Qian Wang   *Editor*

Bones, Genetics, and Behavior of Rhesus Macaques

Macaca mulatta of Cayo Santiago and Beyond

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Developments in Primatology:
Progress and Prospects

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To Li, Leon, Suri, Sevy, and Cody

Foreword

I am most appreciative to Dr. Qian Wang for having invited these few random, and even tatterdemalion, thoughts from an octogenarian who, whatever else he may have lost, has retained his sense of wonderment.

Like Harry Belafonte – and the West Indies cricket team – I love islands in the sun! I was born by the sea and, wherever one goes on a tolerably small island, one is not far from it. I have happy boyhood memories of little Salisbury Island in Durban Bay, South Africa. My adult reminiscences include tiny Heron Island at the southern end of the Great Barrier Reef, off the coast of Queensland, Australia; the Galapagos Archipelago on the equator in the Pacific Ocean; and the charming Mediterranean islands of Majorca, Sardinia, Sicily, Capri, Crete, the Cyclades, and the Dodecanese. I also must not forget the bigger islands of Japan and New Zealand or the island–continent of Australia, and perhaps I should even include the biggest "islands" of them all: Asia and the vast peninsula of Europe, and the Americas.

February 2003 saw me on my first visit to the Caribbean Islands. The International Committee on Anatomical Terminology was meeting on the half-Dutch, half-French, isle of St. Maarten, basking in the unbelievably blue Caribbean Sea. Even as I was writing my report of that visit, the West Indies cricketers were touring South Africa under the captaincy of that brilliant batter, Brian Lara. As with St. Maarten, I have always marveled at how people who dwell on some of these little "worlds" blend insularity with an astonishingly universal outlook.

From an early age, I was well aware of the many nonhuman primate species that abound in Africa. Further, whereas my lifelong department in the School of Anatomical Sciences at the University of the Witwatersrand (Johannesburg, South Africa) focused on human anatomy, nonhuman primates were nevertheless topics of interest and study. Indeed, in the 1930s, Professor Raymond Dart, my predecessor as Head of the School, housed for research chacma baboons (*Papio ursinus*) on the roof of the Old Medical School on Hospital Hill (Tobias 2005; Strkalj and Tobias 2008). As medical students, we were always aware of the presence of the baboons,

especially when one escaped from its cage! Drs. Joseph Gillman and Christine Gilbert and their assistants conducted remarkable sex endocrine research on this caged colony (e.g., Gillman 1935, 1940; Gilbert and Gillman 1944, 1945). For many years, perineal swelling in the baboons was measured daily. The resulting analysis and the researchers' inference that menstrual bleeding is associated with progesterone withdrawal were startling for the time, and shed much light on the perineal turgescence and detumescence associated with the primate menstrual cycle. As a young honors student and medical researcher working in the department under Dr. Gillman, I conducted rudimentary chromosome counts on the baboons, as well as the prosimian *Galago*, and species of the rodent genera *Rattus* and *Tatera*. Other researchers studied baboon skeletal anatomy from specimens collected in the wild.

At the insistence of Professor Dart, the activities of the department expanded to cover the palaeo-anthropological remains that were being uncovered at Taung, Sterkfontein, Kromdraai, and other dolomitic limestone cave sites from 1924 to 1925 onwards. Excavations of a variety of fossil baboon genera and species paved the way for the discovery of hominins in almost all of the South African sites and stimulated numerous studies of extinct primates. I was initially thrust into this dramatic research environment in 1945, an experience that provided the foundation for my subsequent adventures with fossil primates in South Africa and, at the invitation of Louis and Mary Leakey, in East Africa, particularly Tanzania and Kenya.

How islands are populated is a most intriguing problem in the evolution and dispersal of hominins and other animals. Coupled with that problem is how migrating species successfully cross significant expanses of water to populate islands. Apart from the natural distribution of numerous Old World Monkeys in various parts of Africa and Asia, the sudden migration or transport of various species to locations that are far more restricted or isolated geographically has raised the issue of insular micro-evolution. The late Paul Sondaar (1977, 1994) approached the issue by investigating island effects on morphology, especially body size. These investigations inspired a flurry of similar studies on islands in the Mediterranean, South East Asia, and the Americas. Essentially, such insular micro-evolutionary studies suggest that morphological features diversify in size and shape among island and other isolated populations more than mainland populations that are not isolated because of a need to rapidly adapt to changed environmental demands, or because of less competition with other species, or both.

The present book on Cayo Santiago and the Caribbean Primate Research Center presents the intriguing tale of one such venture, in which recent human intervention, not paleo-geographical migration, immediately transported primates from one milieu to another and, in this case, to a circumscribed insular habitat. The enthralling story of the efforts to establish and maintain Cayo Santiago is set forth from an historical perspective. Happily, Professor Donald C. Dunbar, of the School of Medicine at the University of Puerto Rico, has furnished a detailed, blow-by-blow account of the struggles that were required to accomplish this goal. Dr. Wang, the editor of this book, persuaded Professor Dunbar not only to undertake this task but also to provide an invaluable chapter (Dunbar 2011).

In addition to the morphological and behavioral issues that are addressed in this book, micro-evolutionary problems present themselves from Cayo Santiago and its archival records. How long does it take for a population, isolated in an insular habitat

from its parent population, to evolve morphological and biomolecular differences to a degree that justifies micro-evolutionary inferences? How do body size characteristics of the Cayo Santiago population compare with those of rhesus macaques in their parent population or populations in Lucknow, India? One recalls the green monkeys (*Cercopithecus aethiops sabaeus*) that were transported across the Atlantic Ocean from Senegal, West Africa, to the Caribbean islands of St. Kitts (St. Christopher) and Nevis some 350 years ago, as a by-product of the slave trade. Over three centuries of separation from the African parent population should be sufficient for these Caribbean monkeys to have developed characteristics attributable to "Sondaar island effects." Indeed, the research of these monkeys by E.H. Ashton and S. Zuckerman (e.g., Ashton 1960; Ashton and Zuckerman 1950, 1951a, b, c), and by Sade and Hildrech (1965), provides early specific support for the general model of the phenomenon later proposed by Sondaar (1977, 1994). Regarding teeth alone, it has been found that those of the green monkey in the West Indies are bigger than those of its present-day African cousins. There is also decreased variance in the diameters of the cheek teeth, an increased occurrence of malpositions, numerical variations, and other dental abnormalities, and variations in the number of third molar roots. How fascinating it would be to apply Julius Kieser's analysis of fluctuating asymmetry to the West Indies monkeys and their parent populations (Kieser 1990). To what extent are there signs of ecological stress, perhaps differing among the various island populations of monkeys and their several parent populations?

Cayo Santiago challenges such analyses to the extreme, in that only 70 years separates this island population from its parental source. In the case of St. Kitts and Nevis, by contrast, a period of 300–350 years has passed for changes to be wrought on crania, teeth, and even nematode parasitic load. Although we are dealing here with two (or more) different taxa, it would nonetheless be an irresistible challenge to compare and contrast the changes wrought by isolation, under tolerably similar conditions, over 70 years versus over 300 years.

The interest of such studies should by no means be confined to primates. I have long been excited by the research potential of the flightless birds of the Indian Ocean – such as the dodo of Mauritius and related taxa on other islands in the Indian Ocean. Is it possible to trace the historic and prehistoric movements of these remarkable birds, the fatty and chicken-like taste of which excited voracious mariners in the Indian Ocean?

Is there any possible relevance to Flores Island and the fact that tool-bearing humans and elephantids (Stegodon) had crossed three deep-water straits between the Sunda Shelf and Flores around 0.9–0.8 million years ago, as Michael Morwood and his colleagues have shown (Brown et al. 2004; Brumm et al. 2010; Morwood et al. 2005)? Those straits were never so shallow as to permit easy access between the adjacent islands. These migrants floated across the watery expanse using tree trunks, logs, or islands of floating vegetation as rafts, or they paddled while holding floats or they swam. We have no evidence that anyone at this time was constructing boats, but Morwood and his colleagues suggest that Homo erectus was capable of repeated water crossings using watercraft (Morwood et al. 2005). Nevertheless, by whatever means, hominins and elephants managed to cross a stretch of water no less than 19 km wide, nearly 1 million years ago!

Apart from the research it made possible, the introduction of rhesus macaques to Cayo Santiago off the coast of Puerto Rico in 1938 has provided a unique opportunity to determine whether a man-made model of this kind can convey meaningful results, as compared with those furnished by studies in the wild. A fascinating historical example is the comparison of Solly Zuckerman's observations and interpretations of sexual behavior among captive primates on "Monkey Hill" in London's Regent's Park Zoo (Zuckerman 1932) with those made of this behavior by Eugene Marais – a dedicated, but untrained, primate behaviorist – among wild primates living a few hundred kilometers north and northwest of Johannesburg (Marais 1939, 1969). Of course, Marais's observations and analyses were far from perfect, but were the conditions in the London Zoo ideal? Zuckerman's criticism of Marais's work leads one to enquire if we really have objective standards and criteria for appraising behavioral studies conducted in zoos and other artificial environments, as opposed to studies conducted in the wild. Much the same question could be raised through a comparison of Wolfgang Kohler's studies of his banana-loving chimpanzees that were housed in an enclosure on the Canary Islands (1913–1920) and Jane Goodall's studies of wild-living chimpanzees in the Gombe Stream National Reserve in western Tanzania. Perhaps it would not be immodest for us to acknowledge that rigorous models for the study of primate behavior and micro-evolution still need to be developed. In this regard, and in a spirit of hope, we might look to studies comparing the 70-year-old Cayo Santiago island population with its parent population or populations on mainland India in order to provide a foundation for constructing such models.

Late in my life of research in physical anthropology and primate biology, there is a lingering regret that I have not enjoyed the privilege of visiting Cayo Santiago and seeing for myself the basis for the remarkable accomplishments of its scholars. We should be more than thankful that Dr. Wang organized a symposium, which was held in Chicago on 2nd April, 2009, to honor Cayo Santiago on its 70th birthday, and that recognized the scientific contributions of all the units of the Caribbean Primate Research Center. He also deserves our gratitude for taking on the onerous task of editing and publishing the papers arising from this conference. I extend my thanks to him, Professor Dunbar, and my assistants, Felicity Krowitz and Pieter Faugust.

Witwatersrand, Johannesburg   Phillip V. Tobias

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Preface

The introduction of rhesus macaques (*Macaca mulatta)* to Cayo Santiago, Puerto Rico in 1938 and the subsequent development of the Caribbean Primate Research Center (CPRC) for behavioral and biomedical research have generated an unparalleled resource for the physical anthropology and other fields in the social, biological, and medical sciences. The presence of free-ranging groups of rhesus monkeys living under seminatural conditions in an easily accessible location, combined with corralled and caged monkeys and an extensive skeletal collection, all of which are derived from the same population of known biology and familial relationships, provides the rare opportunity to conduct morphological, developmental, physiological, functional, genetic, and behavioral studies across the life span. Thus, the CPRC is invaluable for more than the further development of *M. mulatta* as a biomedical model. Equally, if not more importantly, Cayo Santiago and the other CPRC units enable physical anthropologists and other researchers to gain greater insights into the biology, behavior, and evolution of these animals as a species in their own right and in relation to humans and other animals.

My association with Cayo Santiago and the CPRC started in 2005 when I was granted access to the rich demographic and genealogical database that is available on the Cayo Santiago-derived skeletal collection. Using this database, I was able to study the ontogeny of sexual dimorphism in craniofacial size in general, and in suture morphology in particular. It was through these studies that I became convinced of the incredible potential for research in physical anthropology that this facility has to offer. My determination to advocate for increased physical anthropological research at the CPRC eventually drove me to organize a special symposium to celebrate the 70th anniversary of the Cayo Santiago colony's inception and the subsequent years of unique scientific contributions by researchers working in all the CPRC units. The symposium was entitled "*Bones, Genetics, and Behavior: Physical Anthropology at the Caribbean Primate Research Center*" and was held in Chicago, IL on April 2nd, 2009 as part of the 78th annual meeting of the American Association

of Physical Anthropologists. With the exception of the contribution by Donald Sade, all of the chapters in this volume were derived from the symposium presentations. Whereas the first chapter provides a historical perspective of Cayo Santiago and the other CPRC units, the remaining chapters describe recent investigations into the morphology, genetics, and behavior of the rhesus macaques living on, or derived from, Cayo Santiago. Various chapters also include comparisons with other species living elsewhere.

In Chap. 1, Dunbar initially recounts the beginnings of the Cayo Santiago colony, through the efforts of Dr. Clarence Carpenter and others, and the eventual formation of the CPRC. He then focuses on past and ongoing research in, or related to, physical anthropology, before revealing a few of the numerous research opportunities that still exist at the CPRC.

In Chap. 2, Joganic and colleagues analyze the cranial capacity and craniofacial linear dimensions in two evolutionarily related papionin species: the rhesus macaques from Cayo Santiago and baboons (*Papio hamadryas*) from the Southwest National Primate Research Center. The authors then reveal both the phylogenetic and dietary impact on the development of the craniofacial skeleton in these species.

In Chap. 3, Willmore and colleagues, by investigating the expression of metric and nonmetric traits and studying fluctuating asymmetry in the skulls of Cayo Santiago rhesus macaques, provide new insights into the relationships among craniofacial traits.

In Chap. 4, Turnquist and colleagues examine how structural and architectural parameters of trabecular bone correlate with the occurrence of vertebral fractures and use the Cayo Santiago macaques to establish a rhesus model for osteoporosis.

In Chap. 5, Kohn and Bledsoe study the inheritance of postcranial dimensions and reveal significant differences among social groups that may generate, even over relatively short time periods, the genetic variation and covariation necessary for the evolution of morphological traits.

In Chap, 6, Nelson and colleagues investigate variables that contribute to the establishment of female dominance rank. They approach the issue by determining the ratio of 2nd digit length to 4th digit length (a correlate of the level of prenatal androgen effects) and assessing the significance of this ratio and that of social processes to the relative dominance rank that a female individual achieves.

In Chap. 7, Fellmann studying the mechanical efficiency of forelimb muscles in the Cayo Santiago rhesus monkeys finds that the anatomical proxies of mechanical advantage scale with positive allometry, indicating a trade-off between the limb response speed and mechanical advantage in macaques.

In Chap. 8, Wang assesses sex-related differences in the patterns of tooth eruption in the Cayo Santiago macaques and builds a case for the importance of the biomechanical consequences of sex-based differences in craniofacial form throughout ontogeny.

In Chap. 9, Blomquist demonstrates how female sexual maturation in the Cayo Santiago macaques is influenced by multiple factors such as genetics, the environment, and social rank.

In Chap. 10, Hoffman and Maestripieri integrate longitudinal information from the Cayo Santiago demographic database with recent behavioral, hormonal, and morphological data in order to explain differences among the rank-related, individual life histories.

In Chap. 11, Berman and Kapsalis examine the patterns of temporal variation in social grooming by analyzing the structure of this behavior, focusing on time constraints, social network size among adult females, and other factors.

In Chap. 12, Maestripieri and Hoffman summarize findings on social organization and dynamics within the Cayo Santiago colony, while offering caveats on how these findings may differ from those based on rhesus monkeys in the wild and on related species.

In Chap. 13, Sade attempts to link evolutionary psychiatry with nonhuman primate sociality by focusing on the phylogenetic origins of those social relations and symbolic systems that are similar between humans and other primates.

The research presented in this volume is but a small testament to the multifaceted gem that is the CPRC. Indeed, this effort is only the latest in the following series of publications that are devoted to the research conducted at the CPRC facilities over the last 25 years:

1. *The Cayo Santiago Macaques. History, Behavior and Biology* (State University of New York Press, Albany, 1986). The chapters in this book, which is edited by Richard C. Rawlins and Matthew J. Kessler, are based on several presentations given in a special symposium at the annual meeting of American Society of Primatologist in 1983, in celebration of the 45th anniversary of the Cayo Santiago macaque colony.

2. *Puerto Rico Health Science Journal*, Volume 8, Issue 1, 1989. This special issue was devoted to papers derived from presentations at a meeting in San Juan, Puerto Rico, which was hosted by the University of Puerto Rico School of Medicine, to celebrate the 50th anniversary of the Cayo Santiago colony and the research conducted over the intervening years on the various living and skeletal populations of the CPRC.

3. *Cayo Santiago Macaques – Images* (Blurb 2009). This book by Richard G. Rawlins is a collection of photographs from Cayo Santiago, in celebration of its 70th anniversary.

"Anniversaries are not only times for looking back at the past, nor for appraising where we stand at the present. They are times for looking forward" (Philip V. Tobias). As the CPRC continues to develop through the efforts of its four units, and additional studies are conducted on the rhesus macaques by researchers both inside and outside of Puerto Rico, significant discoveries will continue to be made, providing the foundation for future symposia and celebrations.

I wish to thank the Caribbean Primate Research Center, in particular the Laboratory of Primate Morphology and Genetics, for their support. I am grateful to Paul Dechow and Jim Cheverud for opening my eyes to the Cayo Santiago skeletal collections. Thanks to Don Dunbar – I am deeply appreciative of his friendship, support, and advice, beginning with my initial visit to San Juan. Along with his late

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Chapter 1
Physical Anthropology at the Caribbean Primate Research Center: Past, Present, and Future

Donald C. Dunbar

1.1 Introduction

Physical (biological) anthropology has played a central role in the development of the Caribbean Primate Research Center (CPRC) and has had a profound impact on its research perspectives. Likewise, research arising from the CPRC and its units has helped shape the field of physical anthropology, as we know it today. This latter influence has occurred through publications and the application of techniques and approaches applied or developed at the Center, and also through the mentoring and training efforts of researchers who transmit their professional experiences to future generations of physical anthropologists. In addition, although beyond the scope of this chapter, it is hoped that historians of science will find that the contained information provides the necessary foundation for investigating the degree to which CPRC research has had an impact on the development of theories, concepts, and methods central to physical anthropology.

The CPRC is unusual, if not unique, in that its laboratory and field facilities provide opportunities for integrative studies spanning molecular genetics, organismal and population biology, and behavior of a primate population with known genealogical relationships. This chapter reveals that, whereas some investigations have been conducted that utilize two or more CPRC units, the full potential for integrative primate research remains to be exploited.

The mutual influences between physical anthropology and the CPRC have been demonstrated previously by the contributions to an edited book entitled *The Cayo Santiago Macaques* (Rawlins and Kessler 1986a) and in a special issue of the *Puerto Rico Health Sciences Journal* (Vol. 8, Issue 1, 1989) that contains papers from a

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symposium celebrating the 50th anniversary of Cayo Santiago. The present chapter provides a selective overview of the history surrounding the formation and development of the CPRC and its units. The past and present research conducted on these populations and in these units is then examined. Particular emphasis is placed on those investigations that have been conducted by physical anthropologists, or by specialists from other fields whose approaches and findings have been of direct anthropological relevance. In order to summarize several years of research by numerous investigators in a meaningful and coherent fashion, the chapter focuses on research themes and a select number of individuals contributing to those themes. The disadvantage of this approach, however, is that the relative contribution of co-investigators to a particular study may be misleadingly downplayed or otherwise skewed, a bias of which the reader should be aware. The chapter concludes with suggested future directions that anthropological research may take at the CPRC.

1.2   A Short History of Cayo Santiago, Other Introduced Populations in Puerto Rico, and the Caribbean Primate Research Center

The history of the Cayo Santiago rhesus monkey (*Macaca mulatta*) colony, primate populations on other offshore Puerto Rican islands, and the formation of the CPRC have been documented by Carpenter (1942a, 1972), Frontera (1958, 1989), Altmann (1962), Rawlins (1979a), Windle (1980), Sade and colleagues (Sade et al. 1985), Rawlins and Kessler (1986c), and by others in the special issue of the *Puerto Rico Health Sciences Journal* mentioned above (Benitez 1989; Evans 1989; Goodwin 1989; Kessler 1989; Loy 1989b; Marler 1989; Phoebus et al. 1989; Rawlins 1989; Southwick 1989; Turnquist and Hong 1989; Vandenbergh 1989; Vandenbergh and Nagel 1989; Vessey et al. 1989; Whitehair 1989; Zucker 1989b). As might be expected from such a complex history, specific details can somewhat vary among the sources. Nevertheless, these and other published sources, when combined with the personal recollections of current and former CPRC staff, provide a highly reliable foundation for the following brief history of the CPRC and its units.

In the 1920s and early 1930s, a strong interest had developed in the habits and life styles of nonhuman primates. Virtually nothing was known about these bizarre creatures, however, because they lived in highly remote and unaccommodating locations. Thus, not surprisingly, those investigations that were conducted during this period focused, almost exclusively, on captive animals (Köhler 1927; Kohts 1923; Zuckerman 1932, 1933). Comparative psychologist and primatologist Robert Yerkes, although not a field researcher himself, nevertheless realized the need for investigating monkeys and apes in their natural habitats. To this end, he sent into the wild Henry W. Nissen (1931) to study chimpanzees (*Pan troglodytes*), Harold C. Bingham (1932) to study gorillas (*Gorilla gorilla beringei*), and Clarence Ray Carpenter (1934) to study howling monkeys (*Alouatta palliata)*. Carpenter's 2-year field study, in particular, is considered to be a landmark in modern primatology, not

only for its duration and detail, but also for its emphasis on understanding the animals in their own right, as opposed to models for understanding the human condition (e.g., Jolly 1972). Carpenter (1940) followed the howler study a few years later with a field study of gibbons (*Hylobates lar*) in Thailand.

As indicated through publication (Carpenter 1972) and verbal recollections (see Rawlins and Kessler 1986c), Carpenter and others had been interested from the early 1930s in establishing a colony of one or more Old World primate species on a tropical island in the Americas. Not until 1938, however, was a concrete plan able to take shape. Carpenter began working with Dr. Philip Smith and Dr. Earle Engle of Columbia University, and with Dr. George Bachman, Director of the School of Tropical Medicine in San Juan, Puerto Rico, which was under the auspices of Columbia University. The group approached the Markle Foundation for a grant to fund an expedition to India. The mission of the expedition was to capture rhesus macaques and bring them to one of a number of possible small islands off the coast of Puerto Rico. The purpose was to establish a breeding colony that would provide monkeys for biomedical laboratory research and, at the same time, allow behavioral observations in a seminatural environment. Carpenter also wanted to capture gibbons, primarily because he had become fascinated by their behavior in Thailand. Under the guidance of the financier J.P. Morgan, Jr., the Markle Foundation had recently focused its general philanthropic interests in social welfare onto medical research[1]. The Foundation was interested in the proposed mission, but it was initially hesitant because the ability of rhesus monkeys to breed in Puerto Rico was unproven. A greater concern over the potential loss of access to this species in India due to the developing war in Europe overshadowed these doubts, however, and the funds were granted.

While Carpenter and his colleagues were in Asia collecting monkeys and apes on an expedition that would prove to be laced with intrigue, suspense, and hardship, Bachman remained in Puerto Rico and arranged to lease Cayo Santiago, a small (15.5 ha) island approximately 1 km off the southeast coast of Puerto Rico (Figs. 1.1 and 1.2). Carpenter recruited the Civilian Conservation Corps to prepare the poorly vegetated island for the animals. A variety of plants were introduced, wells were dug, and water catchments, cisterns, living shelters, and a boat dock were built. These physical modifications were carried out with mixed success. Nevertheless, the island was adequately prepared prior to the arrival of its imported inhabitants.

In December 1938, Cayo Santiago was successfully seeded with approximately 400 rhesus monkeys that had been collected near Lucknow, India. Gibbons were also placed on the island, but the exact number is unclear. Curiously, discrepancies exist between the information reported by Windle (1980) and that reported by Rawlins and Kessler (1986c), even though both publications quote directly from transcripts of the same public address given by Carpenter at the University of Puerto Rico, School of Medicine, in 1959. Carpenter himself further confounded the issue in a more recent publication (Carpenter 1972) by providing a description of events

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[1] Based on historical information provided by the Markle Foundation on its website.
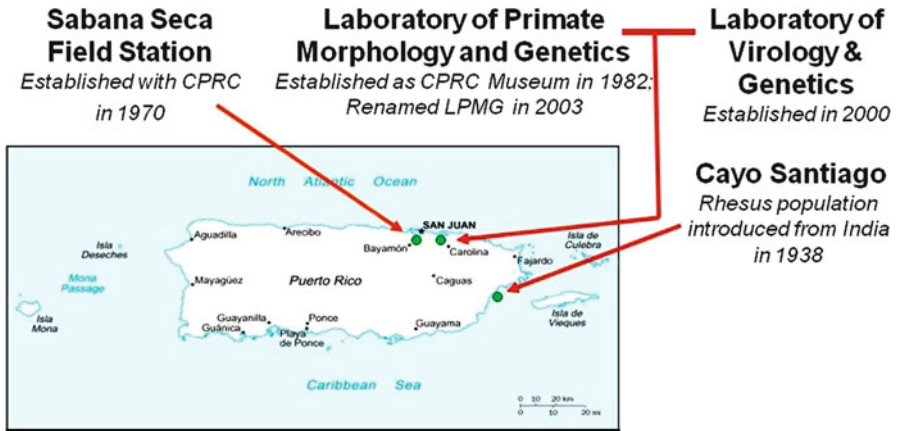
Fig. 1.1 The geographic locations of the Caribbean Primate Research Center units in Puerto Rico. The map of Puerto Rico is from the World Fact Book of the Central Intelligence Agency of the United States Government and is in the public domain

Fig. 1.2 Aerial photograph of Cayo Santiago

that somewhat varies from what he presented in the 1959 address. One source of this discrepancy may be traced to the difficulties in extracting accurate quantitative information from a transcribed oral presentation of a complex series of events that occurred prior to the arrival of the gibbons at Cayo Santiago: their initial capture in Asia and the subsequent loss of several animals through either sale for revenue or exposure during oceanic transit (Rawlins and Kessler 1986c; Windle 1980). A second source may be attributed to the challenge of recalling such specific details 34 years later (Carpenter 1972). Nevertheless, it is sufficient to conclude that between 7 (Windle 1980) and 14 (Carpenter 1972; Rawlins and Kessler 1986c) gibbons were released onto the island.

Primatologist Michael Tomilin, who was the first Scientist-in-Charge on Cayo Santiago and who had only recently arrived on the island to maintain the free-ranging population, received the animals. In 1939, three pigtail macaques (*Macaca nemestrina*), already in captivity at the Institute of Tropical Medicine, were added to the mix. Unfortunately, the gibbons soon proved to be a dangerous threat to human observers on the island and were recaptured and maintained in cages in 1940. Finally, in 1941, the gibbons were sent to Pennsylvania State University and several zoos in the United States. The pigtail macaques, however, were a more successful addition, with the youngest of the three living on the island as late as 1956.

For the first couple of years, the young Cayo Santiago colony strengthened and prospered, and, as with other novel and exotic phenomena of potentially great public interest, it rapidly received extensive local and international media attention, most of which was strongly supportive. Not all the attention proved to be positive, however. The local community on the main island of Puerto Rico, upon hearing (incorrectly) that the monkeys were to be used as test subjects for studies of leprosy and poliomyelitis, became extremely concerned over the risk of contamination to humans, namely, themselves. Through published letters and personal appearances, however, Bachman and others were soon able to quell public fears by clearly explaining that the colony itself would consist only of healthy animals and that studies of induced diseases would not be conducted on the island.

Despite its bright beginnings, Cayo Santiago began to falter in 1941 and the colony would struggle to survive over the next 14 years. The downward slide appears to have been attributed primarily to the combined impact of the Markle Foundation grant being completed, the lack of additional funds, the paucity of scientific use due to involvement of the United States in World War II, and the closing of the School of Tropical Medicine by Columbia University. From 1941 to 1944, a large portion of the colony was sold to various research facilities in the United States in order to raise funds to support the 200 animals remaining on the island. To make matters worse, Tomilin resigned, feeling that conditions had deteriorated to such a degree that he could no longer adequately maintain the colony. Tomilin's departure resulted in Cayo Santiago being left without a Scientist-in-Charge. With the closure of the School of Tropical Medicine, responsibility for the colony was taken up by the College of Natural Sciences at the University of Puerto Rico in 1944.

Although Cayo Santiago would continue to experience severe hardships for the next 11 years, a key figure in its salvation would appear in 1947. At that time, the College of Natural Sciences, desperate for funds to support the island colony, put the monkeys (now numbering around 400) up for sale in the journal *Science*. Fortuitously, Puerto Rican neuroscientist Guillermo Frontera, then a doctoral candidate at the University of Michigan, was extremely interested in using the monkeys for his own research and convinced the Dean of Natural Sciences to delay selling the colony until his return to Puerto Rico the following year. In 1948, the Dean was successful in obtaining NIH funds for 2 years, which would be subsequently extended to a third year. Furthermore, Frontera, who did indeed return to Puerto Rico when promised, not only obtained additional financial support through a grant for neuro-anatomical investigations using the Cayo Santiago monkeys, but also personally paid for and delivered foodstuffs to the island to keep the, by then, underfed animals

alive. The College of Natural Sciences was most likely relieved when it was able to transfer the responsibility of Cayo Santiago over to the newly established University of Puerto Rico, School of Medicine, in 1950. Funding continued to be dismal, however, coming primarily from the Medical School budget. The monkeys were used for in-house biomedical research and were supplied to research institutions in the United States, dropping the colony population to approximately 225.

In 1955, struggling Cayo Santiago was thrown a lifeline when Frontera was able to convince the National Institute of Neurological Diseases and Blindness (NINDB) that it was in everyone's interests to support the island colony. The NINDB's interest was to use the colony to develop a monkey model for perinatal physiology and associated diseases that would parallel their program with humans, and to do so in collaboration with the University of Puerto Rico, School of Medicine. Despite some stumbling in negotiations owing to a separate offer that had been made to Dr. David Rioch of Walter Reed Army Hospital to use the monkeys for behavioral investigations, as well as other details, an agreement was reached in 1956 for the NINDB to establish the Laboratory of Perinatal Physiology (LPP) in San Juan, to financially support the island population, and to use it for research. In an exemplary display of professionalism, Rioch offered to adjust his research efforts to accommodate the NINDB's interests. Furthermore, even though he eventually had to withdraw his claim on Cayo Santiago due to lack of funds, Rioch continued to show his support for the colony's welfare by suggesting that sociobiologist Stuart Altmann, then a Harvard graduate student of E.O. Wilson, be the next Scientist-in-Charge. Altmann was indeed recruited and came to Cayo Santiago that same year, where he established the foundation for the long-term and ongoing animal database. Thus, the NINDB designated the Cayo Santiago colony as its Behavioral-Ecology Section and, in collaboration with the School of Medicine at the University of Puerto Rico, began to vastly improve the well-being of the monkeys and the infrastructure and facilities on the island.

Through the remaining 1950s and the 1960s, improvements continued and the outlook for the Cayo Santiago colony's permanency appeared about as promising as could be expected. During this period, the following individuals followed Altmann to serve as the official Scientist-in-Charge, or in a similar role, while using the colony for their own research: Carl B. Koford, John Morrison, Chester Swett, and, jointly, Margaret Varley and Elizabeth Missakian. In addition, an individual who would prove central to the colony's long-term management and census emerged in the 1950s in the personage of Angel "Guelo" Figueroa, who lived in the neighboring Puerto Rico mainland community of Punta Santiago. Following Figueroa's retirement as Chief Census Taker in 1992, his protégé, Edgar Davila, would assume this critical role, which he continues to fill today.

