 in 2008, approaching the 6.32 ind/group before the hurricane.

Yearly fruit consumption in our *A. pigra* population ranged from 0 % in 2002 to 38 % in 2006, the last year for which an entire annual cycle of data were collected. When fruit first returned to the diet in 2003 (9.8 % of annual diet) the population continued to decrease. In the wet season (June-December) of 2004, the percent of time spent feeding on fruit reached 40 %, equivalent to pre-hurricane levels, and this coincided with the end of the 3-year period of steady population decline (Fig. 13.1). Fruit consumption remained between 30 % of the diet in the dry season (January–May) and 40 % in the wet season, and after a 2-year period of stability, the population density and group size began to rise, which it has continued to do ever since. Both population density and group size were positively correlated with fruit consumption (population density: $N=10$; $r_{sp}=0.635$; $p=0.002$; group size: $r_{sp}=0.572$; $p=0.004$).

Fruit production was an important factor in *A. pigra* reproduction following Hurricane Iris; infant survival showed a significant positive correlation with fruit availability ($N=29$; $r_{sp}=0.805$; $p=0.001$) (Fig. 13.2). No infants were born in the first 12 months after the storm, and the two infants born in the next 6 months did not survive. This was the 18-month period of zero fruit production. As fruit slowly returned to the diet in 2003 and 2004 infant survivorship to age one increased to

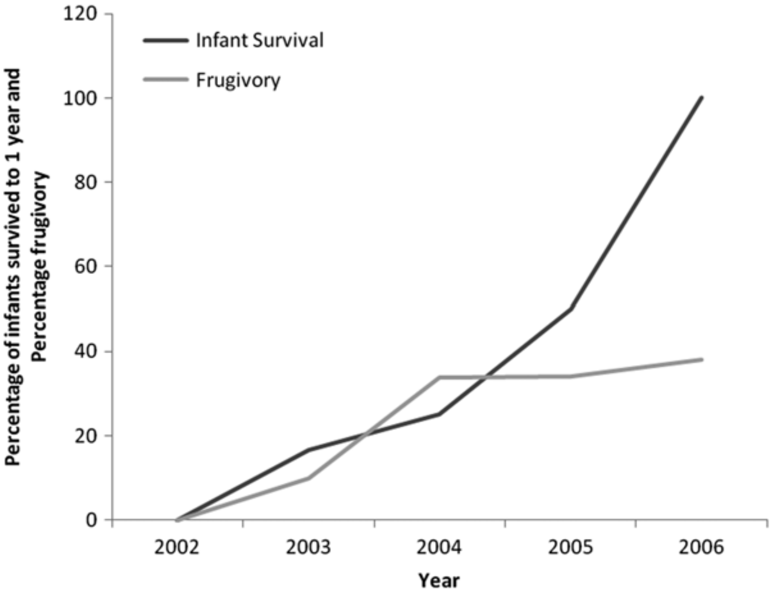

Fig. 13.2 Infant survival in a population of *A. pigra* in relation to annual fruit consumption following Hurricane Iris (2002–2006) at Monkey River, Belize. Infant survival is a measure of the percentage of infants born in for the study groups within the Monkey River site that survived to 1 year of age. Frugivory is the amount of fruit in the annual diet budget, calculated from behavioral data on the same for groups. A significant positive relationship was found between the two variables ($r_{sp}=0.805$; $p=0.001$)

22.2 % (9 infants were born and 2 survived). When fruit consumption increased to 25 % in 2005 infant survival rose to 50 % (2 infants were born and 1 survived) and then to almost 100 % in 2006 (8 infants born and 7 survived) when annual fruit consumption was back to pre-hurricane levels.

13.3.2 *Effect of Fruit Scarcity after Hurricane Iris on Activity Budget in* A. pigra

Monthly fruit consumption varied after the hurricane from 0 to 60.1 %. To compare the effects of fruit scarcity on activity budgets, we grouped data from before fruit production returned to pre-hurricane levels ($N=26$; average annual fruit consumption 4.93 %) and data from after fruit consumption returned to pre-hurricane levels ($N=32$; average annual fruit consumption 28.75 %). We found that during the prolonged period of fruit scarcity, inactivity was significantly higher ($t=-5.104$, $p=0.001$) while both time spent feeding ($t=3.858$, $p=0.004$) and locomoting ($t=-2.743$, $p=0.026$) were significantly lower (Fig. 13.3). After fruit consumption

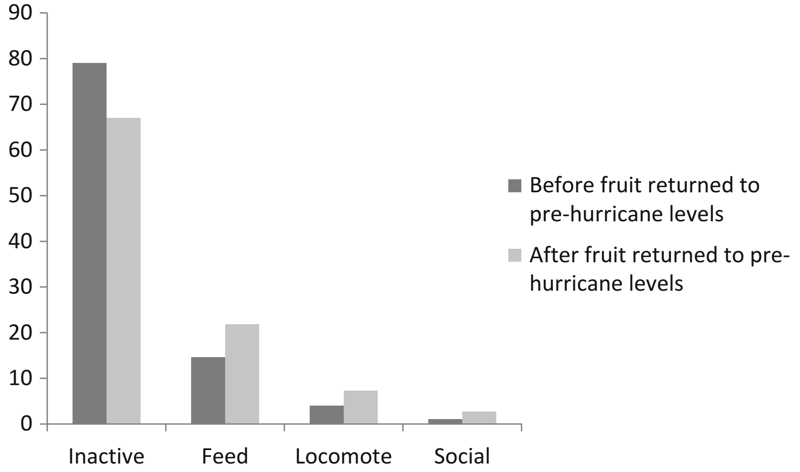

Fig. 13.3 Post-hurricane activity budget of the Monkey River black howler population both before and after fruit returned to pre-hurriane levels. Fruit was at pre-hurricane levels from the hurricane (2001) until mid-2004. Post-hurricane levels of 40% were reached mid-2004 and have remained there since. Activity budgets were calculate based on focal animal data of four study groups, each of which were studied three days per month from 2001 – 2006

returned to pre-hurricane levels, no relationships were found between the time spent eating fruit each month and activity (inactive, locomotion, feed, and social interaction) despite showing significant differences in fruit consumption ($t=-6.798$, $p=0.00$). In other words, seasonal fluctuations in fruit availability were not of sufficient magnitude to cause changes in activity patterns, but prolonged shortages do. Thus, short-term studies showing no change in activity due to changes in frugivory, such as Silver et al. (1998), cannot be interpreted as evidence that dramatic and extended periods of reduced fruit availability will not affect behavior.

13.3.3 Effect of Fruit Scarcity after Hurricane Iris on Birth Seasonality in A. pigra

All births in the study site from 2002 to 2007 ($N=29$) are plotted by month in Fig. 13.4. Births occurred in every month of the year except July and although there is a noticeable decrease in births from May to September and increase in births from February to April (early dry season) and October to December (late wet season) we did not have enough data points (29 births) to determine if this relationship was significant. No significant relationships were found between fruit consumption and month of birth, month of conception, or month of weaning for this population.

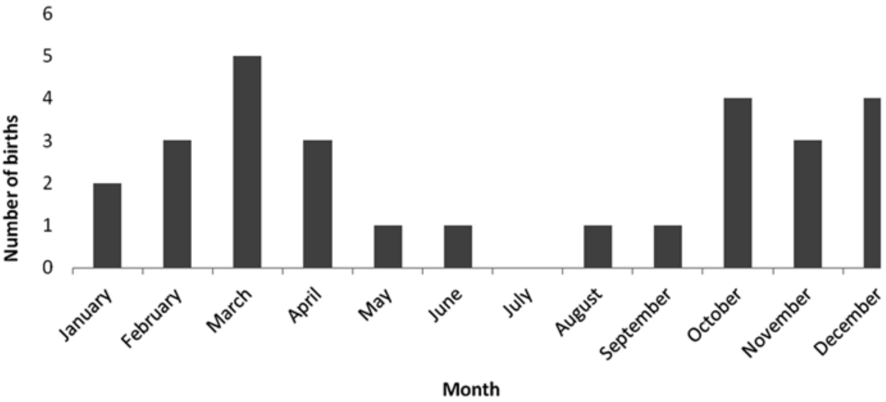

Fig. 13.4 Births by month in the Monkey River study area in the first 5 years following hurricane Iris (2001–2006). While there were no significant differences, there is a small drop in births from May to September and two slight peaks in February–April (early dry season) and October–December (late wet season). Both birth "peaks" occur so that maximum fruit production coincides with either the final stage of lactation or the weaning process

13.3.4 Comparison of A. pigra *to* A. palliata

Our regression (Fig. 13.5) revealed that minimum monthly frugivory, maximum monthly frugivory, and mean frugivory were not affected by forest fragment size ($n = 19$; range = 1.3 ha – 10,800 ha $p > 0.05$) in either *A. pigra* or *A. palliata*. This suggests that differences reported in percent time consuming fruit on these population parameters are occurring independently of fragment size. Our literature review found *A. pigra* live in significantly smaller groups than do *A. palliata*; however, there were no differences between these two species in percent frugivory, forest size, home range size, adult sex ratios, adult female to immature ratios, or in the rainfall and temperature at the study sites. *Alouatta palliata* did show higher variation than *A. pigra* for each of these variables, which may be due to the increased sample size for the comparatively well-studied mantled howlers or reflect species differences in behavioral plasticity or ecology.

As only one significant difference was found between the two species, we pooled the data to investigate the effect of different levels of frugivory in these howler taxa. Population density was positively predicted by minimum monthly frugivory ($F = 4.788$, $N = 15$, $p = 0.024$), supporting our assertion that howlers need a certain amount of fruit in the diet each month to maintain their population numbers. Population density was not predicted by maximum monthly frugivory ($N = 14$, $F = 1.839$, $N = 15$, $p = 0.241$), mean frugivory ($N = 23$, $F = 1.731$, $N = 33$, $p = 0.203$), or rainfall ($N = 22$, $F = 1.832$, $N = 30$, $p = 0.323$). Coefficients of variation for mean frugivory were largest for the populations with the lowest minimum fruit intake, and there was no correlation between minimum monthly fruit intake and either mean fruit intake or maximum monthly intake, suggesting that low minimum

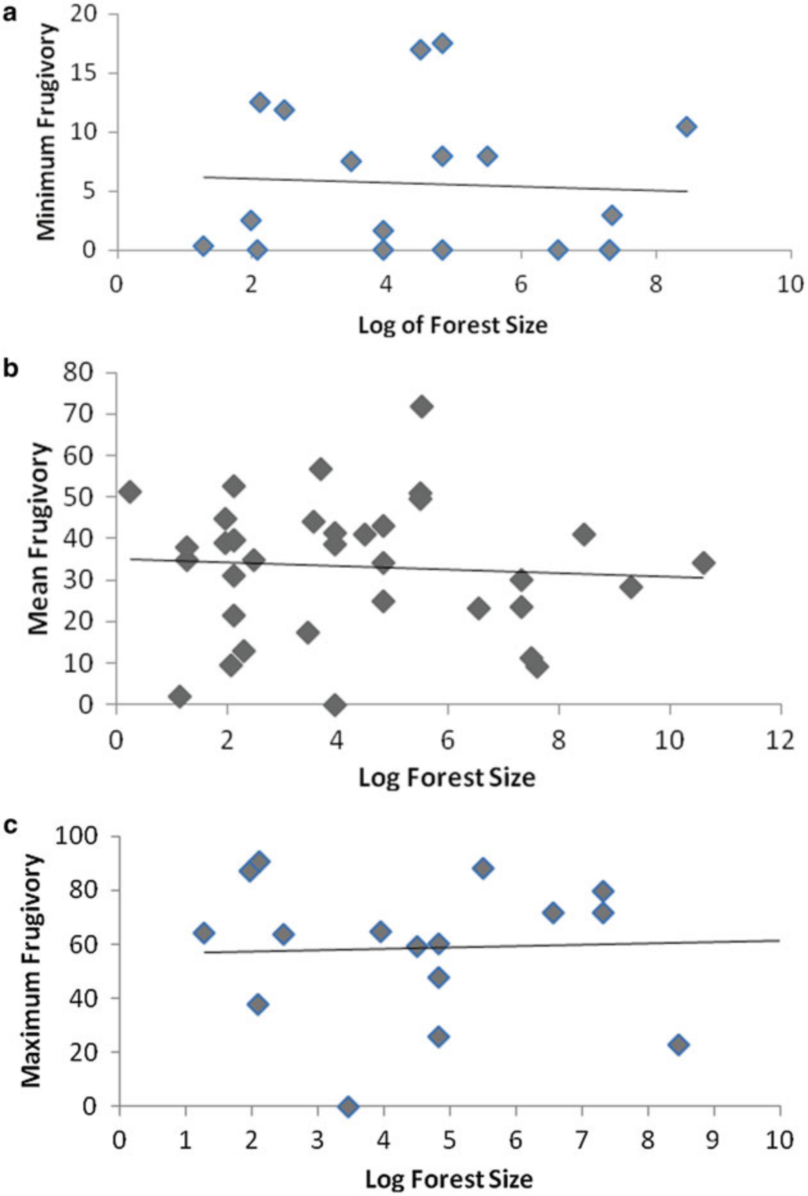

Fig. 13.5 Degree of frugivory for populations of *A. pigra* and *A. palliata* across study sites of various sizes. Forest sizes were log transformed to normalize the data. None of the frugivory variables, including: (**a**) minimum monthly frugivory, (**b**) mean frugivory across the duration of the study, (**c**) maximum monthly frugivory were related to forest size

monthly fruit intake is not simply representative of overall low fruit consumption in the habitat. In other words, this is not an artefact of an environment with overall low fruit production and indicates that even among populations that have the same mean consumption of fruit or experience some months with higher fruit consumption than others, the minimum fruit consumption is important for howler population density.

Of the studies that contained information on the relationship between fruit consumption and activity (Table 13.2), we found no consistency within or between species differences in how populations adjust behavior during periods of fruit shortage. For example, *A. pigra* in Monkey River Belize decrease time spent traveling (from 9.52 to 5.45 %) when resources are scarce (Pavelka and Knopff 2004) yet another population at Community Baboon Sanctuary, Belize did not adjust activity patterns in response to seasonal reductions in fruit intake (Silver et al. 1998). Similarly, while some groups of *A. palliata* do not show changes in activity that correspond to fruit production, the most common response reported in the literature is to increase either travel time [from 18.6 to 35.8 % in *A. palliata* in Nicaragua and from 11.8 to 13.3 % (Williams-Guillen 2003) in *A. palliata* in Mexico (Rodriguez-Luna et al. 2003)] or ranging distance [from a mean of 114.05 m to 502.88 m for the population in Los Tuxlas, Mexico (Estrada 1984) and from 535 m to 675 m a day for a Nicaraguan population (Williams-Guillen 2003)] during fruit shortages; responses that have not been reported for *A. pigra*.

Our survey of birth seasonality in *A. pigra* and *A. palliata* revealed no strict seasonality; however, some studies did report birth peaks at different times of year (Table 13.3). In two of the studies, populations showed an even distribution of births in some years and a clustering of births in other years, indicating a potential relationship between reproduction and yearly variation in resource availability. For the populations that show consistent yearly birth peaks, they occurred during the dry season with more births occurring from December to May than in the rest of the year. However, in one of these studies, the authors suggest that fruit peaks are timed to weaning (Fedigan and Rose 1995) while the other suggests it is timed to the period of conception (Brockett et al. 2000).

