Chapter 1
Why Is It Important to Continue Studying the Anatomy, Physiology, Sensory Ecology, and Evolution 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*: *Adaptive Radiation*, *Systematics*, *and Morphology* are to highlight the importance of morphological, genetic, and physiological studies for understanding the evolutionary adaptations of this highly successful genus. Many questions continue to exist regarding the systematics, anatomy, and physiology of *Alouatta*. Despite being one of the most commonly studied primate taxa in the Neotropics, the number of howler species is unresolved, and the distribution of many species and subspecies is poorly documented. Several attempts have been made to evaluate howler monkey taxonomic

M.M. Kowalewski (✉)
Estación Biológica Corrientes, Museo Argentino de Ciencias Naturales, Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Buenos Aires, Argentina
e-mail: martinkow@gmail.com

P.A. Garber
Department of Anthropology, University of Illinois at Urbana-Champaign, Urbana, IL, USA
e-mail: p-garber@illinois.edu

L. Cortés-Ortiz
Museum of Zoology, Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI, USA
e-mail: lcortes@umich.edu

B. Urbani
Centro de Antropología, Instituto Venezolano de Investigaciones Científicas, Caracas, Venezuela
e-mail: bernardourbani@yahoo.com

D. Youlatos
Department of Zoology, School of Biology, Aristotle University of Thessaloniki, Thessaloniki, Greece
e-mail: dyoul@bio.auth.gr

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diversity based on morphological (e.g., Hill 1962; Gregorin 2006), cytogenetic (e.g., de Oliveira et al. 2002; Steinberg et al. 2014), and molecular (e.g., Bonvicino et al. 2001; Cortés-Ortiz et al. 2003) analyses. More recently, several authors have attempted to integrate available information on genetics, morphology, and biogeography to provide a more comprehensive view of the systematics of this genus (e.g., Groves 2001, 2005; Rylands et al. 2000, 2006; Rylands and Mittermeier 2009; Glander and Pinto 2013; Cortés-Ortiz et al. 2014a, b), identifying two primary radiations: one that originated Amazonian/Atlantic Forest howlers and the other that produced all Central American taxa. Nonetheless, a better understanding of the diversity of howler monkeys will only be possible by continuing integrating different types of data for the same individuals using a thorough sampling across their wide distribution. Howlers (genus *Alouatta*) are distributed from 21°N to 30°S in Central and South America. They occupy the widest range of habitats of any Neotropical genus and are among the most dimorphic of New World primates in body mass and color patterns (Wolfheim 1983; Crockett and Eisenberg 1987; Emmons and Feer 1990; Nowak 1999; Groves 2001; Di Fiore et al. 2010). In all species males are at least 25 % heavier than females and two taxa, *A. caraya* and *A. guariba*, are dichromatic (Crockett and Eisenberg 1987; Neville et al. 1988). There are currently 12 recognized or putatively recognized species in the genus *Alouatta*.

Howlers are found from sea level to ≥3,200 m occupying diverse habitat types from closed canopy wet evergreen forests, including "terra firme" and inundated swamp forests, to open, highly seasonal deciduous and semideciduous woodlands, gallery forests, and llanos habitats containing patches of relatively low trees in open savannah (Crockett and Eisenberg 1987; Camacho and Defler 1985; Wolfheim 1983; Brown and Zunino 1994). Howlers are principally arboreal; however, several species that live in drier areas come to the ground and cross open areas between patches of forest (Crockett 1998; Di Fiore et al. 2010).

Several studies of howler anatomy have been published. These have focused on dental and cranial anatomy, the hyoid apparatus, and the prehensile tail. The study of howler anatomy has been used as a comparative framework for the study of ateline adaptations, studies of parallel evolution of the prehensile tail in atelines and cebines, and as a model to investigate morphological adaptations of Miocene hominoids. Outstanding early examples of anatomical research in howlers include the monograph by W.C.O. Hill (1962), comparison of black howlers (*A. villosa* = *A. pigra*) with other cebid platyrrhines, as part of his comprehensive volume devoted to the group (Hill 1962), and the detailed monograph by Schön (1968) on the muscular anatomy of the ursine howler (*A. arctoidea*). In that same year, M.R. Malinow edited a volume on the biology of *A. caraya*, as part of the series *Biblioteca Primatologica* (Malinow 1968). This volume included chapters on the functional anatomy, skeletal development, ontogeny, hematology, soft tissue anatomy, and general pathology of the black and gold howler monkey.