In 1960, as the Ecology Section Chief of the LPP, biologist and ecologist Carl B. Koford wanted to establish additional monkey colonies that were on islands at the same latitude as Cayo Santiago, but which provided different habitats (Vandenbergh 1989). He was interested in determining what impact a change in habitat would have on breeding patterns and other behaviors in the same species. To this end, Koford gained access that same year to two islands off the southwest coast of Puerto Rico: La Cueva and Guayacán. The two islands together became known as the

La Parguera colony, acquiring its name from the nearest human community on Puerto Rico. Unlike frequently rain-drenched Cayo Santiago, La Cueva and Guayacán were dry and vegetated by small trees, shrubs, cacti, and grassland. In addition, approximately half of each island consisted of mangrove swamp, a much greater proportion than on Cayo Santiago. Initially stocked by nine Cayo Santiago monkeys in 1961, additional rhesus macaques were imported from India in 1962–1963, raising the combined population on both islands to 278. The rhesus colony remained at the La Paguera facility for 18 years and grew to over 1,400 individuals before the entire population was transferred in 1979 and 1980 to Morgan Island, off the South Carolina coast (Taub and Mehlman 1989).

In addition to rhesus macaques, patas monkeys (*Erythrocebus patas*) from Nigeria were also introduced to the La Paguera colony. The history of the patas project and the research derived from it (Loy 1989b), as well as a description of the difficulties encountered in gathering data on this species on Guayacán in particular (Zucker 1989b), have been presented elsewhere through first-hand accounts of La Paguera researchers. To summarize from Loy (1989b), 1 adult male and 4 adult females were placed in corrals on La Cueva in 1971. In two separate shipments the following year, 2 males (1 young adult and 1 juvenile) and 13 females (4 adults and 9 juveniles or infants) were added to the original 5 individuals. Of this total of 20 patas monkeys, 14 individuals (2 young adult males, 1 juvenile male, and 11 females ranging from infant to adult) were released on La Cueva to live under free-ranging conditions in order to establish a breeding colony. By 1973, both the corralled and free-ranging populations began to breed successfully. In the same year, however, it was decided that the free-ranging patas monkeys, now numbering 19 individuals, should be moved to Guayacán, and this transfer was accomplished in 1974. Over the next 5 years, the Guayacán patas population continued to grow through breeding and through the import of an additional 21 individuals, increasing the population to approximately 55–60 individuals (Matt Kessler, personal communication). In 1980, the decision was made to move the free-ranging patas monkeys from Guayacán and back again to La Cueva. Then, in Spring 1982, approximately 2 years after the removal of the rhesus population, the patas monkeys were moved off La Cueva and placed in enclosures at a facility in Sabana Seca on the Puerto Rico mainland (see below), and the La Paguera facility was closed. Some of the patas monkeys lived out their lives at Sabana Seca. Over the next few years, however, the remaining patas population, along with any other primates representing species other than rhesus monkeys (see below), was transported from Sabana Seca to zoos, research institutes, and other facilities (Matt Kessler, personal communication; Jean Turnquist, personal communication).

During the period of the La Parguera colony's existence, individual rhesus and patas monkeys occasionally escaped to the Puerto Rico mainland. Over time, these individuals bred, and eventually established successful rhesus and patas colonies across the southwestern portion of the island. It should be noted, however, that some of the rhesus individuals might have come from zoos, private homes, or other sources (González-Martínez 2004).

Whereas the Cayo Santiago and La Parguera colonies were progressing fairly well throughout the 1960s and 1970s, a far less successful effort at introducing

monkeys to another island environment began in 1966 when 57 rhesus monkeys were transported from Cayo Santiago to Desecheo (Fig. 1.1), a small (1.5 km²), rugged island lying 21 km off the west coast of Puerto Rico (Evans 1989). Desecheo, which is essentially a steep-sided, rectangular-shaped, mountain peak providing only difficult access, was an official United States wildlife reserve (primarily a bird sanctuary) from 1912 to 1940 and then again beginning in 1976. Despite a lack of significant water sources other than intermittent rainfall, arid vegetation, and overall inhospitable conditions, the monkeys appeared to adapt well. As with most introduced species with no natural competition, however, the rhesus macaques were immediately thrust to the top of the food chain. The monkeys soon began to prey so efficiently on seabird eggs that by 1970 Desecheo was devoid of nesting birds well into the normal nesting season. To make matters worse, the monkeys earned the infamous reputation of having obliterated the largest known nesting colony of brown boobies, although resident goats may have also contributed. This painful lesson of how species introduction can go terribly wrong led to the decision to remove the rhesus macaques from the island. Removed monkeys were placed in quarantine in a zoo (Jardín Zoológico de Puerto Rico) in the city of Mayagüez in western Puerto Rico (Evans 1989) before being transported to research institutions in the United States (Matt Kessler, personal communication). Multiple efforts to remove the animals were made in 1977, 1979, and 1981, but it was not until a final extended effort over the 1985–1987 period that their complete removal at least appeared to be successful. Nevertheless, claims of direct sightings and indirect evidence of individual rhesus monkeys on Desecheo have been reported over the intervening years.

Growing administrative disagreements between the NINDB and the University of Puerto Rico, School of Medicine, began to develop in the 1960s. These disagreements finally came to a peak in 1970, when the NINDB closed the LPP and withdrew its operations from Puerto Rico. Arrangements were made, however, for NINDB financial support of Cayo Santiago to continue. In the same year, the University of Puerto Rico, School of Medicine, created the CPRC, which would serve as the umbrella institution encompassing Cayo Santiago as one of its units, and which today is the home to approximately 1,000 free-ranging rhesus macaques. The Sabana Seca Field Station (SSFS), located west of San Juan, became the second unit (Figs. 1.1 and 1.3). The SSFS was formed to house the CPRC's administrative offices and to provide cage and corral facilities for rhesus monkeys that were gleaned from the Cayo Santiago population. The SSFS, which currently houses approximately 2,000 rhesus macaques, also proved to enable more invasive research protocols than were possible at Cayo Santiago. In addition, *Macaca mulatta* and *Erythrocebus patas* were not the only primate species housed at the SSFS. At least from 1977 to 2001, members of the following species were present for various time periods: *Aotus trivirgatus, Cebus apella*, *Cebus capucinus*, *Cercopithecus aethiops, Macaca arctoides* (= *M. speciosa*), *Macaca nemestrina*, and *Saimiri* spp. (Matt Kessler, personal communication, Jean Turnquist, personal communication). Moreover, beginning in 2009, a *Macaca fascicularis* group has been housed at the SSFS for the duration of a reproductive study (Janis González-Martínez, personal communication).

Since its inception, the CPRC has fallen under various levels of administrative jurisdiction, shifting from its initial position in the deanship of medicine to the

Fig. 1.3 Aerial photograph of the Sabana Seca Field Station

chancellorship of the Medical Sciences Campus (MSC). Today, it remains in the chancellorship, but as a subdivision of the Unit of Comparative Medicine, along with the MSC Animal Care Facility. Clinton Conway was appointed the first CPRC Director and over the intervening years, up to the present, the following individuals have served in this role: William Kerber, Sven Ebbesson, Gilbert Meier, Lloyd LaZotte, Delwood Collins, Matt Kessler, and Edmundo Kraiselburd.

Director Conway appointed Donald Sade, a physical anthropologist trained by Sherwood Washburn, as Scientist-in-Charge on Cayo Santiago in 1970, following the formation of the CPRC. Richard Rawlins, another physical anthropologist, followed Sade in 1976. When Rawlins left Cayo Santiago in 1981 to pursue graduate training in reproductive physiology, veterinarian Matt Kessler maintained the colony until 1984, with the aid of Angel Figueroa and John Berard, the latter a graduate student of physical anthropologist Paul Simonds. At that time, sociobiologist Curt Busse, having been hired by Delwood Collins, arrived in Puerto Rico to fill the Scientist-in-Charge position. During his tenure, Busse developed the computerized database for Cayo Santiago. After Busse, the position was filled by Berard, and then by Melissa Gerald and Adaris Mas-Rivera, both of whom are physical anthropologists as well.

In 1969, just prior to the formation of the CPRC and his official appointment as Scientist-in-Charge, Sade proposed a long-term behavioral research plan for Cayo Santiago that would enable the monkey population to remain largely intact (minimal culling of individuals); allow stable, long-term group hierarchies and individual social interactions to develop; and provide the appropriate conditions for the meaningful study of genetic and demographic issues. This proposal, which was adopted by the CPRC upon its formation and implemented for the next several years, required reducing the island population to a size that was manageable and that did not

Fig. 1.4 Rhesus femora and skulls representing the age spectrum available in the skeletal collection of the Laboratory of Primate Morphology and Genetics

overwhelm the infrastructure. To accomplish this population reduction, entire social groups were removed. Beginning in 1971, Sade also began a systematic collection of skeletons from rhesus monkeys that died on Cayo Santiago. This collection was destined to rapidly increase in size when it was decided that one of the social groups (Group K) removed from Cayo Santiago in 1972 would be sacrificed in order to provide a large ($N = 106$) skeletal series for morphological and genetic studies. This action immediately created an invaluable skeletal collection consisting of specimens of known age, sex, weight, and maternity. Prior to their maceration, Richard Rawlins made plaster casts of the hands of Group K individuals for physical anthropologist Robert J. Meier, who used the casts to investigate the design and function of rhesus dermal ridge patterns. Thirty-five years later, Meier would donate this dermatoglyphic collection to the CPRC, where it is housed today with the skeletons of the same individuals from whom the casts were made.

The rapidly growing skeletal collection soon needed a more adequate home. Space was made available in the Department of Anatomy (now the Department of Anatomy and Neurobiology) at the University of Puerto Rico, School of Medicine, in San Juan. Thus, the CPRC Museum was formed in 1982 as the Center's third unit (Figs. 1.1 and 1.4), and Dean Falk, a physical anthropologist and Anatomy faculty

Fig. 1.5 The Laboratory of Primate Virology and Genetics

member, became the first Curator of the collection. In 1984, the National Science Foundation provided funds to maintain the collection, which by then numbered more than 600 specimens. Jean Turnquist, also a physical anthropologist, succeeded Falk as curator in 1986. Under Turnquist's direction over the next 17 years, the collection continued to expand, not only with rhesus skeletons from Cayo Santiago and the SSFS, but also with skeletons of the other SSFS resident species (see above). In 2003, the CPRC Museum was renamed the "Laboratory of Primate Morphology & Genetics" (LPMG) and the Curator position was retitled "Director" in order to more accurately reflect the modern research use and potential of the collection in both these general research areas. Thus far, the LPMG has had two directors: physical anthropologists John G. H. Cant and Donald C. Dunbar. The current collection consists of more than 3,600 primate specimens. Over 3,000 of these specimens are CPRC rhesus monkeys derived from either Cayo Santiago or the SSFS, the latter population of which is also derived from the Cayo Santiago population. The rhesus specimens, like their living CPRC relatives, are both unusual and invaluable because their individual identity and genealogical relationships are known.

When virologist Edmundo Kraiselburd, the current CPRC Director, began his tenure in 2000, he initiated the development of a specific pathogen-free (SPF) rhesus population at the SSFS to help meet the growing demand for "clean" monkeys in biomedical research. Kraiselburd also created the Laboratory of Virology and Genetics (LVG) as the fourth CPRC unit (Figs. 1.1 and 1.5), and recruited physician and biomedical researcher Carlos A. Sariol as the LVG Director. In addition to

virological research, the LVG has collected genetic information on the Cayo Santiago colony. Maternity, as well as parity, was known from census data for the rhesus population since the 1950s, but paternity was unknown. With the services of the German Primate Center, whose rhesus population was also derived from the CPRC population (Arnemann et al. 1989), and later that of the California National Primate Research Center, paternity information has become available for most monkeys born since 1990.

1.3 Physical Anthropological and Related Research

Mentioning every publication that has arisen from research on Cayo Santiago and at the other CPRC units over the last 70 years is beyond the scope of this chapter. Kessler and Rawlins (1986) provide a comprehensive bibliography (and filmography), however, for the period between 1938 and 1985, and the bibliography on the CPRC website begins with 1983 and continues to the present. Rather, this chapter highlights the anthropologically relevant research programs of key scientists, and also provides some examples of studies by others that represent various research themes. In addition, numerous theses, dissertations, and abstracts have resulted from research at the CPRC. In consideration of space limitations, however, the research presented here will be based on published papers and chapters.

1.3.1 Cayo Santiago

Owing to a combination of economic and political factors imperiling the colony's formation and survival, research productivity on Cayo Santiago was slow to develop (Fig. 1.2). In the late 1930s, three publications, originating from the popular press, were aimed at introducing the population to the public and scientific communities. In the 1940s, however, published information switched from public relations to the scientific. Scientists working directly on Cayo Santiago generated ten publications. Perhaps not surprisingly, eight of these early investigations focused primarily on colony health-care issues. Nevertheless, behavioral studies of direct interest to physical anthropologists were being conducted by Carpenter, culminating in two landmark papers on the sexual behavior of the Cayo Santiago macaques that appeared in the *Journal of Comparative Psychology* and *Biological Symposia* in 1942 (Carpenter 1942a, b). Research activities dropped once again, however, during the period when the United States was involved in World War II, and it was not to revive until the 1950s, beginning with the arrival of Stuart Altmann as Scientist-in-Charge.

Although five publications, including two abstracts by Altmann, were produced in the 1950s, it was not until the 1960s that research papers began to appear in earnest. Altmann's detailed sociobiological investigations of the Cayo Santiago rhesus monkeys between 1956 and 1958 formed the basis of his classic series of papers on

overall behavior (Altmann 1962), communication (Altmann 1965, 1968a), and sexual differences (or lack thereof) in affective (emotionally driven) behavior (Altmann 1968b).

At about the time that Altmann was completing his work on Cayo Santiago, a longitudinal growth study of the rhesus monkeys began under the direction of physical anthropologist James A. Gavin. According to Donald Sade and colleagues (1985), physical anthropologists Kirby Chandler (1958–1960), Clyde Snow (1960–1961), and Sade himself (1960–1962) actually collected the data. In the first half of the study, information was gathered on virtually all monkeys in the population, but in the second half, a focal group of 90 individuals was chosen. The data, which were collected while the monkeys were anesthetized, included multiple body measurements, dental eruption status, and blood samples. In addition, radiographs, dental impressions, and prints of the palmar and plantar surfaces of the hands and feet were made on selected individuals. This information was presented in a final NIH progress report (Gavan 1963), but apparently was not otherwise published. Nevertheless, the trapping necessary for data collection in the Gavin study proved immediately beneficial to Carl B. Koford's studies of population dynamics (see below), which were being conducted at the same time (Sade et al. 1985). Moreover, the Gavin longitudinal growth study may have had a fundamental impact on the types and direction of future research on Cayo Santiago (Matt Kessler, personal communication).

As stated earlier, Koford took charge of Cayo Santiago following Altmann; however, it should be remembered that he was also a staff member of the NINDB's LPP, with obligations to that laboratory. Thus, in line with the LPP's interests in developing the rhesus monkey as a biomedical model for perinatal physiology, part of Koford's research focused on the natural occurrence of twins and teratisms in the island population (Koford et al. 1966). Either alone or with Clinton Conway and others, however, Koford also studied other aspects of Cayo Santiago reproduction, as well as demography, population dynamics, and overall social behavior (Conway and Koford 1964; Koford 1963a, b, 1965, 1966), all topics of immediate relevance to physical anthropology.

Donald Sade was not only a prominent administrator of Cayo Santiago, but also a productive researcher. His research, either alone or in collaboration, covered a spectrum of topics, ranging from sexual behavior and reproduction (Sade 1964) to parent–offspring–sibling behavior (Sade 1965,1991), group dynamics (Chepko-Sade and Sade 1979; Chepko-Sade et al. 1989; Sade 1967, 1968, 1972a, b, 1980, 1989, 1992; Sade et al. 1977), demographics (Sade 1990; Sade et al. 1987, 1988), communication (Sade 1973), and data management (Sade 1975).

Comparative psychologist and behavioral biologist Elizabeth Mizzakian, who for a period shared the Scientist-in-Charge duties with Margaret Varley (see above), conducted studies on the Cayo Santiago rhesus population between 1968 and 1970. Papers resulting from these investigations covered a variety of topics, including group dynamics (Missakian 1973b), sex and reproduction (Missakian 1972b, 1973a; Missakian et al. 1969), mother–infant relations (Missakian 1974), and dominance (Missakian 1972a).

Beginning in the mid-1970s, Carol Berman studied infant socialization, focusing on the overlapping themes of play (Berman 1975, 1977), interactions between mother and infant (Berman 1978, 1980b, 1982a, 1983c, 1984, 1989, 1992) and between infants (Berman 1982b, 1983a, b), rank acquisition (Berman 1980a, 1983d), maternalism (Berman 1990a, b), and the impact of matrilines (Berman 1983d, e, 1986) and of being orphaned (Berman 1982c, 1983c). Along with Kathlyn Rasmussen, Stephen Suomi, and others, she looked at the impact of care patterns by, and separation of infants from, mothers (Berman et al. 1993, 1994; Devinney et al. 2003). The mother–infant relationship and infant socialization were also analyzed from a demographic perspective (Berman 1988a, b; Berman et al. 1997).

Richard Rawlins, Cayo Santiago Scientist-in-Charge after Sade, conducted anthropologically relevant studies, either alone or in collaboration with Matt Kessler, Jean Turnquist, and others, on topics that concern reproduction (Rawlins 1979b; Rawlins and Kessler 1985; Rawlins et al 1984), demography (Rawlins and Kessler 1986b, d), group dynamics (Rawlins and Kessler 1987), and locomotion and manipulation (Rawlins 1993). In collaboration with Kessler and others, Rawlins also published more biomedically relevant papers on colony health issues (e.g., Kessler and Rawlins 1983a, b, 1984; Kessler et al. 1984; Rawlins and Kessler 1982, 1983).

Beginning in the 1990s and continuing to the present, psychologist and anthropologist Marc Hauser has pursued studies in cognition by focusing on communication and acoustic perception (Hauser 1991, 1992a, b, c, 1996, 1998, 2007; Hauser and Anderson 1994; Hauser and Marler 1993a, b; Hauser et al. 1998, 2007), handedness and other motor asymmetries (Hauser et al. 1991; Hauser and Akre 2001), and arithmetical abilities and problem solving (Barner et al. 2008; Hauser 2001; Hauser and Carey 2003; Hauser and Spaulding 2006; Hauser et al. 1996, 2000; Wood et al. 2008).

Although most of his investigations in reproduction were conducted with the rhesus population at the SSFS (see below), physical anthropologist and former CPRC staff researcher Fred Bercovitch also studied this topic with the Cayo Santiago population. With John Berard, he conducted a demographic study to determine if rapid reproductive maturation in females exacts a cost in their life history (Bercovitch and Berard 1993). In the early 2000s, along with geneticists Peter Nürnberg and Anja Widdig, among others, he applied genetic (microsatellites and DNA fingerprinting) and behavioral approaches to investigate the impact of paternal relatedness on social interactions among adult females (Widdig et al. 2001, 2002). In addition, along with Nürnberg, Widdig, Berard, Kessler, and others, Bercovitch used genotyping with STR markers to reveal, for the first time in a cercopithecine species, that two different males can sire a single set of dizygotic twins (Bercovitch et al. 2002). In related studies, Berard, Nürnberg, and colleagues used DNA fingerprinting to determine the degree to which dominance rank (Berard et al. 1993) and a variety of behavioral tactics correlate with male reproductive success (Berard et al. 1994).

In the last decade, physical anthropologist Melissa Gerald conducted interdisciplinary and integrated research on mating and competitive interactions within the Cayo Santiago rhesus population. Her investigations, which were made in collaboration with Dario Maestripieri, Corri Waitt, and others, have focused on the impact

of skin coloration on behavior (Dubuc et al. 2009), morphometric measures as an indicator of female fertility (Campbell and Gerald 2004), sex differences in survival costs of reproduction (Hoffman et al. 2008), the stress-related changes of cortisol levels in lactating versus nonlactating adult females (Maestripieri et al. 2008), how the presence of immature maternal relatives within a natal group influences transfer of orphaned males (Waitt et al. 2004), and the social impact of vocalizations (Semple et al. 2009; Whitham et al. 2007).

Besides the above research programs, other investigators have looked at the same and other topics on Cayo Santiago, such as daily activity patterns (Fisler 1967), aggression (Wilson and Boelkins 1970), locomotion and posture or manipulation (Draper 1966; Dunbar 1989, 1994; Dunbar and Badam 1998; Rawlins 1993; Sade 1973; Turnquist and Wells 1994; Wells and Turnquist 2001), obesity (Berman and Schwartz 1988; Schwartz et al. 1993), hormones and behavior (Laundenslager et al. 1999; Rasmussen and Suomi 1989; Rasmussen et al. 1997), aging (Corr 2003), genetics (Beuttner-Janusch et al. 1974a, b; Beuttner-Janusch and Sokal 1977a, b; McMillan and Duggleby 1981; Ober et al. 1980), and the impact of food shortage on behavior (Loy 1970).

Several chapters in this volume demonstrate that research, by both the veteran investigators discussed above and a new generation of researchers, continues to be actively pursued on Cayo Santiago. This research addresses traditional and novel topics. Emma Nelson, Christy Hoffman, Martin Vorcek, Melissa Gerald, and Susanne Shultz use the length ratio of the second digit to the fourth digit of the hand – this ratio is known to be highly heritable and is proposed to be attributed to prenatal androgen effects – as a means to investigate how mothers may be able to genetically transfer dominance rank to their daughters (Chap. 6). Gregory Blomquist focuses on social and demographic factors influencing the age at which females have their first offspring (Chap. 9). Christy L. Hoffman and Dario Maestripieri investigate female stress, disease, and mortality as costs of reproduction (Chap. 10). Carol M. Berman and Ellen Kapsalis look at factors contributing to, or mechanisms underlying, female kin preferences or bias, in terms of how time constraints influence grooming kin bias intensity (Chap. 11). In a second contribution, Maestripieri and Hoffman investigate how ecological and demographic conditions on Cayo Santiago impact the behavior and social dynamics of its rhesus population, as compared to populations in the wild (Chap. 12). Finally, Donald S. Sade demonstrates how concepts from evolutionary psychiatry and tools from social network analysis can open new research areas with the Cayo Santiago rhesus population (Chap. 13).

1.3.2 Other Offshore Colonies and Feral Populations on Mainland Puerto Rico

Although the facilities are no longer in operation, studies were conducted with the Desecheo Island rhesus colony and the populations of rhesus and patas monkeys at the La Parguera colony that are of direct relevance to physical anthropology.

One basic purpose for establishing the Desecheo and La Parguera rhesus colonies was to determine the impact on behavior and social structure of an environment that differed from Cayo Santiago. In addition to these planned colonies, rhesus and patas populations have also been studied that were unintentionally introduced to the southwestern region of the Puerto Rico mainland.

1.3.2.1 Desecheo Island

The period of formal operations (1966–1977) on Desecheo Island was brief when compared to that on Cayo Santiago. This factor, combined with the difficulties of island access and terrain, resulted in this Cayo Santiago-derived rhesus population being little investigated. The only published study of the behavior and ecology of the Desecheo colony is a monograph by John A. Morrison and Emil W. Menzel, Jr. (1972), based on 246 days of observation accumulated through eight visits over a 5-year period (1966–1971). Morrison and Menzel transported to Desecheo a select number of individuals from Group H on Cayo Santiago, a group that had already been studied behaviorally. With an interest in behavioral variation and adaptation, these researchers documented the rhesus response to the unfamiliar Desecheo environment and any changes in their physical condition. They studied differences from, and similarities to, Group H in terms of dominance hierarchy and aggression, group structure, behavioral interactions, reactions to other species, and daily activity patterns. To make these comparisons, Morrison and Menzel used data collected when Group H was still intact on Cayo Santiago, and also made behavioral observations of those Group H members remaining on Cayo Santiago following the removal of those individuals bound for Desecheo Island.

1.3.2.2 La Parguera Colony

The La Parguera colony's existence was also relatively brief (1961–1982), but the populations on the two islands (La Cueva and Guayacán) comprising this facility were much more actively studied than the Desecheo population. Rhesus and patas monkeys occupied both islands, but rhesus studies were conducted primarily on La Cueva, whereas patas studies were carried out primarily on Guayacán. Evan Zucker (1987a, 1989a), however, investigated the interactions of the patas and rhesus monkeys on Guayacán. Vandenbergh (1989), Vessey and colleagues (1989), Loy (1989b), Zucker (1989b), and Phoebus and colleagues (1989) provided overviews of the history and scientific activities that occurred at the La Parguera colony.

Because an established social group from Cayo Santiago-derived rhesus macaques was not initially transported to the La Paguera facility, and due to an excessive number of young males in the colony, zoologist John Vandenbergh had the opportunity to investigate the dynamics of social group formation (Vandenbergh 1966, 1967). He turned next to rhesus reproduction, focusing on hormonal effects on behavior. The first investigation consisted of noninvasive observations of breeding seasons among the free-ranging groups (Vandenbergh and Vessey 1968).

Vandenbergh then conducted experiments to determine if the hormonal state of one sex would impact this state in the other sex. The protocol involved housing captured rhesus males and females in adjacent outdoor cages in the nonmating season and bringing the animals into the mating condition. In two separate studies, females were injected with estrogen (Vandenbergh 1969) and males were implanted with testosterone pellets (Vandenbergh and Post 1976) in order to determine if the opposite sex would become sexually stimulated. Extending the studies to the free-ranging population, two females were trapped, implanted with estrogen pellets, and reintroduced into their group (Vandenbergh and Drickamer 1974).

Lee Drickamer, Douglas Meikle, and Steven Vessey, among others, continued studies of the La Cueva rhesus macaques by investigating group interactions (Vessey 1968, 1971), dominance (Meikle et al. 1984), mating behavior (Drickamer 1974a; Varley and Vessey 1977), seasonal pelage molt (Vessey and Morrison 1970), factors influencing male group transfer (Drickamer and Vessey 1973; Meikle and Vessey 1981; Wilson and Vessey 1968), and sex differences in survivorship and reproduction (Drickamer 1974a; Meikle and Vessey 1988; Meikle et al. 1984). Different methodological issues in studying behavior were also tested, including observability of animals of different ages and ranks (Drickamer 1974b), use of enclosures (Drickamer 1973; Marsden 1968a, b, 1969), behavioral scoring procedures (Drickamer 1975, 1976), conducting experimental studies in the field (Vandenbergh and Drickamer 1974), and the use of demographic data in behavioral analysis, such as in the studies on survivorship and reproduction cited above.

James Loy, Kent Loy, Evan Zucker, Jay Kaplan, and others studied patas monkeys under free-ranging and/or corralled conditions when these African monkeys were at the La Parguera facility (1971–1982). Investigations focused on social organization (Kaplan and Zucker 1980; Zucker 1987b), dominance (Jacobus and Loy 1981; Loy and Harnois 1988; Zucker 1987a;), aggression (Zucker 1994), sexual and associated behaviors (Loy 1975, 1981, 1989a; Loy and Loy 1977; Zucker and Kaplan 1981b), reproductive cycles (Loy et al. 1978), facial color changes during pregnancy and lactation (Loy 1974), allomaternal behavior (Zucker and Kaplan 1981a), early social development (Loy and Loy 1987), and female behavior in the absence of adult males (Loy and Chilton 1987).

During the period when the patas monkeys on Guayacán were being captured for transfer back to La Cueva in 1980 (see above), Matt Kessler, William London, Eric Phoebus, Richard Rawlins, and Jean Turnquist took the opportunity to do blood work on the animals in order to characterize the species (Kessler et al. 1983). In addition, Turnquist measured passive joint mobility in order to determine the impact of sex, age, and caged versus free-ranging conditions on the potential range of joint motion (Turnquist 1983, 1985).

1.3.2.3 Feral Populations in Puerto Rico

Although the rhesus and patas monkeys were never domesticated like farm animals or common pets, the term "feral" is useful to distinguish these fugitive populations from those colonies that were intentionally introduced to the offshore islands.

From 1990 to 1993, Janis González-Martínez, a primatologist and the current CPRC Associate Director, conducted extensive investigations of the feral rhesus and patas populations (González-Martínez 1998, 2004). She was able to collect detailed information, even when the monkeys resided or ventured into habitats that were difficult to access, through the use of focal animals. These individuals were temporarily restrained with ketamine, physically examined, weighed, fitted with radio telemetry-equipped collars for tracking, and then released following recovery from the anesthetic. González-Martínez provided demographic data on group sizes and composition, population density, home range and ranging patterns, water and food sources, environments and habitats, and breeding and birth seasons. Behavioral data included habitat use, mating activity, and interactions between humans and monkeys, rhesus and patas, and members within the same species and group. González-Martínez also addressed the environmental and economic impact of these feral populations at the time of the study and into the future.

1.3.3   Sabana Seca Field Station

The SSFS (Fig. 1.3) differs from Cayo Santiago in that the facilities and infrastructure are designed for more controlled or invasive research protocols, similar to the National Primate Research Centers. Currently, these facilities include enclosures (individual and group cages and covered corrals), surgical suites, digital X-ray, and dual energy X-ray absorptiometry (DEXA) for bone density and body composition. Whereas many investigations at the SSFS are biomedically oriented research at the basic, clinical, and translational levels (ophthalmological, cardiovascular, neurobiological, and virological), these facilities have enabled studies that are relevant to current topics of interest to physical anthropologists, such as reproductive biology, socioendocrinology, bone biology, communication, and aging.

Beginning in the late 1980s and continuing into the late 1990s, Fred Bercovitch conducted studies in socioendocrinology at the SSFS. These investigations of the interaction of hormones and behavior have focused on aspects of male reproduction in rhesus macaques (Bercovitch 1989; 1992, 1993; Bercovitch and Clarke 1995) and patas monkeys (Bercovitch 1996). Along with CPRC veterinarian José Rodríguez, Bercovitch measured the mass of necropsy-derived testes and epididymides, and calculated testicular volume in order to determine the size of the structures relative to body mass (Bercovitch and Rodríguez 1993). These morphological variables largely determine the capacity for sperm production and storage, two components that contribute to the reproductive competitiveness of males. Working on another study with Matt Kessler and other CPRC personnel, Bercovitch weighed and physically palpated SSFS females for pregnancy in order to determine if and how body mass is related to age at first conception and to survival of the first born (Bercovitch et al. 1998). Along with Peter Nürnberg, he used testicular and other morphological variables, combined with multilocus DNA paternity data, testosterone concentrations, and behavioral observations, to determine reproductive

success in corralled rhesus males at the SSFS (Bercovitch and Nürnberg 1996) and at both the SSFS and on Cayo Santiago (Bercovitch and Nürnberg 1997). Along with Marc Hauser and James Jones, Bercovitch also investigated the relationship of the endocrine response (changes in blood cortisol levels) of rhesus mothers to alarm vocalizations by their infants under controlled experimental conditions (Bercovitch et al. 1995). Simultaneous with Bercovitch's program, Kathlyn Rasmussen, Stephen Suomi, and colleagues investigated endocrinological responses of SSFS rhesus macaques to stress and other factors (Suomi et al. 1989).