13.4 Discussion

13.4.1 Fruit Scarcity Effects on Population Density and Infant Survival

The potential for internal and external factors to regulate the density of animal populations has intrigued researchers for decades (Nicholson 1933; Krebs 1978; Boutin 1990). Food supply is commonly recognized as the most common limiting factor for any animal population (Boutin 1990), and because a habitat's carrying capacity is assumed to be principally affected by food availability (although factors

Table 13.2 Observed changes in behaviour in *Alouatta pigra* and *Alouatta palliata* during periods of fruit scarcity

Behavioural response to fruit shortage	Species	Study site	Group size (no. of individuals)	Population density (individuals/ha)	Fragment size (ha)	References
Decrease time spent travelling/ranging	*Alouatta palliata*	Los Tuxlas, Mexico	14	0.22	70	Estrada (1984)
		Arroyo Liza, Mexico	6	4.6	7.3	Asensio et al. (2007)
	Alouatta pigra	Monkey River	6.6	1.01	52	Pavelka and Knopff (2004)
		Cockscomb Basin Wildlife Sanctuary, Belize	6.5	0.1	40,000	Silver and Marsh (2003)
Group fission	*Alouatta palliata*	Agaltepec Island, Mexico	59	9.5	8.3	Asensio et al. (2007)
Increase time spent feeding	*Alouatta palliata*	Los Tuxlas, Mexico	4	?	70	Sheddon-Gonzalez and Rodriguez-Luna (2010)
		La Pacifica, Costa Rica	13	?	1,550	Glander (1981)
Increased time spent travelling/ranging	*Alouatta palliata*	La Pacifica, Costa Rica	25	?	125	Williams-Guillen (2003)
		La Pacifica, Costa Rica	15	?	125	Williams-Guillen (2003)
		La Pacifica, Costa Rica	20	?	125	Williams-Guillen (2003)
		La Pacifica, Costa Rica	13	?	10	Glander (1981)
		Agaltepec Island, Mexico	10	1.21	1.83	Rodriguez Luna et al. (2003)
		Agaltepec Island, Mexico	27	6.87	8.3	Rodriguez Luna et al. (2003)
		Barro Colorado Island, Panama			8	Milton (1980, 1981)
No change in behaviour	*Alouatta palliata*	Los Tuxlas, Mexico	7	1.67	3.6	Estrada and Coates Estrada (1999)
		La Selva, Mexico	20	0.07	1,500	Stoner (1996)
		La Selva, Mexico	11	0.15	1,500	Stoner (1996)
		Santa Rosa, Costa Rica	40	?	10,800	Chapman (1987, 1988)
		Playa Escondida, Mexico	7	0.48	40	Asensio et al. (2007)
	Alouatta pigra	Community Baboon Sanctuary, Belize	5.9	2.5	700	Silver et al. (1998)
Increase in time spent inactive	*Alouatta pigra*	Cockscomb Basin Wildlife Sanctuary, Belize	6.5	0.1	40,000	Silver and Marsh (2003)

Table 13.3 Reproductive seasonality in *Alouatta pigra* and *Alouatta palliata*

Species	Study site	Minimum fruit intake (%)	Maximum fruit intake (%)	Mean fruit intake (%)	Minimum rainfall (mm)	Maximum rainfall (mm)	Total rainfall (mm)	Birth peak?	Infant mortality by season	References
Alouatta palliata	Barro Colorado Island, Panama	10	65	42	120	1,790	2,730	Varies with year	Not reported	Milton (1982)
	La Pacifica, Costa Rica	9	15	13	0	380	1,900	Varies with year	50–100 % for births in scattered years 15–25 % for clustered years 50 % for births outside of cluster months	Glander (1980)
	La Pacifica, Costa Rica	?	?	?	0	380	1,900	No	Males born in wet season have higher mortality	Clarke (1983); Clarke and Glander (1984)
	Los Tuxlas, Mexico	0	65	51	3.5	851	4,500	No	Not reported	Estrada (1982)
	Santa Rosa, Costa Rica	0	55	29	0	919	1,650	Yes (December–May) *Fruit peak times with weaning*	Not reported	Fedigan and Rose (1995)
Alouatta pigra	Community Baboon Sanctuary, Belize	10.5	61.5	41	55	360	1,955	Yes (December–May) *Fruit peak times with conception*	Not reported	Brockett et al. (2000)

such as disease and predation also may be important) during times of scarcity, studies of the quality and quantity of foods available are extremely important (Davies 1994). For Asian and African colobines, the P:F ratio of mature leaves has proven to be an indicator of population abundance (Waterman et al. 1988; Oates et al. 1990; Chapman et al. 2002; Wasserman and Chapman 2003; Chapman et al. 2004), while for frugivores it is the abundance of fleshy fruit that is reported to be a useful predictor of population abundance (Blouch 1997; Chapman and Chapman 1999; Moscovice et al. 2007; Aldana et al. 2008). Howler monkeys are the most folivorous New World monkey, with leaves accounting for between 5 % (Chiarello 1994) and 71.8 % (Juan et al. 2000) of annual feeding time. Despite this, their simple stomach requires howlers to be quite dependent on the ingestion of high energy fruit to meet nutritional demands (Milton 1980). In this chapter we investigated the importance of fruit for one species of howler monkey (*A. pigra*) by examining how a prolonged period of fruit shortage caused by a severe environmental change impacted population density, activity budget, infant survival, and birth seasonality and then put this in the context of what is known regarding frugivory in other populations of this species as well as the other member of the Mesoamerican *Alouatta* clade, *A. palliata*.

The prolonged fruit shortage created by Hurricane Iris had a very clear and direct influence on population size and characteristics in *A. pigra*, indicating for the first time the critical importance of frugivory for a howler monkey population. In the first weeks following the storm, the monkey population declined by 42 %, which was attributed to death and injury from the high winds and falling trees during the storm itself, and then to starvation in subsequent weeks. The continued population decline from 2002 to 2004, however, was likely a response to an overall reduction in food trees, and particularly fruit trees along with an 18-month absence in fruit production (Behie and Pavelka 2005). The reliance on a primarily folivorous diet over this period did not sustain the population and likely resulted in energy malnutrition (Behie and Pavelka 2012).

It is important to try to understand how and why fruit proved to be so important to a monkey previously believed to be able to survive long periods principally consuming leaves. As energy intake must be divided between self-maintenance and reproduction, when animals are facing reduced energy intake they use what energy is available to meet the needs of maintenance (cellular function, thermoregulation, foraging, digestion) first, and only if energy remains will they invest in reproduction (Hau 2001; Gesquiere et al. 2011). This may partially explain the population decline in the Monkey River howler population following Hurricane Iris; however, the picture is undoubtedly more complex.

The low level of post-hurricane fruit consumption was correlated with an increase in the stress hormone cortisol in both adult males and females in the Monkey River population (Behie et al. 2010). When animals suffer from stress, the body induces the fight-or-flight response, which serves to mobilize glucose from cells and tissues into the bloodstream for immediate use (Sapolsky 1992), making the metabolic goal of the stress response to free up energy to be used by the body until the stressor passes. While this mechanism is beneficial in the short term, if it is activated too often or for too long it can have deleterious effects on the body, as energy is constantly being diverted from other body systems. Persistently high cortisol levels can lead to tissue and muscle breakdown, immunosuppression, decreased growth rates, and lower reproductive rates (Abbott 1987; Sapolsky 1992; Ziegler et al. 1995; Saltzman et al. 1998; Avitsur et al. 2001; Bercovitch and Ziegler 2002). Ecological stressors such as extreme temperatures or food deprivation have been recorded in many populations of birds and mammals (Silanikove et al. 2000; Lynn et al. 2003; Filipovic et al. 2007). Similarly, many animals, including wild primates living in low quality and/or disturbed habitats have shown increased cortisol levels (Creel et al. 2002; Homan et al. 2003; Chapman et al. 2006; Martinez-Mota et al. 2007).

The glucocorticoids released in response to stress also can influence reproduction by interfering with normal hormone production, including the release of gonadotropin-releasing hormone and luteinizing hormone. A reduction in these hormones can lead to a reduction in both testosterone and estrogen production, potentially resulting in suppressed ovulation in females (Sapolsky 1992) and reduced sperm production in males (Sapolsky 1986). Following Hurricane Iris, no females produced infants for one complete year, indicating that the stress of the event may have contributed to reduced birth rates. However, after this year, females began producing infants quite regularly, although infant survivorship was low. This suggests that the stress response had a temporary or limited effect on conception and gestation, but had a greater effect on infant health or post-reproductive costs to the mother (lactation).

Females facing malnutrition will often reduce their own energy output to protect fetal health, lowering the birth weight of their infants (Poppit et al. 1994), which is known to be a major source of childhood morbidity and mortality in humans (Kramer et al. 1998; Hack et al. 2002). Thus, to maintain adequate milk production, lactating females may employ similar behavioral strategies as those seen in malnourished pregnant females (Roberts et al. 1985) and reduce their own energy expenditure. Dias et al. (2011) found that lactating *A. pigra* females spent more time inactive and feeding on high energy fruits than other females, which may serve to meet the increased energy demands of lactation. It is important to note that it has recently been found in *A. caraya* that mature leaf intake was positively correlated to the number of infants present each month, suggesting either species differences in howler nutritional ecology and in the ability to extract nutrients from fruit and leaf tissues (see Garber et al. 2014), or that in a flood-affected forest mature leaves may also play an important role in assisting females maintain lactation and ensuring infant survival (Pave et al. 2012). While the high mortality of unweaned infants in Monkey River following Hurricane Iris may have been due to increases in disease or predation, it also is possible that mothers were not producing adequate milk for infants, even after they had returned to more typical activity budgets.

The fact that howler monkeys tend to be quite successful in a variety of habitat types and sizes has been attributed to their ability to flexibly feed from novel plant species and plant tissues (Bicca-Marques and Calegaro-Marques 1994; Crockett 1987; Palacios and Rodriguez 2001; Behie and Pavelka 2005; Dunn et al. 2010). This may explain why many features of the behavior and ecology of the genus such as home range size, dietary diversity, and group size have not been consistently tied to seasonal changes in rainfall and food productivity (Chapman and Balcomb 1998) or fragment size (Bicca-Marques 2003; Cristobal-Azkarate and Arroyo-Rodriguez 2007). Such behavioral flexibility may explain in part, why the results of the Hurricane Iris study do not fit easily into a larger systematic investigation of the importance of frugivory in the genus *Alouatta*. The ability of howlers to adjust feeding behavior to include the ingestion of exotic items such as citrus fruits (Bicca-Marques and Calegaro-Marques 1994) or to increase their consumption of staple food items such as new leaves (Palacios and Rodriguez 2001) or mature leaves (Behie and Pavelka 2012) or in extreme situations to show group fissioning in order to alleviate the negative effects of feeding competition (Asensio et al. 2007) suggests they are able to adapt their diet and behavior in response to a broad range of ecological challenges. This may help to explain the absence of direct evidence that frugivory affects howler population dynamics on a broader scale. Our current study (of the effects of a major hurricane) strongly suggests, however, that there is a point where fruit shortage becomes too prolonged and behavioral flexibility is not sufficient to locate or switch to alternative sources of readily available energy to sustain howler survivorship and reproduction. Our analysis of the *A. pigra* and *A. palliata* literature also shows that population density can be predicted by minimum monthly fruit intake, independent of either mean or maximum monthly fruit intake. This means populations with more pronounced periods of fruit shortages at certain points in the year are expected to exhibit lower population densities. This is true even if they consume high levels of fruit during other months and have an overall frugivory level similar to other populations. Further research on minimum fruit intake and the effect of fruit shortages on population size and reproduction is needed to more fully identify the relationship between fruit deprivation and population density in howler monkeys.

13.4.2 Implications of the Importance of Fruit for Howler Conservation

This study highlights the fact that ripe fruit represents an important component of the howler diet. Although during certain periods of the year leaves may account for nearly 100 % of feeding time, the Monkey River study shows that it is unlikely that howlers can subsist for extended periods without also consuming fruit to increase energy intake. Considering the relationship between minimum monthly frugivory and population density across groups of Central American howlers and the effect that a prolonged lack of fruit consumption had on the fitness of the Monkey River population, it appears that fruit is an essential component of the howler diet and its absence has a negative impact on reproductive success. Population density has been tied to fragment size (Bicca-Marques 2003), which may reflect the fact that smaller fragments generally have lower tree species diversity and fewer large trees that produce large fruit patches (Dunn et al. 2009). From a conservation planning perspective, shorter-term studies of howlers adapting to normal monthly and seasonal fluctuations in fruit availability need to be interpreted cautiously. This also may explain the documented importance of trees from the family Moraceae and particularly of the genus *Ficus* for howler monkeys. *Ficus* tend to grow in secondary forests, fruit asynchronously, and produce a large fruit crop (Silver et al. 1998; Serio-Silva et al. 2002; Bicca-Marques 2003; Pinto and Setz 2004; Agostini et al. 2010). As severe weather events are expected to increase in frequency and intensity, and Hurricane Iris demonstrated that they can be devastating to the fruit supply and subsequently to primate population survival more systematic studies of the importance of frugivory to members of the genus *Alouatta* are needed to fully assess the risk.

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Appendix: Studies from *Alouatta pigra* and *Alouatta palliata* That Were Included in our Analysis of the Effect of Frugivory on Population Density, Group Size, and AF:Immature Ratio

Species	Study site	Forest size (ha)	Minimum monthly frugivory (% of diet)	Maximum monthly frugivory (% of diet)	Mean frugivory (% of diet)	Coefficient of variation for mean frugivory	Population density (individuals/ha)	Group size	AF:Immature ratio	References
Alouatta pigra	Community Baboon Sanctuary, Belize	4,700	10.5	64.5	41.0	41.7	2.5	5.9	0.64	Silver et al. (1998)[a]
	Cockscomb Basin Wildlife Sanctuary, Belize	40,000	?	?	34	?	0.11	6.5	0.70	Silver and Marsh (2003)[a]
	Monkey River, Belize	52	1.65	41.38	84.6	72.31	1.01	6.6	0.88	Pavelka and Knopff (2004)
	Balacan tobasco, Mexico	32	7.5	23	17.4	?	0.06	9	1.00	Pozo-Montuy and Serio-Silva (2006)

Alouatta palliata	Barro Colorado Island, Panama	1,550	?	?	38.8	?	?	?	?	Smith (1977)
	Hacienda La Pacifica, Costa Rica	10	5	30	13	?	?	13	1.20	Glander (1978)
	Barro Colorado Island, Panama	1,550	9.7	46.9	42	?	1.13	17	?	Milton (1980, 1981)
	Field Station, Mexico	700	0	79.5	49.9	132	0.221	14	0.83	Estrada (1982, 1984)
	Santa Rosa, Costa Rica	10,800	?	?	28.5	?	?	40	0.95	Chapman (1987, 1988)
	Santa Rosa, Costa Rica	10,800	?	?	17	?	?	20–28	1.00	Larose (1996)
	La Selva, Costa Rica	1,500	0	71.8	23.5	90.5	0.07	20	2	Stoner (1996)
	La Selva, Costa Rica	1,500	0	87	30	86.7	0.15	11	1.25	Stoner (1996)
	Bala Zapote, Mexico	3.6	0.3	71.6	34.8	74.8	1.94	7	0.67	Estrada (1999)
	Agaltepec Island, Mexico	8.3	?	?	39.5	?	?	29	?	Serio Silva (1999, 2002)
	Los Tuxlas, Mexico	3.6	?	?	38	?	1.94	7	0.67	Solano et al. (1999)
	Parque Yumka, Mexico	101	5	33	16.2	87.76	1.22	?	1.22	Garcia del Valles (2001)
	Agaltepec Island, Mexico	8.3	?	?	31	?	1.21	5	0.13	Rodriguez-Luna (2003)
	Agaltepec Island Mexico	8.3	?	?	52.5	?	6.9	10	1.05	Rodriguez Luna (2003)
	Finca La Luz, Nicaragua	125	0	47.7	25	61	?	25	0.92	Williams-Guillen (2003)
	Finca La Luz Nicaragua	125	17.5	59.1	43	32	?	15	1.14	Williams-Guillen (2003)
	Finca La Luz, Nicaragua	125	7.9	63.9	34	55	?	20	0.064	Williams-Guillen (2003)
	Comalcalco, Mexico	12	11.9	64	35	50.99	?	24	1.38	Munoz (2006)
	Playa Escondida, Mexico	40	?	?	56.88	?	0.48	7	0.67	Asensio et al. (2007)
	Agaltepec Island, Mexico	8.3	?	?	21.35	?	9.5	59	1.11	Asensio et al. (2007)
	Arroyo Liza, Mexico	1.3	?	?	51.18	?	4.6	6	4	Asensio et al. (2007)
	Los Tuxlas, Mexico	244	?	?	49.4	?	0.12	9	1	Dunn et al. (2009)
	Los Tuxlas, Mexico	7.2	?	?	39.1	?	1.11	8	1.5	Dunn et al. (2009)
	Los Tuxlas, Mexico	244	7.95	90.58	50.94	60.41	0.12	9	1	Dunn et al. (2010)
	Los Tuxlas, Mexico	7.2	2.52	88.05	44.67	59.96	1.11	8	1.5	Dunn et al. (2010)

[a] Group composition information from Ostro et al. (1999)

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Chapter 14
Conservation of *Alouatta*: Social and Economic Drivers of Habitat Loss, Information Vacuum, and Mitigating Population Declines

Alejandro Estrada

Abstract Despite being categorized as ecologically flexible primates because of their broad geographic distribution and the diversity of habitats in which they are found, howler monkeys face serious threats of extinction throughout their distribution range. Information reviewed in this chapter indicates that high human population growth rates are prevalent in *Alouatta* range countries, creating important demands for land for food production and the provisioning of other goods and services for the population. Recent global market demands for cattle and food crops and other goods also exert important additional pressures upon *Alouatta* habitats. These interactive processes have resulted in high and continuous rates of habitat loss in the majority of *Alouatta* range countries. Such loss takes place in the context of high levels of poverty and low human development. On average, it is estimated that about 60 % of *Alouatta* populations exist outside protected area boundaries, suggesting that conservation efforts are needed at the landscape level. An important data vacuum exists for the majority of *Alouatta* species, with 58 % of published studies providing information on only two of the 14 recognized species of *Alouatta*. Moreover, 50 % of the published records come from only three countries, suggesting a data vacuum for many geographic regions and localities where *Alouatta* is present. Key conservation gains are represented by increases in the number of natural protected areas in *Alouatta* range countries, but more conservation research is needed outside protected area boundaries. A framework of basic and diagnostic research which incorporates the social dimension of the conservation problem in *Alouatta* is presented as a guideline for scientific and political attention.