Following these publications, Schön and colleagues produced a series of papers examining the appendicular, cranial, and hyoid anatomy of the red howlers (Schön 1968; Schön Ybarra 1984, 1998; Schön Ybarra and Schön 1987). The impact of these publications for evaluating the morphological adaptations of howler monkeys is discussed by Youlatos et al. (2014, see also below). During the same period (mid- and late 1970s to early 1980s), Stern and collaborators explored the functional anatomy and positional behavior of howlers and other atelines through detailed comparative anatomy and electromyography. These authors established the framework of using howler monkeys as morphobehavioral analogs for studies of early hominoids (Stern 1971; Stern et al. 1980). This was followed by an increase in publications on howler cranial, hyoid, and appendicular morphology, in which the genus was considered as integral for understanding the adaptive radiation of platyrrhines, and more particularly of the highly apomorphic atelines, with whom they share large body mass, a prehensile tail, and adaptations to a suspensory way of life (e.g., Rosenberger and Strier 1989). Recent studies have used new morphometric analyses (e.g., geometric morphometrics) to better understand howler functional anatomy. New fossil material has firmly identified the ancestral group that gave rise to modern *Alouatta* (see Rosenberger et al. 2014). This research has revealed significant differences in cranial anatomy, the shape of the hyoid, and specific characters of the long bones across howler species, suggesting that the morphology of *Alouatta* is more variable than previously considered. Ongoing and future studies will need to focus on evidence for ages, sex, and populational differences in functional and evolutionary correlates of howler basicranial morphology, degree of airorynchy, skull size, hyoid shape and size, long bone robusticity, shape of proximal and distal humeral, femoral articular facets, and the morphology of the carpals and tarsals to better understand the adaptive radiation of the genus.

A major goal of this volume is to review and evaluate the current data on howler endocrinology (see Van Belle 2014), their gut microbiome (see Amato and Righini 2014), sensory and communication systems (vision, auditory, and vocal) (see Hernández-Salazar et al. 2014; da Cunha et al. 2014, Kitchen et al. 2014), parasitology (Martínez-Mota et al. 2014), and nutritional ecology (see Garber et al. 2014). An understanding of howler monkeys anatomy and physiology provides a framework for examining how social (Kowalewski and Garber 2014) and reproductive strategies (Van Belle 2014; Van Belle and Bicca-Marques 2014), feeding ecology, and foraging decisions (Dias and Rangel-Negrin 2014; Kowalewski and Garber 2014). Although we argue for the recognition of 12 howler species, the majority of field and laboratory studies have focused on 6 species *A. palliata*, *A. pigra*, *A. caraya*, *A. arctoidea*, *A. belzebul*, and *A. guariba*. Ongoing field research has shown that several howler species consume a diet that includes more fruits than leaves (Garber et al. 2014; Behie and Pavelka 2014), engage in nonaggressive forms of intragroup male–male reproductive competition (Kowalewski and Garber 2014), and that females are more sensitive to social and ecological stress than males (Van Belle 2014). These studies also have demonstrated that female mate choice, male and female migration patterns, extragroup copulations, collective action, and kinship are likely to play a critical role in howler male and female reproductive strategies (Garber and Kowalewski 2014). One goal of this volume is to present new frameworks that integrate data on howler behavioral ecology and reproduction with endocrine function, digestive physiology, host-microbe communities, anatomy, and evolution.

Our knowledge of the sensory physiology of *Alouatta* is biased in terms of their unique vocal repertoire. Detailed studies of sound production in *Alouatta* indicate inter- and intraspecific variability such that Central America howlers (*A. palliata* and *A. pigra*) are reported to have differences in call structure compared to species from South America (see below). Recent research suggests that the howler hyoid has undergone important evolutionary changes towards increased pneumatization, with a large, hollow balloon-like basihyal and enlarged laryngeal cartilages (some of these are partly ossified) that serve, along with air sacs, as a resonating chamber. Changes in the hyoid complex in howlers have resulted in significant modifications in cranial and mandibular shape, leading to a large flat face and airorhynchous skull, elongated basicranial shape, a flat and reduced nuchal plane, a vertically positioned *foramen magnum*, and large and deep mandibular ramus (e.g., Rosenberger et al. 2014; Youlatos et al. 2014).