Marc Hauser and anatomist and primatologist Miguel Schön Ybarra investigated the contribution of lip configuration to the production of vocalizations in SSFS rhesus monkeys, and the ability to adequately produce these vocalizations when the sensorimotor innervation to the lips was blocked by the local anesthetic lidocaine hydrochloride (Hauser and Schön Ybarra 1994).

Melissa Gerald and colleagues used computer graphics to alter facial skin color of infant rhesus monkeys in order to determine if it impacted caregiver responses from caged SSFS adult females (Gerald et al. 2006; Waitt et al. 2007). A comparable technique was also applied in studies to determine how males (Waitt et al. 2006) and females (Gerald et al. 2007) respond to female secondary sexual coloration on the face and sexual skin of the anogenital region, and how both males and females respond to pregnant female facial coloration (Gerald et al. 2009).

Adaris Mas-Rivera, in collaboration with Fred Bercovitch, conducted a study on the cost of reproduction by monitoring postpartum recovery of primiparous rhesus females at the SSFS and the development of their infants (Mas-Rivera and Bercovitch 2008). The study was aimed at determining how the health of a female prior to conception impacted their recovery from the physiological and behavioral demands of caring for infants early in postnatal development.

1.3.4 Caribbean Primate Research Center Museum/Laboratory of Primate Morphology and Genetics

Physical anthropology has had a larger research representation in the CPRC Museum/LPMG (Fig. 1.4) than any other scientific field. The CPRC-derived skeletal collection has facilitated research on topics and themes such as bone biology and pathology, morphometrics (cranial, dental, and postcranial), biomechanics, phenotypic variation, genetics, postnatal growth and development, and evolution. Even before this CPRC unit was formed, Donald Sade's systematic collection of skeletons from Cayo Santiago (see above) induced research activity. Within 3 years of its initiation, studies on the collection led to papers on the relationship between tooth size and body size (Lauer 1975); changes with age in the pubic symphysis (Rawlins 1975); and the occurrence of limb fractures in relation to age, sex, and symmetry (Buikstra 1975). Perhaps the most prolific researcher working with the collection in the 1970s and 1980s, however, was James M. Cheverud. Either alone or with fellow physical anthropologists Jane Buikstra, Joan T. Richtsmeier, and

others, Cheverud used morphometrics to address the issue of how skeletal traits reflect changes in genetics and heritability arising from group fission on Cayo Santiago (Cheverud 1981b; Cheverud and Buikstra 1978, 1981a, b, 1982; Cheverud and Dow 1985). He also pursued related questions regarding morphological integration (Cheverud 1982b), and ontogeny and allometry (Cheverud 1982a; Cheverud and Richtsmeier 1986; Richtsmeier et al. 1984), including his classic developmental study of dental eruption and long-bone epiphyseal fusion that remains an authoritative reference (Cheverud 1981a). Cheverud has continued to work with the collection through collaboration with others, as evidenced by various references below. Conducting independent, but related, research to Cheverud's growth studies, new morphometric techniques for estimating age were developed by physical anthropologist Marianne Bouvier, using mandibular measurements (Bouvier 1988), and by physical anthropologists John G. H. Cant and Richard Kay, using tooth wear and cementum annulus counts (Kay and Cant 1988).

A new ontogenetic program, related thematically to the work of Cheverud and Richtsmeier in particular, emerged in the late 1990s when physical anthropologist Benedikt Hallgrímsson began investigating developmental variability in the LPMG skeletal collection. The initial morphometric study (cranial, dental, and postcranial) investigated fluctuating asymmetry, which is the distribution of random deviations from symmetry of bilateral morphological structures (Hallgrímsson 1999). Along with Katherine E. Willmore and Brian K. Hall, Hallgrímsson then compared limb skeletal data from adult rhesus monkeys in the LPMG collection with those from fetal mice collected elsewhere (Hallgrímsson et al. 2002). Their findings were interpreted in the context of mammalian limb development and primate evolution. Subsequent studies by Hallgrímsson, Willmore, and others that addressed these themes in the skull employed technologically more sophisticated protocols that enabled them to advance from two-dimensional (2D) to three-dimensional (3D) data collection (Hallgrímsson et al. 2004; Willmore et al. 2005). Moving postcranially again, Hallgrimsson, working with Nathan Young, addressed covariation between the serially homologous forelimb and hind limb skeletal elements from the LPMG rhesus collection, and of other mammals from other collections (Young and Hallgrímsson 2005). This study was based on 2D measurement data digitized from images of the bones made on a computer flatbed scanner.

Physical anthropologist Qian Wang continued the ontogenetic theme with the LPMG rhesus collection in the mid-2000s by addressing how age and sexually dimorphic differences in the craniofacial skeleton impact its biomechanics and adaptation. Working at times with physical anthropologist Lorena Havill (see below) and others, Wang used visual observation techniques to determine suture closure patterns. The degree of suture pattern heritability was investigated at pterion in the cranium (Wang et al. 2006b). The sexually dimorphic divergence with age in closure patterns at 28 sutures throughout the cranium and face was also studied in order to determine the differential impact on craniofacial biomechanics in males versus females (Wang et al. 2006a). Similar to Hallgrímsson and Willmore (see above), Wang and colleagues then began to collect 3D measurements of the skull in order to address broader questions about rhesus craniofacial ontogeny and sexual

dimorphism. Specifically, they used the relative 3D positions of 21 craniofacial landmarks to reveal growth rates, directions, and trajectories of, and sexual dimorphism in, the face, palate, neurocranium, and basicranium (Wang et al. 2007).

Beginning in the mid-1980s, several studies of the skeletal collection appeared that used a biomedical approach to address anthropological issues, or more clinical issues that have an anthropological relevance. These studies focused on bone as a biological material (growth and strength) and/or its response to disease processes (e.g., osteoporosis, osteoarthritis, and inflammatory arthritis). Physical anthropologist David Burr used the skeletal collection to investigate, through single photon absorptiometry (Burr et al. 1989) and histological analysis (Burr 1992), the material properties of long bones and the processes of remodeling associated with age, sex, and use. A decade later, Lorena Havill used a histological approach on long bones, combined with the LPMG skeletal collection's database on age, sex, body mass, and matrilineage, to investigate the role genetics plays in osteon remodeling dynamics (Havill 2003a, b).

Also in the mid-1980s, physical anthropologist C. Jean DeRousseau conducted a radiographic study of bone loss with age (DeRousseau 1985). Medical endocrinologists Francisco Aguilo, Jr. and Rafael Cabrera pursued this topic further by studying bone density (bone mineral content) and loss through single photon absorptiometry (Aguilo and Cabrera 1989). Beginning in the late 1980s and continuing into the 2000s, bone biologist Marc Grynpas and medical pathologist Kenneth Pritzker, working together or in collaboration with Matt Kessler, Jean Turnquist, Antonietta M. Cerroni, and others, also studied bone mineralization and osteoporosis using morphometrics, histology, density fractionation, chemical analysis, photon densitometry, and instrumental neutron activation analysis (Cerroni et al. 2000, 2003; Grynpas et al. 1989, 1993a, b; Pritzker 1994; Pritzker and Kessler 1998). Clinical rheumatologist Bruce Rothschild, usually in collaboration with Turnquist and CPRC Museum staff member Nancy Hong, extended the rheumatoid studies on the collection by investigating macroscopic evidence of osteoarthritis, spondyloarthropathic inflammatory arthritis, and articular plate excrescences (Rothschild and Woods 1992; Rothschild et al. 1997, 1999).

Fifteen years after Richard Rawlins's initial study of the pelvis (Rawlins 1975), physical anthropologist Robert G. Tague revisited the topic of changes in pubic symphysis morphology with age, sex, and parity (Tague 1990). Unlike Rawlins, however, Tague's study also investigated changes in preauricular area morphology. Both of these studies were qualitative, in that the data were based on visual inspection. Tague's subsequent studies of the CPRC skeletal collection and those of other anthropoid species in other collections, however, were based on quantitative data. He used calipers, curvometers, and osteometric boards to collect measurements and calculate indices in order to address obstetric, selectional, and broader evolutionary issues (Tague 1991, 1995).

Dean Falk focused much of her research on brain evolution, for which she made several hundred endocasts from the skeletal collection. These collaborative studies, which extended through the 1990s, investigated the sequence of suture closure with age (Falk et al. 1989), the branching patterns of the meningeal arteries

(Falk and Nicholls 1992), the heritability of brain size and surface features (Cheverud et al. 1990b; Konigsberg et al. 1990), sexual dimorphism in brain/body relationships (Falk et al. 1999), and issues related to cortical asymmetry (Cheverud et al. 1990a; Falk et al. 1986, 1990). In a study searching for potential functional associations with cerebral asymmetry, Falk and colleagues also investigated forelimb skeletal asymmetry and its relation to handedness (Falk et al. 1988).

Rather than looking at skeletal morphology, Robert J. Meier investigated the soft tissues of Cayo Santiago macaques (Group K) indirectly by studying plaster casts of the dermal ridge patterns of their hands from a functional perspective (Meier 1973).

As on Cayo Santiago, research on the LPMG's cranial and postcranial rhesus skeletons continues to be conducted by both CPRC veterans and a new generation of investigators. Jessica L. Joganic, Katherine E. Willmore, Charles C. Roseman, Joan T. Richtsmeier, and James M. Cheverud conduct a quantitative genetic analysis on the rhesus skeletal collection, focusing on cranial capacity and craniofacial morphology, and compare their findings with those derived from a collection of baboon crania from the Southwest National Primate Research Center (Chap. 2). In a thematically similar chapter, Willmore, Cheverud, and Richtsmeier, along with Jane E. Buikstra, use functional cranial analysis to investigate the relationship between metric and nonmetric traits during cranial morphogenesis in Cayo Santiago rhesus skulls (Chap. 3). Jean E. Turnquist, Antonietta M. Cerroni, Kate J. Faccia, Steven K. Boyd, and Benedikt Hallgrímsson use micro-CT technology to investigate the bone mineral density of lumbar vertebrae in adult females of known matrilineages from the LPMG skeletal collection (Chap. 4). The purpose is to determine how characteristics of trabecular structure and the underlying genetic components provide insight into the accurate assessment of osteoporosis. In an evolutionary dynamics study, Luci A. P. Kohn and Zachary Bledsoe measure specific dimensions of the axial and appendicular skeletons from the Cayo Santiago population in order to determine the influence of genetics on morphology and the impact of social group fission on heritability (Chap. 5). Connie Fellmann addresses the question of whether ontogenetic changes in musculoskeletal design occur in order to provide mechanical advantage for particular age groups during locomotion (Chap. 7). A cross-sectional growth series from the Cayo Santiago skeletal collection is compared with those of other monkey species (*Macaca fuscata, Macaca fascicularis, Cebus paella,* and *Cebus albifrons*) and rabbits (*Lepus* sp.) to investigate the issue in terms of relative lever arm lengths for the biceps brachii and deltoid muscles. Qian Wang then looks at sexual dimorphism during ontogeny in Cayo Santiago skulls to determine the impact of changing biomechanical and functional design (Chap. 8).

1.3.5   *Laboratory of Virology and Genetics*

Research to date in the LVG (Fig. 1.5), having focused primarily on virological topics (e.g., Ellenberger et al. 2006; Sariol et al. 2005, 2006, 2007), may be considered peripheral to the traditional interests of physical anthropologists. Nevertheless, the

LVG has made a significant contribution to the CPRC database that is fundamental to moving forward anthropologically relevant genetic studies of the Cayo Santiago rhesus population. In conjunction with the German Primate Center and the California National Primate Research Center, the LVG has successfully established the paternity for the majority of Cayo Santiago monkeys born between 1990 and the present, and even for some individuals born prior to this date. These data have been collected through the use of STR marker profiles, DNA fingerprints, and MHC genotype data. The ever-increasing database currently consists of 80,808 genotypes from about 2,886 monkeys. This paternity information offers new opportunities for investigations of heredity and genetics in both health and disease for the living populations on Cayo Santiago and at SSFS, and for the LPMG skeletal collection, as specimens enter it in the future (see below).

1.4 Future Research Potential for Physical Anthropology at the Caribbean Primate Research Center

As with any scientific field, the boundaries of physical anthropology are limited only by the interest, imagination, innovation, vision, and competency of its scholars. Many of the investigations at the CPRC, several of which are presented in this chapter and other chapters within this volume, have not exhausted their topics, and both should and will continue to be pursued.

Genetics and other research areas that incorporate genetic information have particular potential for new and expanded growth. The recently available DNA/paternity database continues to build through the extensive efforts of the LVG, and will soon be available for research that addresses issues in genetics and behavior. The genetics database provides the foundation for future advances on anthropologically relevant topics such as reproductive success, inbreeding avoidance, migration, and infant kidnapping. On a broader level, which encompasses genetics, the biomedically oriented SSFS and LVG, along with the LPMG and Cayo Santiago, provide opportunities to address anthropological questions on health and disease and on psychological adaptations that are central to evolutionary medicine and evolutionary psychology, respectively.

Perhaps the greatest value of the CPRC, however, lies not in the types of questions that can be asked, but rather, in the broad spectrum of approaches and protocols that the four administrative units can accommodate to address these questions. Whereas other institutions and facilities offer opportunities for studying nonhuman primates from either behavioral, physiological, morphological, or, genetic perspectives, the CPRC allows investigations of the same closed population of known pedigree that combine all these perspectives. Indeed, the most innovative future anthropological studies or research programs may address issues that require the integration of behavior, physiology, morphology, and genetics in both health and disease. Such studies or programs will be possible at the CPRC through a combination of protocols that encompass the free-ranging Cayo Santiago rhesus colony,

the corralled and caged SSFS population, the LPMG skeletal collection, and the LVG database. Regardless of the topic or approach, however, the CPRC will remain uniquely positioned to facilitate these research endeavors.

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Chapter 2
Comparative Quantitative Genetic Analysis of Cranial Capacity and Craniofacial Morphology in Two Closely Related Primate Species

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Abbreviations

CC   Cranial capacity
CFC   Craniofacial complex
SNPRC   Southwest National Primate Research Center
VCV   Variance/covariance matrix

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2.1   Introduction and Background

Evolutionary change in a character is due to a combination of the direct effects of selection on that character and the indirect effects of selection on characters that are genetically correlated with the character in question (Lande and Arnold 1983; Cheverud 1996). Therefore, selection on a single component within a correlated unit will result in coordinated evolution of the entire complex (Lande 1979; Cheverud 1982, 1984; Falconer and MacKay 1996). Due to the ubiquity of phenotypic correlations among traits, natural selection appears to act on many characters simultaneously. However, genetic correlations among traits can pose constraints on phenotypic evolution because these correlations are capable of altering both the rate and direction of evolution from the optimal path defined by natural selection (Cheverud 1984; Wagner and Altenberg 1996). If traits that are inherited together ultimately evolve together, then the challenge in explaining the correlated appearance of particular characters and understanding coordinated evolution lies in identifying genetically integrated morphological traits.

Various units have been identified in the primate craniofacial complex (CFC) that are genetically integrated as a consequence of shared developmental origins and/or function (Cheverud and Buikstra 1981a, b; Cheverud 1995; Marroig et al. 2004). These units are typically comprised of statistically correlated landmark data collected from the surface of the face and cranial vault and reflect coordinated evolution relating to behaviors and actions that have been important in primate evolution, such as mastication, ossification patterning, reliance on visual cues, and locomotor patterns (Ross 1996; Bruner 2007). Encephalization, or the possession of a relatively large brain for a given body mass, is another trend that has been important in our lineage. It has been well established through developmental studies that brain growth ceases prior to most facial growth (Schumacher 1997). As a result of this differential growth timing, the brain completes its growth prior to the activation of the growth hormone axis, which is active during and influences the growth of facial features (Cheverud 1996). Consequently, the brain and its surrounding cranial bones are subject to different genetic controls than the face, although they do share some controls since they compose a single adult structure. The hypothesis of shared genetic controls despite differential growth timing is supported by empirically measured correlations among facial and neurocranial morphological units. This suggests that, although the two are functionally and developmentally independent, they are genetically correlated such that selection on one will cause coordinated evolution in the other (Cheverud 1982).

In addition to empirical evidence for genetic correlation between the neurocranium and face, developmental experiments demonstrate that tinkering with skull base morphology results in altered facial form. These results suggest that the general relationship between the skull base and facial skeleton is that the former acts as a blue print upon which the latter is patterned (Persing et al. 1991). Despite evidence of the interrelatedness of neural, basicranial, and facial components, the specific nature of these relationships and the degree to which measures of each are related remains unknown.

Because both encephalization and morphological changes in facial patterning caused by specific dietary adaptations are recognized trends in primate evolution, appreciating the relationship between measures of neural size and facial pattern is critical for studying primate evolution. To understand how trends in increased brain size, as measured by cranial capacity (CC), and the unique structure of the primate face have enabled or constrained evolution in the hominin lineage, it is necessary to examine the coordinated evolution of these characters. To achieve this, we will quantify the degree to which cranial measurements are correlated with CC in two closely related primate species and reconstruct the selection vector that represents the total amount of change differentiating the morphologies of the two lineages.

Questions regarding the nature of phenotypic evolution can be approached with two different but complementary methods. The first asks how a phenotype like the CFC evolves in a direct sense by examining the attributes and relationships of physical traits able to be selected for or against by natural selection. The second asks how genetic correlations among these same traits affect the potential for Darwinian evolution since correlations can constrain phenotypic variation. By first defining the variance of a phenotype within a population and then partitioning that variance into its genetic and environmental components, we can establish the relative importance of the determinants – heredity (nature) versus environment (nurture) – of phenotypic variation. The heritable portion of variance is termed heritability and is defined as the proportion of phenotypic variance that is determined by genes passed from parents to offspring, or the additive genetic variance (Falconer and Mackay 1996). Heritability is an important concept in the study of phenotypic evolution because it represents the portion of phenotypic variation that can be transmitted between generations and, therefore, contribute to changing genotype frequencies. This evolution is typically measured as the response to selection, or the change in the population mean phenotype between the offspring and parental populations, and is represented by the equation

$$R = h^2 S, \tag{2.1}$$

where R is the response to selection, h^2 is the heritability, and S is the selection differential or the strength of selection being applied to the parental population measured as the covariance between the phenotype and relative fitness. The incorporation of heritability in the response to selection equation highlights the integral nature of this element in the study of evolution. The heritability of a trait is estimated by measuring the degree of resemblance among relatives in the phenotype of interest. Therefore, both a quantitative assessment of the full range of phenotypic variance and a detailed knowledge of familial relationships are necessary for predicting the response to selection of a trait in a population. For this reason, large populations of pedigreed individuals are important for the quantitative study of complex traits.

Closely related primate species for which extensive data on morphological characters and familial relatedness have been collected are critical to the study of morphological and genetic integration as it relates to questions of CC and CFC evolution in the human lineage. Because estimating genetic parameters of complex traits in general requires populations of animals with well-recorded pedigrees, most

research focuses instead on phenotypic variance and its correlation with behavioral and physiological traits. For example, McNab and Eisenberg's (1989) findings of the independence of brain size increase and deviations of basal metabolic rate from the expected mammalian scaling factor (mass to a power of 0.6–0.75) are responsible for the proposal of various models explaining the source of increased energy required for larger brains. In primates, dietary quality, dietary type, and the relative size of the various visceral organs appear correlated with brain size (Stephan et al. 1988; Aiello and Wheeler 1995; Fish and Lockwood 2003; Taylor and van Schaik 2007), suggesting an evolutionary link between ecology and physiology and a potential source of brain energy. However, to move such observations from the realm of correlation into that of causation, studies incorporating genetic correlations as well as experimental work in model species are necessary.

Baboons (genus *Papio*) and macaques (genus *Macaca*) are both members of the tribe Papionini, a division of the larger family Cercopithecidae (i.e., Old World Monkeys, Image 2.1 and Fig. 2.1). They are our closest nonhuman primate relatives next to apes and, as such, papionins make excellent models for examining questions of human evolution. Although the apes are phylogenetically closer to us, no large-scale, multigeneration pedigrees of apes exist from which to obtain variance component estimates for craniofacial morphology. In addition, several life history traits of Old World Monkeys, such as their short interbirth intervals and fast growth trajectories, make them preferable to apes for research requiring large sample sizes.

We have chosen a sample of rhesus macaques from the large colony living on the Caribbean island of Cayo Santiago (hereafter referred to as the Cayo macaques) and a complementary sample of baboons from those housed in Texas at the Southwest National Primate Research Center (SNPRC, hereafter referred to as the SNPRC baboons) for our research. Our study samples are drawn from data collected previously from the Cayo macaque and SNPRC baboon populations. Cheverud et al. (1990) demonstrated moderate to high heritability of both gross regional morphology and overall size of the brain, respectively, in the Cayo macaques. A similar study conducted in the SNPRC baboons yielded high heritabilities for total brain volume as well as for regional volume and shape (Rogers et al. 2007). Results from both brain studies contribute to our knowledge of the genetic controls of brain size and internal brain structure.

Additionally, comparative research among mouse strains on the relationship between brain size and craniofacial variation suggests that growth of the CFC is largely stimulated and patterned by brain growth (Boughner et al. 2008; Lieberman et al. 2008). Therefore, understanding the molecular determinants of brain size is crucial for our understanding of craniofacial variation. Further empirical evidence of phenotypic integration of the brain and skull in human subjects (Richtsmeier et al. 2006) suggests that the use of cranial capacity as a proxy for brain size is appropriate when measurement of the brain itself is not possible. As bone is the only tissue that typically survives the fossilization process, understanding heritable variation in the skull of extant populations is our best hope for understanding evolutionary processes relating to the brain in the primate lineage and for characterizing the range of variation observed in extinct populations.
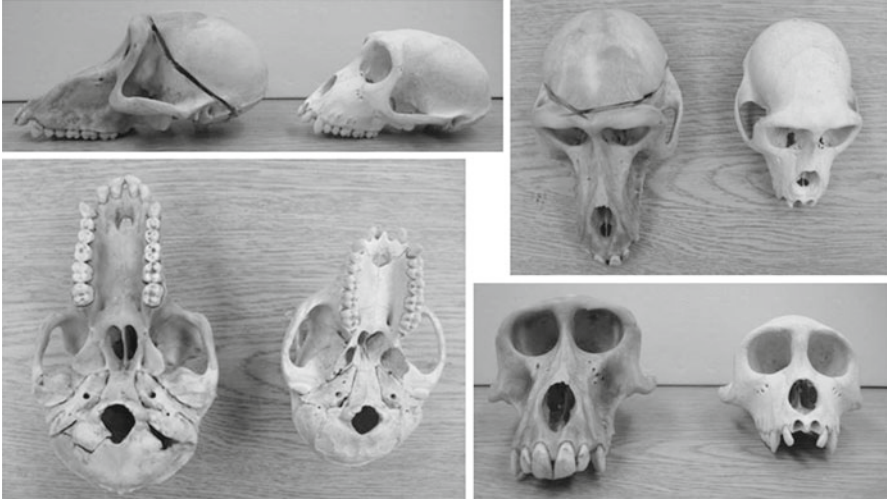
Image 2.1 Each image shows an adult female SNPRC baboon skull on the *left* and an adult female Cayo rhesus macaque skull on the *right*. Starting with the *upper-left* image and continuing clockwise the views shown are lateral, vertex, frontal, and basal
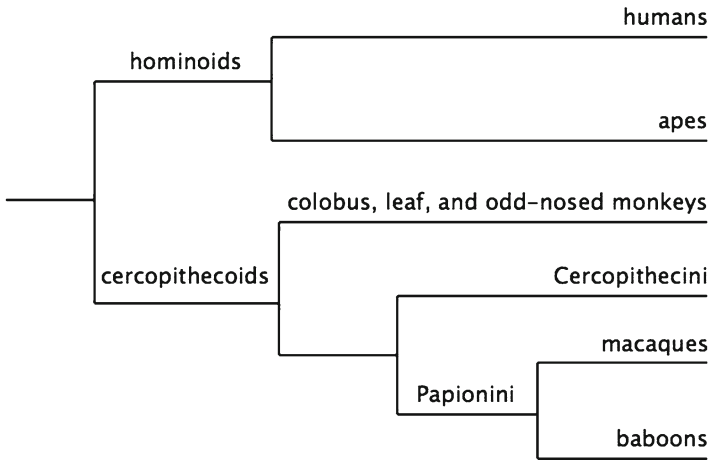
Fig. 2.1 Phylogeny of catarrhine primates (adapted from Xing et al. 2005). Branch lengths are arbitrary and do not represent time since divergence between species

Lande (1979) noted that the evolutionary response to selection depends upon genetic variation and is mediated by natural selection acting upon intraspecific phenotypic variation and, as such, both types of variation are necessary for evolution to occur. Therefore, intraspecific patterns of variation are an important source for understanding observed differences between species. Reconstruction of the pattern of

selection responsible for such species differences is possible and informative for understanding the pressures, environmental or otherwise, that have affected the evolutionary history of a species. Cheverud (1996) reconstructed selection patterns for craniodental traits in tamarins, from which he was able to develop hypotheses relating to the role of dietary composition in speciation events within the genus. Studying the differences in patterns of variation between closely related species affords us the unique opportunity to discern the effects of genetic drift and natural selection and formulate explanatory models for further testing. We hope to be able to generate such hypotheses about the ecology of papionin evolution for future research.

In this study, we will compare the pattern of craniofacial phenotypic correlations in baboons and macaques to understand how these correlations may have affected the potential for morphological evolution in papionins and we will reconstruct the selection gradient that contributed to the differences in CFC morphology between these two species in an attempt to explore the selective pressures responsible for these differences. Using distances calculated from 3D landmark data of 668 baboon crania, CC measured from CT scans of 478 baboon skulls, and distances and CC measured from the skulls of 420 macaques, all from known genealogies, we estimated variance components for 14 craniofacial traits. We hypothesize that, given the close phylogenetic relationship between *Papio* and *Macaca*, patterns of correlation between CC (as a proxy for brain size) and craniometric distances in the head and face will be similar in the two genera.

2.2 Materials and Methods

2.2.1 Primate Populations and Data Collection

2.2.1.1 Cayo Santiago: *Macaca mulatta*

Cayo Santiago is a 15.2 ha island off the southeast coast of Puerto Rico that is home to a free-ranging rhesus macaque (*Macaca mulatta*) population founded in 1938 with 500 wild-trapped animals imported from India by C.R. Carpenter (Rawlins and Kessler 1986). One of the single greatest advantages offered by the colony is the long-term genealogic information. Pedigree records have been meticulously maintained since the arrival of Stuart Altmann in the early 1950s by recording maternal parentage and annually tattooing all yearlings. Additionally, complete skeletons of deceased animals have been routinely collected since 1970. This unique combination of genealogic and phenotypic information affords primatologists, biologists, and anthropologists the opportunity to explore the nature of the interaction between genes and the environment in producing observed behaviors and morphologies.

The Cayo macaque skeletal collection contains both immature and mature animals of all ages from 1 year to over 20 years of age. Exact ages of many of the Cayo macaques in the skeletal collection are known but some are not. The monkeys of known age were divided into seven age-by-sex cohorts based on dental eruption and epiphyseal union patterns. Individuals of unknown age were binned into one of

these cohorts by matching their skeletal growth and dental eruption status with the patterns of individuals of known age (see Cheverud 1981 for a more detailed description of these methods). Although data were collected from 420 Cayo macaques, not all of the individuals included in the analysis are adults and not all of the adults are members of the main recorded genealogy, some being unidentified individuals while others are members of different genealogies for which they are the only representative. Because the relationship between CFC and CC changes with age (Ackermann 2005), only adults were included in these analyses. This explains why the sample sizes recorded in Table 2.2 are smaller than the total population size. Although the measurements from 370 adults were used in the calculation of total phenotypic variance, the average number of individuals that were members of the full genealogy and, therefore, included in the heritability calculations is 253.

The genealogic relationships among the full collection of skeletal remains is known and includes 367 nuclear families, 788 individuals, 426 founders, 724 parent–offspring pairs, 411 half-sibships, 464 grandparent–offspring pairs, and 705 half-avuncular pairs. Because paternities are unknown, all sibships are assumed to be half-sibships. This systematically underestimates genetic relationships, meaning that all estimates of trait heritabilities in the Cayo macaques are conservative and, therefore, true values are likely slightly greater than we estimate in these analyses (Konigsberg and Cheverud 1992).

For the present study, the phenotypes of interest include CC and various craniometric interlandmark distances measured from dry Cayo macaque skulls with sliding, needlepoint calipers by JMC in the 1970s (see Table 2.2). Prior to measuring Cayo macaque CC, we filled the orbital canals and fissures with cotton balls to prevent escape of mustard seeds. The volume of seed used to fill the cranium was measured with a graduated cylinder.

Brain size and interlandmark differences are sexually dimorphic in the Cayo macaques so the difference in means between males and females was added to each female's measurement so that males are compared to the male mean and females to the female mean in the genetic analysis. No correction for age was performed since there is no relationship between CC and age among known-age adults in the Cayo macaque sample (Cheverud et al. 1990). Individuals who fell outside of two standard deviations from the trait mean were considered to be outliers and were removed. On average, 12 individuals were deemed to be outliers for each trait and were removed from the data set. This was done under the assumption that these outliers represented either an error in measurement or an extreme trait value. Either way, those individuals would exert excessive leverage in the statistical analyses, greatly affecting the resulting regression coefficients. Only the datum for that trait was removed from the individual's record; the individual as a whole was not removed from the analysis.

2.2.1.2 Southwest National Primate Research Center: *Papio hamadryas* ssp.

A large pedigreed colony derived from east African populations of olive (*Papio hamadryas anubis*) and yellow baboons (*P.h. cynocephalus*) has been maintained for the past 40 years at the SNPRC at the Southwest Foundation for Biomedical

Research in San Antonio, Texas. Animals are housed in polygynous social groups in large outdoor enclosures to ensure the integrity of the pedigree. Upon death, baboon heads are transported to Washington University in Saint Louis for processing and data collection.

We macerated each cranium over a period of 2 weeks to remove all soft tissue. Calottes had been removed for brain extraction from all specimens during necropsy so, to prepare the specimens for CT scanning, we affixed calottes using modeling clay to approximate the amount of bone lost during brain removal and taped mandibles into proper anatomical position. The 668 individuals we analyzed for craniometric landmark data consisted of 267 males and 446 females. The average age of the specimens at death was 18.09 ± 6.49 (range 0.02–33.7 years). Only subjects deemed adult – full occlusion of M3 and fusion of the sphenooccipital synchondrosis – were included in this study. The individuals analyzed for CC were a subsample of the larger population ($N=478$). The genealogic relationships among the full baboon population are known and include 933 individuals, 279 founders, 1,178 parent–offspring pairs, 284 sibships, 4,366 half-sibships, 643 grandparent–offspring pairs, and 155 avuncular pairs.