Resumen A pesar de ser catalogados como primates ecológicamente flexibles debido a su amplia distribución geográfica y a la diversidad de hábitats en que se encuentran, los miembros del género *Alouatta* enfrentan serias amenazas de extinción en todo su rango de distribución geográfica. La información revisada en este capítulo indica que

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las altas tasas de crecimiento de la población humana en los países en donde *Alouatta* ocurre genera demandas para la producción de alimentos y la provisión de otros bienes y servicios del campo para la población. Asimismo, la creciente demanda del mercado global por alimentos y otros productos del campo ejercen fuertes presiones sobre los hábitats de *Alouatta*. La interacción de estos procesos se ha traducido en tasas elevadas y continuas de pérdida de hábitat en los países del área de distribución de *Alouatta*. Esta pérdida se da en el contexto de altos niveles de pobreza y un bajo desarrollo humano. Se estima que cerca del 60 % de la distribución para las 12 especies de *Alouatta* actualmente reconocidas existe fuera de los límites de áreas naturales protegida, lo que sugiere que se requieren esfuerzos de conservación a nivel de paisaje. Asimismo, existe un fuerte vacío de datos para la mayoría de las especies de *Alouatta*. Por ejemplo, el 58 % de los estudios publicados proporcionan información para sólo dos de las 12 especies de *Alouatta*. Además, el 50 % de los registros publicados provienen de sólo tres países, lo que también sugiere un vacío de datos para muchas regiones geográficas y localidades donde *Alouatta* está presente. Se propone un esquema de investigación básica y de diagnóstico que incorpora la dimensión social del problema de conservación de *Alouatta* y que podría ser motivo de atención pública y política.

Keywords Landscape changes • Neotropics • Protected areas • Human population growth • Deforestation

14.1 Introduction

In 2011, the world's human population reached a milestone in size, seven billion, and it is expected to increase to nine billion by 2050. As of 2005, there were ca. two billion humans in primate range countries. Human populations in these regions are projected to have steep growth through the next three decades (UNFPA 2011). The estimated average growth rate from 1980 to 2005 for the Neotropics, Sub-Saharan Africa, and Southeast Asia was ca. 3 %/year, greatly exceeding the world average (1.8 %/year) and that of European countries (0.2 %/year). Population density in 2005 was estimated at 51 people/km^2 in the Neotropics, 99 people/km^2 in Sub-Saharan Africa, and 116 people/km^2 in Southeast Asia (UNFPA 2011). The rapidly growing human population and increases in local and global market demands exert an extreme burden on the natural resource base for food production, water, and living space (Lambin and Meyfroidt 2011) that in turn have significant consequences for native primates. For example, average annual deforestation rates for the period 1990–2005 for the Neotropics have been estimated at 10.9 % (21 countries), for Sub-Saharan Africa at 11.3 % (30 countries), and for Southeast Asia at 8.9 % (13 countries) (FAO 2011).

Conversion to agriculture has been a major cause of tropical habitat degradation, loss and fragmentation, and of changes in the distribution of primates (Donald 2004; Laurance et al. 2011), with stochastic forces playing an important role in the decline of populations and the local extinction of species (Henle et al. 2004; Mittermeier et al. 2009). Studies of the consequences of habitat fragmentation on animal communities in the tropics have centered on profiling the biological richness of forest, woodland, and rangeland fragments, and on understanding how species richness is affected by isolation, degradation, edge effects, invasive species, and management practices (Cowlishaw and Dumbar 2000; Chapman et al. 2006; Bennett and Saunders 2010; Laurance et al. 2011). However, as is the case for other geographic regions, in the Neotropics this task is further complicated by the high diversity and endemism of many animal taxa including primates (Rylands et al. 2006; Rylands and Mittermier 2009). Moreover, human-induced fragmentation of primate habitats and populations together with the existence of large and expanding human populations brings humans and nonhuman primates into close spatial contact. Such forced proximity may alter host–parasite relationships leading to new vectors of parasite and disease transmission that are of critical relevance to issues of public health and management of remnant primate populations (Cowlishaw and Dumbar 2000; Altizer et al. 2003; Kowalewski and Gillespie 2009). Hunting and the pet trade are additional important pressures upon primates in the Neotropics (Ráez-Luna 1995; Cullen et al. 2001; Jerozolimski and Peres 2003). Furthermore, the impact of climate change upon primate habitats and populations has yet to be investigated (Wright 2007).

It is clear then that we confront a conservation challenge of great magnitude. Recent assessments indicate the existence of 612 primate species and subspecies recognized by the International Union for Conservation of Nature RedList (IUCN 2012), but it is estimated that about 50 % of the world's primate taxa are threatened with extinction as a result of human pressures (Mittermeier et al. 2009). Such pressures heavily tax the limits of primate behavioral and ecological plasticity, including those of species of the genus *Alouatta*, a genus categorized as ecologically flexible because of its broad geographic distribution and diversity of native habitats and human-modified landscapes in which it is found (Bicca-Marques 2003; Di Fiore and Campbell 2007). Importantly and rarely discussed, such challenges are exacerbated by a data vacuum on the majority of *Alouatta* species.

Here I provide a regional-level view of conservation pressures affecting the persistence of *Alouatta* habitats within its range. Some of these pressures come from regional human population growth and economic development and from global market demands which translate into growing demands for food crops and other resources which in turn translate into high rates of forest loss. I do not attempt untangling the complex web of interacting forces that locally or regionally drive the conservation problem of native habitat for *Alouatta*. My intention here is to illustrate trends and patterns for future scientific and political attention. Below I list the specific aims of the chapter and the sources used to assemble information on social and economic aspects of relevance to the conservation problem.

14.2 Aims

I examined (1) the conservation status of species of *Alouatta* according to the IUCN RedList, (2) trends in human population growth and in forest loss within the geographic distribution of *Alouatta* in the Neotropics, (3) trends in local and global market demands and their impact upon the persistence of native habitat, and (4) the overall growth of natural protected areas (NPAs) in *Alouatta* range countries. I further estimated range extension for each species and the extent of protected areas found within it. Additionally, I explored the volume of published reports available on each *Alouatta* species with the goal of assessing the richness of information. To achieve this, I tackled the following sets of information.

Using the IUCN RedList database (IUCN RedList 2012), I tracked the number of recognized species of *Alouatta* and their IUCN conservation and population trends status. I also noted the number of species hosted by each country and those groups of countries sharing species. I profiled trends and projections in human population growth in *Alouatta* range countries by consulting the data banks of the Population Division of the United Nations Department of Economics and Social Affairs (UNDES 2012). For each country, I further profiled the level of human development of the population as expressed by the Human Development Index (HD) of the United Nations Development Program (UNDP 2012).

I also profiled trends in expansion of pasture lands and permanent crop lands and in loss of forest cover in *Alouatta* range countries using information from FAO (Food and Agriculture Organization of the United Nations) databases (Food and Agricultural Production Division (FAO-Stat-land 2012) and use these metrics as proxies of trends in habitat loss for the genus. Using information from the World database on protected areas of the United Nations environment programme (UNEP 2012), I profiled the overall growth (from 1970 to 2010) of NPAs throughout *Alouatta*'s range and mapped onto this the growth of the human population.

I obtained maps with the expected range for each *Alouatta* species from the GIS archives of the IUCN (IUCN RedList 2012). To these maps I added a layer of information, from the same database, on the NPAs within the range for each species. I then digitized the range boundary of each species to estimate the land area it encompasses and did the same for the NPAs found within this range.

I explored the published literature on *Alouatta* using the PrimateLit database (PrimateLit 2012) to assess the richness of information on each species of the genus for the period 1940–2010, and profiled the distribution of these records for each country within the range of the genus. In the examination of the PrimateLit database, I avoided reports mentioning *Alouatta* species in keywords. Instead, I searched the database by tracking the scientific name in the title. While the taxonomy of *Alouatta* was recently updated, sorting out the literature by species did not allow for separation of the original *A. seniculus* group into the current six species (*A. arctoidea, A. juara*, *A. macconnelli*, *A. puerensis*, *A. sara*, *and A. seniculus*). Records available are flagged in the PrimateLit only as *A. seniculus*.

Quantitative information was processed for both Mesoamerican and South American *Alouatta* range countries as a group and for some analysis I separated each of these regions to illustrate convergence or divergence in regional trends in human demographics and social condition, in forest cover loss, in expansion of agricultural activities as a result of local and global market demands, and in growth of NPAs. While hunting and the pet trade are important pressures upon extant primate populations in the Neotropics, including those of *Alouatta*, I did not examine or discuss these in this chapter because I consider habitat loss as the major cause of declines in *Alouatta* populations.

For Mesoamerica, *Alouatta* range countries considered in this analysis were Mexico, Belize, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, and Panama. For South America, information was examined for Brazil, Peru, Ecuador, Bolivia, Colombia, Venezuela, Guyana, French Guyana, Suriname, Argentina, Paraguay, Uruguay, and Trinidad and Tobago. Uruguay was included due to reports indicating the possible presence of *A. caraya* and *A. guariba* in the Department of Artigas (Villalba et al. 1995) and Rivera (EOL 2012).

14.3 Official IUCN Conservation Status of Species in the Genus *Alouatta*

According to the IUCN RedList, there are 19 genera, 7 subfamilies, and 199 recognized species and subspecies of monkeys in the Neotropics, making platyrrhines one of the most taxonomically, behaviorally, and anatomically diverse primate radiations (Rylands et al. 2006; Rylands and Mittermier 2009). Among these, *Alouatta* is represented by 14 recognized species (but see Cortés-Ortiz et al. 2014), and is the most widely distributed genus in the Neotropics, with species ranging from southern Mexico to northern Argentina (Table 14.1).

Table 14.1 *Alouatta* species as listed in the IUCN RedList database

Species	Common name	IUCN RedList conservation status	IUCN Population trend	Countries
Mesoamerica				
Alouatta palliata	Mantled howler	Least concern	Unknown	Mexico, Guatemala, Honduras, Costa Rica, Nicaragua, Panama
Alouatta pigra	Yucatan black howler	Endangered	Decreasing	Mexico, Guatemala, Belize
South America				
Alouatta arctoidea	Ursine howler	Least concern	Unknown	Venezuela
Alouatta belzebul	Red-handed howler	Vulnerable	Decreasing	Brazil
Alouatta caraya	Black-and-gold howler	Least concern	Decreasing	Brazil, Paraguay, Argentina, Bolivia, Uruguay
Alouatta discolor	Spix's red handed howler	Vulnerable	Decreasing	Brazil
Alouatta guariba	southern brown howler	Least concern	Decreasing	Brazil, Argentina, Uruguay (?)
Alouatta juara	Juará red howler	Least concern	Decreasing	Brazil, Colombia, Venezuela
Alouatta macconnelli	Guianan red howler	Least concern	Unknown	Brazil, French Guiana, Guyana, Suriname, Venezuela
Alouatta nigerrima	Black howler	Least concern	Unknown	Brazil
Alouatta puruensis	Purús red howler	Least concern	Unknown	Brazil, Peru
Alouatta sara	Bolivian red howler	Least concern	Decreasing	Bolivia
Alouatta seniculus	Colombian red howler	Least concern	Decreasing	Brazil, Peru, Colombia, Venezuela
Alouatta ululata	Maranhão red-handed howler	Endangered	Decreasing	Brazil

For definition of conservation and population trend categories http://www.iucnredlist.org/technical-documents/categories-and-criteria/2001-categories-criteria

In Mesoamerica, the genus *Alouatta* is represented by two species. *Alouatta palliata* with a broad geographic distribution through southern Mexico and through Central America, but *A. pigra*, the other recognized species in this region, has a distribution restricted to the area shared by Mexico, Belize, and northern Guatemala (IUCN RedList 2012), with 80 % of its range found in Mexico (eastern Tabasco, northeast Chiapas, and the Yucatan peninsula). In South America, Brazil harbors 10 of the 12 species of *Alouatta* recognized by the IUCN. Of these, four only occur in Brazil (*A. belzebul*, *A. discolor*, *A. nigerrina*, *and A. ululata*). *Alouatta arctoidea* is present only in Venezuela and *A. sara* is found only in Bolivia (Table 14.1). According to the IUCN RedList conservation classification, 10 *Alouatta* species are broadly classified as Least Concern, two as Endangered, and two as Vulnerable (Table 14.1). The IUCN classifies trends in population for three species (*A. palliata*, *A. arctoidea*, and *A. macconnelli*) and one subspecies (*A. puruensis*) as unknown and for the rest ($N=10$) as decreasing (Table 14.1). While the IUCN classifies most *Alouatta* species as Least Concern, it also classifies 70 % of these as decreasing in population.

14.4 Trends in Human Population Growth in *Alouatta* Harboring Countries

In Mesoamerica, human population in 2010 was estimated at about 53 million (for Mexico, only the states of Veracruz, Tabasco, Oaxaca, Chiapas, and the Yucatan peninsula were considered because they harbor tropical forests where *Alouatta* has been reported (Estrada and Coates-Estrada 1988)). With a growth rate of 3 % since the 1950s, the population is expected to double in size in 20–35 years (Fig. 14.1a). In 2010, South American *Alouatta* range countries were inhabited by an estimated 396 million people. Brazil accounted for 50 % of the population; Colombia and Argentina together contributed another 24 %; and Peru, Venezuela, and Ecuador accounted for 20 %. The rest of the countries accounted for the remaining 6 %. Average growth rate projection (2010–2015) for the population of *Alouatta* range countries is estimated at 1.34 % (±0.54 %), but this varied from 0.2 %/year in Guyana to 2.5 %/year in Guatemala. In contrast, in developed nations the projected growth rate for the period is 0.4 % (UNFPA 2011). In *Alouatta* range countries in South America, the human population increased from ca. 232 million in 1980 to ca. 396 million in 2010, and projection estimates place the population at ca. 500 million by 2030 (Fig. 14.1a). Increasing demand for land, water, and food production from a rapidly growing human population are enhanced by global market to produce animal and plant food products (see sections 8 and 9 below). Continued growth of human populations and the negative relationship found between human population density and forest cover as percent of land area for the 21 *Alouatta* harboring countries in the Neotropics (Fig. 14.1b), suggests future and growing pressures upon the persistence of *Alouatta* habitats and populations.