One unexpected aspect of howler physiology that distinguishes them from other New World primates are derived features of their visual system resulting in routine trichromatic color vision in both males and females in *A. seniculus* and *A. caraya* (Jacobs et al. 1996). In other taxa of New World primates, there are sex-linked differences in color vision with males being dichromatic, approximately 60 % of females also are dichromatic, and 40 % of females are trichromatic. The main theories proposed to explain the adaptive advantages of this apomorphy include leaf and fruit selection, visual social signals, increased ability to detect camouflaged predator, and the use of color by males or females to determine health or reproductive condition (Sumner and Mollon 2000, 2002; Dominy and Lucas 2001; Regan et al., 2001; Dominy 2004; Jacobs 2007).

After Malinow's early book on the biology of *A. caraya* (Malinow 1968), and individual publications focusing on howler morphology, systematics, and physiology, Neville et al. published a review of *Alouatta* in the book, *Ecology and Behavior of Neotropical Primates Volume 2* (edited Mittermeier et al. 1988). However, it took another decade before the publication of another volume dedicated to *Alouatta.* This was a special issue of the *International Journal of Primatology* (Vol. 19: 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. Of the 11 articles in this volume, 2 dealt with anatomical issues: 1 on the forelimb anatomy of *A. arctoidea* (Schön Ybarra 1998) and 1 on cranial pathology of *A. palliata* (DeGusta and Milton 1998). The remainder of the articles focused on behavior, ecology, and conservation.

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 two comprehensive companion volumes, one titled *Howler Monkeys*: *Adaptive Radiation*, *Systematics*, *and Morphology* and a second *Howler Monkeys*: *Behavior*, *Ecology and Conservation*. These volumes integrate our current knowledge of the behavioral, ecological, social, and evolutionary processes that have shaped the evolution, biology, physiology, and life history of this taxon. In this first volume we include 15 chapters divided into 5 sections

(1) Introduction; (2) Taxonomy, genetics, morphology, and evolution; (3) Physiology; (4) Ontogeny and sensory ecology; and (5) Conclusions. Each chapter identifies directions for further research on howler monkeys using a comparative framework. In developing this volume, we have relied on the expertise of researchers from habitat countries. Sixty-four percent of the chapters in the 2 volumes are led by a Latin American or non-Latin American that lives permanently in this region, and 89 % of the chapters have at least 1 Latin American coauthor. Thus, we acknowledge the growing number of Latin American scholars that 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 our understanding of Latin American primates.

1.1.1 The Taxonomy, Genetics, and Evolution of Howler Monkeys

This first part of the volume is focused on the evolutionary history of the genus Alouatta. In Chap. 2, Rosenberger and collaborators offer a unique summary of fossil alouattines arguing that fossils such as *Paralouatta* (16.5 Ma), *Stirtonia* (13.5–11.8 Ma), *Solimoea* (6.8–9 Ma), and *Protopithecus* (ca. 20,000 BP) are ancestors to extant howler monkeys. The chapter also includes an examination of some fossil taxa that previously have been only briefly discussed in the literature (e.g., *Protopithecus* and the non-alouattine *Caipora*) as well as *Solimoea*, which was originally considered a stem ateline, but the authors advocate its inclusion in the alouattines. Of these fossil genera, only *Stirtonia* can be considered a committed leaf-eater similar to extant howlers. This is based on detailed functional traits in molar morphology shared with *Alouatta*. In contrast, the molars of *Paralouatta* (and *Solimoea*) are apparently more primitive, while the lesser-known dentition of *Protopithecus* presents a different anatomical pattern, perhaps closer to atelines and thus possibly morphotype-like for alouattines. The authors suggest that these features in *Protopithecus* represent adaptations to howling rather than adaptations to the consumption and mastication of a leaf-based diet. Another important idea from this chapter is that relatively small brain sizes evolved in the alouattines prior to their dental commitment to leaf-eating. Thus, perhaps in alouattine evolution morphological constraints associated with loud howling result in changes in cranial design that limited space available for an expanded brain volume.