On the processed SNPRC baboon skulls, three-dimensional coordinate locations were captured with a Microscribe MX digitizer for 13 craniometric landmarks, of which seven were bilateral for a total of 20 collected data points (Table 2.1, Fig. 2.2). Points were chosen to best characterize the shape and size of the cranial vault. To ensure repeatability, measurements were taken twice and averaged. Euclidean distances between landmarks were calculated by first averaging the bilateral measurements (Table 2.2). These Euclidean distances correspond to the interlandmark distances measured on the Cayo macaques with calipers by JMC. Outliers were removed from the SNPRC baboon data as well. On average, there were two individuals per trait that were removed because they possessed trait values greater than two standard deviations from the mean.

Table 2.1 Craniometric landmarks recorded from crania using a three-dimensional digitizer

Landmark	Description	Position(s)
BR	Bregma	Midline
LD	Lambda	Midline
AS	Asterion	Right, left
PT	Pterion	Right, left
TSJ	Temporo-sphenoidal junction	Right, left
APT	Anterior petrous temporal	Right, left
JP	Jugular process	Right, left
NA	Nasion	Midline
NL	Nasale	Midline
ZTS	Superior zygo-temporal suture	Right, left
FMO	Frontomalare orbitale	Right, left
BA	Basion	Midline
OP	Opisthion	Midline
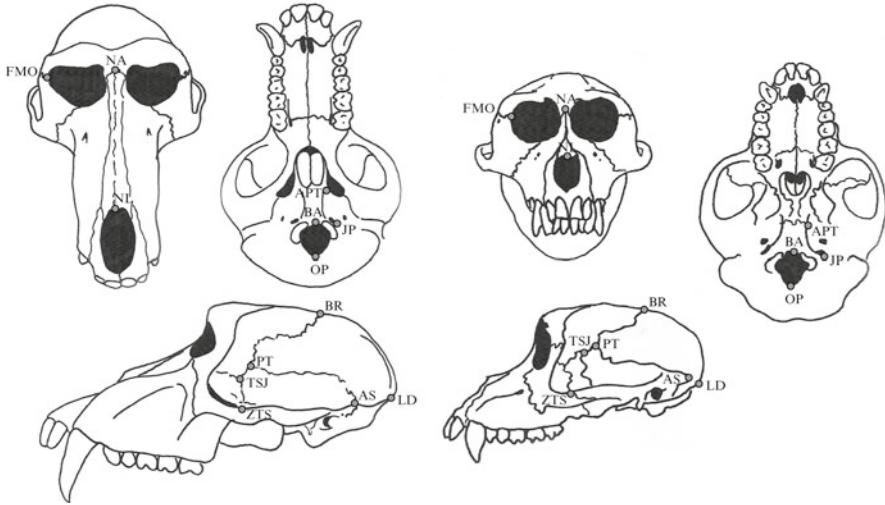
Fig. 2.2 *Top row*, from *left*: oblique vertex and basal view of a *Papio* cranium and frontal and basal view of a *Macaca* cranium. *Bottom row*, from *left*: lateral views of a *Papio* and a *Macaca* cranium. Adapted from Ackermann et al. 2006 and Hershkovitz 1977. Landmark identifications are given in Table 2.1

Table 2.2 Linear craniofacial measurements calculated from the landmarks in Table 2.1

Abbreviation	Description
BRNA	Bregma-nasion length
BRLD	Bregma-lambda length
BRPT	Bregma-pterion length
BRAS	Bregma-asterion length
ASPT	Asterion-pterion length
ASJP	Asterion-jugular process length
ASAS	Biasterionic breadth
LDPT	Lambda-pterion length
LDBA	Lambda-basion height
LDAS	Lambda-asterion length
PTPT	Bipterionic breadth
PTFM	Pterion-frontomalare length
JPJP	Bijugul breadth

CT scans of the SNPRC baboon skulls were analyzed using Amira 5 (Visage Imaging, Berlin, Germany). We rendered volumes for the slice data of each specimen and measured cranial capacity with an image segmentation technique. This allowed us to define the negative space between the bones of the neurocranium and then calculate the volume of the segmented voxels according to the equation

$$CC = \left[V \times T \times \left(\frac{F}{J} \right)^2 \right] / 1000, \qquad (2.2)$$

where V is the sum total of segmented voxels, T is the slice thickness, F is the field of view, and J is the CT matrix. Slices were sequentially adjacent with a thickness of either 0.6 mm or 0.75 mm, depending on which of two CT scanners were used over the 2 years data were collected. The difference in slice thickness does not introduce a significant source of error given that the slices were acquired on both scanners with no intervening gaps and, therefore, capture the entire skull without any loss of information. The field of view is the square image area containing the object of interest. For instance, the field of view for one of our CT scans would be the measurements of a square that encompasses the entire length and width of the monkey's skull. The field of view value varies per specimen and is measured in mm^2. The CT matrix (J) is the number of readings the scanner takes along the horizontal and vertical axes, a constant 512 for each. Therefore, within the field of view (F) for a skull measuring 350 mm long, the scanner will record the number of X-rays absorbed by the skull along the x and y axes every $F/J = 350/512$, or 0.68 mm.

Even though considering the negative space between calvarial bones as entirely brain space – thus discounting the presence of cerebrospinal fluid, meninges, and vasculature – is an overestimation, our application of this protocol to every specimen ensures both consistency and reproducibility of measurement within the baboon sample. Because we are interested in the relative relationships, not the absolute values, of these measurements among specimens, the potential for overestimation is not problematic as long as it is consistently applied with every measurement. In addition, a similar overestimation was applied to the Cayo macaques by completely filling the negative space within the cranium with mustard seeds. Although the methods of data collection differ in the two species, this will not materially affect results since we compare the *pattern* of variation and covariation between the two species and any biases in the measurement values themselves are small and consistent between species.

Adult cranial capacities in the SNPRC baboons vary by sex and with age among adults. To account for this, the quantitative genetic analyses in the SNPRC baboons included sex, age, and the interaction between sex and age as covariates in the model. For the Cayo macaques, there is no age variation in CC or cranial measurements with adult age and sex differences were eliminated prior to the genetic analysis.

The average number of baboons used in the calculation of heritability of the craniofacial measurements is 632 out of the possible 668 individuals. Since only a subset of baboons was used to estimate the heritability of CC, this analysis is based on 458 individuals. Minor fluctuations in the number of animals included in the analyses are due to the removal of outliers and incomplete data for certain traits. The landmarks AS and PT are particularly vulnerable to obliteration from saw marks during post-mortem removal of the brain.

2.2.2 Statistical and Quantitative Genetic Analyses

2.2.2.1 Quantitative Genetic Model

We conducted initial summary statistical analysis and data transformations in Excel 2008 (Microsoft Corporation, Redmond, Washington, USA). Transformations were chosen to produce a trait distribution with a residual kurtosis value less than 0.8. In all cases except one (JPJP for SNPRC baboons), z-score standardization of the log-transformed measurements produced an appropriate value for the residual kurtosis. In this single case, we went forward with the analysis although there was significant kurtosis. As described previously, the measurements were transformed differently in each species because of the nature of the age data recorded for the Cayo macaques. Because of this, sex and age were not included as covariates during the quantitative genetic analysis of Cayo macaques while sex, age, and the interaction between sex and age were used as covariates for SNPRC baboons. Visualization of distributions and outlier removal took place using JMP v 5.0.1.2 (SAS Institute, Inc., Cary, NC, USA).

SOLAR v 4.2.0 (Almasy and Blangero 1998) was used to estimate variance component heritability values. The program employs maximum likelihood variance decomposition algorithms to calculate heritable variation using the relationship:

$$\Omega = 2\Phi\sigma_g^2 + I\sigma_e^2, \tag{2.3}$$

where Ω is the pedigree covariance matrix, Φ is the kinship matrix holding the pairwise kinship coefficients between animals, σ_g^2 is the additive genetic variance, I is the identity matrix, and σ_e^2 is the variance due to random environmental effects. The strength of the SOLAR program is that variance components are estimated while maximizing a model that considers all multigenerational pedigree relationships among individuals, not just traditional parent–offspring, midparent–offspring, or sibship pairs (Blangero et al. 2001).

Covariate screens were conducted with age, sex, and the interaction between age and sex as potential covariates in baboons but not in macaques where age- and sex-related variation were controlled as described above. Narrow-sense heritability (h^2) is determined as the proportion of total variance in the sample measurement that is attributable to the additive genetic variance, σ_g^2, as calculated in (2.3). It is a measure of the extent to which variation in a trait is under heritable genetic control (Lynch and Walsh 1998). Significance is determined by comparing the likelihood of the model where heritable variance is estimated to a null model in which it is constrained to zero.

For the purposes of this analysis, we assume multivariate normality across individuals. Univariate normality was supported by statistical tests (e.g., Cramér–von Mises test of normality) for all traits in the Cayo macaques and for most traits in the SNPRC baboons. Only PTPT ($P=0.01$), PTFM ($P=0.002$), BRLD ($P=0.01$), LDBA ($P<0.001$), and ASJP ($P=0.03$) deviate from normality to a statistically

significant extent with a Cramér–von Mises test despite the large sample size used here. These deviations are minor and after a Bonferroni correction for multiple comparisons only LDBA and PTFM continue to deviate slightly from a normal distribution. This deviation is unlikely to have any discernable effect on the quantitative genetic analysis. It is also assumed that these characters have no dominance or epistatic variance. According to the quantitative genetic model, total phenotypic variance (σ_P^2) is the linear sum of additive genetic variance (σ_g^2), dominance genetic variance (σ_d^2), epistatic (i.e., interaction) genetic variance (σ_i^2), and a residual error term, assumed to be environmental variance (σ_e^2). In the case of the Cayo macaques, dominance and epistatic variance are entirely subsumed within the environmental variance component since all sibships are half-sibships, while in the SNPRC baboons σ_d^2 and σ_i^2 are largely contained in the σ_e^2 component since most pairs of relatives are not full sibs. Finally, as is standard in quantitative genetic analyses, it is assumed that there is no environmental covariance among relatives.

2.2.2.2 Correlations

All craniofacial measurements were included in partial regression analysis with CC using ordinary least-squares according to the model $CC = constant + trait_1 + trait_2 + \ldots + trait_n + error$. Multiple regressions were conducted in SYSTAT v 12 (Cranes Software International, Chicago, Illinois, USA) using trait values standardized to a mean of zero and a standard deviation of one. Species-specific vectors of the resultant beta coefficients from the regression equations were constructed (Fig. 2.3).
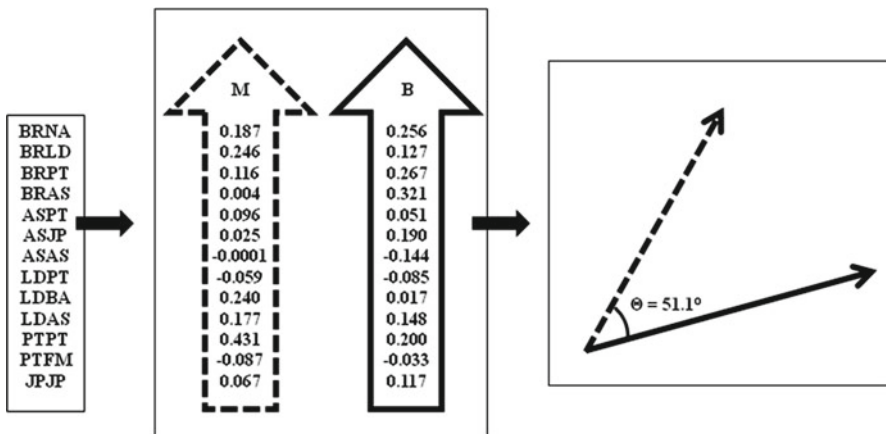
Fig. 2.3 Species-specific vectors constructed from the partial correlation coefficients of CC regressed on the significantly heritable craniometric distances. Cayo macaques are represented by a *dashed-line vector* (M) and SNPRC baboons by a *solid-line vector* (B). The angle of dispersion between them (θ) is 51.1°

To assess the degree of similarity in the patterns of correlation between CC and craniofacial landmark distances, the angle (θ) between the two vectors was determined thus:

$$\cos\theta = r \tag{2.4}$$

where r is the correlation between the baboon and macaque vectors as measured by:

$$r = \frac{\Sigma(M \times B)}{\sqrt{(\Sigma M^2 \times \Sigma B^2)}} \tag{2.5}$$

where $\Sigma(M \times B)$ is the sum of the cross-products of the macaque (M) and baboon (B) vectors, ΣM^2 is the sum of squares of the M vector, and ΣB^2 is the sum of squares of the B vector. The angle of dispersion (θ) indicates whether the patterns of trait correlation in these closely related primates are similar, the degree of similarity increasing as $\theta \to 0$. A similarity in CFC-CC patterning, as measured by the correlation between CC and interlandmark distances, would suggest that the phenotypes of these species potentially respond similarly to environmental pressures or have been subjected to similar selection gradients in the past.

In order to determine which of the thirteen coefficients are significantly different in Cayo macaques and SNPRC baboons, thus influencing the Pearson correlation, an ANCOVA was performed. CC was defined as the dependent variable and species, trait, and the interaction between species and trait as the covariates. Significance indicates that the slopes of the species' multiple regression coefficient for that trait are statistically different.

2.2.2.3 Diversifying Selection

The selection required to produce the observed morphological differences between Cayo macaques and SNPRC baboons was calculated using a rearrangement of (2.1) into a two-group linear discriminant function equation:

$$\beta = \mathbf{G}^{-1}\left[z_i - z_j\right] \tag{2.6}$$

where β is a vector of selection gradients summed over the generations responsible for the divergence between macaques and baboons, $\mathbf{G}^{-1}$ is the inverse of the within-species genetic variance/covariance matrix, and $[z_i - z_j]$ is a vector of the difference in means between species i and j (Lande 1979). Discriminant analysis, and therefore selection reconstruction analysis, assumes homogeneity of within-group variance/covariance patterns. However, it has been empirically shown that moderate deviations from homogeneity do not severely affect such analyses (Blackith and Reyment 1971; Manly 1986; de Oliveira et al. 2009). Even though the species-specific matrices vary, we adopted the suggestion of Lovsfold (1988) and used an average variance/covariance matrix. As is generally accepted in cases where the genetic

variance/covariance is unknown, we substituted the inverse of the species average phenotypic variance/covariance matrix (VCV) for the G^{-1} matrix because the two have often been shown to be proportional to each other for morphological traits (Cheverud 1988; Roff 1995; Marroig and Cheverud 2001; see Ackermann and Cheverud 2002 for an example). We performed a MANOVA in R v 2.7.1 (R Foundation for Statistical Computing, Vienna, Austria) using species, sex, and the interaction between species and sex as factors and used the residual variance/covariance as the VCV pooled across sexes and species.

2.3 Results

2.3.1 Heritabilities and Genetic Variances

Heritabilities and standard errors for Cayo macaques are presented in Table 2.3 while heritabilities, standard errors, proportion of variance attributed to the covariates, and statistically significant covariates for SNPRC baboons are presented in Table 2.4. For the Cayo macaques, heritability estimates range from 0.106 to 0.865 with 50% of the estimates significantly greater than zero with an alpha of 0.05. The estimates have a mean of 0.395 and a standard deviation of 0.21 with a distribution that does not deviate significantly from normal (Cramér–von Mises $W = 0.05$, $P = 0.54$). Similar results are observed for the SNPRC baboons with heritability measurements ranging from 0.165 to 0.595 with 100% of the estimates significantly greater than zero at the 5% level. The estimates have a mean of 0.398 and a standard deviation of 0.13 with a distribution that does not deviate significantly from normal

Table 2.3 Maximum likelihood narrow-sense heritability estimates for Cayo macaques

Measurement	n	Maximum likelihood ($h^2 \pm SE$)
BRNA	254	0.51 ± 0.19[a]
BRLD	254	0.30 ± 0.21
BRPT	254	0.20 ± 0.18
BRAS	253	0.16 ± 0.23
ASPT	253	0.27 ± 0.25
ASJP	252	0.11 ± 0.13
ASAS	250	0.34 ± 0.26
LDPT	252	0.28 ± 0.22
LDBA	254	0.56 ± 0.19[a]
LDAS	254	0.33 ± 0.21[a]
PTPT	254	0.67 ± 0.18[a]
PTFM	253	0.46 ± 0.22[a]
JPJP	253	0.49 ± 0.15[a]
CC	253	0.87 ± 0.18[a]

[a]Significantly different at $P < 0.05$ level from model $h^2 = 0$

Table 2.4 Maximum likelihood narrow-sense heritability estimates for SNPRC baboons

Measurement	n	Maximum likelihood ($h^2 \pm$ SE)	Proportion of variation due to covariate	Significant covariate[a]
BRNA	630	0.50 ± 0.08[b]	0.006	Age
BRLD	630	0.29 ± 0.08[b]	NA	None
BRPT	636	0.52 ± 0.10[b]	0.012	Age, Age&Sex
BRAS	636	0.53 ± 0.10[b]	NA	None
ASPT	630	0.17 ± 0.08[b]	NA	None
ASJP	630	0.41 ± 0.09[b]	0.009	Sex
ASAS	629	0.38 ± 0.09[b]	0.056	Age, Sex
LDPT	625	0.29 ± 0.09[b]	0.004	Age
LDBA	638	0.20 ± 0.09[b]	0.035	Age, Age&Sex
LDAS	632	0.32 ± 0.09[b]	0.056	Age, Sex
PTPT	629	0.49 ± 0.09[b]	NA	None
PTFM	633	0.59 ± 0.08[b]	0.011	Age&Sex
JPJP	636	0.35 ± 0.09[b]	NA	None
CC	458	0.52 ± 0.15[b]	0.011	Age, Age&Sex

[a]"Age&Sex" indicates the interaction effect between the covariates "Age" and "Sex"
[b]Significantly different at $P < 0.05$ level from model $h^2 = 0$

(Cramér–von-Mises $W = 0.05$, $P = 0.43$). The total phenotypic variance of each SNPRC baboon trait was assessed for the proportion due to significant covariates (e.g., sex, age, and the interaction of sex and age). An average of 2.2% (± 2.1%) of the phenotypic variance is due to covariates. It is important to note that in the SNPRC baboon sample there are three potential covariates while in the Cayo macaque sample there are none.

2.3.2   Correlations

The partial correlation coefficients and standard errors of CC regressed on the craniofacial traits are presented in Table 2.5 as well as the P-values from the ANCOVA analysis. The Pearson product moment coefficient between vectors of partial regression coefficients as calculated from (2.5) is 0.627. This corresponds to an angle of dispersion (2.4) of 0.89 radians or 51.1°. Figure 2.3 presents a visual representation of the Cayo macaque and SNPRC baboon vectors of partial correlation coefficients.

2.3.3   Diversifying Selection

The difference in species' mean phenotypes and calculated selection coefficients are given in Table 2.6. The magnitude of the standardized selection coefficients determines the degree of deviation from the expected pattern. The pattern of covariation among traits constrains the change in trait shape and size but, since baboons are

Table 2.5 Regression coefficients (standard errors) and ANCOVA probabilities from the partial correlation between CC and the 13 craniofacial measurements

Measurement	Cayo macaques	SNPRC baboons	ANCOVA P[b]
BRNA	0.187 (0.05)[a]	0.256 (0.06)[a]	0.37
BRLD	0.246 (0.08)[a]	0.127 (0.05)[a]	0.23
BRPT	0.116 (0.05)[a]	0.267 (0.05)[a]	0.04[a]
BRAS	0.004 (0.07)	0.321 (0.07)[a]	0.002[a]
ASPT	0.096 (0.06)	0.051 (0.06)	0.61
ASJP	0.025 (0.05)	0.190 (0.04)[a]	0.02[a]
ASAS	−0.0001 (0.05)	−0.144 (0.05)[a]	0.05
LDPT	−0.059 (0.09)	−0.085 (0.05)	0.81
LDBA	0.240 (0.05)[a]	0.017 (0.03)	0.0005[a]
LDAS	0.177 (0.07)[a]	0.148 (0.07)[a]	0.78
PTPT	0.431 (0.04)[a]	0.200 (0.04)[a]	0.0003[a]
PTFM	−0.087 (0.05)	−0.033 (0.05)	0.41
JPJP	0.067 (0.04)	0.117 (0.04)[a]	0.33

[a] Significance indicates that the regression coefficients of the two species are statistically different from each other
[b] Significant at $P<0.05$ level

Table 2.6 Vectors of the selection reconstruction analysis: $[z_i - z_j]$ and β

| Measurement	Difference in means[a]	Selection coefficient	Standardized selection coefficients[b]
BRNA	10.19	−1.00	−0.26
BRLD	6.30	0.11	0.03
BRPT	8.82	0.95	0.33
BRAS	10.98	−0.97	−0.31
ASPT	5.49	0.89	0.23
ASJP	8.93	0.28	0.08
ASAS	18.88	−0.08	−0.01
LDPT	10.63	−0.06	−0.01
LDBA	12.89	−0.01	−0.001
LDAS	13.25	1.61	0.47
PTPT	10.67	0.64	0.22
PTFM	8.94	0.97	0.30
JPJP	4.05	−0.01	−0.004
CC	61.59	0.27	0.02

[a] Calculated as the least-squares average species means of the linear measures pooled across the sexes. Difference in phenotypic averages between the species as measured by subtracting the macaque mean from the baboon mean. Measurements are in 1.0 mm increments and cranial capacity (CC) is in cubic centimeters
[b] Calculated as a selection coefficient divided by its standard deviation. This will allow comparisons to be made among coefficients by placing them all along the same scale of magnitude

absolutely larger than macaques, we would still expect all baboon traits to be bigger than those of macaques. A coefficient close to zero indicates that the baboon trait is as large as expected given indirect responses to selection on the other traits included in the analysis. Coefficients larger or smaller than zero indicate that some measurements are longer or shorter, respectively, than expected based on indirect selection on other traits, which suggests they experienced direct selection over the time since divergence of the two species. It is important to note that this reconstruction does not define what selection was per se, but rather how selection would have had to operate in order to produce the observed species differences. It is entirely possible that all of these traits are correlated with others that we did not measure and that selection was actually on those undefined traits.

With no additional taxa to root the direction of changing morphology, the decision to derive one species phenotype from the other is arbitrary. Taking the Cayo macaques as the standard, differences in mean phenotypes were calculated. If the SNPRC baboons were selected to be the standard instead, the results would be the mirror image of those we obtained here. Applying the mean phenotype data and the inverse VCV to 2.6 asks the question: what morphological features have been selected for that explain the differences in morphology between the two species? Two principal patterns are recognized in the SNPRC baboon cranium that differentiates it from that of the Cayo macaques. First, selection has affected cranial vault and cranial base measurements differently. Specifically, measurements of the superior cranial vault including the borders of the parietal bone (BRPT, ASPT, LDAS, PTPT, and PTFM) have been increased more than would otherwise be expected and those of the posterior cranial base (ASAS, ASJP, LDBA, and JPJP) demonstrate no signatures of direct selection. Additionally, BRAS is decreased, which indicates a less globular vault. The resultant shape of the SNPRC baboon skull in comparison to that of the Cayo macaques is that the former is relatively broader across the vault in a mediolateral direction, similar to the differences in shape between a hot air balloon and a sphere. Intriguingly, this alteration in cranial vault shape resulted in an increased CC in baboons as an indirect response to selection on vault shape with no direct selection on CC.

The second trend evident in these data is that the bony orbits of the SNPRC baboons project forward from the neurocranium relative to the configuration of that region in the Cayo macaque skull. Although the distance from the top of the cranial vault to the top of the orbits (BRNA) has experienced a negative selection gradient, the distance between the orbits themselves and the vault (PTFM) has been positively selected upon. If one visualizes the face as a triangle attached to a circle (the neurocranium) with the tip of the triangle pointing upward, then it is easy to envision a scenario that explains these seemingly contradictory results (Fig. 2.4). When facing the triangle-circle figure, if you grasp the base of the triangle and pull it toward you, the tip of the triangle will tilt backward and into the circle. In the same way, the face can be seen to angle back into the neurocranium along its superior margin (BRNA) around the orbits as the mid-face is elongated (PTFM). The result of this morphological shift in craniofacial relationship is seen in a gross comparison of the relative degree of prognathism in the two species (see Image 2.1).
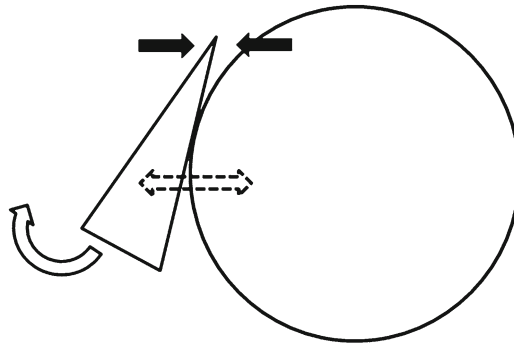
Fig. 2.4 A representation of the relationship between the neurocranium (*circle*) and face (*triangle*). As the lower face is pulled away from the neurocranium (*curved arrow*), the distance between the mid-face and the neurocranium is increased (double-headed, *dash-lined arrow*) while that between the upper face and the neurocranium is decreased (*solid arrows*)

2.4   Discussion

The heritability estimates for the six heritable traits (BRNA, LDBA, LDAS, PTPT, PTFM, and JPJP) do not differ in magnitude between the two species to a statistically significant extent (paired *t* test $t = -0.04$, $P = 0.97$). However, the number of significantly heritable traits in the SNPRC baboon population is larger. This can be explained by a number of reasons. First, as mentioned previously, relatedness is unknown in many cases within the Cayo macaque pedigree and, therefore, all sibling relationships are assumed to be half-sibships when some may actually be full-sibships. As such, heritabilities are slightly underestimated but have relatively large standard errors (Konigsberg and Cheverud 1992) compared to similar pedigrees known through both the paternal and maternal lines. Second, because exact age data are not available for some Cayo macaques, it is impossible to correct for age directly as a covariate. Because correlations fluctuate throughout ontogeny – phenotypic patterns for an infant may differ from those of an adult, thereby reducing the similarity among relatives – heritability estimates will be correspondingly decreased. Finally, the Cayo macaque heritabilities have larger standard errors than those of the SNPRC baboons, mainly because the sample size of Cayo macaques is relatively small. The use of standard errors in computing statistical significance means smaller standard errors, and therefore larger sample sizes, are needed in order to reach statistical significance. The larger sample size, and therefore greater precision in estimating heritabilities, explains why more of the estimates for SNPRC baboons are statistically significantly different from zero than are those of the Cayo macaques. Of course, many more animals have been added to the Cayo macaque skeletal collection since the data analyzed here were collected and their inclusion in future studies would rectify this problem.

With an average of 0.40, the heritability estimates for these craniofacial traits are consistent with those typically estimated for morphological phenotypes in vertebrates (Mousseau and Roff 1987). Conducting a partial regression of CC on the craniofacial measurements allows us to control for the variance of 12 traits while examining the effect of the thirteenth on the variance of CC. In both species, only LDPT, ASAS, and PTFM have negative regression coefficients. All others increase with increasing CC. Since the brain is primarily responsible for inducing bony cranial growth, these results may suggest that: (1) select regions of the brain in the two species are receiving growth signals and (2) these regions are likely to be the same in both species. Despite the gross similarities in sign between Cayo macaques and SNPRC baboons, only a moderate degree of correlation ($r=0.627$) between the species vectors was calculated, suggesting that relative contributions of neurocranial bones to the measurement of CC differ in these papionins.

This result of differential cranial patterning is supported by the ANCOVA results. Five of the 13 traits show significantly different contributions to CC (BRAS, BRPT, ASJP, LDBA, PTPT). If you think of the neurocranium as the Earth, upon which float land masses of varying size and orientation, then it is easy to understand these results. The 13 traits are separate land masses and eight of them are aligned similarly on the macaque Earth and the baboon Earth. However, for those significant five measurements, the trait land masses are larger or smaller on one Earth than on the other. These parts of the skull are not contributing to CC similarly in the two species, which may suggest a functional difference in neurocranial component composition. On the one hand, this may be a surprising result given the close phylogenetic relationship between baboons and macaques and the lack of overt differences in ecology that might explain the differences in patterning of craniofacial morphology. The large degree of shared ancestry should tend to maintain phenotypic similarity if only because genetic correlations often need time to decouple. Additionally, the physical and dietary environment inhabited by these species is similar. Although the geographic ranges of the species are very distinct – baboons are primarily confined to sub-Saharan Africa and a small part of Arabia while macaques range over much of Asia and parts of northern Africa – both are terrestrial quadrupeds with home ranges across a wide landscape of climates and ecozones who subsist off a diverse omnivorous diet.

On the other hand, it may be the similarity in their use of habitats that necessitates a divergence in the morphology of their CFC. By capitalizing on a particular feature of the landscape, ancestral populations of cercopithecines might have ensured their fitness by expanding into previously uninhabited geographies, creating environmental differences that would eventually result in a speciation event. Many possibilities exist for explaining how a phenotype as seemingly well integrated as the CFC could be altered in divergent ways in two closely related species. For instance, a change in the rate of growth of various cranial modules during ontogeny or the differential selection on individual cranial components could explain how patterns of covariation within the skull could differ in these two species.

Upon examination of the skulls of the two species (see Image 2.1), the most immediate gross morphological difference is the degree to which the face projects

from the skull. The face of the baboon is much longer and more prominent, particularly in the nasal region. The allometry of the mid-face differs drastically between the two species but visually the shape of the brain case appears remarkably similar. The results of this study indicate that, quantitatively, the relative contribution of various elements of the neurocranium contributes to differences in overall cranial shape variation. Our reconstruction of selection gradients responsible for the divergence of macaque and baboon crania suggests a neurocranial expansion and a forward placement of the mid-face relative the brain case in the baboon skull resulting in a baboon skull that is relatively wider and longer than that of macaques. This change may have been mediated by an increase in soft tissue growth, perhaps of the temporalis muscle, which passes through the infratemporal fossa, one of the regions to demonstrate a large, positive selection coefficient. Alternatively, muscular forces acting on the ectocranial surface, potentially those exerted by the muscles of mastication, could have produced these morphological features of the baboon skull. This might suggest a quantifiable difference in diet between ancestral populations of baboons and macaques, but the relative plausibility of these scenarios cannot be determined from these data. Either possibility or a combination of the two could explain the pattern of selection gradients reconstructed from these data.

The polarity of these morphological changes cannot be established without additional data from fossil primates or an outgroup species analyzed in a phylogenetic context. For instance, whether selection has been for prognathism in baboons or orthognathism in macaques is not defined. Although it is beyond the scope of this paper, a more wide-ranging comparative analysis that includes both fossil cercopithecines and extant species would provide additional insight regarding the history of selection and evolutionary change in the primate lineage. Despite this drawback, preliminary hypotheses regarding the selective pressures contributing to the appearance of these recognized trends in the craniofacial patterns of extant populations can be formulated.