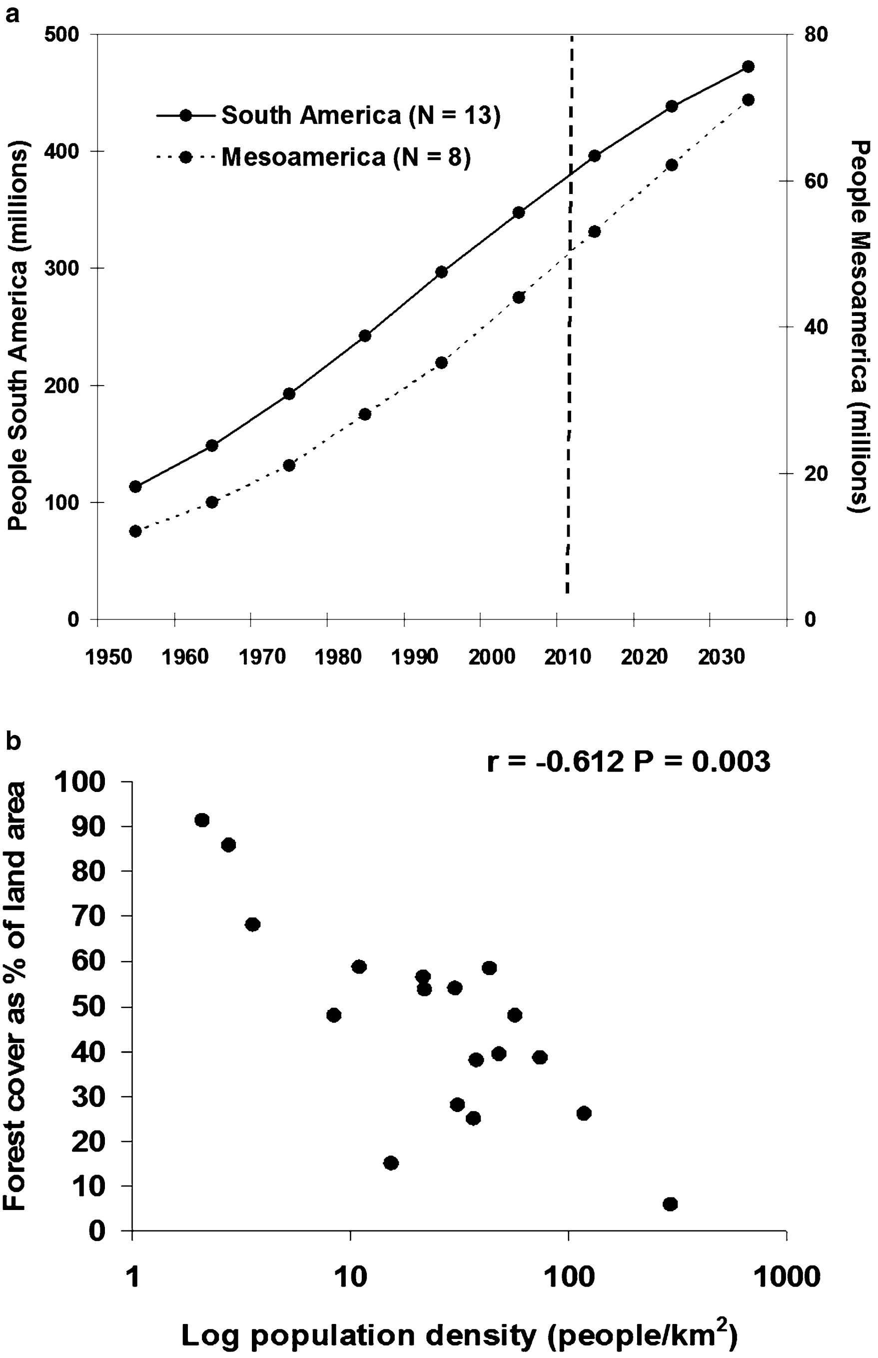

Fig. 14.1 (**a**) Human population growth trends in *Alouatta* harboring countries (*trend lines* after *broken line* are projections based on average annual growth rates for 2010 (*numbers* in parenthesis are the number of countries in each case), (**b**) relationship between human population density for Neotropical countries harboring *Alouatta* and forest cover as percent of land area. Human population growth data and projections from the UN Population Division [UNFPA 2011]. Forest cover as percent of land area from FAO [FAO 2011]

14.5 Human Development and Poverty in *Alouatta* Range Regions

It is inconsistent that amidst the enormous biological wealth of *Alouatta* range countries, high poverty and low human development are, according to the United Nations' (UN) Human Development Index (HDI), predominant features of their human inhabitants. The HDI focuses on three measurable dimensions of human development: living a long and healthy life (life expectancy), being educated (school enrollment and literacy), and having a decent standard of living (GDP per capita). Thus, it combines measures of life expectancy, school enrollment, literacy, and income to allow a broader view of a country's development than does income alone (UNDP 2011). A comparison of the mean HDI for the top 25 developed countries in the world with those of *Alouatta* range countries clearly shows a large gap between these two groups and stresses the need to improve living conditions for the inhabitants in the latter (Fig. 14.2).

According to the UNDP, the lack of steady economic growth in many tropical regions harboring primate populations and habitats makes it difficult or impossible to significantly reduce rural poverty, which in turn will continue to foster enormous pressure on natural habitats and weakly protected reserves (UNDP 2011). As a result, conservation approaches are required not only within, but also outside of protected area boundaries. The matrix of surrounding agricultural habitat may play an important role in long-term primate and biodiversity preservation and must be considered in landscape-level approaches to conservation (Estrada et al. 2012).

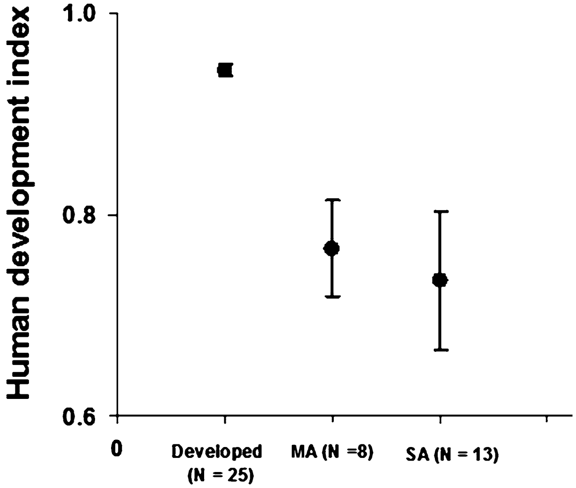

Fig. 14.2 Mean Human Development Index (HDI) for the top 25 developed countries in the world, and for *Alouatta* range countries in Mesoamerica (MA) and South America (SA) (UNDP 2012). Top developed nations: Norway, Iceland, Australia, Ireland, Sweden, Canada, Japan, United States, Switzerland, Netherlands, Finland, Luxembourg, Belgium, Austria, Denmark, France, Italy, United Kingdom, Greece, Singapore, Spain, New Zealand, Hong Kong China (SAR), Israel, Germany

14.6 Deforestation Trends in *Alouatta*'s Range

Data from FAO databases indicates that forest loss has been increasing over the last few decades in *Alouatta* range countries and that similar trends are evident in Mesoamerica and South America (Fig. 14.3). A business as usual scenario calculated at 50 and 100 years using an exponential decay model and deforestation rates for the period 1990 to 2010 projects further losses of forest cover with expected declines in the sustainability of extant *Alouatta* populations (Fig. 14.3).

Such changes are pressing if we consider that for Mesoamerica with a land area consisting of 750,656 km^2, the estimated average original forest cover as percent of land area (8,000 years ago assuming current climatic conditions) was 99 % (range 90 %–100 %). In 2005, forest cover as percent of land area was estimated at 32 % or a loss of almost 70 % of the original forest cover. This difference has been caused mainly by human activity (Estrada et al. 2006). For example, in this region deforestation rates for the period 1990–2010 resulted in the loss of 6, 218,000 ha of forest or about 310,000 ha per year (FAO 2011). Similar land cover changes can be observed in South America. It is estimated that in this region approximately 64 % of the total land area of *Alouatta* range countries (ca. 16,836,950 km^2) was originally covered by forests. As of 2005, estimated forest cover was about 7.5 million km^2 or 45 % of the total land area (Estrada 2009). Loss of forest cover for the period 1990–2010 was estimated at 82,103,000 ha or about 4,105,150 ha/year (FAO 2011).

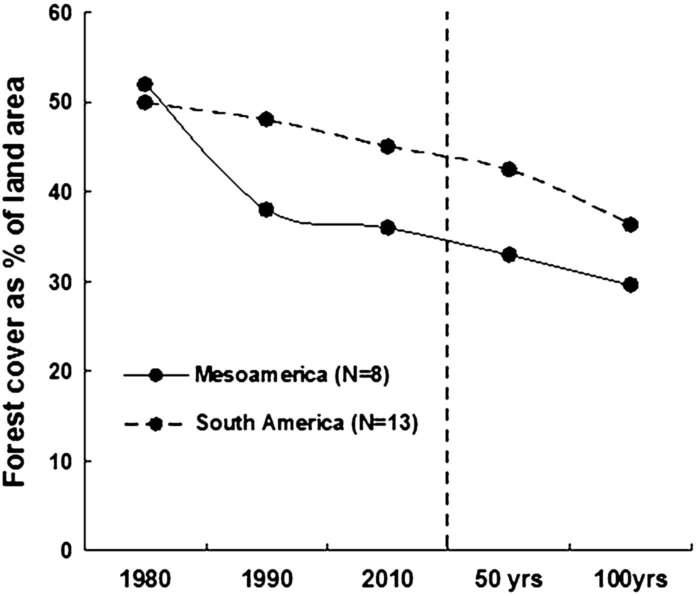

Fig. 14.3 Trends in forest loss for *Alouatta* range countries in Mesoamerica and in South America. Data points after the broken line are projections calculated by the author using deforestation rates for 1990–2005 fitted into an exponential decay model. Source of raw data: (FAO-Stat-land 2012)

14.7 Pasture Lands, Cattle Stock, Local and Global Market Demands, and Forest Loss

Nearly one third of the world's land area is used for food production, making agriculture the largest single cause of habitat conversion on a global basis (WWF 2011; USDA 2003). Such pattern is evident in many *Alouatta* range countries, where human-induced pasturelands and arable and permanent crop lands dominate significant portions of the landscape (Wassenaara et al. 2007).

For example, in the Neotropics, forest loss has been paralleled since the 1960s by significant increases in the extension of pasturelands and permanent croplands, with pasture lands accounting for about 80 % of this kind of land use (Fig. 14.4a). While this demand has been driven by population growth, urbanization, and increasing incomes in *Alouatta* range countries, more recently such land use has been more intensively driven by global market demands for livestock products (Delgado 2005; Lambin and Meyfroidt 2011).

Poverty and inadequate land tenure in *Alouatta* range countries drive the process of agricultural expansion and extensive cattle production, which offers economic flexibility and low financial risks (Steinfeld et al. 2006). The rapid growth of the cattle populations in the Neotropics in the last few decades (Fig. 14.4b) seems to be a response not only to local, but also to global demands, with 50 % of production exported to the United States and to the European Union (Steinfeld et al. 2006; Thornton 2010).

Because of the extensive nature of cattle production in the Neotropics, pasture degradation is common, thus maintaining the process of expansion. While the growth in local and global demands is in part met by enhanced productivity, it is done by increasing the number of animals which further fuels the transformation of forest into agricultural land (Thornton 2010). The importance of cattle in the economies of *Alouatta* range countries cannot be underestimated. Because the livestock sector is increasingly organized in long market chains, at a world scale it employs at least 1.3 billion people globally and directly supports the livelihoods of 600 million poor smallholder farmers in the developing world (Thornton et al. 2006; Thornton 2010). Currently, livestock is one of the fastest growing agricultural subsectors in developing countries (Steinfeld et al. 2006). Expansion of pasture into forest seems to be greater than that of crop land and this process is also responsible for the expansion of crop land into forest. For example, Amazonian biological hot spots in Brazil and Bolivia harboring populations of *Alouatta* are adjacent to large soybean production zones, the creation of which, largely driven by increasing animal feed needs, has caused large-scale deforestation in the recent past (Casson 2003; Hecht 2005; Morton et al. 2006; Greenpeace 2008).

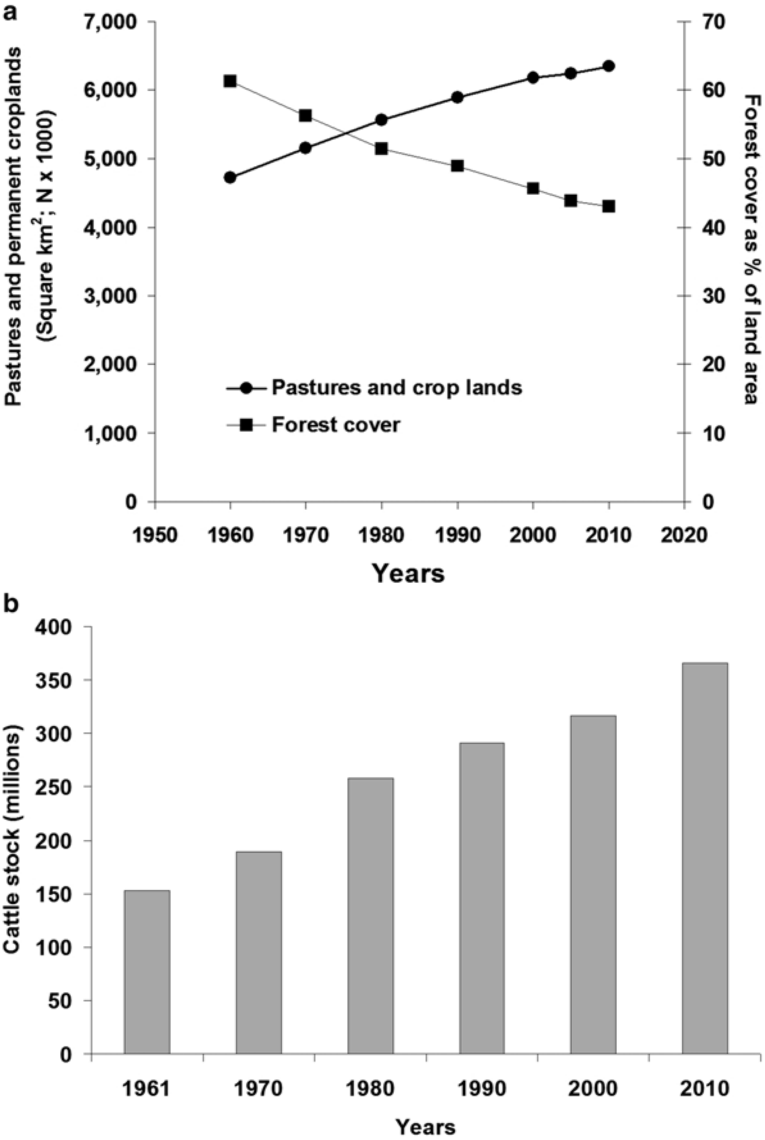

Fig. 14.4 (**a**) Expansion of pastures and croplands and declines in forest cover in primate range countries in the Neotropics; (**b**) trends in growth of cattle stock in *Alouatta* range countries (source: http://faostat.fao.org; Accessed 15 April 2012)

14.8 Global Market Demands for Soybeans and Oil Palm and Habitat Loss in *Alouatta* Range Countries

Soybeans (*Glycine max*) and oil palm (*Elaeis guineensis*) are increasingly of global importance not only as a source of food products for humans and domestic animals, but also and more recently, for liquid biofuel production (Fitzherbert et al. 2008; Koh and Ghazoul 2010). Soymeal is used for livestock production (single stomach animals: chickens/pigs) (Oil World 2002; Delgado 2005). Soy oil (a by-product of soymeal production) is used by the food industry to produce various food products (e.g., soy sauce, cooking oil, miso, soy milk, soy curd, tempeh, and tofu products) and by other industries to produce detergents, cosmetics, and various chemicals, among others (Oil World 2002; Casson 2003; USDA-FAS 2010). The oil palm, native to West Africa, is now cultivated in large-scale plantations throughout the tropics. It is used in a number of commercial products including cooking oil, soap, cosmetics, and margarine (USDA-FAS 2010). Both soybeans and oil palm are also used to produce biodiesel (Koh and Ghazoul 2010).