In Chap. 3, Cortés-Ortiz and colleagues review the taxonomy of howler monkeys and in comparing morphological and genetic data provide support for nine species: mantled howlers (*A. palliata*), Central American black howlers (*A. pigra*), red howlers (*A. seniculus*), ursine howler (*A. arctoidea*), red-handed howlers (*A. belzebul*), Bolivian red howler monkey (*A. sara*), Guyanan red howler (*A. macconnelli*), brown howlers (*A. guariba*), and black and gold howlers (*A. caraya*). These authors also suggest that three more taxa should be tentatively considered as full species

(*A. nigerrima*, *A. ululata*, *A. discolor*). Final confirmation of species status awaits but for which additional genetic and/or morphological studies are required to confirm status. Cortés-Ortiz et al. (2014a, b) also propose five subspecies in *A. palliata* (*A. p. mexicana*, *A. p. palliata*, *A. p. coibensis*, *A. p. trabeata*, and *A. p. aequatorialis*), three subspecies in *A. seniculus* (*A. s. seniculus*, *A. s. juara*, and *A. s. puruensis*), and two in *A. guariba* (*A. g. guariba* and *A. g. clamitans*). These authors further acknowledge the possibility that *A. pigra* may contain two subspecies (*A. p. pigra* and *A. p. luctuosa*). This chapter constitutes the most complete taxonomic evaluation of howlers to date. Steven Nash has generously provided plates with accurate drawings of each *Alouatta* species and subspecies.

In Chap. 4, Mudry et al. provide a comprehensive review of howler cytogenetic studies, highlighting the differences in chromosome number among the different taxa, some of which are due to the presence of microchromosomes. They review the evidence of multiple sexual systems present in *Alouatta* including the formation of trivalents X1X2Y in males of *A. belzebul* and *A. palliata*; quadrivalents X1X2Y1Y2 in males of *A. seniculus*, *A. pigra*, *A. macconnelli*, *A. sara*, and *A. caraya*; and possible pentavalents X1X2X3Y1Y2 in males of *A. guariba*. Based on cytomolecular analyses they propose an independent origin of the sex chromosome systems in the Mesoamerican and South American lineages.

In Chap. 5, Cortés-Ortiz and colleagues explain the importance of hybridization in the evolutionary history of howler monkeys and examine the morphological, behavioral, and genetic data available from the few known howler monkey hybrid zones: between *A. palliata* and *A. pigra* in Mexico and between *A. guariba* and *A. caraya* in Argentina and Brazil. Morphological data from these hybrid zones indicate the existence of individuals with intermediate phenotypes; however, genetic studies of the *A. palliata*×*A. pigra* hybrid zone show that it is not always possible to distinguish pure forms from admixed individuals. Furthermore, the genetic analyses demonstrated that most individuals in the hybrid zone are multigenerational backcrossed hybrids. The lack of early-generation male hybrids, consistent with Haldane's rule, which states that in hybrid systems if one sex is absent it is the heterogametic sex, provides strong support for the contention that reproductive isolation is already present between these taxa. Further behavioral, cytogenetic, and molecular studies are required to understand the mechanisms promoting reproductive isolation between howler species and the maintenance of species integrity despite hybridization.

1.1.2 The Anatomy and Physiology of Howlers

This section of the volume describes the anatomical and physiological characteristics of howlers. For example, in Chap. 6, Canales-Espinosa and collaborators focus on blood biochemistry and hematology. By doing so, they not only review the published information (*A. caraya*) but also provide novel information from the howlers of Mexico (*A. palliata* and *A. pigra*) and French Guyana (*A. macconnelli*), providing reference values for these species. Among the patterns found include evidence of a higher concentration of white blood cells in females (except in *A. caraya*) than in males and a higher concentration of white blood cells overall in *A. caraya* and *A. palliata* than in other species. Additionally, creatinine levels were found to be higher in males, in relation to body mass differences, and protein levels were found to be lower in Mexican species than in other *Alouatta* species. Although some differences between males and females may follow a sexual dimorphic pattern (i.e., creatinine level), some results may be associated with ontogeny, aging (i.e., mean corpuscular volume and mean corpuscular hemoglobin), or health status (i.e., white blood cells). The variability present among *Alouatta* species may reflect the ability of howler monkeys to live in marginal and highly variable habitats.