Of interest is the fact that these craniometric landmark traits, which are clearly correlated with each other as well as with CC, differ in their patterns of correlation in the two species. This has interesting implications for the evolution of correlated characters. Although these are cousin species and once shared a common ancestral pattern of character correlation around six to eight million years ago (Steiper and Young 2006), they have since evolved divergent patterns. This raises two intriguing problems that further research will need to explore: how is correlated character evolution maintained and what mechanisms can interrupt or alter this type of evolution? A myriad of possibilities present themselves as explanations for the first question. Pleiotropic loci, or regions that influence multiple phenotypes, could maintain correlation among characters. Epistasis, or gene-by-gene interactions, could also maintain this correlation. Natural selection within a constant environment could be simultaneously selecting for a suite of advantageous traits. Even physiological processes that act on a set of morphologies to the exclusion of others could maintain correlation among phenotypes. Understanding how correlated evolution occurs will suggest methods or events by which it can be altered, which may contribute to our general knowledge of evolutionary processes.

2.5   Conclusion

The purpose of this study was threefold. First, to determine and compare heritability estimates for traits associated with the CFC in two closely related primate species. Second, to gauge the similarity between the species in covariance patterns among these traits and to highlight the craniofacial measurements strongly correlated with CC, a trait strongly correlated with brain size. Finally, to reconstruct selection gradients necessary to explain the difference in craniofacial patterning between these two species. It is important to determine the amount of heritable variation present in a population because it is the only variance component that can contribute to phenotypic evolution. If the heritability of the traits in question is large enough, we can proceed with gene mapping to identify candidate genes that will allow us to test hypotheses regarding the evolutionary pressures driving encephalization in the primate lineage.

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Chapter 3
Developmental Origins of and Covariation Between Metric and Nonmetric Cranial Traits

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3.1 Introduction

Determination of how the underlying cause(s) of variation in metric and nonmetric skeletal traits compare has remained elusive despite active research (Bennett 1965; Berry and Berry 1967; Kellock and Parsons 1970; Rightmire 1972; Corruccini 1976; Cheverud et al. 1979; Cheverud and Buikstra 1982; Richtsmeier et al. 1984; Hartl et al. 1995). This question has been of particular importance to anthropologists trying to measure the biological or the genetic distance between populations, using fragmentary skeletal material (Berry and Berry 1967; Kellock and Parsons 1970; Rightmire 1972; Konigsberg 1988; Ishida and Dodo 1993; Prowse and Lovell 1996; González-José et al. 2001; Hallgrímsson et al. 2004, and others). There is an ongoing debate over which skeletal traits yield the most accurate affinities between populations. This debate has generally been centered on the assumed highly heritable nature of nonmetric traits. However, the few studies that have estimated the

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heritability of nonmetric traits have shown that heritabilities are much less than 1.0 (Self and Leamy 1978; Cheverud and Buikstra 1981; Sjøvold 1984; Carson 2006). Cheverud (1982) calculated the mean heritability of cranial metric traits in this sample of macaques as $h^2 = 0.327$, while Roseman et al. (2010) recently estimated the mean heritability of cranial metric traits as approximately 0.40. Therefore, variation in both metric and nonmetric traits has a genetic and environmental component.

Understanding the factors that cause variation in metric and nonmetric traits is also of interest from a strictly skeletal biology perspective. Both types of traits are osseous and result from bone morphogenesis, but are their variations modulated through the same genetic and developmental pathways and affected similarly by environmental factors? To address this question, several studies have compared patterns of metric and nonmetric trait variation and covariation (Berry and Berry 1967; Bennett 1965; Corruccini 1976; Cheverud et al. 1979; Richtsmeier et al. 1984; Hartl et al. 1995). The reasoning behind this type of comparison is that the interdependence or the integration of traits – as measured by covariation – reflects a common influence from functional and/or developmental factors. Therefore, significant covariation between metric and nonmetric traits may indicate that the underlying factors causing variation are shared, or partly shared, by both types of traits.

In this study, we compare patterns of covariation between metric and nonmetric traits using rhesus macaque skulls from Cayo Santiago. Our two main aims are: (1) to determine the relationship between covariation in cranial metric and nonmetric traits and (2) to determine whether sources of covariation for both types of traits are the same. We are expanding on previous work that used these same data. Cheverud and colleagues have used these data to measure patterns of cranial variation (Cheverud 1981; Cheverud et al. 1983) to estimate heritability and genetic correlations using both metric (Cheverud 1982) and nonmetric data (Cheverud and Buikstra 1981; McGrath et al. 1984), as well as for comparisons of variation and covariation between both types of data (Cheverud and Buikstra 1982; Richtsmeier et al. 1984). Our study differs from previous investigations of these data sets by dividing the causes of covariation into two categories (direct and parallel – see below), based on the patterns of covariation observed.

For traits to be integrated, or to covary, there are two requirements: (1) there must be variation and (2) there must be a process that associates the traits so that the variation affects them jointly (Klingenberg and Zaklan 2000; Klingenberg et al. 2003; Klingenberg 2005). Sometimes, the source of variation itself is the mechanism by which the traits are associated, and other times the source of variation and the process of association are distinct. Klingenberg and colleagues have suggested that the sources of variation can be divided into two main categories, those due to direct developmental interactions and those due to parallel variation (Fig. 3.1) (Klingenberg and Zaklan 2000; Klingenberg et al. 2003; Klingenberg 2005).

Direct developmental interactions refer to a direct interaction between two or more developmental pathways such as a division of a cell population or interactions between signaling factors. The direct interaction passes on the variation to all pathways simultaneously. With direct interactions, variation arising in one pathway can be passed onto other associated pathways (Klingenberg and Zaklan 2000;
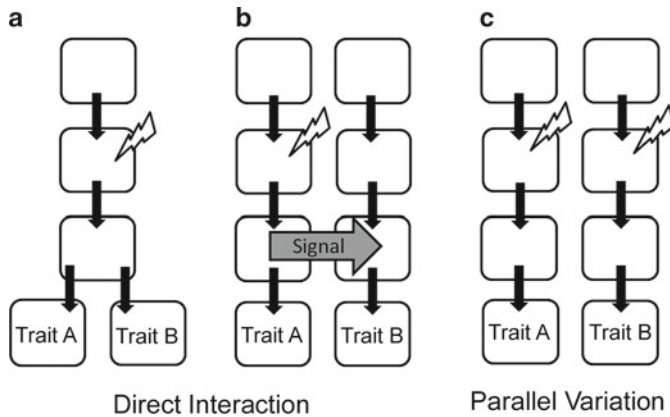
Fig. 3.1 Schematic of the two sources of variation – direct interaction and parallel variation – leading to covariation among traits. Diagrams (**a**) and (**b**) depict how variation can be passed between traits directly through multiple developmental steps. In (**a**), variation is passed onto two traits by the division of one trait. A signal that is passed directly between two separate developmental pathways is responsible for covariation of traits A and B in diagram (**b**). Diagram (**c**) illustrates an example of parallel variation. In this example, a source of variation (*lightning bolt*) has a simultaneous effect on both developmental pathways leading to traits A and B. There is no direct interaction between the separate pathways. Adapted from Klingenberg (2005: p. 227)

Klingenberg et al. 2003; Klingenberg 2005). For parallel variation, an outside factor acts on multiple pathways simultaneously, causing covariation between traits. Therefore, with parallel variation, the source of variation is also the mechanism of association between traits. Environmental factors such as temperature or nutrition can be sources of parallel variation as can allelic variation of genes and pleiotropic effects (Klingenberg and Zaklan 2000; Klingenberg et al. 2003; Klingenberg 2005). With parallel variation, the association between traits is due to the simultaneous effects of an outside source of variation on the development of multiple traits, rather than due to an interaction between the developmental pathways producing the traits.

The two sources of variation can be distinguished if genetic and environmental variation can be eliminated. Under these circumstances, any covariation between traits will be due to direct developmental interactions. It is possible to parse out covariation caused by direct interactions by using covariation of fluctuating asymmetries (Klingenberg and Zaklan 2000; Klingenberg et al. 2003; Klingenberg 2005). Fluctuating asymmetry (FA) is the distribution of random deviations from perfect symmetry in bilaterally symmetric traits (Ludwig 1932; as cited by Van Valen 1962). Variation between left and right sides is thought to be due to direct developmental interactions, as bilaterally symmetric traits presumably share the same environment and genetic background (Reeve 1960; Palmer and Strobeck 1986; Clarke 1998). Therefore, FA refers to within-individual variation, and the covariation of FA is caused by direct developmental interactions. Fluctuating asymmetry has traditionally been thought to arise from microenvironmental variation or environmental

variation that arises within the organism (Reeve and Robertson 1953; Waddington 1957; Clarke 1998). Similarly, we assume that FA is due to direct developmental interactions. Among-individual covariation incorporates covariation caused by both parallel variation and direct developmental interactions.

In this study, we use the methods outlined by Klingenberg and colleagues to distinguish integration due to parallel variation from integration due to direct developmental interactions by measuring the covariance among individuals and the covariance of FA (or the covariance of within-individual variance) (Klingenberg and Zaklan 2000; Klingenberg et al. 2003; Klingenberg 2005). We measure the integration of both kinds of variance data and compare the patterns of integration between metric and nonmetric traits of the macaque cranium. This method allows us to not only compare the patterns of integration between metric and nonmetric data, but to also compare the underlying cause of integration for the two types of data.

We expect that both metric and nonmetric traits will share a similar pattern of integration and that the underlying cause of variation, as reflected by their patterns of integration, will be similar for both types of data. Our reasoning behind both hypotheses is interrelated.

The variation for the metric and nonmetric traits used in this study show both a heritable and a nonheritable (or environmental) component (Cheverud and Buikstra 1981; Cheverud 1982; McGrath et al. 1984). In fact, with the exception of foraminal nonmetric traits (presence of extra foramina), heritability estimates for both metric and nonmetric traits are quite similar (Cheverud and Buikstra 1982). These results do not support the idea that nonmetric traits have a greater heritable component than metric traits. Additionally, studies of the effects of an environmental factor, such as cranial deformation, on nonmetric traits support the idea that variation in nonmetric traits has an environmental component (Bennett 1965; Kellock and Parsons 1970; Ossenberg 1970; Konigsberg et al. 1993).

These results agree with standard views on the contribution of variance components to trait expression in threshold (or nonmetric) traits (Roff 1998). Falconer and McKay (1996) describe nonmetric trait variation as continuous, with a threshold that imposes a discontinuous trait expression. The underlying continuously distributed variable is the liability of expression of that trait – or the underlying determinant of whether or not the trait will be expressed. This liability is determined by both genetic and environmental factors (Fraser 1976). Therefore, while nonmetric trait expression is triggered by factors crossing a threshold, such as a critical amount of a morphogen, or a critical amount of physical contact between tissues, the underlying liability for nonmetric traits is determined by genetic and environmental factors, as are metric traits (Hallgrímsson et al. 2005).

Since the variation in both metric and nonmetric traits has a genetic and an environmental component, we assume that both genetic and environmental (both micro and macro) factors influence variation in the two types of traits similarly. As we expect that variation in both types of traits share similar causative factors, we further expect that the patterns of covariation among traits will be similar for metric and nonmetric data.

3.2 Materials and Methods

Our data were collected from 110 macaque skulls from the Cayo Santiago skeletal collection. The sample includes 58 females and 52 males that range in age from 0.8 to 18.5 years. Both metric data in the form of 3D landmarks and nonmetric data were previously collected by two of the authors (JC and JB). A diagraph was used to collect the landmark data, and we have used these data to calculate 13 linear distances that are used in the analyses. The original metric data set consists of 42 bilateral and midline landmarks from 208 macaque skulls, and the original nonmetric data includes 43 bilateral and midline traits from 442 individuals. Because we wanted to compare metric and nonmetric traits, we limited our study to those individuals who had complete sets of both types of data, yielding a sample of 110 individuals. Adults and juveniles of both sexes were included. Table 3.1 provides a description of the 13 distances and the 13 nonmetric traits used. Figure 3.2 outlines the metric distances used in the analyses.

Table 3.1 List of metric and nonmetric traits with their abbreviations used in this study as well as the area of the skull in which they are located Metric and nonmetric traits were matched according to their location on the skull. Matching traits are listed in the same row. All traits were measured/counted on both left and right sides

Metric traits (distances)	Nonmetric traits	Region
Temporomalar junction to external auditory meatus (N1)	Frontotemporal articulation (fta)	Neurocranium
Pterion to bregma (N2)	Epipteric bone (epi)	Neurocranium
Lambda to pterion (N3)	Asterionic bone (ast)	Neurocranium
Asterion to jugular process (N4)	Divided hypoglossal canal (dhyc)	Neurocranium
Asterion to temporo-sphenoidal junction at petrous (N5)	Number of occipital foramina (occfn)	Neurocranium
Frontomalar junction to zygomaxillare superior (F1)	Frontal–nasal contact (fnc)	Face
Pterion to frontomalar junction (F2)	Accessory supraorbital structures (asos)	Face
Zygomaxillare inferior to spheno-fronto-malar junction (F3)	Number of zygomaticofrontal foramina (zffn)	Face
Zygomaxillare inferior to inferior pterygomaxillary junction (F4)	Number of infraorbital foramina (iof)	Face
Spheno-fronto-malar junction to zygomaxillare superior (F5)	Number of zygomaticofacial foramina (zff)	Face
Zygomaxillare inferior to zygomaxillare superior (F6)	Infraorbital suture (ios)	Face
Inferior pterygomaxillary junction to premaxilla-maxillary junction at alveolus (F7)	Lateral pterygoid bridging – medial aspect (lbpm)	Face
Superior pterygopalatine fossa to inferior pterygomaxillary junction (F8)	Lateral pterygoid bridging – lateral aspect (lbpl)	Face
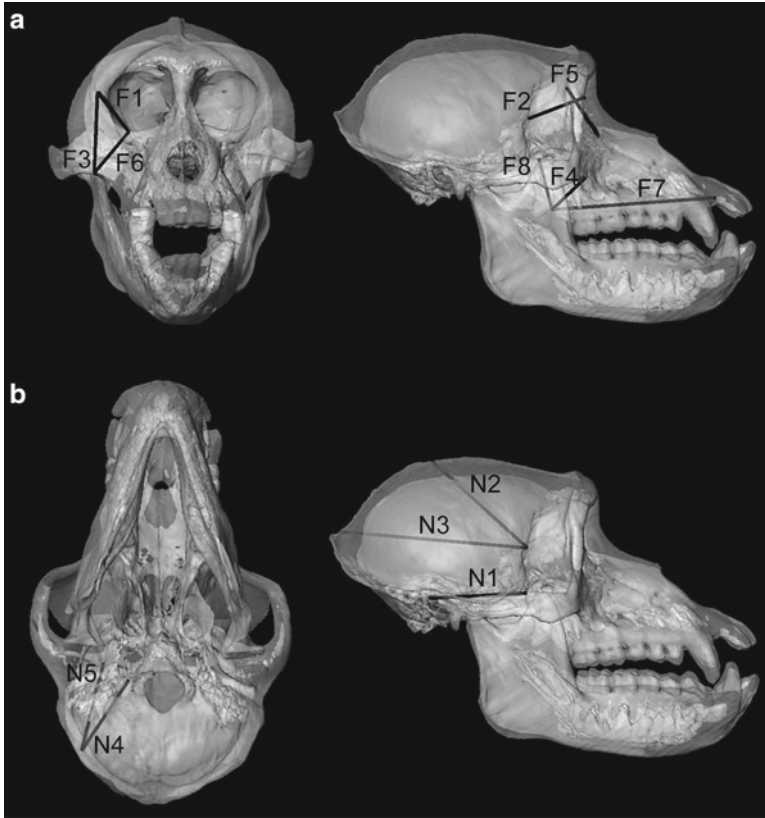
Fig. 3.2 Metric distances used in analyses shown on a 3D reconstruction of computed tomography scan of a skull. In order to visualize many of the linear distances used (Table 3.1) that pass through the interior of the skull, the 3D reconstruction is shown as transparent. Transparency also makes the endocranial and ectocranial surface of the vault and internal structures of the mandible visible. Linear distances that are on or close to the surface of the skull are shown in *black*, while those linear distances (or parts of linear distances) that pass through the skull are shown in *gray*. Part (**a**) illustrates facial distances in anterior (*left*) and lateral (*right*) views. Part (**b**) illustrates distances located within the neurocranium in inferior (*left*) and lateral (*right*) views. Descriptions and labels of each distance are listed in Table 3.1

Nonmetric traits were originally scored using a multistate system, but we have dichotomized these data into present/absent categories using the methods described in Cheverud and Buikstra (1981: pp 48–49). Binary data make it easier to compute correlations among traits.

We chose distances that spanned the regions where the nonmetric traits are located. To allow for the most informative comparisons between correlation matrices of metric and nonmetric data, we paired each metric trait with a nonmetric trait based on proximity: these pairs are listed in the same row in Table 3.1. We then used this pairing to construct the correlation matrices. We labeled all traits according to whether they were located on the neurocranium or the face.
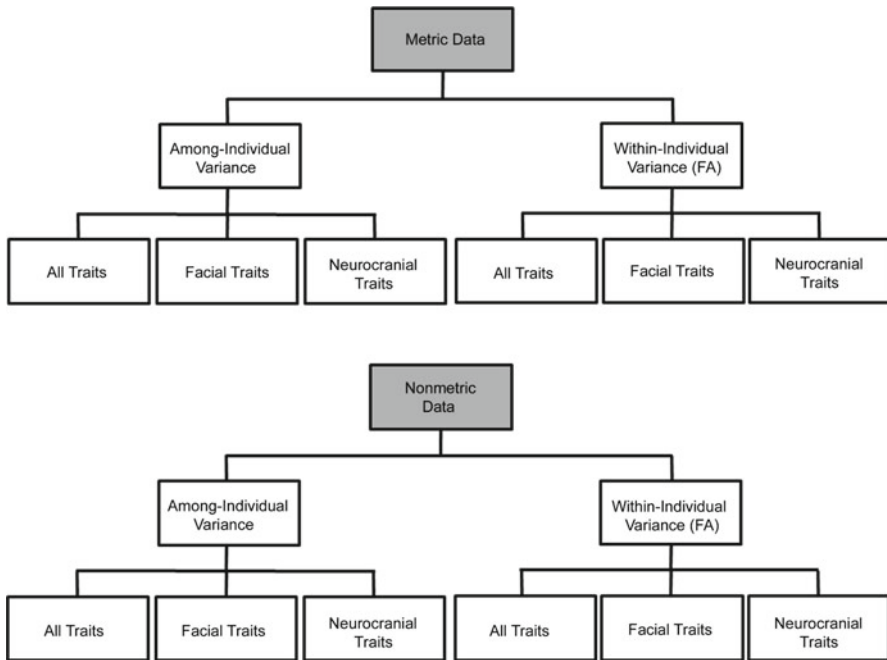
Fig. 3.3 Schematic of the data used in analyses

3.2.1   Analyses

Our analyses used several sets of data, which we outline in Fig. 3.3. From our metric data and nonmetric data, we calculated correlation matrices using among-individual variance data and within-individual variance (or FA) data. We also assigned each trait to one of two modules: a facial module or a neurocranial module (Table 3.1). We then constructed correlation matrices using data from the facial module only and from the neurocranial module only from both among-individual variance data and within-individual variance data, for both metric and nonmetric traits, using the statistical software R (Fig. 3.3).

3.2.2   Metric Data

We tested all distances for possible age and sex effects using ANOVA. We found that all but two of the distances showed significant age effects and that over half of the distances had significant sex effects. To remove these effects, we regressed distance data on sex and age and used the residuals from these regressions in all subsequent analyses as our data. To account for possible scaling effects, we also natural log-transformed all distances.

We used right-sided distances only for among-individual variance data calculations. For each individual, we calculated the absolute difference between the distance for that individual and the mean distance of the sample. We then calculated the variance of this difference across all individuals and used this variance data to calculate the correlation matrix using the statistical software R.

To calculate FA, we used the difference between left and right sides for each distance, and then used these data to calculate the FA correlation matrix. We checked our FA data for both directional asymmetry and antisymmetry. Directional asymmetry is indicated if the mean of the signed difference between right and left sides is significantly different from zero and to check for it, we used a *t*-test (Palmer and Strobeck 1992). We calculated skew and kurtosis for the FA data to determine if antisymmetry was present. We calculated standard errors as $\sqrt{6/N}$ for skewness and $\sqrt{24/N}$ for kurtosis, where N is the sample size (Sokal and Rohlf 1995: p. 138). Antisymmetry artificially inflates measures of FA, and therefore any traits exhibiting antisymmetry should be excluded from FA analyses (Palmer and Strobeck 2003). We did not find directional asymmetry for any of the traits, but we found that nearly half of the traits showed signs of either kurtosis or skew. We graphed these data for visual inspection; the degree of antisymmetry was minimal, and we therefore included all distances. Graphs of data for kurtosis and skew are available from the authors upon request.

3.2.3 Nonmetric Data

As with the metric data, we checked our nonmetric data for age and sex effects using ANOVA. We did not detect any age effects, but some of the traits displayed sex effects. Because our data are binary, we could not remove the effects of sex using regression. Instead, we calculated separate correlation matrices for males and females, and then used the average for further analyses.

We used tetrachoric correlations between traits to construct the correlation matrices. Tetrachoric correlation is preferred for binary data because it estimates the correlation as if the data were based on a continuous scale (Pearson 1901). We calculated the tetrachoric correlations and their associated standard errors using the statistical software R.

We calculated fluctuating asymmetry as the absolute difference between right and left sides. We used the absolute difference between sides to maintain binary data for the tetrachoric correlations. We checked for the presence of directional asymmetry using McNemar tests for each trait, employing the sequential Bonferroni procedure to evaluate significance. The McNemar test determines whether the proportions of the two labels (in our case, left- and right-sided data) are equal. This is essentially a sign test that is appropriate for binary data (Leamy 1997; Sokal and Rohlf 1995: pp 779–783). To test for antisymmetry, we followed the method described by Leamy (1997) whereby the signed difference between right and left sides for each individual is summed across all traits. Therefore, we tested for antisymmetry using the entire

Table 3.2 List of comparisons used in analyses

Data		Data
Metric among-individual variance – all traits	with	Nonmetric among-individual variance – all traits
Metric among-individual variance – facial traits	with	Nonmetric among-individual variance – facial traits
Metric among-individual variance – neurocranial traits	with	Nonmetric among-individual variance – neurocranial traits
Metric within-individual variance – all traits	with	Nonmetric within-individual variance – all traits
Metric within-individual variance – facial traits	with	Nonmetric within-individual variance – facial traits
Metric within-individual variance – neurocranial traits	with	Nonmetric within-individual variance – neurocranial traits
Metric among-individual variance – all traits	with	Metric within-individual variance – all traits
Metric among-individual variance – facial traits	with	Metric within-individual variance – facial traits
Metric among-individual variance – neurocranial traits	with	Metric within-individual variance – neurocranial traits
Nonmetric among-individual variance – all traits	with	Nonmetric within-individual variance – all traits
Nonmetric among-individual variance – facial traits	with	Nonmetric within-individual variance – facial traits
Nonmetric among-individual variance – neurocranial traits	with	Nonmetric within-individual variance – neurocranial traits

data set, rather than for each trait individually. For each trait, an individual could have a signed difference of −1, 0, or 1 and, summed over all 13 traits, could range from −13 to +13. We used these summed, signed differences to calculate kurtosis and skew and calculated their associated standard errors using the same formulas we used for metric data. None of our McNemar tests were significant, indicating that directional asymmetry was insignificant for all traits. Our results for kurtosis and skew were also insignificant, indicating that these data do not display antisymmetry.

3.2.4   Integration Comparisons

We compared the pattern and strength of integration between several sets of data that are outlined in Table 3.2. The main comparisons are between metric and non-metric traits, using both among-individual variance and within-individual variance (FA) data. Our comparisons were refined by assigning each trait (metric and non-metric) to one of two modules: a facial module or a neurocranial module (Table 3.1). Consequently, our integration comparisons were done using data from the whole skull as well as data from each module.

Our first test follows the method developed by Cheverud (Cheverud et al. 1989; Cheverud 1995; Marroig and Cheverud 2001) and involves comparisons between theoretical correlation matrices, based on assumed associations within the skull and our empirically derived correlation matrices. We constructed the theoretical matrices based on our two skull modules, the face and neurocranium. The assumption used to construct our theoretical matrices is that there is a perfect correlation among traits of the module of interest and that there is no correlation among all other traits. For example, we constructed the facial theoretical matrix by placing a value of 1.0 in any cell that represents the correlation among facial traits and a value of 0.0 in cells that correlate a facial trait with a neurocranial trait or that correlate two neurocranial traits. Using this same method, we constructed a neurocranial theoretical matrix. Additionally, we constructed a theoretical matrix that recognized the possible association of both facial and neurocranial traits. In this matrix, we placed a value of 1.0 in any cell that represented a correlation between two facial traits or between two neurocranial traits and a value of 0.0 in any cell that represented a correlation between a facial and neurocranial trait.

We used Mantel's tests to compare the observed correlation matrices with the theoretical matrices. This method allows us to compare patterns of integration between metric and nonmetric data as well as between within-individual variance and among-individual variance. It does not, however, allow us to statistically compare the strength of integration between the different types of data. We calculated Mantel's tests using Microsoft Excel and evaluated significance using 1,000 permutations.

Additionally, we calculated the average within-module correlation and the average between-module correlation for both the facial and neurocranial modules. We then calculated the difference of the average between-module correlation from the average within-module correlation assessing the significance of the differences in correlation, using the permutation results from Mantel's tests. This test gives a relative estimate of the strength of integration within a module compared with the strength of integration among all other traits that are not included in the module.

Our second test of integration uses the method outlined by Wagner and colleagues (Wagner 1984; 1990; Pavlicev et al. 2009), whereby the variance of the eigenvalues for a correlation matrix is calculated. A trait that is strongly integrated will have only a few eigenvalues that are quite large in comparison to the rest of the eigenvalues. The premise of this integration index is that when there are only a few large eigenvalues, the variation of the traits is confined to a smaller subspace in the overall multivariate phenotypic space (Wagner 1984; 1990).

We used the statistical software R to calculate the variance of eigenvalues for each correlation matrix. We conducted multiple comparisons of the variance of eigenvalues, as listed in Table 3.2. Before each comparison, we standardized the estimated variance of the eigenvalues by the number of traits by dividing the observed variance of the eigenvalues by the number of traits minus 1 (Pavlicev et al. 2009). For each comparison, we calculated the significance of the difference by bootstrapping each data set using 1,000 iterations, and then tallied the number of iterations in which the difference between the two resampled values exceeds zero, divided by the number of iterations.

We also directly compared correlation matrices using Mantel's tests. We compared the correlation of metric traits with the correlation of nonmetric traits using both among-individual variance and within-individual variance data. We also compared the correlation of among-individual variance data with within-individual variance data for both metric and nonmetric traits. To evaluate statistical significance, we used 1,000 permutations. We calculated matrix repeatabilities for each correlation matrix by subtracting the average error variance of the correlation estimates from the observed variance of correlation estimates divided by the observed variance. Repeatabilities provide an estimate of the maximum correlation that can be expected when two sample matrices are drawn from a common population. We then standardized all matrix correlations by the matrix repeatabilities. For example, we corrected the correlation between the metric matrix of among-individual variance data using all traits and the nonmetric matrix of among-individual variance data using all traits using the following formula:

$$\text{Corrected } r_{m/nm} = r_{m/nm} \Big/ \sqrt{t_{metric} \times t_{nonmetric}}$$

where $r_{m/nm}$ is the correlation between the metric and nonmetric phenotypic correlation matrices and t_{metric} and $t_{nonmetric}$ are the repeatabilities for the metric and nonmetric correlation matrices, respectively (Cheverud 1996: pp. 15–16).

3.3 Results

3.3.1 Correlation Matrices

Our correlation matrices for metric traits and nonmetric traits using both among-individual variance and within-individual variance data can be found in Appendix. Correlations are located below the diagonal of the matrix, and their associated standard errors are found above the diagonal. Statistically significant correlations at the $P < 0.05$ level are highlighted in gray. The correlation matrix constructed from among-individual variance data for metric traits shows several statistically significant correlations among facial distances. There are also several significant correlations among facial traits and the neurocranial distances between the temporomalar junction and the external auditory meatus (N1), between asterion and the jugular process (N4), and between asterion and the temporo-sphenoidal junction at the petrous bone (N5). The correlation matrix constructed from within-individual variance data for metric traits shows fewer significant correlations among facial traits. Significant correlations between facial and neurocranial distances show less of a pattern than found for among-individual variance data.

In general, correlations among nonmetric traits using both among-individual and within-individual variance data are quite strong. However, few of these correlations are statistically significant due to their high standard errors.

3.3.2   Hypothetical Matrix Results

We tested the correlation between the correlation matrices constructed from our empirical data and the hypothetical correlation matrices based on assumed relationships within the skull. Our results show similarities in patterns of integration for among-individual variance data and within-individual variance data for metric and nonmetric traits. We also found that in general, traits that are strongly integrated for metric data are weakly integrated for nonmetric data (Table 3.3).

For our metric traits, the whole skull hypothetical matrix (which represents integration among neurocranial traits and among facial traits) is significantly correlated with both among-individual variance data ($r=0.269$, $P=0.026$) and within-individual variance data ($r=0.294$, $P=0.022$). Our nonmetric traits are significantly correlated with the neurocranial hypothetical matrix using among-individual variance data ($r=0.338$, $P=0.016$) and are nearly significantly correlated with the neurocranial module using within-individual variance data ($r=0.321$, $P=0.052$).

Our nonmetric data are negatively correlated with the facial hypothetical matrix for among-individual variance data ($r=-0.138$, $P=0.359$) and significantly negatively correlated for within-individual variance data ($r=-0.408$, $P=0.026$). These results indicate that facial nonmetric traits are negatively correlated with each other. Our results for the difference in correlations within-modules and between-modules correspond with our hypothetical matrix correlations. For nonmetric traits using among-individual variance data, traits within the facial module have an average correlation of $r=0.053$, whereas the average correlation of all traits outside of the facial module is $r=0.125$. Similarly, the average correlation within the facial module using within-individual variance data is $r=0.045$, and the average correlation between modules is $r=0.215$ (Table 3.3). The high average correlation between modules is likely due in part to the high correlation among neurocranial traits. Still, the average correlation among facial nonmetric traits for both among-individual variance data and within-individual variance data is very low.

3.3.3   Variance of Eigenvalues

Results from our comparisons of variance of the eigenvalues between metric and nonmetric traits are similar to our hypothetical matrix results. Facial traits are significantly more integrated for metric traits compared with nonmetric traits for among-individual variance data (Table 3.4). Conversely, nonmetric traits show significantly greater integration within the neurocranium compared to metric traits for both among-individual and within-individual variance data (Table 3.4).

Our comparisons of integration of among-individual variance data with within-individual variance data revealed a significant difference for the integration of facial traits. For both metric and nonmetric data, facial traits are significantly more integrated for among-individual variance data than within-individual variance data (Table 3.5).