Because of rapidly growing markets in the European Union, the United States, Japan, and China and to a lesser extent in other countries, there has been a meteoric expansion in soybean and oil palm agriculture. In the Neotropics, and as a response to global markets, production of soybeans and oil palm has undergone an accelerated growth, especially in *Alouatta* range countries harboring large expanses of tropical forests such as Brazil, Colombia, Bolivia, and Ecuador (Fig. 14.5a). For example, forest-rich and *Alouatta* species-rich Brazil accounted in 2010 for 50 % of the land area (46 million ha) dedicated to soybean crops (FAOStats 2012; Fig. 14.5a).

Oil palm and soybean production have a significant direct and indirect impact on native habitat in *Alouatta* range countries because plantations are primarily large-scale, commercial monocultures. Development of monoculture plantations results predominantly in the total clearing of natural vegetation, and the use of pesticides and herbicides, which largely eliminate remaining vestiges of indigenous biodiversity, significantly diminish the chances of habitat restoration (Fearnside 2001; Laurance 2007; WWF 2010;). Soybean and oil palm production in pristine areas also requires the construction of massive transportation networks and other infrastructure projects. This in turn sets free a number of indirect consequences associated with opening up large, previously isolated environments to population migration and to other land uses, contributing directly and indirectly to declines in *Alouatta* habitat (WWF 2006).

14.9 Industrial Logging and Declines in *Alouatta* Habitat Quality

There is a good body of evidence indicating that industrial-scale logging operations in tropical countries have an important and long-lasting impact on tropical biodiversity, including primates. Reduction of canopy cover and increase canopy disturbance, destruction of forest undergrowth, decline of large tree species, and declines in tree

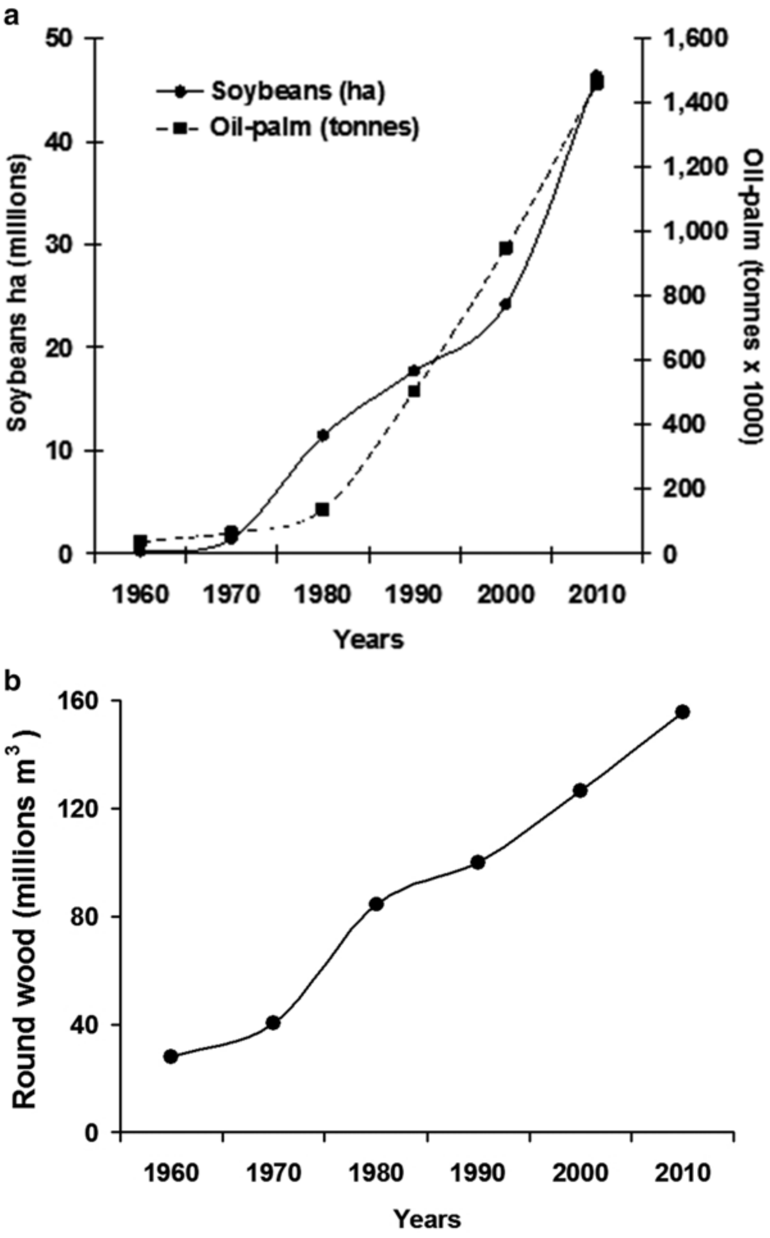

Fig. 14.5 Trends in production of (**a**) soybeans and oil palm, and (**b**) industrial round wood in *Alouatta* range countries (source: http://faostat.fao.org; Accessed 15 April 2012)

species of importance for primates as a source of food and shelter are, among others, important effects of high-intensity logging upon primates (Chapman and Peres 2001; Bawa and Seidler 1998). Recently, globalized financial markets and a worldwide commodity boom for tropical woods have led to an expansion of industrial logging (Butler and Laurance 2008). However, industrial logging promotes deforestation not only directly but also indirectly, by generating a potent economic impetus for road building in and near forests (Laurance and Peres 2006).

Alouatta range countries are responding to global market demands from developed countries and from China by expanding their industrial logging activities to increase economic growth. In 2010, the Neotropics accounted for 67 % of production of industrial round wood (ca. 300 million m^3), followed by Sub-Saharan Africa (23 %) and SE Asia (10 %) (FAO ForesSTAT 2012). Data for the period 1960 to 2010 show that logging operations (measured as production of industrial round wood in m^3) have grown rapidly in the Neotropics (Fig. 14.5b). Overall, in the Neotropics, industrial round wood production ranged from 28 million m^3 in 1960 to 155 million m^3 in 2010 (Fig. 14.5b). A large proportion of industrial round wood extraction takes place in Brazil, the largest country in the Amazon basin, accounting for 60 % of total industrial round wood production in 2010 (FAO ForesSTAT 2012). It is evident then that industrial round wood production is a major driver of current forest degradation, very likely impacting the persistence of population of many *Alouatta* species.

14.10 Natural Protected Areas and Conservation of *Alouatta*

Despite overpopulation, poverty and underdevelopment, and concerned with the conservation of their biodiversity, *Alouatta* range countries have taken important steps toward preserving their natural resources. All have ratified the International Convention on Biodiversity and have taken measures to protect natural ecosystems in their territories. NPAs are defined by IUCN as “A clearly defined geographical space, recognized, dedicated, and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values." (Dudley 2008). They are internationally recognized as a major tool in conserving species and ecosystems. NPAs as biosphere reserves, national parks, ecological reserves, and community reserves also provide a range of goods and services essential to sustainable use of natural resources.

Alouatta range countries have been building up their systems of NPAs (Fig. 14.6), but the number of protected areas vary considerably from country to country, depending on national needs and priorities, and on differences in legislative, institutional, and financial support (Rodrigues et al. 2004; Chape et al. 2005). According to the World Database on Protected Areas of the United Nations Environmental Program indicates that, as of 2010, there were a total of 860 NPAs and 2,830 NPAs in Mesoamerican and South American *Alouatta* range countries, respectively (Fig. 14.6a, b) (UNEP 2012). These NPAs protect an estimated 146,805 km^2 in Mesoamerica (about 20 % of total land area, 750,000 km^2) and 3,032,897 km^2 in South America (about 18 % of total land area, ca. 16,836,950 km^2). The same data set shows that the number of NPAs has steadily increased in *Alouatta* range countries since 1970 (Fig. 14.6). This also has been paralleled by increases in the number of square kilometers protected (from 43,008 km^2 in 1970 to 146,805 km^2 in 2010 in Mesoamerica and from 715,125 km^2 in 1970 to 3,032,898 km^2 in 2010 in South

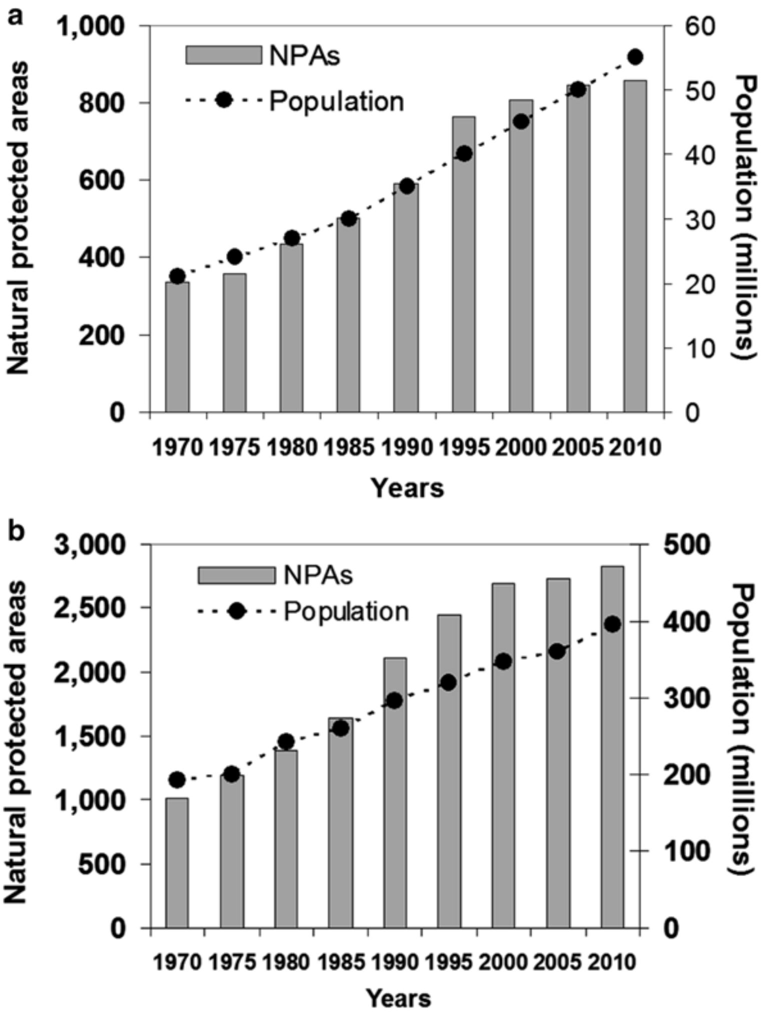

Fig. 14.6 Growth in number of natural protected areas from 1970 to 2010 in *Alouatta* range countries in (**a**) Mesoamerica ($N = 8$) and (**b**) South America ($N = 13$). Also shown is the trend in human population growth for the same time period for each region. Source of raw data for natural protected areas: (UNEP 2012); for human population growth: (UNDES 2012)

America), stressing the efforts by countries in these two regions to enhance conservation of their natural ecosystems.

Although protection of undisturbed habitat in NPAs (e.g., parks and reserves) is crucial for *Alouatta* conservation, it has been argued that these areas alone may not meet long-term conservation goals. To begin, the average landmass protected in many cases is not large enough, many of the NPAs may not be suitable for habitation by particular species, and in other cases species of interest may not be found within park boundaries (Carey et al. 2000; Chape et al. 2005). Other problems have to do with the fact that few of the areas are actually protected. More than 50 % of the protected areas are less than 10,000 ha in size, only some have specific management plans, many are understaffed, some are paper parks, and most are poorly delimited. Research projects are only being carried out in few of these protected areas, deforestation rates in surrounding areas are particularly high, and in many cases protected areas are virtual islands of vegetation surrounded by altered landscapes (Rodrigues et al. 2004; DeFries et al. 2007).

Despite these conditions, the UNEP considers that habitat conservation is vital for curtailing the decline in biodiversity and that the establishment of protected areas is an important mechanism for achieving this aim (UNEP 2012). In addition to protecting biodiversity, including many primate taxa, protected areas have become places of high social and economic value (Rodrigues et al. 2004; DeFries et al. 2007; Andam et al. 2008; WWF 2011; UNEP 2012).

Since it is likely that important segments of *Alouatta* populations occur outside of protected areas (see section 11 below), continued loss or degradation of natural habitats in these landscapes diminishes the ability of *Alouatta* to persist over generations. For example, among the Amazon basin countries, Brazil which harbors in its territory populations of 10 recognized species of *Alouatta* had, for the period 1990–2005, the highest loss of forest cover (423,290,000 ha), followed by Bolivia (61,274,000 ha), Venezuela (43,130,000 ha), and Ecuador (29,640,000 ha). While these four countries as a group accounted for 92 % of total estimated forest loss for this period, Brazil alone accounted for 76 % of this loss (Estrada 2009).

Pressure from human population growth upon NPAs is another issue that merits attention. Data from the UN Population Division shows that high human population growth has been running parallel to the growth of NPAs in *Alouatta* range countries in Mesoamerica and in South America (Fig. 14.6). This translates into rapidly growing demands for land for food production and for the extraction of other goods and services, which translates into local and regional landscape-level agricultural intensification, placing enormous pressure on *Alouatta* habitats, including protected areas. As a result, most protected areas are surrounded by, or are part of, a matrix of human-altered habitats (Mora and Sale 2011).

14.11 Estimated Range Extension and Protected Area Within the Estimated Range of *Alouatta* Species

Based on the IUCN RedList range maps database, the estimated ranges of each *Alouatta* species and of the protected area existing within each are shown in Table 14.2. The range shown for each species is a gross estimate made by the IUCN RedList based on historical and current records. The digitized measures of range extension for each *Alouatta* species indicate that this varied from 15,000 km^2 (*A. ululata*) to 340,000 km^2 (*A. seniculus*) with an overall mean of 145,517 ± 108,478 km^2 (Table 14.2; Fig. 14.7). Species such as *A. seniculus*, *A. juara*, *A. macconnelli*, and *A. pigra* have estimated range extensions >200,000 km^2.