In Chap. 7, van Belle reviewed data on hormones and behavior from six species of howlers (*A. palliata*, *A. arctoidea*, *A. caraya*, *A. pigra*, *A. belzebul*, and *A. seniculus*). Although the database is limited, this chapter explores relationships between the concentrations of sexual and stress-related hormones and growth patterns, mating relationships, intra- and extragroup male–male competition, resource scarcity, habitat fragmentation, translocation, and sociality that serve to better understand the physiological response of howlers to changes in the social and ecological environment. Data suggest that in male *A. palliata*, fecal androgens increase at 3 years of age. However these results are equivocal as 3-year-old males that were evicted from their natal groups show lower levels of fecal androgens than males of similar age who remained in their social groups. Data on ovarian cycles are available from three species (*A. arctoidea*, *A. caraya*, and *A. pigra*). Although different techniques have been used to estimate the length of the ovarian cycle, in most species the range falls between 13 and 25 days.

Endocrine function in *Alouatta* also may reflect nutritional status and food availability. In a long-term study on *A. pigra* in Belize (Behie et al. 2010; Behie and Pavelka 2012, 2014), glucocorticoid levels were higher during periods of fruit scarcity compared to periods of fruit abundance in a population recovering from a collapse and habitat destruction caused by a hurricane. In *A. pigra*, glucocorticoid levels were found to increase as a consequence of intragroup competition (Van Belle et al. 2008). In contrast, Rangel-Negrín et al. (2011) reported that in *A. palliata* glucocorticoid levels increased in response to intergroup competition. As it is stated by Van Belle (2014), these differences may reflect differential hormonal responses to variable social situations within and between groups and to changing demographic patterns, provide a framework for understanding behavioral individuals and species-specific differences in male and female mating strategies and social interactions.

In Chap. 8, Amato and Righini evaluate the role of the gut microbiome in howler heath and feeding ecology. Primates and other mammals rely on mutualistic microbial communities in their gut to provide them with energy via the fermentation of otherwise indigestible material such as fiber. Howler monkeys, as are all other primates, are dependent on their gut microbiota for the breakdown of plant structural carbohydrates, and Amato and Righini use recently collected data to describe the gut microbiome of captive and wild black howler monkeys (*A. pigra*) to test two models of host–microbe interactions and bioenergetics. The two models tested focus on (1) general host–microbiota interactions and (2) measures of bioenergetics that include gut microbiota effects. Their results indicate that individual howler monkey microbial community composition differs more across habitats than across seasons, and that these differences are strongly associated with the nutrient composition of the diet. Examining how spatial and temporal fluctuations in resource availability and the plant and animal tissues consumed affect the primate gut microbiome, and in turn, how this influences host nutrition and physiology is critical for examining questions regarding age- and sex-based differences in feeding ecology. In particular, whether adult males, adult female, and juveniles can consume the same diet, but due to differences in their microbiome, differently extract nutrients. This has important implications for examining the role that the gut microbiota plays in primate ecology, health, and conservation. There is only one howler species represented in their dataset (*A. pigra*), and this highlights the need to conduct comparative studies on other howler species.

In Chap. 9, Martínez-Mota and collaborators offer an overview and a meta-analysis of gastrointestinal parasites that are hosted by howler monkeys. They explore how ecological factors affect parasitic infection in this primate genus analyzing eight howler monkey species (*Alouatta palliata*, *A. pigra*, *A. macconnelli*, *A. sara*, *A. seniculus*, *A. belzebul*, *A. guariba*, *and A. caraya*), at more than 35 sites throughout their distribution. Some factors such as human presence and annual precipitation may influence the prevalence of intestinal parasites. For example, precipitation, latitude, altitude, and human proximity may differentially influence the prevalence of parasite type. For example, nematode prevalence increases with precipitation, trematodes appear to be unaffected by these climatic/anthropogenic variables (no trend was found), cestode presence was higher in remote habitats than in rural habitats, amoebae were found to exhibit higher prevalence at lower latitudes and at sites with high precipitation, *Trypanoxiuris* sp. showed a trend of decreasing prevalence towards higher altitudes, *Giardia* sp. was found to decrease with increasing precipitation, and *Plasmodium* sp. was not found to be strongly associated with any of the variables measured. In addition, the authors found that parasitic infection in howlers appears to be biased towards few individuals within a group. Given that infectious diseases are serious threats for primate survival, this study provides a baseline for evaluating the dynamics of parasite–howler interactions and for comparative studies in other platyrrhines.