Table 3.3 Results from Mantel's tests between correlation matrices from metric and nonmetric data with hypothetical matrices for the whole skull, neurocranium, and face, as well as the average within-module correlation and between-module correlation with significance values for their differences

	Metric data				Nonmetric data			
	r	Within-module r	Between-module r	P value	r	Within-module r	Between-module r	P value
	Among-individual variance				Among-individual variance			
Whole skull	**0.269**	**0.299**	**0.209**	**0.026**	0.094	0.123	0.076	0.395
Neurocranium	–0.120	0.200	0.261	0.505	**0.338**	**0.318**	**0.067**	**0.016**
Face	0.364	0.335	0.207	0.097	–0.138	0.053	0.125	0.359
	Within-individual variance (FA)				Within-individual variance (FA)			
Whole skull	**0.294**	**0.092**	**–0.012**	**0.022**	–0.177	0.118	0.188	0.1
Neurocranium	0.084	0.025	0.041	0.496	0.321	0.321	0.129	0.052
Face	0.248	0.097	0.006	0.053	**–0.408**	**0.045**	**0.215**	**0.026**

The between-module correlation represents the average correlation of all traits that are not within the module of interest. For instance, for the facial module, the within-module correlation is the average correlation for all facial traits, and the between-module correlation is the average correlation of all other traits. Significant correlations and differences in correlations at the $P=0.05$ level are highlighted in *bold*

Table 3.4 Comparison of the variance of the eigenvalues for correlation matrices from metric and nonmetric data using both among-individual variance and within-individual variance (FA)

	Metric	Nonmetric	P value
Among-individual variance			
Whole skull	0.010	0.078	0.554
Neurocranium	**0.082**	**0.209**	**0.01**
Face	**0.152**	**0.060**	**0.027**
Within-individual variance (FA)			
Whole skull	**0.035**	**0.068**	**0.001**
Neurocranium	**0.068**	**0.193**	**0.001**
Face	0.043	0.028	0.386

Comparisons include the whole skull as well as neurocranial and facial modules. Data used in the comparisons were corrected for the number of traits included. The significance of the differences in variance of the eigenvalues for each comparison are indicated by *P* values with statistically significant differences highlighted in *bold* (*P*<0.05)

Table 3.5 Comparison of the variance of the eigenvalues between among-individual variance and within-individual variance (FA) using both metric and nonmetric data

	Among-individual	Within-individual	P value
Metric			
Whole skull	0.010	0.035	1
Neurocranium	0.082	0.068	0.279
Face	**0.152**	**0.043**	**0.001**
Nonmetric			
Whole skull	0.078	0.068	0.381
Neurocranium	0.209	0.193	0.444
Face	**0.060**	**0.028**	**0.037**

Comparisons include the whole skull as well as neurocranial and facial modules. Data used in the comparisons were corrected for the number of traits included. The significance of the differences in variance of the eigenvalues for each comparison are indicated by *P* values with statistically significant differences highlighted in *bold* (*P*<0.05)

3.3.4 Direct Comparisons of Correlation Matrices

We compared correlation matrices directly using Mantel's tests. We made four comparisons: between metric and nonmetric traits using among-individual variance data, between metric and nonmetric traits using within-individual variance data, between among-individual and within-individual variance data for metric traits, and between among-individual and within-individual variance data for nonmetric traits. We corrected all correlations using the repeatabilities of the matrices involved. Both correlations between metric and nonmetric data were negative and statistically insignificant (among-individual variance data $r=-0.265$, $P=0.155$; within-individual variance data $r=-0.045$, $P=0.681$). Correlations between among-individual and within-individual variance data were positive and statistically significant for both metric and nonmetric traits (metric traits $r=0.501$, $P=0.001$; nonmetric traits $r=0.273$, $P=0.006$).

3.4   Discussion

In general, our results support our hypothesis that there is a common source(s) of integration for both metric and nonmetric traits. However, we found that their patterns of integration differ. Facial traits are strongly integrated for metric data, whereas, nonmetric data are more strongly integrated among neurocranial traits.

We found that the relative contribution of among-individual covariance and within-individual covariance is quite similar for metric and nonmetric traits; that is, parallel variation and direct developmental interactions provide a similar contribution to the integration of both types of cranial traits. The similarity between metric and nonmetric traits could be due to the same degree of exposure to among- and within-individual variance and potentially indicates that the same combination of genetic, developmental, and environmental factors might be influencing both types of traits. Or, the similarity could be due to both types of traits *reacting* similarly to parallel variation and direct developmental interactions rather than due to similar sources of variation.

While we are able to partition the underlying causes of variation into those due to direct developmental interactions and those due to parallel variation, we are not able to establish precisely the underlying developmental cause(s). Rather, our analysis reduces the number of possible sources of variation that lead to the patterns of integration, which provides a useful guide for further studies that empirically test for the possible sources of variation.

Our metric data show strong integration among facial traits using both among-individual and within-individual variance data. Results from our eigenvalue variance analyses show that metric facial traits are significantly more strongly integrated than nonmetric traits, using among-individual variance data and that they are more strongly, though not statistically significantly integrated, using within-individual variance data. Our correlation matrices also reveal strong integration among facial traits. This pattern is especially prominent in the matrix using among-individual variance data. Not only are facial traits strongly and significantly correlated, they are also significantly correlated with traits found in the temporal region of the neurocranium. This pattern of integration could represent the influence of the forces of mastication on structuring variance in the skull. Our findings of strong facial integration are consistent with studies of other monkeys (Cheverud 1995; Ackermann and Cheverud 2000; Marroig and Cheverud 2001), of apes and humans (González-José et al. 2004; Ackermann 2005; Mitteroeker and Bookstein 2008), of mice (Willmore et al. 2006), and across a wide range of therian mammals (Goswami 2006; Marroig et al. 2009; Porto et al. 2009).

Conversely, our nonmetric traits are more strongly integrated within the neurocranium. Comparisons of our nonmetric correlation matrices with the neurocranial hypothetical matrix reveal a strong and significant correlation for among-individual variance data and a strong and nearly significant correlation for within-individual variance data. Likewise, nonmetric neurocranial traits are significantly more tightly integrated than metric neurocranial traits, using both among- and within-individual variance data.

Interestingly, our nonmetric facial traits are negatively correlated with each other for both among- and within-individual variance data. Given the theoretical importance of facial integration to ensure efficient mastication and the empirical evidence involving metric data that supports this theory, it is difficult to explain a negative correlation among facial traits. On closer inspection of the nonmetric traits of which the facial module is comprised, we noticed that four of the eight traits are foraminal, that is, traits that involve the presence or absence of foramina. The other half of the facial nonmetric traits are either hyperostotic or hypostotic. Hyperostotic traits represent an excess of ossification, such as the ossification of something that is normally cartilage, ligament, or dura (Ossenberg 1970). Lateral bridging of the pterygoid process (both medial and lateral aspect) are examples of facial hyperostotic traits. Hypostotic traits represent insufficient osseous development such as a patent suture or a sutural bone (Ossenberg 1970). Hypostotic nonmetric traits of the face used in this study include frontal–nasal contact and infraorbital suture. Both hyperostotic and hypostotic nonmetric traits involve changes in ossification, whereas foraminal traits essentially represent variation in the degree and position of branching in the peripheral nerves and/or the vascular system.

It is possible that our negative correlations among nonmetric facial traits are due to the composition of our nonmetric data, rather than a lack of integration among facial traits. To check for this possibility, we constructed two more hypothetical matrices, one representing foraminal traits of the entire skull (not just the face), and one representing both hyperostotic and hypostotic traits of the entire skull. Our results show that indeed there is a negative correlation between our empirical nonmetric correlation matrices and the foraminal hypothetical matrix (among-individual variance data $r = -0.101$, $P = 0.397$; within-individual variance data $r = -0.104$, $P = 0.531$). Our finding indicates that foraminal traits are not strongly correlated with each other, and that perhaps our negative correlation among facial nonmetric traits is at least partly due to the large number of foraminal traits used.

Our neurocranial nonmetric trait set included four hyperostotic/hypostotic traits and one foraminal trait. It is possible that the strong integration found within the neurocranium using nonmetric traits is due to the make-up of the trait set. Mantel's tests between our empirical correlation matrices and the hyperostotic/hypostotic hypothetical matrix revealed positive but statistically insignificant correlations (among-individual variance data $r = 0.149$, $P = 0.289$; within-individual variance data $r = 0.163$, $P = 0.402$). However, comparisons between our data and the neurocranial hypothetical matrix were twice as strong as comparisons between our data and the hyperostotic/hypostotic hypothetical matrix (Table 3.4). Our results indicate that while the strong integration among nonmetric neurocranial traits may be due in part to the traits used, there seems to be another factor or set of factors that are responsible for integrating the neurocranium. Given that three of these neurocranial nonmetric traits (fta, epi, and ast) involve the establishment of suture patterns, the relatively increased correlation of neurocranial nonmetric traits may indicate an underlying propensity for early patterning of the sutures between calvarial plates.

We suggest that the relatively heterogeneous nature of our nonmetric trait set compared with our metric trait set could be causing the differences in integration patterns observed. Cheverud and Buikstra (1982) have shown previously that estimates of heritability differ between types of nonmetric traits in this same group of macaques. They found that hyperostotic traits are more heritable than foraminal traits, which support earlier findings reported by Ossenberg (1970). Foraminal traits do not have a particularly low genetic component; in fact, they have heritability estimates similar to cranial metric traits (Cheverud and Buikstra 1982). Rather, hyperostotic traits have relatively high heritabilities. Perhaps further studies that compare the different types of nonmetric traits will help us better understand their patterns of integration.

We still cannot link the knowledge we have of gene function at the molecular level and our knowledge of the processes that result in the production of osseous phenotypes. Here we compared metrics representing the linear distances among landmarks located on the skull to the expression of cranial nonmetric traits. Since the linear distances connect separate anatomical regions, the distance itself may only reflect magnitude of the distances and not any particular developmental origin. Nonmetric traits embody specific, though seemingly disparate developmental processes, some of which are direct representatives of vascular and/or neural anatomy. When evaluating the contribution of general causes, we get similar results for metric and nonmetric traits in the relative contribution of parallel variation and direct developmental interactions. However, it may be that the development underlying each nonmetric trait is so dissimilar that they cannot be considered as a single class but rather as consisting of several etiologically distinct classes. The developmental basis of traits may provide a more cogent basis for their classification than their anatomical position on the adult structure.

3.5 Conclusion

In summary, we found that variation in metric and nonmetric cranial traits are due to a similar combination of direct and parallel sources of variation. These results do not mean that metric and nonmetric traits are influenced by the same factors. To make such a claim, we need to determine the specific developmental underpinnings of the variation in both types of traits. However, our results do suggest that it is at least *possible* that metric and nonmetric cranial traits are influenced by the same factors.

Our results also revealed a puzzling difference in the patterns of integration between metric and nonmetric traits. We found strong integration among facial traits for our metric data, a pattern that has been commonly reported for a variety of primates and mammals. Our nonmetric traits however, were strongly integrated within the neurocranium and negatively correlated among facial traits. Generally, strong integration among facial traits is attributed to the coordinated movements involved in chewing. Our metric data support this suggestion, especially since our

facial traits are also strongly integrated with traits in the temporal region of the neurocranium – a region of attachment for the muscles of mastication.

The strong integration among neurocranial traits for the nonmetric data is more difficult to explain. We suggest that the selection of nonmetric traits used in this study could be responsible for the patterns of integration observed. In this study, we have combined three different kinds of nonmetric traits in our analyses: foraminal, hyperostotic, and hypostotic. Little is known about the etiology of these different types of nonmetric traits, and we suspect that each type has a distinct developmental program. Our study does not allow us to uncover the specific developmental underpinnings of each nonmetric trait type and therefore, we have no evidence to support our supposition. We are uncertain why our nonmetric traits are so strongly integrated within the neurocranium and negatively integrated within the face. We suggest that the nearly 50/50 mix of foraminal traits and hyperostotic and hypostotic traits within the face are causing the negative correlation and that the more homogeneous group of nonmetric traits used for the neurocranium allow for a stronger pattern of integration.

Given that we found similar sources of direct and parallel variation for metric and nonmetric traits, it is surprising that we find such disparate patterns of integration for each trait type. Our results highlight the need for further study. A logical first step is to re-examine cranial integration of nonmetric traits using a much larger trait set with separate tests for foraminal, hypostotic, and hyperostotic traits. Such a study would help determine if the heterogeneous nature of the nonmetric traits used in our study affects integration patterns. It is also necessary to gain a greater understanding of the specific developmental underpinnings of each trait – both metric and nonmetric.

For anthropologists trying to determine affinities between populations, knowledge of the underlying causes of variation for metric and nonmetric traits is of great importance. If both types of traits are influenced by the same factors, then it is possible to increase the number of traits used for comparison. When fragmentary samples are common, increasing trait number is essential. If metric and nonmetric traits are influenced by different developmental factors, then study of each trait type will provide separate insight for a common question.

Appendix

Table A1 Metric correlation matrix using among-individual variance data

	N1	N2	N3	N4	N5	F1	F2	F3	F4	F5	F6	F7	F8
N1		0.095	0.096	0.093	0.094	0.095	0.093	0.093	0.092	0.096	0.090	0.083	0.094
N2	0.131		0.095	0.095	0.096	0.096	0.096	0.096	0.096	0.096	0.095	0.096	0.095
N3	0.031	0.173		0.096	0.094	0.096	0.096	0.096	0.095	0.095	0.096	0.095	0.095
N4	0.253	0.165	0.079		0.074	0.095	0.086	0.086	0.087	0.096	0.091	0.080	0.082
N5	0.190	0.111	0.232	0.637		0.096	0.093	0.089	0.092	0.096	0.095	0.088	0.087
F1	0.137	−0.077	0.109	0.130	0.076		0.096	0.092	0.090	0.092	0.093	0.093	0.095
F2	0.249	0.043	0.017	0.454	0.247	0.048		0.085	0.089	0.095	0.089	0.086	0.094
F3	0.238	0.015	−0.010	0.459	0.368	0.297	0.463		0.084	0.095	0.089	0.074	0.087
F4	0.289	−0.007	0.139	0.433	0.278	0.351	0.370	0.479		0.094	0.089	0.073	0.088
F5	0.081	0.091	0.143	0.016	0.092	0.286	0.125	0.149	0.193		0.093	0.095	0.094
F6	0.350	0.145	0.122	0.315	0.175	0.262	0.377	0.391	0.379	0.250		0.087	0.089
F7	0.503	0.110	0.126	0.555	0.412	0.242	0.444	0.638	0.646	0.181	0.422		0.082
F8	0.235	0.180	0.165	0.521	0.429	0.177	0.221	0.423	0.415	0.229	0.390	0.521	

Table A2 Metric correlation matrix using within-individual variance data

	N1	N2	N3	N4	N5	F1	F2	F3	F4	F5	F6	F7	F8
N1		0.095	0.096	0.096	0.095	0.090	0.096	0.096	0.096	0.096	0.096	0.095	0.096
N2	0.164		0.088	0.096	0.096	0.096	0.089	0.096	0.094	0.096	0.096	0.096	0.096
N3	0.012	0.412		0.095	0.096	0.096	0.081	0.094	0.096	0.096	0.096	0.096	0.095
N4	−0.048	−0.036	−0.168		0.080	0.095	0.096	0.096	0.096	0.096	0.096	0.095	0.096
N5	−0.127	0.033	−0.018	0.549		0.096	0.096	0.095	0.096	0.096	0.096	0.096	0.096
F1	0.352	0.096	0.089	−0.123	−0.023		0.094	0.091	0.094	0.089	0.091	0.095	0.096
F2	0.007	−0.391	−0.536	0.065	−0.003	−0.212		0.091	0.096	0.096	0.096	0.096	0.096
F3	0.085	0.020	0.219	−0.094	0.160	0.324	−0.314		0.096	0.096	0.093	0.096	0.096
F4	0.050	−0.236	−0.099	0.042	0.038	0.209	0.028	0.042		0.095	0.094	0.091	0.093
F5	−0.011	0.090	0.098	−0.043	−0.091	0.392	−0.086	−0.089	0.148		0.092	0.095	0.096
F6	0.059	−0.066	0.017	0.053	0.075	0.313	0.019	0.260	0.199	0.288		0.096	0.095
F7	0.180	−0.122	−0.090	−0.161	−0.060	0.174	0.096	0.121	0.311	−0.142	0.023		0.096
F8	−0.088	−0.025	−0.127	0.044	0.082	0.074	0.029	0.020	0.265	0.009	0.159	0.051	

Table A3 Nonmetric correlation matrix using among-individual variance data

	fta	epi	ast	dhyc	occfn	fnc	asos	zffn	iof	zff	ios	lbpm	lbpl
fta		0.362	0.391	0.341	0.415	0.387	0.438	0.346	0.327	0.352	0.429	0.346	0.336
epi	0.596		0.336	0.393	0.409	0.452	0.427	0.413	0.394	0.408	0.421	0.412	0.400
ast	0.654	0.728		0.506	0.468	0.482	0.403	0.489	0.489	0.502	0.443	0.506	0.505
dhyc	0.052	0.241	−0.020		0.244	0.233	0.325	0.229	0.225	0.209	0.283	0.209	0.212
occfn	0.008	0.281	0.401	0.240		0.259	0.264	0.277	0.274	0.228	0.246	0.248	0.254
fnc	−0.016	0.034	0.270	0.204	0.179		0.274	0.241	0.247	0.233	0.324	0.228	0.239
asos	0.295	0.427	0.623	0.044	0.525	0.412		0.375	0.354	0.337	0.325	0.326	0.324
zffn	0.183	0.131	0.272	−0.022	−0.101	0.199	−0.192		0.238	0.192	0.312	0.219	0.228
iof	−0.313	−0.307	−0.269	−0.024	0.100	0.040	−0.053	0.254		0.232	0.297	0.202	0.225
zff	−0.090	0.126	0.100	−0.178	−0.425	−0.259	−0.280	0.494	0.0119		0.289	0.200	0.215
ios	0.138	0.274	0.505	0.098	0.463	−0.263	0.401	−0.162	−0.096	−0.093		0.263	0.279
lbpm	−0.166	0.044	0.036	−0.034	−0.215	0.255	−0.232	0.097	0.428	0.323	0.103		0.203
lbpl	−0.066	0.217	0.047	−0.034	−0.027	0.009	−0.012	−0.070	−0.152	0.067	0.083	0.170	

Table A4 Nonmetric correlation matrix using within-individual variance data

	fta	epi	ast	dhyc	occfn	fnc	asos	zffn	iof	zff	ios	lbpm	lbpl
fta		0.381	0.370	0.454	0.433	0.427	0.413	0.435	0.451	0.435	0.417	0.427	0.452
epi	0.595		0.424	0.402	0.374	0.428	0.449	0.430	0.407	0.416	0.384	0.367	0.435
ast	0.628	0.569		0.420	0.411	0.424	0.393	0.371	0.419	0.434	0.436	0.432	0.397
dhyc	0.204	-0.066	0.084		0.266	0.255	0.328	0.243	0.231	0.249	0.304	0.270	0.209
occfn	0.377	0.424	0.300	0.098		0.307	0.326	0.299	0.265	0.290	0.346	0.334	0.283
fnc	0.407	0.180	0.203	-0.046	0.099		0.323	0.339	0.276	0.307	0.344	0.310	0.281
asos	0.478	0.311	0.296	-0.129	0.264	0.277		0.364	0.264	0.372	0.353	0.376	0.337
zffn	0.363	0.128	0.453	0.168	0.024	-0.132	-0.056		0.275	0.290	0.338	0.331	0.270
iof	0.234	0.060	0.120	0.204	0.172	-0.016	0.459	-0.082		0.273	0.269	0.268	0.248
zff	0.363	0.122	0.157	0.265	0.177	0.077	-0.154	0.152	0.042		0.336	0.311	0.258
ios	0.457	0.387	0.279	-0.084	-0.073	0.083	0.274	0.015	0.122	0.015		0.371	0.294
lbpm	0.407	0.464	0.208	0.082	-0.168	0.151	0.016	0.067	-0.024	0.073	-0.153		0.285
lbpl	0.224	-0.028	0.092	**0.422**	-0.204	-0.277	0.090	0.008	-0.056	0.244	-0.028	0.085	

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Chapter 4
Fragile Spines on Cayo Santiago: Bone Mineral Density, Trabecular Morphology, and the Potential for Exploring the Genetics of Osteoporosis in Rhesus Monkeys

Jean E. Turnquist, Antonietta M. Cerroni, Kate J. Faccia, Steven K. Boyd, and Benedikt Hallgrimsson

4.1 Introduction

4.1.1 The Definition and Diagnosis of Osteoporosis: Limitations of the Current Paradigm

Osteoporosis, a reduction in bone mass associated with an increased risk of fracture, is defined by the World Health Organization as a measurement of bone mineral density (BMD) that is greater than 2.5 standard deviations (SD) below the mean value of a young adult same-sex reference population. Established osteoporosis is defined as a BMD measurement that lies 2.5 SD below the young adult average,

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Fig. 4.1 Aged female rhesus monkey on Cayo Santiago, with Dowager's hump

in addition to the presence of one or more fragility fractures. A diagnosis of osteopenia, a milder form of this condition, is defined as a BMD measurement that is between 1 and 2.5 SD below the mean value of the reference population (Kanis 1994; Wasnich 1996; World Health Organization (W.H.O.) 1994). The standard definition of osteoporosis does not include a description of the microarchitecture of the trabecular component of bone, nor does it include the actual BMD as part of the diagnosis. Although osteoporosis affects both cortical and trabecular bone, the most obvious location in which to observe the result of decreased bone density is the trabecular bone of the vertebral body, where fracture results in vertebral collapse and the familiar kyphosis (Dowager's hump) that is associated with established osteoporosis. The condition observed in human patients is similar to its counterpart in rhesus monkeys as shown in Fig. 4.1, which illustrates Dowager's hump in an aged female rhesus monkey on Cayo Santiago.

The standard criterion for the presence of vertebral fracture is a decrease of at least 20% in vertebral height when compared with adjacent vertebrae (Genant et al. 1993). Riggs et al. (1991) reported that fractures occur in the human femur and spine when bone density falls below a critical threshold level, which is about 1 g/cm^2 for both sites, and the known risk factors for osteoporosis include age, gender, nutrition, positive family history, physical activity, and lifestyle (Riggs et al. 1991; Stini 1990; Wasnich 1996). In addition to these variables, the attainment of higher peak bone mineral density early in life may play a critical role in postmenopausal bone loss in women (Lin et al. 2003). A large, longitudinal population-based investigation of bone loss at the distal radius, distal tibia, and lumbar spine using quantitative computed tomography (QCT) (Riggs et al. 2008) found that substantial cortical bone loss begins in women during middle age, but does not begin in men until after the age of 75 years. However, significant trabecular bone loss begins in both *young adult* men and women at all three sites and continues throughout life, but accelerates
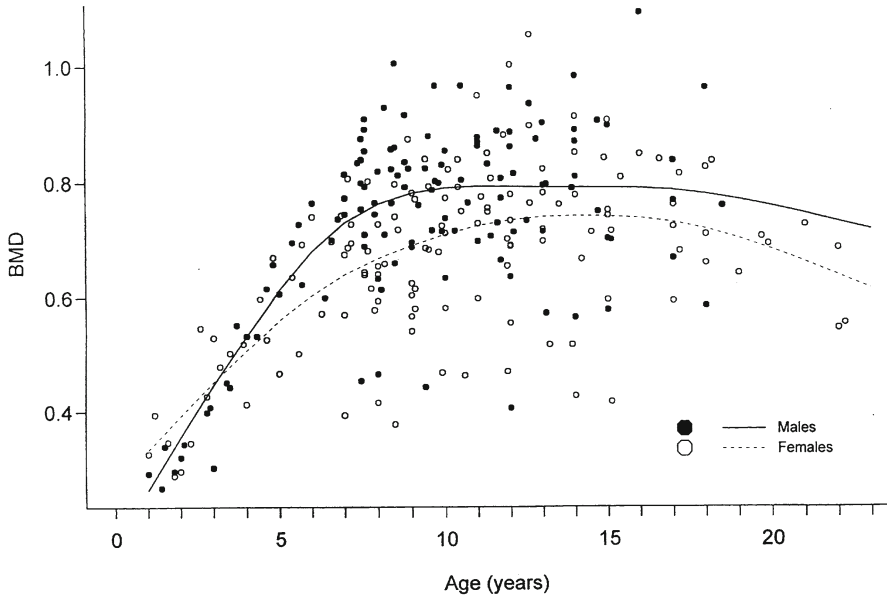
Fig. 4.2 Bone mineral density (BMD, g/cm^2) of the centrum by age (years), with smoothing spline fit, assessed by DEXA (dual energy X-ray absorptiometry, Lunar). $N=254$; *broken line* and *open symbol* = females. Female areal BMD peaks at ~9.5 years, remains constant until 17.2 years, and then declines. The difference in areal BMD between adult females and males is significant ($p<0.0001$). Originally published in Cerroni et al. 2000

in women during their perimenopausal years. The authors of this study conclude that the late onset of cortical bone loss is associated with sex hormone deficiency, but the phenomenon of trabecular bone loss observed in both sexes in the absence of hormone deficiency is unexplained, "…and indicates that current paradigms on the pathogenesis of osteoporosis are incomplete" (Riggs et al. 2008).

Osteoporosis is a well-documented naturally occurring disorder among rhesus monkeys (*Macaca mulatta*) on Cayo Santiago, Puerto Rico, where it disproportionately afflicts more females than males (Cerroni 2000; Cerroni et al. 2000, 2003) (Fig. 4.1). One of our previous studies has demonstrated that, like their human counterparts, female rhesus monkeys experience an age-related decline in bone mineral density and increased fracture risk. As reported in Cerroni et al. (2000), Fig. 4.2 shows the areal BMD of the vertebral body determined by DEXA (dual energy X-ray absorptiometry) of 254 individuals from Cayo Santiago in a plot of BMD (g/cm^2) by age (years), with smoothing spline fit.

The areal BMD of female rhesus monkeys peaks at around 9.5 years, remains constant until 17.2 years, and then subsequently declines. The difference in areal BMD between adult females and males is significant ($p<0.0001$) (Cerroni et al. 2000). We also noted that the areal BMD values of the osteoporotic and osteopenic monkeys with vertebral fractures overlapped with those of the nonfractured individuals with similar osteoporotic status, supporting the view that *low bone*

density may not always precede fracture (Cerroni 2000; Cerroni et al. 2000). It is well known that bone density measurements as determined by DEXA do not clearly discriminate patients with osteoporotic fractures from those who have not yet sustained a fracture. Previous studies on human subjects have noted a large overlap in BMD values of patients with spine, forearm, and hip fractures relative to controls (Heaney 1992, 1993; Johnston et al. 1996; Melton III et al. 1989) and suggested that the presence of structural defects in vertebral bone may explain why prior fracture appears to predict future fracture in a patient, even when bone density is relatively high (Heaney 1996). Low bone density is a significant, but not necessarily sufficient, cause of fracture. Areal bone mineral density accounts for 75–85% of the variance in the ultimate strength of bone tissue in humans (Melton III et al. 1988), and, therefore, these BMD values provide an indication of the strength of whole bones, but not a complete assessment of their structural integrity.

Although DEXA is the standard for defining osteoporosis, it only assesses bone quantity, not the *quality* of trabecular bone architecture, and thus does not access which, if any, morphological features are most likely to predict the susceptibility to fracture or nonfracture. In vertebral bones, both the microstructure of the trabecular bone of the centrum and its bone mineral density are important determinants of its strength and structural integrity and thus contribute to susceptibility to fracture or nonfracture. To further explore this issue in the hope of identifying which features of bone morphology might be better predictors of actual fracture risk and to later determine which characters may have potential for "building better bone," we examined a subset of the samples from the original DEXA study using micro-CT (micro-computed tomography) to analyze trabecular structure per se. Parameters of trabecular structure were examined in relation to volumetric BMD, and BMD data derived from DEXA were compared to volumetric BMD values from micro-CT in the same individuals.

In human females, pregnancy and lactation are known to impose stress on the maternal skeleton, which is the main repository of calcium in the body. There is, however, a complex hormonal regulatory mechanism which effectively counteracts bone loss by retaining excess calcium in the circulation (Kumar et al. 1980; Wieland et al. 1980). A retrospective approach uses "parity," a term that refers to the number of offspring born to a female, to study the long-term effects of reproductive history on bone mineral density in females. We employed this approach in one of our previous cross-sectional studies of the relationship between parity and BMD in rhesus monkeys from Cayo Santiago (Cerroni et al. 2003), and this subject is also re-visited in our current investigation using BMD data derived from micro-CT.

4.1.2 Hypotheses Tested in Our Current Research

The hypotheses addressed in our current research (Turnquist et al. 2007, 2009) are as follows: (1) areal BMD as measured by DEXA (g/cm²) is highly correlated with

the micro-CT volumetric BMD (mg/cm^3 HA), the closest equivalent to the areal BMD parameter; (2) trabecular structure as reflected in number of trabeculae/unit volume is highly correlated with volumetric BMD (mg/cm^3 HA); (3) trabecular structure as reflected by trabecular thickness is highly correlated with volumetric BMD (mg/cm^3 HA); and (4) bone architecture is a better predictor of fractures elsewhere in the vertebral column than is trabecular structure or volumetric BMD (mg/cm^3 HA).

4.2   Materials and Methods: Description of Our Research Methods in Past and Current Studies

4.2.1   Micro-CT Technology and Method

Micro-computed tomography (micro-CT) measurements of the vertebrae (Fig. 4.3) were obtained, providing high-resolution isotropic resolutions, at 55 kVp, 108 μA (vivaCT40, Scanco Medical, Bassersdorf, Switzerland).

The scanned images were digitally reconstructed, and the data were subsequently evaluated to determine morphological parameters related to bone architecture (IPL v.5.01). Output of a typical scan includes a three-dimensional reconstruction in addition to the raw data (Fig. 4.3). Figure 4.4 depicts various micro-CT reconstructions of a vertebra: 3D whole bone, sagittal section, mid-coronal section, mid-transverse section, and the core of the trabecular bone. The three-dimensional core of the trabecular bone of the vertebral body was utilized in the analyses.

Based on potential relevance to bone strength, the nine variables analyzed for each specimen included: a volumetric BMD variable (mg/cm^3 HA), the closest equivalent to areal BMD from DEXA; BV/TV (bone volume/total bone tissue); three parameters that describe trabecular structure and four variables that describe bone architecture (Table 4.1). These variables have also been investigated in other studies (Hulme et al. 2007; Sran et al. 2007).

Micro-CT is a noninvasive technology that provides a three-dimensional approach for assessing BMD. In contrast to BMD estimates using DEXA, micro-CT-based estimates take bone architecture into account and allow separate assessments of architectural parameters and density. One micro-CT variable, described as mg/cm^3 HA, is the closest equivalent to the areal BMD parameter derived from DEXA. Our current research explores which aspects of trabecular bone architecture most highly correlate with BMD, and more importantly, which more accurately predict potential fracture risk. The focus of the current analysis is on variables which are most relevant to the hypothesis that specific architectural features of the trabecular bone are more highly correlated with fracture risk than BMD alone (Turnquist et al. 2007, 2009).