Table 14.2 Estimated range of each *Alouatta* species and estimated area protected within each range by existing systems of protected areas

Alouatta species	Species estimated range (km^2)	Estimated extensión of NPAs (km^2)	% of range protected	Range map URL
A. seniculus	339,625	109,511	32	http://maps.iucnredlist.org/map.html?id=43929
A. juara	333,730	109,511	33	http://maps.iucnredlist.org/map.html?id=922
A. macconnelli	253,434	126,963	50	http://maps.iucnredlist.org/map.html?id=40642
A. pigra	213,000	85,050	40	http://maps.iucnredlist.org/map.html?id=914
A. guariba	186,517	31,770	17	http://maps.iucnredlist.org/map.html?id=39916
A. puruenses	155,574	78,640	51	http://maps.iucnredlist.org/map.html?id=136787
A. belzebul	140,626	64,300	46	http://maps.iucnredlist.org/map.html?id=39957
A. caraya	121,775	30,890	25	http://maps.iucnredlist.org/map.html?id=41545
A. palliata	96,392	25,697	27	http://maps.iucnredlist.org/map.html?id=39960
A. discolor	68,613	40,000	58	http://maps.iucnredlist.org/map.html?id=43912
A. arctoidea	61,408	19,465	32	http://maps.iucnredlist.org/map.html?id=136486
A. nigerrima	35,564	14,735	40	http://maps.iucnredlist.org/map.html?id=136332
A. sara	15,759	7,100	45	http://maps.iucnredlist.org/map.html?id=41546
A. ululata	15,218	5,210	40	http://maps.iucnredlist.org/map.html?id=918
Average		53,489		
Total	2,037,235	748,842		
Overall %			37	

Estimates made by digitizing range maps and natural protected areas (NPAs) within each map for each *Alouatta* species from the IUCN RedList database (IUCN 2012). Species are ranked from largest to smallest estimated range. Also shown are the URL for each map

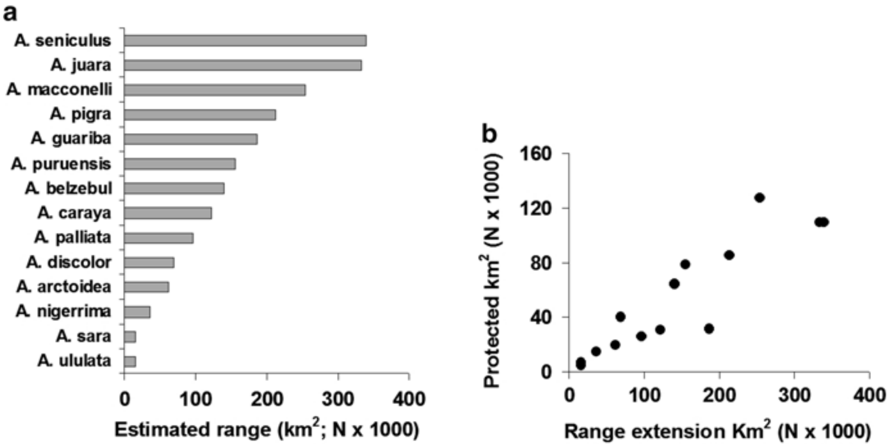

Fig. 14.7 (**a**) Square kilometer protected, as natural protected areas (NPAs), within the estimated range of each species of *Alouatta* as per the IUCN RedList database. (**b**) Relationship between expected range extension of *Alouatta* species and square kilometer protected within their range by NPAs. Source of raw data: (UNEP 2012)

While species such as *A. guariba*, *A. puruensis*, *A. belzebul*, *and A. caraya* have range extensions >100,000 km^2 and <200,000 km^2. Species such as *A. palliata*, *A. discolor*, *and A. arctoidea* have ranges >50,000 km^2 and <100,000 km^2. Finally, three species, *A. nigerrima*, *A. sara*, *and A. ululata*, have ranges <50,000 km^2 (Table 14.2; Fig. 14.7a). Range extension and number of km^2 protected within the range were strongly correlated ($r = 0.90$ $P < 0.001$; Fig. 14.7b), suggesting that, in general, species with large geographic ranges tend to have larger areas under protection within their estimated range.

The estimated number of square kilometers protected via NPAs within the range of each species varied from 5,000 km^2 (*A. ululata*) to 127,000 km^2 (*A. macconnelli*), with an overall average of 53,489 km^2. Percent of range protected varied from 17 % in *A. guariba* to 58 % in *A. discolor*, with an overall value of 37 % (±11.3 %) (Table 14.2; Fig. 14.7). In general, cumulative range for *Alouatta* species in the Neotropics was estimated at 2,037,235 km^2 of which 37 % is under some form of government protection (biosphere reserves, national parks, or other). This in turn suggests that about 63 % of the distribution of *Alouatta* species is found outside protected areas. As commented in the earlier section, many protected areas suffer many problems of sustainability and hence *Alouatta* populations found within may also be at risk.

Considering the above, it is important to keep in mind that this is a theoretical exercise and that significant extensions of *Alouatta*'s native habitat have been destroyed by human activity over the last five to six decades in many segments of the range of each species and that the range of each *Alouatta* species in many local areas is largely unknown. Projected future human population growth paralleled by growing local and global market demands will continue to expand the agricultural frontier in *Alouatta* range regions, exerting important pressures upon extant *Alouatta* habitats, including those in NPAs, and upon the long-term capacity of populations to persist.

14.12 Information Vacuum on Some *Alouatta* species

Examination of the PrimateLit database revealed the existence of 1,318 published papers for the genus. Thirty-six percent of these belonged to reports on *A. palliata*. An additional 20 % were reports on *A. caraya*. Three species (*A. pigra*, *A. seniculus*, and *A. guariba*) accounted for 34 % of records and three more (*A. fusca*, *A. belzebul*, and *A. ululata*) for <10 % of records (Fig. 14.8). No records existed for *A. discolor*. Almost 60 % of records come from studies of two *Alouatta* species (*A. palliata* and *A. caraya*), strongly suggesting an important lack of information on the majority of species in the genus. It is evident from this examination that the distribution of published reports on *Alouatta* is heavily skewed toward a few species (Fig. 14.8a). Hence, the contention that *Alouatta* is one of the most studied primates in the Neotropics may need to be reconsidered.

The PrimateLit database also indicates that about 50 % of published information on *Alouatta* comes from studies conducted in Brazil (25 %), Mexico (16 %), and

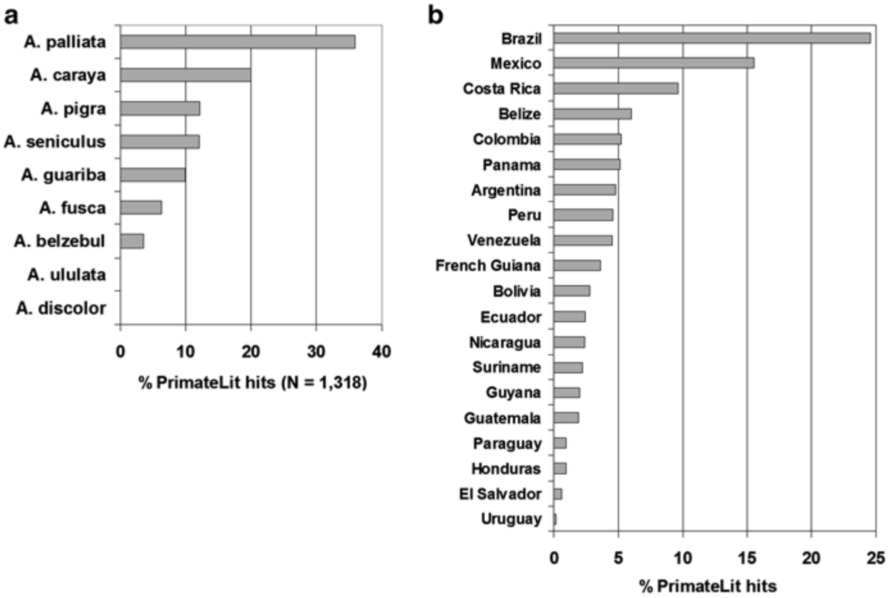

Fig. 14.8 PrimateLit hits on (**a**) *Alouatta* species and (**b**) *Alouatta* range countries. Source of raw data (PrimateLit 2012; 1,318 hits)

Costa Rica (10 %) (Fig. 14.8b). Another 30 % is contributed by research in Belize, Colombia, Panama, Argentina, Peru, and Venezuela. The remaining 20 % comes from research in 12 additional *Alouatta* range countries (4 from Mesoamerica and 8 from South America). These patterns suggest that while research efforts, as seen in the published literature, have accumulated information for each *Alouatta* species, there is still a large data vacuum for many geographic localities and regions and countries where *Alouatta* is present.

14.13 Land Management Scenarios that May Mitigate Reduction in *Alouatta* species Range

Among key initiatives undertaken by *Alouatta* range countries to protect their biodiversity as a national priority are (1) the establishment of systems of NPAs, along with more local initiatives such as community-based reserves, ecological reserves, and biological field stations (Carey et al. 2000; Chape et al. 2005; UNEP 2012); (2) programs promoting community-based sustainable use of the forest, e.g., growing shade coffee and cacao, forest-shade spices, ornamental plants, and ecotourism projects, among others (3) projects promoting restoration of native habitats in human-altered landscapes such as reforestation, establishment of biological and biodiversity corridors, and species reintroductions (Sanderson et al. 2003; DeFries et al. 2007).

Using remote sensing technology and ground surveys involving social, economic, demographic, and biological assessments, *Alouatta* range countries may significantly improve monitoring of land cover changes caused by human activity over vast and over specific regions and across years (DeFries et al. 2007). Such technology can also be used to project networks of biodiversity corridors that would connect protected areas in each country and between countries (Transboundary conservation; GTBCN 2012a). The cardinal principle of this strategy must be to avoid fragmentation of natural areas and the resulting isolation. A major focus of the biodiversity corridor concept is to integrate conservation and sustainable use of biodiversity within the framework of sustainable economic development (Chazdon et al. 2009). The significance of biodiversity corridor projects for conservation of *Alouatta* populations and species cannot be underestimated. Biodiversity corridors can result in (1) increased area of habitat available, (2) increased habitat connectivity, (3) a possible increase in effective population size, and (4) increased probability of persistence (Sanderson et al. 2003). An example of this approach is the Mesoamerican Biological Corridor project involving eight countries and now in its implementation phase (GTBCN 2012b).

Considering that high rates of human population growth in *Alouatta* range regions runs parallel to the growth of NPAs, suggesting important pressures upon their integrity (Fig. 14.6), and that in several cases important segments of *Alouatta* populations may occur outside protected areas, other complementary conservation approaches are required. More research is needed on landscape-level approaches to *Alouatta* conservation. Here, the potential of some land-use practices associated to production of commercially important crops for *Alouatta* conservation needs evaluation (Schroth et al. 2004; Estrada et al. 2012). Human-modified landscapes used for agricultural and cattle production in the Neotropics may range from highly homogenous, where monocultures (e.g., pasturelands, soybeans) dominate the landscape, to highly heterogeneous, in which the landscape space is shared by various types of agroforests, forest fragments, and pastures (Estrada 2006; Estrada et al. 2012). In these landscapes, the presence of networks of linear strips of vegetation represented by live fences and hedge rows planted by humans and of riparian corridors preserved by humans for water conservation and shade may support the dispersal of primates (Estrada 2006).

Highly heterogeneous landscapes, in particular, may play an important role in medium and long-term primate preservation and must be considered in landscape-level approaches to *Alouatta* conservation (Didier 2010). A recent review reports populations of five *Alouatta* species (*A. palliata*, *A. pigra*, *A. caraya*, *A. seniculus*, *and A. guariba*) using 15 types of arboreal agroecosystems as temporary or permanent habitats in human-modified landscapes (Estrada et al. 2012). Occasionally, plantation managers/owners benefit from the presence of primate groups, especially when tourism generates extra income. In southeast Mexico, for example, a cacao plantation successfully integrated the presence of *A. palliata* into marketing as a conservation strategy attracting tourists (see https://www.facebook.com/fincacholulatabasco).

While howler monkey populations that disperse into the anthropogenic landscapes as a result of habitat fragmentation and isolation may face important risks such as increased predation by humans and dogs, and increased exposure to disease (e.g., pathogens and parasites) from humans and domestic animals and contaminated sources of water, in heterogeneous landscapes they may find shelter, food, and opportunities to disperse into new groups. Such opportunities may allow *Alouatta* populations to persist for many years in anthropogenic landscapes and thus active conservation efforts are required not only within but also outside of protected area boundaries (Naughton-Treves and Nick 2004; Estrada et al. 2012).

14.14 Conclusions

One critical aspect related to conservation of *Alouatta* within its natural range is the lack of sufficient information on its natural history, ecology, behavior, and general biology. Without such knowledge, conservation initiatives are likely to be of limited success. For many *Alouatta* species and populations, there is limited information regarding their current range, the specific location, number and density of groups, and about their status of conservation. Only a very few *Alouatta* species have been studied in some detail, and even for these species only certain aspects of their behavioral ecology, reproductive biology, and life history are known (e.g., diet, ecological interactions, and social behavior) (see Dias and Rangel-Negrin 2014; Cristóbal-Azkarate et al. 2014, and Barbisan-Fortes et al. 2014). For the rest, there is no information or, at best, anecdotal information because of the short-term nature of the studies. In addition, there is a need to determine how many of these studies simply replicate each other, what information on *Alouatta* is lacking, and what specific research questions need to be addressed over the coming decade.

The broad geographic distribution of the genus *Alouatta* in the Neotropics is taken as proof of ecological and phenotypical variability, but we fail to recognize that much of this may be the result of adaptation to past evolutionary events and may not necessarily reflect sustainability in twenty-first century ecosystems (Cavender-Bares and Wilczek 2003; Cavender-Bares et al. 2009). We infer much from a few data points and seek shelter into the canon of extreme ecological and behavioral plasticity as a quick and easy explanation for what we see today. The truth is we do not have enough information. The limited data available for many *Alouatta* species seriously hinders our ability to make accurate predictions concerning the current and future danger of local extinctions of populations, as howler monkey habitats and populations face unparalleled threats of human origin, ranging from extensive land cover changes where native habitat is rapidly converted to cropland and pasture, to habitat fragmentation and isolation, to the introduction of invasive species, to increasing risk of infection from human pathogens, to overhunting, and to climate change (Gardner et al. 2006; Laurance and Peres 2006).

It is also evident that there is a critical data vacuum on detailed and quantitative information on the conservation status and sustainability of *Alouatta*. The current information on the natural history, ecology, behavior, and biology available of the genus comes from a less than handful of species. Important anthropogenic pressures seem to be reducing and shifting the distribution and range of *Alouatta* populations and species, but no precise information on this is available. Populations of ten species of *Alouatta* have been identified as declining by the IUCN and for four additional species the status of the population is unknown. Detailed information on the current local distribution of each species does not exist. We have no accurate information about the proportion of populations of each species existing in NPAs. Local and global demands from tropical land continue to mount with expected further reductions in available *Alouatta* habitat. The fate of populations in fragmented landscapes is uncertain while in many instances primatologists continue to employ traditional approaches to conservation that may be of limited application to the successful conservation of populations.

More research is needed to fill this void of information and on the impact of local and global market demands for particular localities, regions, and countries. More assessments are needed on human population growth projections and on profiling intensification of agricultural activity and of extraction of other goods and services from *Alouatta* native habitats at the local and country level. These may inform us of current and future pressures and thus conservation initiatives could be adjusted accordingly. Remote sensing can be an important tool to monitor land cover changes at the local-, region-, and country-level scales. Consideration should be given to the use of drones, a new emerging technology less expensive than remote sensing, for monitoring land cover changes, potential connectivity among protected areas and/or forest remnants, and even may be used for primate censuses. Drone technology, originally for military use, is now beginning to be employed in surveying land use and wildlife, including orangutans in South East Asia (Kohn and Wick 2012).

It is evident that the above overview of *Alouatta* conservation is by no means comprehensive, but some general patterns emerge which are informative. It is palpable that the problem of *Alouatta* conservation has a complex multidimensional, social, and economic base that deserves research efforts, both at local and regional levels. Special attention needs to be paid to the role that global economic activity is playing in enhancing existing conservation problems and creating new ones. The fact that the Neotropics seems to be a major source of production of cattle stock, industrial round woods, and crops such as soybeans to satisfy local and global market demands, and that this has an important negative impact on the persistence of forest cover and increased degradation of native vegetation, is an issue of direct relevance to the conservations equation involving *Alouatta*, and merits vigorous investigation.