In Chap. 10, Youlatos and colleagues provide a comprehensive review of howler morphology. The authors examine howler cranio-mandibular and hyoid shape and form using three-dimensional geometric morphometrics. This methodology offers advantages over more traditional approaches by measuring shape, estimating shape variability, and calculating variance in allometry and form. The authors also review howler dental and postcranial anatomy. The results indicate that howler monkeys possess a skull with a robust prognathic, airorynchous face, small braincase, and posteriorly directed occipital condyles and *foramen magnum* and a hypertrophied hyoid with enlarged laryngeal cartilages. These represent distinctive morphological traits that characterize this genus compared to other atelines and platyrrhines. The results indicate that the unique morphology of *Alouatta*'s cranium and hyoid is strongly associated with a shift to a loud communication lifestyle. Additionally, the arrangement and morphology of the dentition including small incisors and flat elongated crested molars suggest an increased ability to process leaves and possibly seeds, while the appendicular morphology reveals an emphasis on an above-branch quadrupedal positional repertoire and short-distance travel. Limb morphology associated with these positional behaviors includes relatively short forelimb long bones with joints that allow ample movements at the level of the shoulder and elbow and more restricted movement at the wrist. Moreover, the howler hip, knee, and tarsal joints are quite flexible, and both *manus* and *pes* provide stable grasping on arboreal supports, with the help of a comparably short prehensile tail. These major behavioral axes, enhanced sound production functioning in long-distance vocal communication, variable but generally increased ability to dentally process leaves, and above-branch locomotor and posture behavior describe a suite of traits that distinguish *Alouatta* from other atelines.

1.1.3 The Ontogeny and Sensory Ecology of Howlers

The final section of the volume presents information on the ontogeny and sensory systems of howler monkeys. In Chap. 11, Raguet-Schofield and Pavé present data on the ontogeny of *Alouatta* examining the degree to which howler development follows a "fast-slow" continuum and whether individual life history traits are best understood in terms of dissociated development. Although, howlers have traditionally been characterized as having fast life histories compared to other atelines, the authors point out the need for a change of paradigm when interpreting ontogeny. For example, *A. palliata* seem to reach age at first reproduction earlier than *A. caraya* and *A. seniculus*, but has a longer interbirth interval (IBI) and later age at weaning. These patterns do not correspond with the paradigm of a fast vs. slow developmental trajectory. Also, the authors suggest that compared to other atelines, *Alouatta* females shift resources from current to future offspring more rapidly. Thus, howler females reach reproductive age earlier, exhibit a shorter gestation period, shorter IBI, and wean infants earlier than other atelines; however, female growth rates are indistinguishable between *A. caraya* and *Ateles geoffroyi* (Leigh 1994), indicating that the fast-slow evolutionary model misrepresents the pattern and pace of primate development. Sexual dimorphism also is expressed at different phases of development including postnatal growth rate, craniodental maturation, and initiation of solid food intake in *Alouatta*. For example, males exhibit more rapid postnatal growth than females; moreover, male growth does not remain uniformly accelerated and instead alternates between periods of slower growth and periods of faster growth, supporting a pattern of life history dissociability. The authors make a strong argument about the necessity of using a dissociability model to analyze *Alouatta* life history traits, indicating that some traits develop relatively early in ontogeny and others develop late in ontogeny compared to other atelines, and therefore howler development does not conform to the predictions of a fast-slow continuum.