Fig. 4.3 Example of the results of a typical micro-CT scan. The entire bone is scanned and a 3D reconstruction of images is created and displayed along with the raw data for each variable
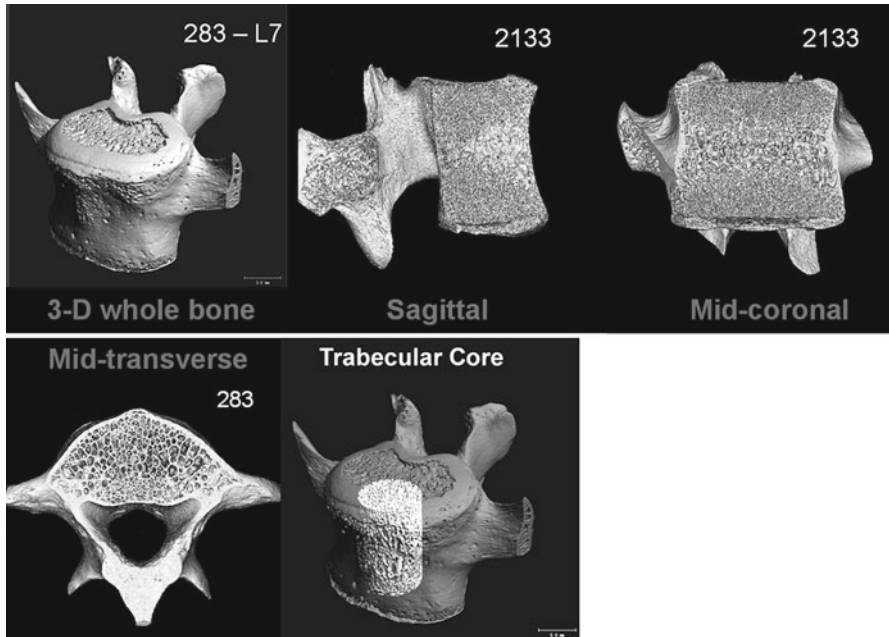
Fig. 4.4 Micro-CT reconstructions of a vertebra: 3D whole bone, sagittal section, mid-coronal section, mid-transverse section, and the core of the trabecular bone

Table 4.1 Micro-CT variables of interest

Micro-CT variable	Measurement	Definition
BMD (volumetric)	mg/cm^3 HA	Closest equivalent to areal BMD (bone mineral density)
BV/TV	Percent	Bone volume/total bone tissue
Trabecular structure		
Tb.N	per mm^3	Number of trabeculae per mm
Tb.Th	mm	Mean trabecular thickness
Tb.Sp	mm	Mean trabecular separation
Bone architecture		
Conn.D	per mm^3	Connectivity density of the bone
SMI	0 for plate-like, 3 for rod-like	Structural model index – proportion of rods and plates
BS/BV	per mm^3	Bone surface to volume ratio
DA	1 = isotropic, >1 is anisotropic	Degree of anisotropy – directionality of bone architecture; i.e., preferential alignment of trabeculae along a directional axis

Table 4.2 DEXA variables

DEXA variable	Measurement	Definition
BMC	grams	Bone mineral content (hydroxyapatite)
Projectional area	cm^2	Areal region of interest – entire vertebral body, in cranio-caudal projection, following outline of endplate
BMD (areal)	grams/cm^2	Bone mineral density: BMD = BMC/ projectional area
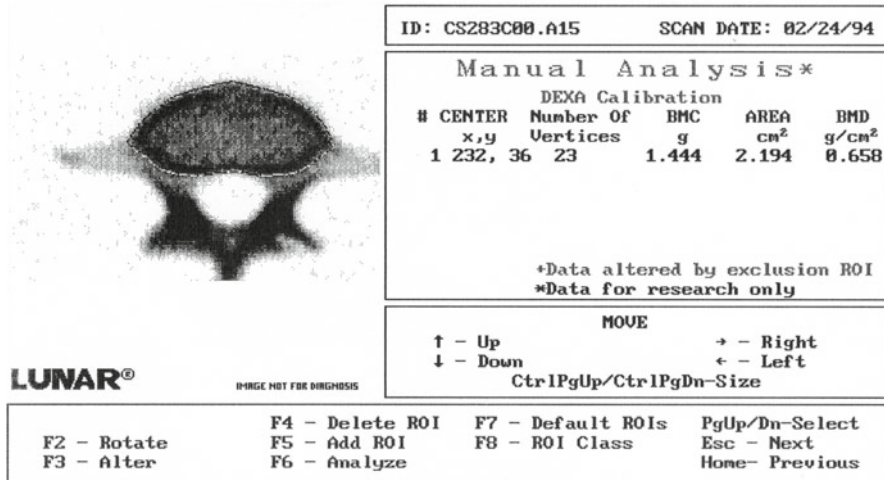
Fig. 4.5 Typical DEXA scan of a vertebra, showing raw data and BMD results

4.2.2 The DEXA Technique

DEXA also provides a noninvasive method for assessing bone mineral density, but the result is not a true volumetric value. The densitometer measures the quantity of hydroxyapatite in bone, as bone mineral content (BMC) in grams, and calculates the areal bone mineral density (BMD, g/cm^2), expressed as grams of mineral per unit area scanned. Areal BMD, the variable of interest in this research, was determined as described in Table 4.2 using macerated bone and includes only the vertebral body, assessed in cranio-caudal projection, following the outline of the endplate. BMD is the BMC normalized for bone size, thus providing a degree of standardization for differences in bone size among individuals. In a previous cross-sectional study, DEXA measurements of the same vertebrae (Fig. 4.5) were obtained (DPX-L Lunar Bone Densitometer) at high resolution (76 kVp, 150 μA, 1/64 sample interval, fine collimation 0.84 mm) and analyzed with Lunar DPX-L X-ray Bone Densitometer Small Animal software version 1.0c, 1992 (Cerroni et al. 2000, 2003).

4.2.3   The Study Population, the Sample, and Data Analysis

The sample in our cross-sectional micro-CT study included the macerated last lumbar vertebral body (mostly L7, and two L6) from 36 female free-ranging rhesus macaques ranging in age from 5.4 to 23.7 years from the Cayo Santiago colony at the Caribbean Primate Research Center (CPRC) in Puerto Rico. These bones are a subset of the sample from the original cross-sectional DEXA study reported in Cerroni et al. (2000, 2003) and consist of intact specimens from the CPRC Museum (Laboratory of Primate Morphology and Genetics). Data on each individual include: matrilineal affiliations and parity, as well as sex and exact age at death (Turnquist et al. 2007, 2009). Bone mineral density measurements determined by DEXA are available for each individual in the sample (Cerroni et al. 2000, 2003). The presence of vertebral fractures elsewhere in the spine has been documented previously, as well as the presence of other conditions such as vertebral osteophytosis and vertebral osteoarthritis (Cerroni 2000; Cerroni et al. 2000, 2003). The lumbar vertebrae included in this sample are normal in all respects, but four of the females exhibit fractures in other areas of the spine.

Female rhesus monkeys on the island of Cayo Santiago have a seasonal reproductive cycle. They attain sexual maturity at 3 years of age, usually produce their first offspring in their fourth year of life, and continue to reproduce until the end of their lives, although aged female rhesus monkeys tend to experience a longer birth spacing and the viability of their neonates is reduced (Koford 1965; Rawlins et al. 1984). Hoffman et al. (2010) found that although these monkeys have the physical and physiological capacity to conceive and give birth virtually until the end of their lives, they are not able to sustain lactation, particularly during the last 5–10 years of life, and consequently infant survival rates decline steadily during this period (Hoffman et al. 2010). Thus, age adjustment with respect to age at menarche and years since menopause, a necessary requirement for studies on human subjects, is not an issue for this investigation of the impact of parity on BMD. Another advantage of using these monkeys as study subjects is the uniformity of environment and similar rearing conditions experienced by all members of the colony. The majority of the monkeys on the island live to advanced age and expire from natural causes, including the specimens in this cross-sectional study and our original investigation. The matrilines of all members of the colony can be traced back to 1956, and paternity has been determined for individuals born since 1990. Thus, genetic studies based on this population are greatly facilitated by this information, which provides a basis for future investigations (Arnemann et al. 1989; Nurnberg et al. 1998; Rawlins and Kessler 1986; Rawlins et al. 1984; Turnquist and Hong 1989).

Our study utilized multivariate statistical analysis, which was performed with SPSS and Excel programs, and includes Regression, ANOVA (Analysis of Variance), Pearson's *r*, and principal components analysis (PCA) (Turnquist et al. 2007, 2009).

4.3 Current Research: Results

4.3.1 Summary of the Results of Our Current Research

A comparison between the two methods, micro-CT and DEXA, reveals that areal BMD (g/cm^2) measured by DEXA is significantly correlated ($r=0.80$) with the micro-CT volumetric value (mg/cm^3). Table 4.3 summarizes the results of our current study. Multivariate analysis (alpha=0.05) of micro-CT trabecular structure and architecture reveals that the micro-CT BMD variable (volumetric BMD, mg/cm^3 HA) that is most similar to DEXA BMD (areal BMD) is *most highly correlated* with *trabecular thickness* ($r=0.94$) and *bone volume ratio* ($r=0.99$). Volumetric BMD as assessed by micro-CT shows high positive correlation with trabecular thickness, bone volume ratio, more plates than rods, and less bone surface area per bone volume. However, the correlation between volumetric BMD and the bone architectural elements of connectivity, bone surface ratio, and number of trabeculae is not significant. Age, connectivity, directionality of bone architecture, and trabecular number and separation are not strongly correlated with bone density, although the latter two are correlated with each other (Turnquist et al. 2007, 2009).

Micro-CT reconstructions of 3D whole bones, 3D cores, and 2D mid-transverse slices of the seventh lumbar vertebrae of two females whose BMD values lie at opposite ends of the distribution are shown in Fig. 4.6. The top row of images is from the individual with the *highest* BMD value as assessed by both DEXA (1.16 g/cm^2) and micro-CT (257.66 mg/cm^3 HA). The bottom row of images is from the individual with the *lowest* areal BMD (0.38 g/cm^2) and the *6th lowest* volumetric BMD

Table 4.3 Summary of results

1. Micro-CT variable, volumetric BMD (mg/cm^3 HA), is most similar to areal BMD (by DEXA, g/cm^2) ($r=0.80$, $p<0.001$), and shows *high positive correlation* with
   - Trabecular thickness
   - Bone volume ratio
   - More plates than rods
   - Less bone surface area per bone volume
2. Multivariate analysis (alpha=0.05) of micro-CT trabecular structure and architecture reveals volumetric BMD (mg/cm^3 HA) is most *highly correlated* with
   - Trabecular thickness ($r=0.94$)
   - Bone volume ratio ($r=0.99$)
3. Correlation between volumetric BMD (mg/cm^3 HA) and these bone architectural elements is *not significant*
   - Connectivity
   - Bone surface ratio
   - Number of trabeculae
4. Age, connectivity, directionality of bone architecture, trabecular number, and separation are *not strongly correlated* with volumetric BMD
5. After controlling for age, there is a *positive association* between parity and volumetric BMD ($r_p=0.42$, df=33, $p<0.01$)
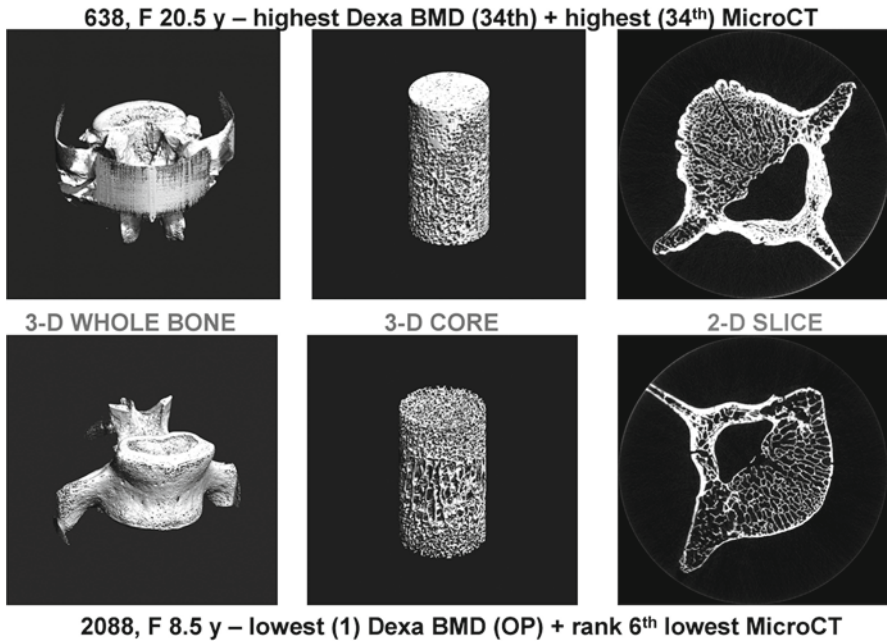
Fig. 4.6 Micro-CT reconstructions (3D whole bone, 3D core, and 2D mid-transverse slice) of the seventh lumbar vertebrae of two female rhesus monkeys with BMD values at opposite ends of the distribution. *Top row*: 20.5-year-old female (#638) with the highest BMD as assessed by both micro-CT (257.66 mg/cm^3 HA) and DEXA (1.16 g/cm^2). *Bottom row*: 8.5-year-old female (#2088) with the lowest areal BMD (0.38 g/cm^2) and the sixth lowest volumetric BMD (81.78 mg/cm^3 HA). Note the greater fenestration of trabecular bone in #2088. These individuals demonstrate that low BMD and osteopenia/osteoporosis are not restricted to aged cohorts in this colony

(81.78 mg/cm^3 HA) in the sample. It is interesting to note that the individual with high BMD is 20.5 years old (#638), while the individual with low BMD is only 8.5 years old (#2088).

4.3.2   The Role of Trabecular Thickness

Our current research has highlighted the importance of one variable of vertebral bone microstructure – trabecular thickness. The micro-CT variable mean trabecular thickness is not strongly associated with age in this sample of 36 individuals. Trabecular thickness, however, is highly correlated with volumetric BMD (g/cm^3 HA), $r = 0.94$ (Turnquist et al. 2007, 2009). Thus, there is a significant increase in bone density in the vertebrae as mean trabecular thickness increases. Conversely, bone loss will likely be reflected in the *thinning of trabeculae*, not in the loss of struts or their connectivity as evidenced by the lack of strong correlation between

these variables and volumetric BMD as assessed by micro-CT. With continued thinning of trabecular struts, structural failure will eventually occur as the weakest trabecular struts fail first. The severity of structural collapse may depend on local factors, such as position in the vertebral column, and associated stresses.

4.3.3 Predictors of Vertebral Fracture

This research has also identified certain potential predictors of vertebral fracture (Turnquist et al. 2007, 2009). Multivariate analysis (principal components) suggests that there is no correlation between the micro-CT variables related to bone architecture assessed for the last lumbar vertebra and the presence of fractures in vertebrae in other regions of the spine. Thus, bone architecture is *not* a better predictor of fragility fractures elsewhere in the spine than is trabecular structure or volumetric BMD. However, due to the small sample size in this analysis, these results should be interpreted with caution and verified in a larger study. Figure 4.7
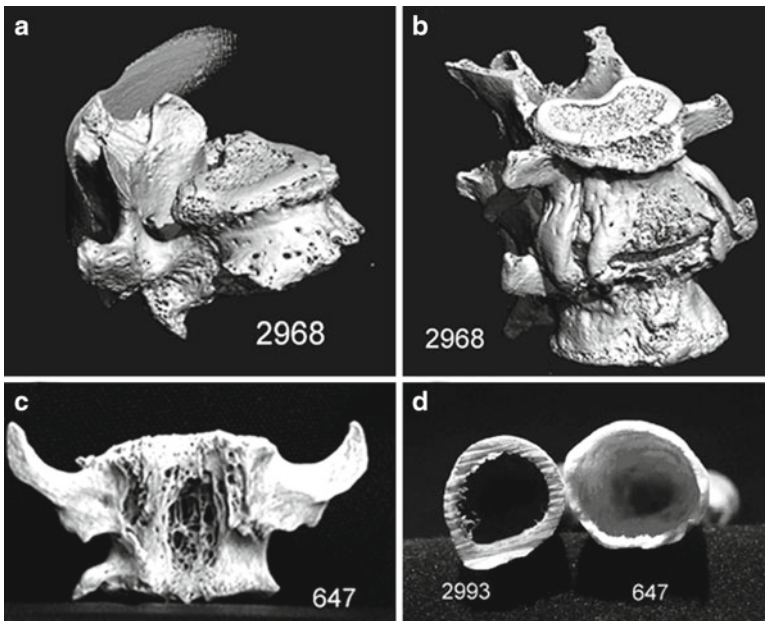
Fig. 4.7 Photographs of significant wedge fractures in the ninth thoracic (T9) vertebra (**a**), and in the second and third lumbar (L2–L3) vertebrae, with subsequent fusion (**b**), in a 22-year-old female (#2968). (**c**) A dorsal perforation in an osteoporotic lumbar vertebra from a different individual (#647) revealing the fenestrated trabecular structure. (**d**) Example of cortical thinning in a femur from the same osteoporotic individual (#647), pictured on the *right*; on the *left*, a normal femur (#2993)

shows examples of significant wedge fractures in the ninth thoracic (T9) (Fig. 4.7a) and the second and third lumbar (L2-3) (Fig. 4.7b) vertebrae, with subsequent fusion, in a 22-year-old female (#2968) whose appearance in life would have been similar to that seen in Fig. 4.1. Data on bone architecture of L7 in this individual did not predict the presence of these fractures. A dorsal perforation in a sixth lumbar vertebra from a different osteoporotic individual (#647) reveals its fenestrated trabecular structure, thus providing an actual anatomical image that corresponds to the digital micro-CT reconstructions (Fig. 4.7c). A photograph of a sectioned femur from the same osteoporotic individual (Fig. 4.7d, #647) depicts concurrent pronounced thinning of cortical bone; a normal femur from a different individual is pictured on the left (#2993).

4.3.4   Comparing Micro-CT and DEXA

Although areal BMD (g/cm^2) measured by DEXA is significantly correlated ($r = 0.80$) with the micro-CT volumetric value (mg/cm^3), neither reveals significant differences between last vertebrae of individuals with or without fractures elsewhere in the vertebral column (Turnquist et al. 2007, 2009). Bone morphology is the primary determinant of variation in bone density as shown by the high correlation between principal component 1 (PC1) and bone density as measured by either micro-CT ($r = -0.96$, df $= 35$, $p < 0.01$) or DEXA ($r = -0.82$, df $= 35$, $p < 0.01$). The first PC is loaded most highly by trabecular thickness, structural model index, bone volume fraction, and bone surface to volume ratio. These parameters all correlate highly (>0.9) with PC1 and indicate that as volumetric bone density changes, bone microarchitecture also changes. As volumetric BMD decreases, the change in bone microarchitecture involves a decrease in bone volume fraction, thinning of the trabecular struts, an increase in the ratio of bone surface to volume, and a more rod-like architecture. In principal-components analysis of morphology, the results of micro-CT are more tightly clustered than those of DEXA indicating a better predictive ability using micro-CT, since as bone density decreases the probability of structural failure tends to increase (Turnquist et al. 2007, 2009).

4.3.5   The Impact of Parity

An earlier study of this colony has shown that parity and age are closely associated variables ($r = 0.84$) (Cerroni et al. 2003). A plot of parity versus age at death in the sample, with the line describing average parity across age, shows a significant positive correlation between parity and age, and, as expected, parity generally increases with age beginning at 5 years of age (Fig. 4.8a). After controlling for age, there is a positive association between parity and volumetric bone density ($r_p = 0.42$, df $= 33$, $p < 0.01$),
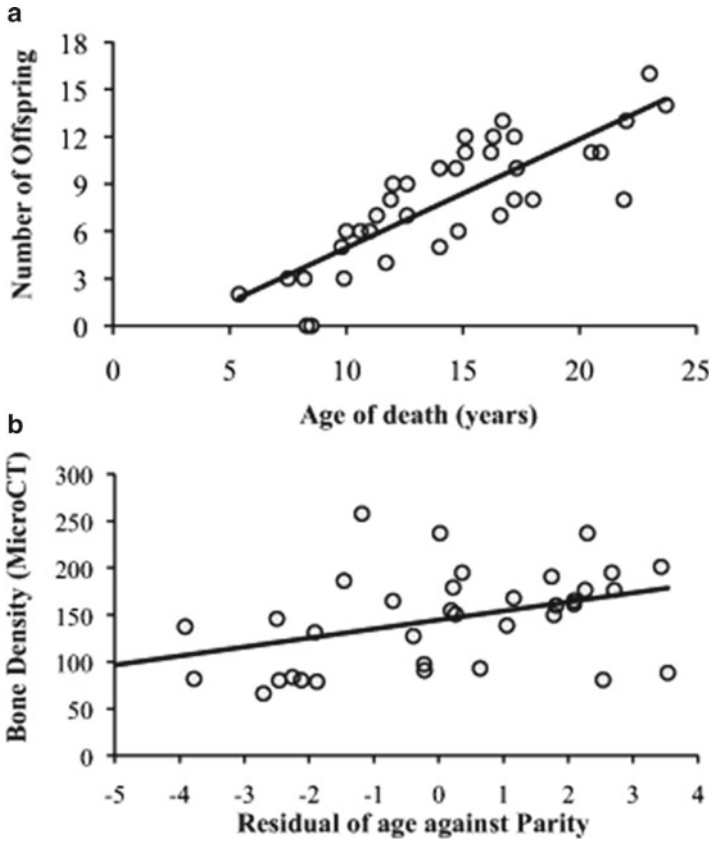
Fig. 4.8 Impact of parity (number of offspring) on volumetric BMD as assessed by micro-CT. (**a**) Line fit plot of parity versus age at death (years). Line describes average parity across age. There is a significant positive correlation between parity and age beginning at 5 years. (**b**) Line fit plot of volumetric BMD versus residual of age against parity. After controlling for age, there is a positive association between parity and volumetric bone density

which reveals that bone density increases steadily as parity increases (Fig. 4.8b). Thus, these analyses suggest that measurements of bone density are enhanced for female monkeys with more offspring. Furthermore, the protective effect of parity appears to be a specific effect on trabecular thickness in vertebral bones. Trabecular thickness shows a positive correlation with parity after controlling for age ($r_p=0.42$, df$=33$, $p<0.05$).

Although our study demonstrates the lack of importance of age and the significant impact of parity on bone morphology, particularly trabecular thickness, the strength of these interesting findings may, at least in part, reflect the relatively small sample size ($N=36$). Nevertheless, they do suggest some interesting avenues to consider in a larger study.

4.4   Discussion

4.4.1   Placing Our Current Research Results in the Context of the Literature

The rhesus macaques of Cayo Santiago spontaneously develop osteoporosis in a free-ranging environment making them an excellent animal model for the study of vertebral microstructure and osteopenia/osteoporosis. In humans, osteoporotic fractures are generally more common in the spine. The eighth thoracic to the third lumbar vertebrae are the most susceptible to fragility fractures, and advanced cases of osteoporosis may culminate in dorsal kyphosis of the spine. Our earlier study (Cerroni et al. 2000) notes that the lower thoracic and lumbar vertebrae of rhesus monkeys are also most susceptible to fragility fractures, and in aged monkeys, advanced osteoporosis leads to dorsal kyphosis of the spine, as illustrated in Fig. 4.1. Complete compression fracture is a common form of vertebral fracture in humans affected with osteoporosis where the pattern of vertebral fracture is dictated by the effects of vertical loading on the spine, coupled with the force of gravity. Since the line of gravity is anterior to the thoracic vertebrae, but passes *through* the lumbar vertebrae, fractures in human thoracic vertebrae tend to be wedge-shaped anteriorly, while fractures in the lumbar spine tend to be biconcave (Bullough and Boachie-Adjei 1988). It is noteworthy that complete compression fractures have not been observed in the spines of the osteoporotic macaques of Cayo Santiago; only anterior wedging of the centrum has been detected. A study of the Hamann-Todd collection (Mensforth and Latimer 1989) reported no statistically significant difference in the frequency of vertebral compression fractures between the sexes in humans. This contrasts with our previous study in rhesus monkeys that identified more osteopenic/osteoporotic females than males (21:16) but the difference in frequency is also not significant (Cerroni et al. 2000).

Although cortical bone has also been implicated in vertebral compression fracture, studies of osteoporosis have focused primarily on the role of trabecular bone in the collapse of the vertebral body. A recent study of regional differences in morphological parameters found that bone volume, trabecular thickness, and trabecular number correlate with sites of vertebral fracture (Sran et al. 2007). Another study on regional differences within human lumbar vertebral bodies, using classic histomorphometric methods, found that trabecular bone volume, trabecular number, and connectivity density decreased significantly faster with age compared with other parameters (Thomsen et al. 2002b). In contrast, our study found that volumetric BMD is not strongly correlated with trabecular number or connectivity. A descriptive study of human vertebral trabecular bone, using scanning electron microscopy (SEM), found that bone remodeling causes an age-related loss of connectivity in the trabecular network, describing a process whereby thinned, disconnected horizontal trabeculae are resorbed while vertical trabeculae frequently show microcallus formation in samples from elderly individuals (Mosekilde 1990). In their analysis of

trabecular properties associated with fragility fractures, Kreider and Goldstein (2009) suggested that what differentiates a person in terms of risk for failure is his or her propensity to remodel or adapt to habitual damaging or nondamaging loads (Kreider and Goldstein 2009). An in vivo assessment of bone microarchitecture of the distal radius and tibia by high-resolution peripheral QCT (Boutroy et al. 2005) found that in osteopenic women with similar spine and hip BMD, the fractured osteopenic women exhibited significantly lower trabecular density and greater heterogeneous trabecular distribution at the distal radius compared with unfractured osteopenic women. Compared with healthy premenopausal women, the postmenopausal osteoporotic and osteopenic group showed significantly lower density and trabecular number and decreased cortical thickness at both long bone sites (Boutroy et al. 2005). A study by Cooper et al. (2003) of the microarchitecture of cortical bone using micro-CT has identified various parameters associated with Haversian canals that may be useful for investigating the mechanical properties of long bones and a variable that quantifies connectivity between the canals that may permit the assessment of cumulative change related to bone remodeling (Cooper et al. 2003). A study by Block et al. (1989) provides normative data on spinal trabecular bone density in 538 healthy women ranging in age from 20 to 80 years using QCT and notes that significant losses in BMD correspond with the time of menopause and continue into old age (Block et al. 1989). However, as mentioned previously, Riggs et al. (2008) suggested that the late onset of cortical bone loss in humans is associated with sex hormone deficiency, but the phenomenon of trabecular bone loss that occurs in both sexes *in the absence of hormone deficiency* is currently unexplained by existing paradigms (Riggs et al. 2008).

Our current investigation of rhesus monkeys examines the relationship between trabecular patterns and architecture as visualized by micro-CT and BMD results obtained by DEXA, the clinical standard for diagnosis of osteoporosis, and demonstrates which structural components most closely predict BMD and indicate potential for structural failure. These results are consistent with those reported in humans, lending further support to the appropriateness of the rhesus macaque as an animal model for osteoporosis. Previous studies of bone architecture have shown that BMD is an imprecise estimate of the relative risk for vertebral fracture. Trabecular architecture, particularly the preferential thinning of transverse trabeculae and increased anisotropy, has been implicated but a satisfactory "fracture risk index" has yet to be developed (McDonnell et al. 2007). An additional compounding factor is that recent reports have shown that although pharmacological treatment for osteoporosis increases BMD, this is *not* necessarily predictive of decreased fracture risk (Judex et al. 2003; Watts et al. 2004). A recent review article notes that, despite its limitations, the monkey OVX (ovariectomy) model is one of the most important large animal models in osteoporosis research and drug development (Smith et al. 2009), but in vivo fracture prediction and prevention remain elusive. The urgency of these issues is further highlighted by a recent study that documented a significant increase in the incidence of spinal, rib, hip, radial, ulnar, and pelvic fractures among perimenopausal and postmenopausal American women over a 3-year period following the publication of the results of

the Women's Health Initiative and Heart and Estrogen/Progestin Replacement Study II, a trend that is associated with a decline in the use of hormone therapy and an increase in the use of other bone-modifying agents (Islam et al. 2009). The identification of risk factors for low bone mineral density, osteoporosis, and fractures in premenopausal women is reviewed in a recent article (Vondracek et al. 2009), as well as the importance of examining the role of bone quality in fracture prediction. In view of these issues, we suggest that the female rhesus monkeys of Cayo Santiago present an excellent alternative nonhuman primate model for the study of bone mineral density, and the etiology of age-related bone loss and osteoporosis in a population where osteoporosis occurs naturally without the imposed limitations of the OVX model.

The multivariate analyses of our current study (Turnquist et al. 2007, 2009) suggest that bone architecture is *not* a better predictor of fragility fractures elsewhere in the spine than is trabecular structure or volumetric BMD. The micro-CT variables related to trabecular structure include trabecular thickness, separation, and number. It is noteworthy that progression of trabecular bone failure appears to show a different pattern than that which is observed in the development of bone (Ryan and Krovitz 2006). In our study, trabecular thickness appears to be a more important variable in structural failure – not complexity of architecture or trabecular number. A vertebral bone with thinner trabeculae is expected to have a lower volumetric bone density and is more likely to experience structural failure at some point in the individual's life. Whether or not structural failure occurs may depend on other factors, such as the position of the bone in the vertebral column since intraskeletal variability in mass is tethered to a specific mechanical loading environment (Peck and Stout 2007).

In a quadrupedal animal such as the rhesus monkey, the apex of curvature of the spine is in the lower thoracic-upper lumbar region, which may experience different biomechanical stressors in comparison with other areas of the spine. A study of the biomechanics of the human spine (Ferguson and Steffen 2003) has found that in the vertebral body, individual trabeculae are oriented along the lines of principal forces and play a critical role in the transfer of compressive forces along the spine. Ferguson and Steffen (2003) also noted that age-related changes to the trabecular core of the vertebral body included trabecular thinning, loss of trabecular connectivity, and increased spacing between trabeculae. Thomsen et al. (2002a) reported that trabecular thickness of vertical trabeculae in human lumbar vertebrae is independent of age in all regions of the bone, while the thickness of horizontal trabeculae decreases significantly with age, and no significant gender-related differences were noted in their sample of 48 study subjects. They also noted that a biomechanical implication of their findings is that compressive bone strength in the horizontal and vertical direction must exhibit different age-related changes. One limitation of their study is that the classification of vertical versus horizontal trabeculae was based on the appearance of trabecular networks on thin histological sections, and thus, it is not apparent how well this represents the actual three-dimensional structure of trabecular bone (Thomsen et al. 2002a). In our recent study of rhesus monkey vertebrae, however, we found no significant correlation between bone density and trabecular

connectivity and trabecular number, but there is a very high positive correlation between BMD and trabecular thickness and bone volume ratio. In this model, trabecular thickness is the *primary* and *essentially the only* architectural determinant of volumetric bone mineral density (Turnquist et al. 2007, 2009). A study of postmenopausal osteoporotic women who were treated with parathyroid hormone (PTH 1–84) showed a 45–48% increase in trabecular bone volume (BV/TV) of the iliac crest relative to controls, as measured by micro-CT and histomorphometry, a result of higher trabecular number and thickness; in addition, a more plate-like architecture and higher trabecular connectivity were all consistent with lower vertebral fracture incidence (Recker et al. 2009). Although our study did not find a strong correlation between volumetric BMD and trabecular number or connectivity, we did find a high positive correlation with bone volume ratio, trabecular thickness, and a more plate-like architecture.