In reality, net forest loss continues at very high rates per year and the distribution of *Alouatta* habitats and populations continues to decline, a reason why more research efforts are needed to design ways to protect ecosystems, not only via NPAs but also through sustainable use initiatives outside of protected areas. Such an approach needs to consider that high rates of growth of the human population and high levels of poverty and low human development represent the pattern in *Alouatta* range nations.

To document, understand, and predict conservation pressures caused by human activity upon *Alouatta* habitats, populations, and species in particular geographic regions or localities is not an easy task. We need to examine multiple factors that vary across spatial and temporal scales, and realize these are distinct from species to species (Chapman and Peres 2001). In addition, country- and regional-level conditions vary depending on particular historical, demographic, ethnic, political, and economic conditions of each locality, country, and region. However, by examining some key sociological and economic contexts associated with habitat loss in *Alouatta*, we can gain insight into the past, current, and future impact of anthropogenic activities upon the persistence of howler monkey populations within their range. Equally important in this approach is to examine country- and regional-level conservation efforts, which may mitigate the negative effects of anthropogenic pressures upon *Alouatta* habitats and populations.

As evidenced by this review, I would like to conclude this chapter by emphasizing that much information is needed to adequately assemble conservation approaches aimed at ensuring the persistence of *Alouatta* populations and species in the twenty-first century. Clearly it is the human dimension of the conservation problem that merits our total attention if we are to gain important footholds in finding solutions. Moreover, conservation-oriented primatologists working with *Alouatta* need to conduct basic and diagnostic research and link information from these two areas to the human social dimension of the conservation problem (Fig. 14.9). Such an approach

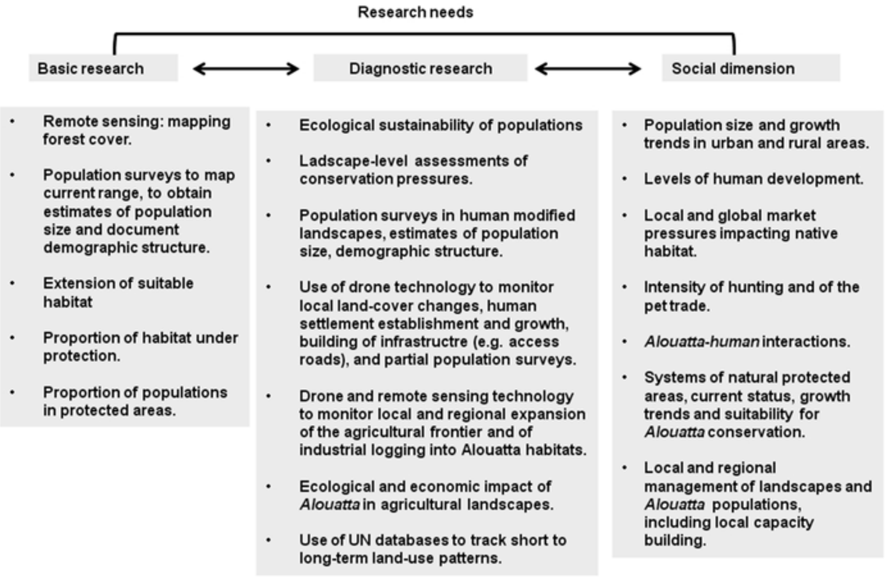

Fig. 14.9 Conservation-oriented research priorities for the current and the next decade. These revolve around three principal and mutually dependent areas of investigation

will yield the needed diagnostic platform upon which conservation programs at the local and regional level can be built.

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Part IV
Conclusion

Chapter 15
New Challenges in the Study of Howler Monkey Behavioral Ecology and Conservation: Where We Are and Where We Need to Go

Paul A. Garber and Martín M. Kowalewski

Abstract Howler monkeys comprise some 12 species of fruit, leaf, and flower feeding New World primates (see Cortés-Ortiz et al. 2014) that range from southern Mexico through southern Argentina and Brazil. *Alouatta* has the most widespread distribution of any platyrrhine genus and can exploit forest types that vary from undisturbed rainforest to severely anthropogenically impacted forest fragments adjacent to pastures, agricultural fields, and human communities (Estrada 2014). In many instances, howlers are the only primate species found in these highly disturbed habitats. Although there exist numerous short-term and long-term studies on individual howler species, the goal of this volume is to bring together a set of expert scholars, many from habitat countries, to contribute to a comprehensive volume that reviews, integrates, and evaluates current information on howler behavior, ecology, nutrition, reproduction, evolution, and conservation. Moreover, recently published studies on howler nutritional ecology, patterns of habitat utilization, mating strategies, collective action, and conservation highlight the growing importance of the genus *Alouatta* as a comparative model for examining parallel solutions to social and ecological challenges faced by species of prosimians, New World monkeys, Old World monkeys, and apes (Kowalewski and Garber 2010; Di Fiore et al. 2011; Garber and Kowalewski 2011).

Keywords Howlers • Conservation • Challenges • Research priorities

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15.1 Introduction

Howler monkeys comprise some 12 species of fruit, leaf, and flower feeding New World primates (see Cortés-Ortiz et al. 2014) that range from southern Mexico through southern Argentina and Brazil. *Alouatta* has the most widespread distribution of any platyrrhine genus and can exploit forest types that vary from undisturbed rainforest to severely anthropogenically impacted forest fragments adjacent to pastures, agricultural fields, and human communities (Estrada 2014). In many instances, howlers are the only primate species found in these highly disturbed habitats. Although there exist numerous short-term and long-term studies on individual howler species, the goal of this volume is to bring together a set of expert scholars, many from habitat countries, to contribute to a comprehensive volume that reviews, integrates, and evaluates current information on howler behavior, ecology, nutrition, reproduction, evolution, and conservation. Moreover, recently published studies on howler nutritional ecology, patterns of habitat utilization, mating strategies, collective action, and conservation highlight the growing importance of the genus *Alouatta* as a comparative model for examining parallel solutions to social and ecological challenges faced by species of prosimians, New World monkeys, Old World monkeys, and apes (Kowalewski and Garber 2010; Di Fiore et al. 2011; Garber and Kowalewski 2011).

Although there have been several recent volumes published on the ecology and behavior of Neotropical primates including capuchins (Fragaszy et al. 2004), spider monkeys (Campbell 2008), marmosets (Ford et al. 2009), and pitheciines (Veiga et al. 2013), as well as a set of companion volumes on Mesoamerican (Estrada et al. 2006a) and South American primates (Garber et al. 2009a), the current volume is distinguished by its focus on integrating data on howlers as a framework to understand other primate radiations. In addition, several of the chapters in our volume have advanced our understanding of howler behavioral ecology by defining the limits of and constraints of howler variability. Simply describing a taxon as plastic, variable or flexible, without quantifying how specific changes in the social and ecological environment directly affect the costs and benefits of particular behavioral and physiological responses, provides no information on how individual differences in behavior influence fitness. For example, the underlying substrate that determines behavioral variability may be genetic or physiological—following for example a developmental program—or it could be cognitive and reflect changes in decision-making in response to newly acquired or accumulated information (Maestripieri 2003). What is required to understand behavioral variability is information regarding the variance or norm of reaction of a particular behavioral pattern or physiological system (phenotype) in response to changes in the social and ecological environment (Pigliucci 2001; West-Eberhard 2003) and then to examine how selection may act to limit or expand this norm of reaction (Callahan and Pigliucci 2002). Individuals in all primate species modify certain aspects of their activity budget, diet, social interactions, ranging behavior, and life history traits (e.g., inter-birth interval and time of first reproduction) under changing conditions. However, in some species the expression of variability in these traits is very narrow whereas in other species the expression varies more widely. For example, certain aspects of howler behavior such as devoting 60–80 % of their daily activity budget to resting and 10–15 % to travel, or consuming a diet that principally includes fruits and leaves or utilizing a day range of 200–500 m to satisfy daily nutritional and social demands vary minimally across species (Di Fiore et al. 2011; Garber et al. 2014). Other aspects of howler behavior and demography such as group size and composition, population density, patterns of migration, risk of infanticide, and reproductive seasonality vary more widely. For example, in *Alouatta guariba* population density ranges from 48 to 117 ind/km^2, whereas in *A. palliata* population density ranges from 5 to 30 ind/km^2, and in *A. caraya* population density ranges from 81 to 280 ind/km^2 (Di Fiore et al. 2011). Similarly, mean group size in *A. caraya* ranges from 6 to 18, 9 to 22 in *A. palliata*, but only 6–7 in *A. guariba* (Di Fiore et al. 2011). Thus, we need to identify the social, ecological, and physiological factors that set limits on howler demography and distribution. For example, do site-specific differences in the availability and nutrient content of food constrain howler group size, composition, and demography? Or, do individual differences in social tolerance, conditions favoring collective action, kinship, the operational sex ratio (number of fertilizable females to adult males), and/or risk of infanticide set limits on howler group size, composition, and demography? In this regard, authors in this volume have attempted to define or outline the general howler adaptive pattern, as well as the range of species-typical responses that distinguish a given howler species or species group from another.

15.2 New Directions

A second goal of this volume is to identify a set of new research techniques and new research questions that can advance our understanding of primate behavior and ecology. Although traditional methods such as time spent feeding on fruits, leaves, and flowers or the number of plant species consumed in a given month or year have served to distinguish the basic dietary patterns that characterize different primate taxa, at a more fine-grained level, these data are limited in identifying how diet, nutrition, and feeding ecology are linked to primate fertility, health, social organization, and fitness, and the implications this has for primate conservation. Below we describe several new approaches to the study of primate feeding ecology that we feel can better address research questions linking primate feeding ecology to issues of nutrition, health, reproduction, and conservation.

15.2.1 Nutritional Ecology

The idea that animals have the ability to efficiently locate, consume, and process resources that offer a nutritionally balanced diet during both food limited and food abundant periods of the year is a commonly held assumption of models of optimal foraging (Milton 1980; Stephens and Krebs 1986; Snaith and Chapman 2007). Within this framework, animals are assumed to behave as rational consumers, accurately evaluating and comparing the net benefits of alternative foraging strategies and selecting the most efficient feeding patch or food item (Timberlake et al. 1987). Similarly, there is general agreement that primates living in anthropogenically disturbed and fragmented forests face significant challenges in obtaining sufficient resources to meet their energetic and nutritional requirements for maintenance, growth, and reproduction. Thus, there appears to be an important link among diet, feeding ecology, nutrition, and the ability of primate populations to survive in disturbed habitats. However, the specific behavioral, cognitive, social, physiological, and neurological mechanisms that underlie primate food choice, decisions of when to leave a food patch, and which patch to visit next are poorly understood. In this regard, a major question in primate behavioral ecology is the degree to which individuals are able to "detect" short-term deficits in nutrient intake and respond by altering their feeding behavior in an appropriately compensatory way. Recent models of nutrient balancing (Felton et al. 2009a; Rothman et al. 2011; Raubenheimer and Rothman 2013; Behie and Pavelka 2014; Garber et al. 2014; Amato and Righini 2014) offer a critical framework for examining foraging strategies and food choice in howler monkeys, and the ability of primates to associate particular foods with their micro- and macronutrient content.

15.2.2 Nutrient Balancing

There is evidence that animals have "appetites" and can learn to associate the color, flavor, taste, smell, and/or texture of particular foods with their protein, carbohydrate, and lipid content (Di Battista and Holder 1998; Sclafani 2004). In this regard, it has been argued (Stricker 2000: 6) that internal signals "provided by neural input…. blood-borne substrates, or hormones detected in the brain" help guide or stimulate the ingestion and appetite for particular nutrients. Moreover, studies on human subjects indicate that individuals fed a nutrient-poor or a nutrient-rich food will compensate and select subsequent meals that balance nutrient intake over time intervals that range from as short as 30 min to several days (de Castro 1998; Rolls 2000).

Different plant parts and food species consumed by nonhuman primates vary in their energetic value, protein, lipid, carbohydrate, and mineral content, as well as the presence of secondary compounds (Garber 1987; Simmen et al. 2007; Felton et al. 2009b; Norconk et al. 2009; Lambert 2011; Righini and Garber 2012). Under conditions of nutrient mixing, a forager is expected to leave a productive food patch before it is depleted or below the average patch value in order to locate a new food type or food species that offers a different or complementary set of nutritional rewards (Charnov 1976; Freeland and Janzen 1974; Westoby 1974; Stephens and Krebs 1986; Ganzhorn and Wright 1994; Jimenez 2004; Zhao et al. 2013). This might mean switching from ripe fruits to insects to increase protein and lipid intake, switching from leaves of an evergreen species to leaves of an early successional plant species to reduce the intake of fiber and secondary compounds, or switching from one species of ripe fruit to another species of ripe fruit in order to increase the consumption of lipids or nonstructural carbohydrates (Milton 1979; Glander 1981; Jimenez 2004; Simpson et al. 2004). For example, in a study of the nutritional composition of nine fig species in Uganda, Conklin and Wrangham (1994: 149) argue that although "figs provide an acceptable baseline level of ME [metabolizable energy] and protein," given differences in the nutritional content across fig species, the ripe fruits of one species of fig are not substitutable or nutritionally equivalent to the ripe fruit of another species of fig. These authors report that some species of *Ficus* in the same forest contained 4–5 times more proteins and lipids, and twice the metabolizable energy than other fig species (Conklin and Wrangham 1994). Similarly, one must use extreme caution in assuming that in different forests particular food items such as young leaves and mature leaves differ predictably in their nutrient content. A recent study by Righini (2014) on the feeding ecology of *Alouatta pigra* in Mexico found no significant differences in crude protein, available protein, non-detergent fiber, hemicellulose, cellulose, lipids, nonstructural carbohydrates, and condensed tannins in mature and immature leaves consumed by black howlers. Thus, it appears that individual howlers were targeting leaves that had a particular nutritional profile, regardless of stage of maturity, and avoiding leaves produced by trees that failed to provide them with an adequate nutritional/toxin profile. In addition, Chapman et al. (2003) report considerably temporal, interspecific, and intraspecific variability in the concentration of proteins, structural carbohydrates, and toxins in the leaves of trees fed in by red colobus (*Piliocolobus tephrosceles*) and black and white colobus (*Colobus guereza*) inhabiting Kibale National Park, Uganda. In this regard, meaningful studies of howler food choice, food sampling, and dietary strategies whether in continuous forest, forest fragments, or in highly disturbed areas will need to include, as part of their research protocol, the nutritional analysis of plant tissues from the individual trees fed in and not fed in by howlers.

15.2.3 Female Energy Requirements

In a recent study, McCabe et al. (2013) examined the energetics of primate reproduction by measuring C-Peptide levels in the urine of wild female Sanje mangabeys (*Cercocebus sanjei*) to assess energy balance. C-Peptide is a biomarker associated with the production of insulin and is an indicator of the body's response to changes in plasma glucose levels (Slabber et al. 1994; Emery Thompson et al. 2009). Increased levels of C-Peptide are indicative of a positive energy balance and the ability to store glucose in the form of glycogen. McCabe et al. (2013) outline three nutritional strategies female primates might use during periods of high fruit availability to insure energy surplus and energy storage that could be mobilized during more energetically demanding periods such as late pregnancy and lactation. These include increasing time spent feeding, increasing feeding rates (amount ingested), or increasing dietary selectivity and targeting resources that are high in available energy. Each of these feeding strategies might enable females to store resources during periods in which high energy foods are most available. The results of this study indicate that periconceptive mangabey females (females who were preconceptive or in the early phase of gestation) and nonpericonceptive females (females during late gestation and early lactation) did not increase time spent feeding, time spent foraging, or their feeding rate. However, the proportion of lipids in the diet of periconceptive females increased from approximately 7–14 %, and the proportion of both lipids and proteins in the diet of nonpericonceptive females increased from approximately 7–18 % and 27–33 %, respectively (Fig. 3 in McCabe et al. 2013). Nonpericonceptive females also consumed food at a faster rate than did periconceptive females (106.5 vs. 58.3 g/h) (McCabe et al. 2013). Lipids represent an energy-rich nutrient that contains more than twice the concentration of energy than proteins or carbohydrates (9 vs. 4 kcal/g; Ullrey et al. 2003). Given that female mangabeys are considered capital breeders (capital breeders store energy when food is abundant for use during nutritionally expensive reproductive periods (Brockman and van Schaik 2005)), they appear to consume and store calorie-rich foods such as fruits high in lipids and sugars as part of a nutritional strategy to support reproduction during food limited times of the year (McCabe et al. 2013).