In Chap. 12, Hernández-Salazar and colleagues review data exploring how howler monkeys perceive the world. Although there are several studies on howler vision, there are limited data on other senses. This chapter focuses on a review of the anatomy, physiology, genetics, and behavioral relevance of hearing, tactile communication, taste, vision, and olfactory communication in howler monkeys in comparison to other platyrrhines, and in particular to *Ateles* sp. Some specific differences among howlers and other atelines are (1) howler monkeys exhibit a form of trichromatic color vision that make them more similar to the Old World monkeys, apes, and humans than to other platyrrhines. In this regard, it has been argued that routine trichromatic vision may be linked to a diet where leaves represent a critical component; (2) the ability to use loud calls to increase group cohesion, intergroup communication, and between group male spacing. Unfortunately, we lack specific information of the sense of smell, touch, and taste to better understand its role in food selection and social–sexual interaction within and between groups. Overall, we continue to lack accurate measures of physiological performance for the majority of sensory communication in howlers and other atelines.

In Chaps. 13 and 14, da Cunha, Kitchen, and collaborators provide a thorough review of the diversity of vocal communication in howler monkeys. Chapter 13 focuses on the acoustic structure of the vocalizations, particularly loud calls, and the variation among different species. A striking division between Central and South American howlers is difference in male loud calls parallel genetic differences that separate two identified phylogenetic clades of the genus *Alouatt*a (Cortés-Ortiz et al. 2003). Thus, both *A. palliata* and *A. pigra* produce only simple, short-duration roars, their barks are essentially just shorter syllables of their species-typical roars, and both barks and roars usually occur in the same bout of loud calling. However, although their individual vocalizations are shorter than in South American howlers, they are produced during bouts that last much longer than in the southern species, with pauses between calls. The authors present information on the anatomy of the vocal organs, and discuss the limited information available regarding the vocal repertoire of "of more subtle calls" in *Alouatta.* The chapter concludes by offering a set of standardized methodologies to study vocal communication in this genus. Chapter 14 reviews the functional studies conducted to date on loud vocalizations in howlers, highlighting both inter- and intraspecific variation. The authors explore the role of male loud calls in group cohesion, predator avoidance, attraction of females, and competition over resources and address the understudied role of female loud calling. Their main results indicate that calls have a major function in assessment of rivals. The rate and patterns of vocal battles and intergroup encounters and the likelihood that groups will escalate these conflicts after physical aggression vary among species and populations. Although there is strong support that howling evolved at least in part under male intrasexual selective pressures, the importance of resource competition remains unclear.

1.2 Conclusions

A major goal of this volume is to integrate published and unpublished data on howler monkey evolution, systematics, genetics, and anatomy into a framework that can be used to study other primate radiations. Thus, we feel that this book will be of great interest to students and researchers examining a range of issues in evolutionary biology, genetics, anthropology, primatology, physiology, and endocrinology. In addition, 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 this book as a centerpiece, contributing to the scientific literature on primates, as well as adding to our understanding of Neotropical community ecology. 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 of howler physiology, anatomy, demography, evolution, and conservation that are not included in this volume. However, their contributions have made this volume possible. Most certainly this includes Clarence Raymond Carpenter, Margaret Clarke, Alejandro Estrada, Kenneth Glander, Robert Horwich, Katharine Milton, Miguel Schön Ybarra, and Gabriel Zunino. Additionally absent are many graduate students currently gathering new and innovative data and whose work 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 ecological communities in order to understand the adaptability of the genus *Alouatta*. In addition, we need to collect data to more clearly define the set of conditions that promote phenotypic variability in howlers. Furthermore, long-term data on a broad set of taxa will facilitate comparative analyses needed to explore the underlying mechanisms of behavioral, ecological, morphological, and genetic variability. New available methodologies are critical for addressing twenty-first century questions in primatology. These techniques include molecular genetics, 3D geometric morphometrics, GIS technology, portable high-definition and high-speed video recording, hormone analyses, nutritional analyses of plant foods, and the use of molecular methods for examination of disease, the gut microbiome, and invertebrate and vertebrate DNA present in primate feces. Although these technologies may increase the cost of research, the information they will provide will surely be of significant value in advancing our understanding of howler monkey behavior, ecology, and evolution. These new studies will require the collaboration of multidisciplinary research teams across countries. Many of the chapters in this volume are the result of such collaboration and an irrefutable proof that we, as primatologists, are heading in the right direction.

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