Although little is known regarding nutritionally based reproductive strategies in howler monkeys, in some populations infants tend to be born during a limited period of the year, often the dry season, whereas in other populations there is no evidence of reproductive seasonality (Crockett and Rudran 1997; Kowalewski and Zunino 2004; Di Fiore et al. 2011). Assuming that female howler monkeys are able to alter food choice in such a way as to (1) overeat and store energy during one time of year and later reinvest this energy in response to the elevated costs of reproduction or (2) target high energy foods during lactation, then future studies need to examine evidence for sex-based differences in nutritional strategies. A recent study by Righini (2014) examining this question in black howler monkeys (*Alouatta pigra*) found that although females consumed more energy than males throughout the year, these differences were not significant. Thus, in the absence of additional studies, the degree to which differences in the availability and nutritional content of foods consumed in different habitats affect howler reproductive ecology and female food choice remain unclear. However, new methodological techniques such as stable isotope analysis (SIA) (Reitsuma 2012; Sandberg et al. 2012) and identifying the taxa of insect DNA present in primate feces (Pickett et al. 2012) offer researchers new tools to document individual, age, sex, and species-based differences in diet and patterns of canopy and habitat utilization (Dias and Rangel-Negrin 2014). Both SIA and insect DNA techniques rely on fecal samples which are relatively easy to collect and store in the field, and provide quantitative complementary data strengthening behavioral observations.

15.2.4 Gut Microbial Ecology

As indicated by Amato and Righini (2014), changes in the ratio or type of gut microbacteria can play a critical role in host nutrition, metabolic activity, and immune function. Although studies of the nonhuman primate microbiome are limited, it is possible that during seasonal changes in resource availability or increased nutritional demands (growth, reproduction, development of secondary sexual characteristic) individual variation in the host gut microbial community may enable individuals exploiting the same diet to differentially extract and assimilate nutrients. For example, in a recent study by Amato (2013), changes in the diet of wild black howler monkeys (*A. pigra*) across time were correlated with shifts in gut microbial community composition and function. Amato (2013) found that females and juveniles were able to extract more energy and vitamins than adult males while consuming a similar diet. Moreover, although Firmicutes, Bacteroidetes, and Proteobacteria were the three most common gut bacterial taxa present in all group members, individuals differed in their proportion of particular gut microbes (Amato and Righini 2014). Thus, age and sex-based shifts in microbiome diversity may enable group members to satisfy their individual nutritional requirements without major shifts in diet, activity budget, or patterns of habitat utilization.

Moreover, there is evidence in black howler monkeys that host microbial communities differ among individuals living in distinct habitats, possibly in response to differences in the nutritional profile of resources consumed or differences in gut microbial diversity in these habitats (Amato 2013). This has important implications for primate conservation and the ability of howlers to survive in altered landscapes, as the reduction or loss of natural microbial communities or the introduction of new microbial communities in response to environmental change, pollution, or other factors, can affect host nutrition, health, and immune function. As a result, it is critical that discussions of behavior, ecology, diet, and conservation consider host–microbe interactions. New research projects that emerge from the study of primate-microbial ecology and host-microbial coevolution include: (1) analyzing soil, plant, and environmental microbial community composition during different times of the year and in different primate habitats; (2) testing the assumption that if the gut microbiota adapts to host diet and/or life history stage (i.e., reproduction and growth) and acts to increase digestive efficiency, then host energy balance is expected to remain relatively constant over time, while the gut microbiota and products of microbial fermentation should vary; (3) obtaining measurements of glucocorticoid levels, Immunoglobulin A, Immunoglobulin B, and T-cell levels, in conjunction with data on parasite prevalence and abundance (Martinez-Mota et al. 2014) to evaluate immune function, and relationships between gut microbial diversity and indicators of stress. Recent studies indicate that a reduction in gut microbial diversity has been associated with increased host glucocorticoid levels (indication of increased stress) in some primate taxa (Martinez-Mota et al. 2014). Finally, (4) researchers may consider developing experimental studies in which nonhuman primates receive controlled probiotic (live bacteria) supplementation to determine how changes in the gut microbial community affect host health and nutrition independent of changes in diet.

Relatedly, challenges researchers face in evaluating the health consequences and severity of parasite loads in howler populations exploiting habitats differentially exposed to humans, cattle, and other domesticated animals are (a) applying recently developed molecular tools to accurately identify parasite taxa, (b) determining the life cycles of individual parasite species infecting howlers, and (c) determining exactly how habitat disturbance and forest fragmentation affects parasite survivorship. The collection of these data represents an important advancement in determining parasite pathogenic potential, and in evaluating the conditions that promote the proliferation of different parasites within their howler hosts (Martinez-Mota et al. 2014).

15.2.5 Seed Dispersal

There remain several important questions that need to be addressed to improve our understanding of the effect that howler monkeys have on forest regeneration in their role as seed dispersers and seed predators. Although howlers, like virtually all fruit-eating primates both prey upon and disperse seeds, studies of intraspecific and inter-specific differences within the genus are lacking. Such differences in the quality of seed dispersal among howler species are likely to exist, given differences across *Alouatta* populations in the plant species composition of the diet, the proportion of fruits consumed, and the biomass of howlers relative to other frugivorous animals (see Dias and Rangel-Negrin 2014; Garber et al. 2014). To date, most studies of howler seed dispersal have occurred in well-conserved or protected forests. Thus, more research is needed in fragmented/degraded forests in order to assess, for example, if seed dispersal effectiveness is lower or higher in these habitats (possibly higher given the absence of other large bodied frugivores or possibly lower in small forest fragments because a large proportion of seeds are deposited at the same latrine sites), whether the loss of particular members of a primate community and/or a reduction in primate population size negatively affects patterns of forest regeneration, and the potential compensatory role of howlers in sites lacking other dispersal agents. Finally, although the quantity component of seed dispersal in *Alouatta* and other primates has received much attention, aspects of dispersal quality (e.g., moving seeds to sites suitable for germination) require additional study. More research is needed on (1) the effects of pulp removal (deinhibition) on seed fate, not only for defecated seeds but also for spat and dropped seeds; (2) the effects of gut passage on decreasing the viability of insect larvae present in ingested fruits/seeds; and (3) the impact of gut passage rate on seedling survival and growth.

Regarding the impact of howler monkeys on the spatial distribution of plants, no study to date has adequately assessed the effect of seed shadows created by howler monkeys on the current spatial distribution of adult trees of howler dispersed plant species. Future studies also must focus on post-dispersal seed fate (Garber and Lambert 1998; Vulinec and Lambert 2009) and secondary dispersal of seeds voided by primates. This includes an assessment of the importance of ants, dung beetles, rodents, other insect predators, and fungal pathogens in determining the fate of seeds dispersed by howler monkeys and other primates (Garber and Lambert 1998). Finally, detailed investigation of differences between clumped (e.g., in latrines) and scattered seed deposition patterns on seeds/seedlings survival and plant recruitment are needed (Lambert 1998) in order to test the hypotheses that seed dispersal by howler monkeys creates a patchy spatial distribution of preferred fruit-tree species (e.g., food gardens within the forest; Milton 1980) and that howler latrine sites improve the nitrogen level and fertility of tropical soils and aids in seedling establishment and survival (Estrada et al. 2006b; Arroyo-Rodríguez et al. 2014).

15.3 Conservation, Sustainability, and Environmental Change

Persistent habitat change in response to human population growth, deforestation, cattle ranching, the mining of precious metals, and the conversion of previously forested areas into monocultures (e.g., oil palm, maize, sugar cane, bananas, pineapples, soy) has resulted in expanded human encroachment into habitats traditionally occupied by natural animal and plant communities (Estrada et al. 2006b; Estrada 2014). Unfortunately, this situation will likely continue, as the global demand for these products increases. Net loss of forests is occurring at very high annual rates and as the availability of *Alouatta* habitats and populations declines, new natural protected areas and a priority to promote sustainable use initiatives outside of protected areas are critically needed (Estrada 2014). For example, in Costa Rica, natural parks are becoming islands, isolated from one another resulting in limited opportunities for gene flow or repopulation. Therefore, private reserves and land purchased by conservation-oriented NGOs are becoming more and more critical for primate conservation (Garber et al. 2009b). Sadly, in many primate habitat countries the conversion of forests for economic development has not resulted in lower rates of human population growth, a reduction in human poverty, an increase in educational opportunities, or elevating human development at the local or regional level (Estrada et al. 2006c). The fact that howlers have the ability to survive in close proximity to humans should not necessarily be of great comfort to conservationists. Genetic data indicate that in highly fragment forests group size often decreases, as does opportunities for gene flow increasing the likelihood of endogamy (Oklander et al. 2010). Also in these small forest patches, howlers may face increased exposure to parasitic or infectious diseases (Martinez-Mota et al. 2014).

In the case of *Alouatta*, populations of ten species have been identified as declining by the IUCN and for two additional species the status of the population is unknown. In the case of *A. caraya* (and possibly other howler species) regional evaluations describing them as ubiquitous and non-threatened only 10 years ago have been reevaluated and now this species is listed as vulnerable in Northern Argentina (Ojeda et al. 2012). Detailed information on the current local distribution of each species is not fully available, and this must be a conservation priority. In addition, we lack accurate information regarding the proportion of each howler species that is currently found in natural protected areas, and have even less information on the sustainability of populations in non-protected areas. New technologies such as use of remote sensing or drones may be required to map howler distribution across local and regional landscapes. These tools can be used to evaluate present distribution in response to the growth of human settlements and industrial-level agriculture, mining and logging, and the economic needs of local communities (Estrada 2014).

Given the ability of howler populations to survive in highly impacted habitats and in close proximity to human settlements, new studies of *Alouatta* also would benefit from a greater inclusion of "matrix" habitats into field research (Estrada 2009; McKinney et al. 2014). Howlers living in agroecosystems, forest fragments, ecotourism sites, and other modified landscapes are valuable populations for applied conservation efforts. In addition, the study of these human commensal populations will allow us to better define the limits of howler variability and the fitness costs to howlers of inhabiting environments characterized by specific types of habitat change. This should result in new theoretical frameworks for understanding the implications of behavior flexibility and behavioral rigidity across a wide range of specific behavioral and ecological contexts and allow us (1) to determine the minimum ecological requirements (e.g., plant species diversity, nutrition, microbacteria, disease vectors, space) for the persistence of a healthy sustainable population in anthropogenic habitats; (2) to quantify the risks (disease transmission, stress, immune suppression, reduced fertility) that traditional tourists, ecotourists, and the local human communities impose on *Alouatta* populations; and (3) to compare these risks with alternate uses of the landscape. These research initiatives are not only of scientific interest, but also will contribute to developing more effective conservation policies to ensure the survival of howler populations. Ultimately long-term research projects that provide economic and education opportunities for governments, business leaders, and members of local human communities and result in the collection of long-term data on changes in environment, primate demography, diet, disease, and the genetic structure of the population are essential for sustaining both the local human population and the local nonhuman primate population. Finally, as severe weather events become more frequent and intense in response to global warming, documenting the ability of individual primate populations to survive and recover in areas devastated by hurricanes, tsunamis, monsoons, flooding, and other catastrophic events will serve as a research tool essential for informed conservation planning (Behie and Pavelka 2014).

The captive management of howler monkeys is critical to efforts to rescue, rehabilitate, and release confiscated or injured primates back into the wild. In many cases zoos and rehabilitation centers are well positioned to expand their mission and programs of conservation management. These facilities provide an opportunity to generate scientific knowledge on howler monkey digestive physiology, focusing on the impact of adequate nutrition and the role of intestinal microbiota on health, stress, and fertility. Combining comparative studies of gastrointestinal microflora diversity and richness in captivity and in the wild represents the type of interdisciplinary and integrated research that will most effectively address questions concerning digestive and nutritional ecology, as well as identify digestive pathologies associated with low fiber diets and the development of howler monkey wasting disease.

15.4 Lacunae or Gaps in the Study of Howlers

Several important questions and gaps in our knowledge regarding the behavior, ecology, and conservation biology of howler monkeys remain. For example, despite the fact that endocrine studies have been incorporated into research on howler monkeys only recently, these studies have revealed several important insights into howler biology and sociality that were not anticipated based on behavioral data alone. This includes nonaggressive forms of intragroup male–male competition over access to females and the apparent greater sensitivity of females to social and ecological stress than males (Van Belle and Bicca-Marques 2014). Future research needs to correlate changes in baseline steroid hormonal profiles with data on intra- and intergroup mating patterns, paternity assignment, and the costs and benefits of inter- and intrasexual social relationships in order to better understand the effectiveness of individual mating strategies on reproductive success.

Although there exist numerous studies of howler behavioral ecology, these have concentrated on only a few species, most noticeably *A. caraya*, *A. seniculus* (*arctoidea*), *A. palliata*, and *A. pigra*. Kowalewski and Garber (2014) evaluated collective action and the collective action problem associated with cooperative male defense during intergroup encounters. Although empirical data show that in several howler species resident adult males collectively defend resources such as fertile females from solitary males and resident males in neighboring groups, how howlers (or other primates) negotiate the cost/benefit ratio of collective action remains unclear. The presently available data suggest that intergroup encounters of multimale groups may offer opportunities where collective action problems may arise, and is negotiated and solved through joint actions by central males and noncentral males. Future studies that try to understand the evolution of cooperation and coordinated actions should focus on comparing differences in individual male and female behaviors associated with mate defense, access to reproductive partners, female mate choice, and individual reproductive success between howlers that reside in unimale groups and howlers that reside in multimale groups.

15.5 Conclusions

Howlers offer an instructive model in addressing a broad range of research questions regarding the behavioral, ecological, reproductive, and social strategies present in living primates. This volume has shown, however, that despite numerous howler field studies, most of these efforts have focused on a relatively small number of species within the genus. Clearly, there is a priority to study other howler species such as *A. sara*, *A. belzebul*, *A. macconnelli*, *A. discolor*, *A. ululata* and *A. nigerrima*, and subspecies of *A. seniculus* such as *puruens*is and *juara*; and to employ new research tools and data collecting methodologies to address the next generation of research questions on *Alouatta* foraging patterns, diet, social organization, genetics, and evolution. We also need to rethink traditional socioecological models that attempt to explain primate social organization in terms of feeding competition and rigid social hierarchies and instead highlight the benefits that individuals receive as members of a well-functioning social unit (Sussman and Garber 2011). In this regard we need to develop models of primate sociality that include the costs and benefits of nutrient balancing, cooperative behavior, and predator (including infanticide) and disease risk across different habitats and under conditions of changing population density.

Finally, it explains very little to refer to howlers as a plastic taxon, although this is commonly stated in publications on *Alouatta*. Clearly, behavioral modification or adaptability has limits, and these limits are likely to differ across phenotypes within the same species and across species. Individual traits can be described as variable, plastic, or flexible relative to other traits as long as the limits of this variability are described and it is recognized that along different points across this continuum the cost/benefit ratio can increase or decrease. Moreover, for different species, different individuals, and under different social and ecological conditions, the cost/benefit ratio of this variability will likely differ. The fact that howlers can survive in highly disturbed habitats gives the impression that they are highly adaptable. However, howler may be less successful than other primates in less marginal or less disturbed habitats, including habitats characterized by indigenous hunters. We anticipate that as our knowledge of understudied howler species increases, we will be able to better model the set of demographic and ecological factors that most strongly affect howler distributions. These data will allow us to develop effective management and conservations to protect threatened howler populations across their range.

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