Placing the results from our recent study in the context of changes over the life cycle (Fig. 4.9) may lead to a better understanding of normal changes in trabecular bone over time and what processes lead to structural failure of vertebral bones. It is known that volumetric bone density increases during growth and development and declines with advanced age, and since trabecular thickness is highly correlated with bone density, it follows that it may also reveal a similar pattern with age but this has yet to be confirmed in a larger sample. Since volumetric BMD also shows a high positive correlation with bone volume ratio and more trabecular plates than rods, it would be interesting to follow these parameters over the life cycle in this population as well.

Furthermore, age-related loss of bone mineral density and thinning of the vertebral endplate, which is cortical bone, increases the risk of endplate fracture (Ferguson and Steffen 2003). This suggests that analysis of both trabecular and cortical bone in future studies might provide additional insight into susceptibility to, and location of, osteoporotic vertebral fractures (Oleksik et al. 2000; Ritzel et al. 1997). A recent study of elderly human subjects (Yang et al. 2009) found that osteoporosis is associated with expansion of the center of the intervertebral disk with corresponding collapse of the vertebral bodies, most likely the outcome of secondary changes to the vertebral endplate, but there is no relationship between osteoporosis and disk degeneration or preservation.

Life history parameters such as parity may also play a significant role with respect to the status of trabecular thickness in vertebral bones and relative fracture risk. After controlling for age, a significant positive association between parity and bone density as determined by micro-CT is demonstrated in our current study. Thus, bone density increases steadily as parity increases, and beginning at the age of sexual maturity, females experience an increase in their vertebral bone density as they have more offspring. This increase in bone density is likely accomplished by an enhancement in the thickness of individual trabeculae, as suggested by the high correlation between trabecular thickness and volumetric BMD. Our new analyses confirm the results of our previous DEXA study on 119 females from the same colony which also demonstrates that, after controlling for age, there is a significant increase in areal BMD with increasing parity (Cerroni et al. 2003). However, the previous DEXA study also
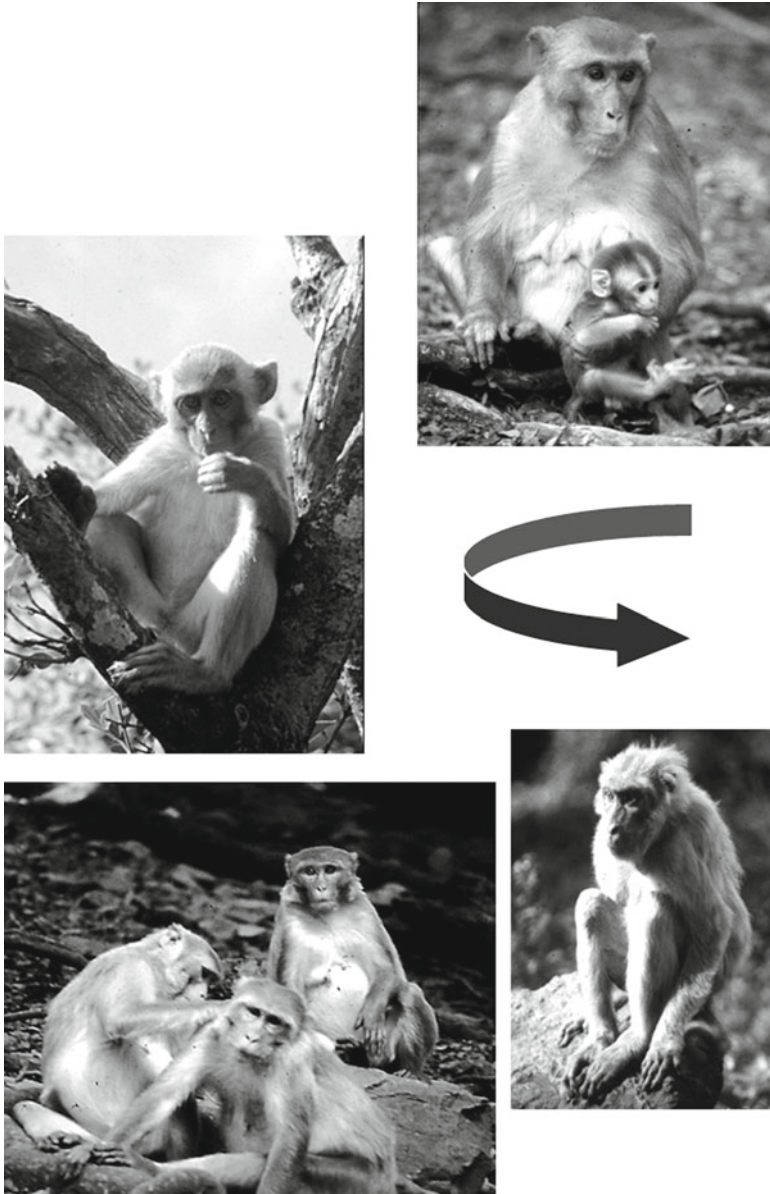
Fig. 4.9 Rhesus monkeys on Cayo Santiago at various stages of the life cycle, from infancy to old age exemplify bone mineral density, trabecular thickness, and structural failure of vertebral bone in the context of life history

reveals that there is a positive association only up to a parity of about seven offspring. While high parity initially has a positive effect on areal BMD, this effect disappears with parities greater than seven offspring ($p = 0.0006$). It is surmised that this initial positive effect of parity on areal BMD in rhesus monkeys was eventually over-whelmed by the aging process (Cerroni et al. 2003). Our current micro-CT analyses suggest that this eventual age-related decline in bone density is likely caused by the thinning of vertebral trabeculae, not by the loss of trabecular struts or their connectiv-ity. Our recent results also suggest that bone density measurements are enhanced for female rhesus monkeys with more offspring, and the protective effect of parity appears to be a specific effect on trabecular thickness in vertebral bones.

A number of studies on human subjects have also reported increased bone den-sity with parity in women (Aloia et al. 1983; Cure-Cure et al. 2002; Fox et al. 1993; Goldsmith and Johnston 1975; Grainge et al. 2001; Honkanen et al. 2000; Mariconda et al. 1997; Murphy et al. 1994; Sowers et al. 1991; Valenzuela et al. 1987). In their study of bone mineral density in women from an Old Order Amish community, a population characterized by a homogeneous lifestyle and high par-ity, Streeten et al. (2005) found that parity is strongly associated with BMD of the hip in women aged 50–59 years, even after adjusting for age and body mass index, but there is no significant association between these variables in the older age group, or in women younger than 50 years of age. Interestingly, the authors note that the benefit of high parity on BMD appeared to dissipate soon after the transi-tion to menopause in the older age group, and that the long-term effect of high parity on bone health is neither beneficial nor detrimental (Streeten et al. 2005). These data support our findings for rhesus monkeys reported in a previous paper (Cerroni et al. 2003). A cross-sectional study of postmenopausal Sri Lankan women, a population in a developing country, has shown that a history of multipar-ity or prolonged lactation has no detrimental effects on maternal BMD of the lum-bar spine and femoral neck (Lenora et al. 2009). Postmenopausal Saudi Arabian women with high parity (>6) show BMD values of the hip and lumbar spine that are significantly higher than those of their low-parity and nulliparous counterparts, even after prolonged periods of lactation, and the women with high parity were also assessed as less osteoporotic and at lower risk of fracture (Sadat-Ali et al. 2005). Women in Cambridge, U.K. also show a positive relationship between par-ity and BMD of the hip and lumbar spine, with an average 1% increase in BMD per live birth (Murphy et al. 1994). These reports lend support to the conclusions of our study.

4.4.2   Nonhuman Primate Models of Bone Density and Osteoporosis

Many nonprimate large animal models have been used in osteoporosis research (Reinwald and Burr 2008; Turner 2001), and are reviewed in Reinwald and Burr (2008), which outlines their limitations, and the lack of exact mimicry of the progression of bone loss and development of osteoporosis that occur in human

postmenopausal females. The nonhuman primate is the most relevant model for the study of human disease processes due to general similarities between human and primate subjects with regard to metabolism, physiology, and responses to therapeutic interventions (Archer 2004). The literature records a number of studies on nonhuman primates that demonstrate the relationship between experimentally induced menopause or hormone deficiency and bone density and osteoporosis (Brommage 2001; Jayo et al. 1990; Jerome et al. 1986, 1992, 1994; Longcope et al. 1989; Lundon et al. 1994, 1997; Lundon and Grynpas 1993). Cross-sectional and longitudinal studies of bone mass in female cynomolgus macaques have also been conducted (Jayo et al. 1994, 1991). A study that evaluated the BMD of the lumbar spine (L2–L4) and total body of live female cynomolgus monkeys reports that peak bone density in the lumbar spine occurs at around 9 years of age and that mature individuals older than 10.5 years experience bone loss through time (Jayo et al. 1994). The effects of age, sex, and heredity on bone mass have also been studied in pedigreed baboons (Kammerer et al. 1994, 1995; Mahaney et al. 1997), and in one study, an investigation of bone mass and density by radiographic morphometry of the left second metacarpal in pedigreed baboons reports that age-related changes are similar to those observed in humans (Kammerer et al. 1995). Older baboons also experience a marked reduction in spinal bone mineral density, and they exhibit dorsal kyphosis and fractures of the spine (Aufdemorte et al. 1993). Shively and Clarkson (2009) reviewed the unique value of macaque models for research involving the reproductive, central nervous, cardiovascular and musculoskeletal systems, the diseases of aging, as well as conditions such as obesity and diabetes. They also noted that in order to further the understanding of women's health, researchers need good primate models of natural menopause, hypertension, and colon and breast cancer (Shively and Clarkson 2009). We believe that the colony of rhesus monkeys on Cayo Santiago provides natural models of many age-related human conditions, including age-related bone loss, osteopenia, and osteoporosis.

4.4.3 The Rhesus Monkey Model of Bone Density and Osteoporosis

The rhesus monkey has been established as a model of human estrogen-depletion bone loss (Binkley et al. 1998; Colman et al. 1999). A few studies using the rhesus monkey OVX model have reported that certain drugs commonly used to treat osteoporosis in humans have interesting effects on trabecular architecture (Fox et al. 2007a, b, 2008). According to Fox and colleagues, treatment of skeletally mature OVX rhesus monkeys with parathyroid hormone (PTH) stimulates bone remodeling, which increases trabecular BMD, trabecular bone volume and number, and trabecular bone formation rate at the proximal femur, rendering it more fracture resistant (Fox et al. 2007b). Also, treatment of OVX rhesus monkeys with PTH increases bone formation, bone strength, bone volume and density, and improves trabecular architecture of the lumbar spine by increasing trabecular bone volume primarily via augmenting trabecular number, but the highest doses result in

excessive stimulation of bone remodeling, causing reduced trabecular thickness in the vertebral body by markedly increasing intra-trabecular tunneling (Fox et al. 2007a). Micro-CT scans of the tenth thoracic vertebrae reveal that trabecular bone volume and connectivity are higher in the treated monkeys compared to controls (Fox et al. 2008). The fact that trabecular thickness was significantly reduced by excessive amounts of parathyroid hormone in these studies is an intriguing result, demonstrating that this bone microstructural parameter responds to external stimuli and can be affected by altered levels of circulating hormones in females. Interestingly, a comparative study of the trabecular microarchitecture of thoracic vertebrae in hominoids, including humans, reports that trabecular thickness is positively associated with bone volume fraction, which is also correlated with structural model index and trabecular number and separation (Cotter et al. 2009).

Previous studies have examined the effects of reproductive parameters such as pregnancy, lactation, and parity on bone physiology and bone mass in the rhesus monkey as well as other species of nonhuman primates (Bowden et al. 1979; DeRousseau 1985; Grynpas et al. 1989; Hiyaoka et al. 1996; Jerome and Peterson 2001; Lees and Jerome 1998; Lees et al. 1998; Ott et al. 1999; Power et al. 1999; Sumner et al. 1989). Given the availability of detailed information on life history parameters, our current studies and a previous investigation (Cerroni et al. 2003) demonstrate that the female rhesus monkeys of Cayo Santiago provide a particularly good model of the effect of parity on the microstructure of vertebral trabecular bone and bone mineral density of the spine. Indeed, this colony of rhesus monkeys offers an excellent model of osteoporosis because the disorder occurs naturally in this free-ranging population without ovariectomy, and its manifestation is very similar to that which occurs in humans, exhibiting vertebral fractures, loss of trabeculae, and cortical bone thinning. It provides an ideal model of naturally occurring age-related bone loss in both adult female and male intact rhesus monkeys that survive to advanced age in a semi-natural, freeranging environment.

A longitudinal DEXA study of age-related bone loss in normal, intact male and premenopausal female rhesus monkeys reports an age-related decline in forearm BMD and total body BMC in both sexes, which suggests that the rhesus monkey is a good model for age-related changes in the human skeleton (Black et al. 2001). A study by Havill (2004) that characterizes normal age and sex variation in osteon remodeling in the femur of immature and adult rhesus monkeys also supports the use of this animal model for investigating bone turnover, and age-related changes and pathology in the human skeleton. Similar to humans, age and skeletal maturity are the two factors that contribute significantly to variation in osteon population density, activation frequency, and bone formation rate (Havill 2004). Noninvasive markers of bone metabolism in the rhesus monkey have been shown to be useful for measuring the effects of potential treatments for osteoporosis (Cahoon et al. 1996) and this study also notes an age-related decline in bone density among older animals. Using single photon absorptiometry, Pope et al. (1989) studied the effects of age and sex on bone density of the humerus and lumbar and caudal vertebrae in rhesus monkeys at the Yerkes Primate Center. Age and sex differences are reported among the rhesus monkeys in their study which included animals of all ages from

less than 1 year through geriatric. Their findings include an age-related decrease in bone density of lumbar vertebrae in both sexes and an age-related decline in the bone density of the humerus in females (Pope et al. 1989).

A cross-sectional DEXA study of bone density in 178 live female rhesus monkeys at the Wisconsin Regional Primate Research Center examined the effect of age on bone-area and body-weight adjusted bone mineral content of the distal radius, lumbar spine (L1–L4) and total body (Champ et al. 1996). Champ et al. (1996) reported that bone mass of the lumbar spine significantly increases with maturation up to 11 years of age, and then remains stable with advancing age. This reported age of peak bone mass is similar to our results for the Cayo Santiago rhesus monkey females, who attain peak bone mass in the spine at around 9.5 to 10 years of age. However, unlike our results for the Cayo Santiago female monkeys, the study by Champ et al. (1996) did not observe a decrease in bone mass of the lumbar spine with advancing age but noted that this may reflect artificially elevated BMC due to degenerative arthritis or other factors and thus cautioned that it may be difficult to model age-related bone loss. Our cross-sectional studies excluded lumbar vertebrae with extensive osteophytosis, and results indicate that both female and male free-ranging rhesus monkeys from the Cayo Santiago population provide good models for the study of osteoporosis and age-related changes in bone mineral density, and that DEXA of the lumbar vertebra is a reliable site of measurement provided all specimens with moderate to advanced vertebral osteophytosis and degenerative disk disease are excluded from the analysis. Furthermore, if an entire vertebra or a complete section of spine is to be scanned and analyzed, it is recommended that bones with osteoarthritis of the zygapophyseal joints also be excluded. The exclusion of individuals with vertebral osteophytosis, degenerative disk disease, and vertebral osteoarthritis from longitudinal and cross-sectional studies using live animals avoids the possible influence of mineralized evidence of pathological conditions on vertebral bone density readings (Cerroni 2000; Cerroni et al. 2000, 2003).

4.4.4   The Cayo Santiago Rhesus Monkey Model of Naturally Occurring Osteoporosis and Age-Related Bone Loss

An early study that used single photon absorptiometry (SPA), the precursor of DEXA, reports an age-related decrease in bone density in the radius and femur of rhesus monkeys from Cayo Santiago (Aguiló and Cabrera 1989). Other previous studies on Cayo Santiago macaques (Grynpas 1992; Grynpas et al. 1989, 1993) also demonstrate that osteoporosis is associated with age, that females are predilected, and that high parity is a protective factor. Using the skeletal collection associated with the colony of rhesus monkeys on Cayo Santiago, several of us were involved in a study that established a baseline of vertebral areal bone mineral density measurements in the rhesus monkey, and identified two distinctive patterns of bone mineral density of the lumbar spine, one for females and another for males (Cerroni 2000; Cerroni et al. 2000, 2003). The observed differences in areal BMD of the lumbar spine between

adult females and males are significant ($p < 0.0001$). In both sexes, there is little variation in areal BMD values among the young (age 1–7 years), but greater variability among older animals at every age. In the female rhesus monkeys, areal BMD increases with age to a peak of about 0.72 g/cm^2 around the age of 9.5 years, and remains constant until 17.2 years, after which there is a steady decline in areal BMD with advancing age. In contrast to the pattern in humans, the male rhesus monkeys attain a peak areal BMD of about 0.78 g/cm^2 at an *earlier* age than do females, at around 7 years of age, and between the ages of 7 and 18.5 years, there is no apparent effect of age on areal BMD. At every age after the age of sexual maturity, which occurs at 3 years of age, males have a higher areal BMD than do females. Male rhesus monkeys acquire bone mass at a faster rate than do females, attain a higher peak BMD, and reach this peak areal BMD at a younger age (Cerroni 2000; Cerroni et al. 2000). In this colony, both females and males attain mature linear adult morphology at 6.5 years of age. By this age, there is full epiphyseal closure in all long bones, and the dentition, with the possible exception of the third molar (M_3), is fully developed (Cheverud 1981; Turnquist and Kessler 1989). Thus, although growth of the body is complete in females by 6.5 years of age, full bone mineralization is not and the acquisition of bone mass continues until a peak areal BMD is attained by around 9.5 years. In contrast, males complete their growth at 6.5 years of age and peak areal BMD is attained only slightly later, by around 7 years of age. Both male and female osteopenic and osteoporotic monkeys were identified in the colony, at a combined frequency of 12.4% (37/298) (Cerroni 2000; Cerroni et al. 2000).

Evolution has endowed the female primate skeleton with specific mechanisms that balance the requirements of the developing fetus and neonate for calcium with the mother's need to maintain calcium homeostasis. The female rhesus macaques from Cayo Santiago exhibit a significant increase in bone mineral density of the spine with increasing parity, after controlling for age (Cerroni 2000; Cerroni et al. 2003; Turnquist et al. 2007, 2009), up to a parity of around seven offspring (Cerroni et al. 2003). Parity has an augmenting effect on bone mineral density, while age has a reducing effect, beginning several years after the attainment of peak BMD at around 9.5 years of age. Initially, parity appears to mitigate the effects of aging on BMD, but after a certain age, the positive effect of parity on BMD of the spine appears to be overwhelmed by the aging process. Previous work by some members of our group noted that mean BMD values of low-parity females are significantly lower than those of age-matched controls, and osteopenic and osteoporotic females are present in much higher frequency in the low-parity group (Cerroni 2000; Cerroni et al. 2003). These results suggest that there are interesting underlying mechanisms that should be explored in future research by examining the matrilineal affiliations of these osteoporotic, low-parity females.

4.4.5   Directions for Future Research

Bone mineral density is known to have a genetic component (Havill et al. 2005, 2007, 2010; Lipkin et al. 2001; Morrison et al. 1994; Salamone et al. 1996;
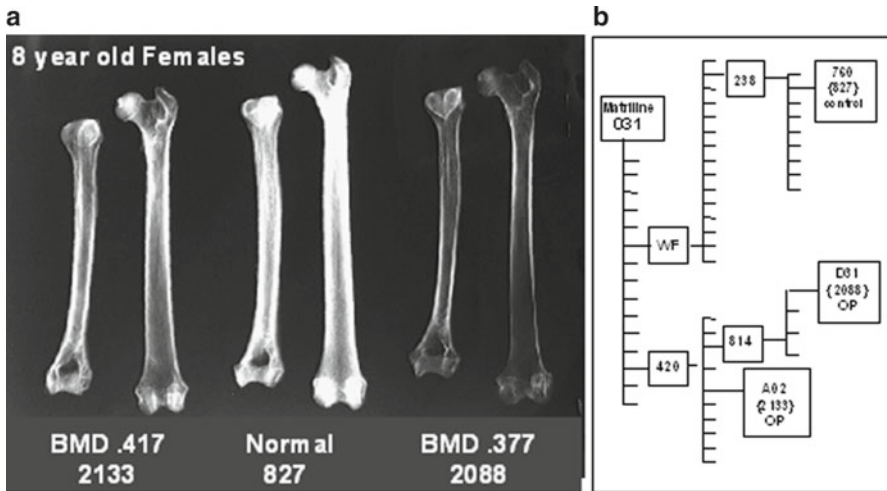
Fig. 4.10 Radiograph (**a**) shows the *left* femur and humerus of two osteoporotic females who exhibit very low bone density by both DEXA and micro-CT, but no fractures in the spine or long bones. Significant trabecular and cortical bone loss is evident. An age-matched control animal is imaged in the center. (**b**) Cayo Santiago matrilineage data show that these two osteoporotic females are in the same matriline and therefore genetically related. Radiograph originally published in: Cerroni et al. 2000

Uitterlinden et al. 1996; Wang et al. 2007), and strategies for using nonhuman primates in genetic research on complex multifactorial diseases such as osteoporosis are available in an extensive review paper (VandeBerg and Williams-Blangero 1996). Matrilineal affiliations of the rhesus monkeys on Cayo Santiago are known, and this unique database of information has been utilized, to great effect, in other studies (Berman 1986), as has the use of genetics using this colony (Kohn and Bledsoe 2011). DNA fingerprinting for maternity and paternity has also been conducted successfully in past studies (e.g., Arnemann et al. 1989; Berard 1989). The previous studies conducted by members of our team (Cerroni 2000; Cerroni et al. 2000) indicate that low bone mineral density and osteoporosis may be more prevalent in certain matrilines, suggesting an exciting opportunity to explore the genetics of the natural occurrence of this disorder in rhesus monkeys. The radiograph in Fig. 4.10a shows the left femur and humerus of two osteoporotic females who exhibit very low bone density, by both DEXA and micro-CT, but no fractures in the spine or long bones. An age-matched control animal is imaged in the center of the radiograph. Significant trabecular and cortical bone loss is evident in the osteoporotic females, and yet structural failure of bone did not occur in these individuals. According to the chart in Fig. 4.10b, the two osteoporotic females in this image are in the same matriline.

This indicates that it may be possible to trace the matrilineages of all the known osteoporotic females in the skeletal collection with the goal of identifying a possible genetic component that can be followed to their descendants in the living population. Micro-CT can provide a tool to help further delineate characteristics of

vertebral bone architecture associated with vulnerability to fragility fracture and potentially be integrated with molecular studies to provide a better understanding of the impact of heritability and genetics on this process. Common variants in multiple genetic loci have recently been associated with bone mineral density and fractures in humans (Hirschorn and Gennari 2008; Sigurdsson et al. 2008; Styrkarsdottir et al. 2008), suggesting that using the rhesus monkeys of Cayo Santiago to study the contribution of genetic factors to bone density may afford the significant advantage of being able to better control the lifestyle variables that are commonly found in similar studies on human subjects (Deng et al. 2000). For example, human studies often encounter challenges necessitating statistical adjustments for age and body weight, as well as other lifestyle variables, which can obscure any possible effect of parity on BMD (Lekamwasam et al. 2009).

4.5   Conclusions

Our recent and past research projects have demonstrated the utility of the Cayo Santiago rhesus monkey colony as an intact nonhuman primate model for naturally occurring age-related bone loss, bone mineral density, and osteoporosis. We have shown that bone mineral density as measured areally by DEXA (g/cm^2) is *highly correlated* with the micro-CT 3D measurement of bone density (mg/cm^3 HA). Multivariate analysis of micro-CT trabecular structure and architecture reveals that volumetric bone density (mg/cm^3 HA) is most *highly correlated* with trabecular thickness (Tb.Th) and bone volume ratio (BV/TV). Trabecular architecture as reflected in number of trabeculae/unit volume (Tb.N) and connectivity (Conn.D) are not highly correlated with volumetric BMD (mg/cm^3 HA). Bone architecture is not found to be a better predictor of fractures elsewhere in the vertebral column than is trabecular structure or volumetric BMD. Bone morphology is the primary determinant of variation in bone density as demonstrated by the high correlation between principal component 1 and bone density as measured by either DEXA or micro-CT.

These insights into trabecular structure and bone density suggest the potential for more accurate assessment of osteoporotic status, including relative fracture risk by focusing on morphological characteristics involved in vertebral structural failure. In future studies, a closer examination of the matrilineal affiliations of the osteoporotic individuals in the Cayo Santiago colony of rhesus monkeys may provide further insights into the role of genetics in bone density, metabolic bone disease, and fragility fracture.

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Chapter 5
Genetic and Social Group Influences on Postcranial Morphology in Rhesus Macaques of Cayo Santiago

Luci Ann P. Kohn and Zachary Bledsoe

5.1 Introduction

Recent studies have renewed discussions concerning the importance of quantitative genetic studies of natural populations for the understanding of evolutionary dynamics, including the effects of natural selection, migration, inbreeding depression, and genetic drift (Moore and Kukuk 2002; Kruuk 2004; Kruuk and Hill 2008; Pemberton 2008). Evolution requires genetic variation and covariation among traits, and natural selection on phenotypes (Lande 1979). Such studies require individual identification of relatively large numbers of individuals of known genetic relationship. While individuals of a single generation may be studied, such as siblings or half-siblings, inclusion of multiple generations and multiple types of relationships provides additional information. Population structure, mating patterns, and individual behaviors may significantly influence patterns of genetic variance and covariance and therefore the "raw material" of evolution. There are relatively few animal populations that have been studied in sufficient depth to provide data for quantitative genetic studies.

The rhesus macaque colony on Cayo Santiago has provided a unique opportunity to study the effects of social structure on genetic differentiation of social groups. The colony was founded in 1938 by C. R. Carpenter with 409 rhesus macaques imported from India (Rawlins 1989). Detailed life history data have been collected since 1956, including date of birth, gender, maturity status, group affiliation, matriline, and date and cause of death. Animals live in naturally formed social groups consisting of one to four matrilines. Each matriline includes an adult female, her adult female offspring, and their juvenile and infant offspring (Kessler and Berard 1989).

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Upon sexual maturity, males migrate from their natal social group to join other social groups. Several social groups have undergone lineal fission between matrilines (Missakian 1973; Chepko-Sade and Sade 1979; Sade et al. 1977), and the dates of fission and resulting group membership have been recorded. Skeletons of individuals from the island colony were collected after 1960 and are housed at the Caribbean Primate Research Center museum at the University of Puerto Rico (San Juan, Puerto Rico). With its known colony history, rich demographic and ethological records, and accompanying museum collection, the ongoing effects of microevolutionary processes within the free-ranging rhesus macaque colony can be observed.

Initial analyses of social structure on genetic differentiation on Cayo Santiago examined associations of blood group allele frequencies (Buettner-Janusch et al. 1974; Duggleby 1977, 1978; Chepko-Sade and Olivier 1978; Olivier et al. 1981), migration (Cheverud et al. 1978), nonrandom mating among lineages (McMillan and Duggleby 1981), and genetic drift (Melnick and Kidd 1983) on genetic structure within the colony. Each of these studies found that lineal fission along matrilineal lines resulted in genetic differentiation between the groups with respect to blood group proteins. Nonrandom mating within social groups (McMillan and Duggleby 1981) and founder effects and genetic drift (Melnick and Kidd 1983) may explain observed genetic patterns of social group differentiation.

The extensive skeletal sample derived from the Cayo Santiago colony provides an additional resource for the study of genetic differentiation of social groups. Quantitative traits include continuous traits, such as a limb dimensions or body height, as well as discrete traits with an underlying continuous distribution, such as presence of a supraorbital foramen or a cleft palate. It is assumed that quantitative traits represent the influence of multiple genetic loci as well as environmental (nongenetic) factors (Falconer and Mackay 1996; Lynch and Walsh 1998). A sample that includes individuals of known genetic relationship can be used to assess the relative role of genetic and environmental factors in the phenotypic variability of a trait at many levels, including between groups, populations, and species. Quantitative traits can be analyzed in situations in which DNA, blood group alleles, or protein polymorphisms are unavailable (Relethford 2006). In addition, evolutionary forces may have differing magnitudes of influence on quantitative traits and DNA loci or alleles.

Traditionally, F_{st} has been used as an estimate of population differentiation based on allele frequencies (Wright 1965, 1969). As a standardized estimate of gene frequency differentiation, F_{st} can be compared between populations. Estimates of F_{st} can range from 0.0 to 1.0, with 0.0 indicating no genetic differentiation and 1.0 representing alleles that are fully differentiated between the populations considered. Quantitative traits can also be used to study population structure and genetic distances (Relethford 2006). Methods introduced by Williams-Blangero and Blangero (1989), Relethford and Blangero (1990), and Relethford and colleagues (1997) extend the analysis of allele frequencies to the study of more complex quantitative traits.

Only two studies have used quantitative traits to study population structure on Cayo Santiago, and both predate the methods introduced by Williams-Blangero and Blangero (1989) and Relethford and Blangero (1990). Cheverud and Buikstra (1978)

examined eight discrete cranial traits in order to assess the genetic differences associated with the formation of one social group, comparing the fission product groups with the parent group. They found cranial trait differences between social groups to be within the range of random, and suggested that the pattern of male migration associated with the fission event may be responsible for the lack of significant differences. Cheverud (1981) assessed discrete and dimensional cranial traits for significant phenotypic, genetic, and environmental differences among eight social groups. This study found significant genetic differences among social groups, but limited environmental effects.

This study examined the effect of social group fission on dimensions of the postcranial skeleton of rhesus macaques on Cayo Santiago. Specifically, we tested for significant heritability of 49 postcranial dimensions of the axial and appendicular skeleton, and tested whether there was significant genetic differentiation between social groups. These morphological traits are quantitatively inherited, influenced by multiple alleles (Kenney-Hunt et al. 2008). Between 1958 and 1971, the number of social groups on Cayo Santiago increased from two to ten. Significant genetic differentiation between social groups over this short period of time, especially with quantitative traits, has implications for our understanding about the evolution of morphological traits.

5.2 Materials and Methods

5.2.1 Sample

The data for this study consist of 285 rhesus macaque skeletons, including 135 males and 150 females. While most individuals were born into the colony between 1956 and 1982, the birth year of 47 individuals was unknown, and was probably before the regular recording of demographic material began. All included individuals were skeletally mature, and individuals ranged in age from 6 to 28.8 years. Four individuals were of unknown age. The sample included individuals from 34 matrilines ranging in size from 2 to 35 individuals. Forty-four individuals had no known relatives within the sample. Many matrilines included a number of generations and varied relationships, and the sample included 149 mother–offspring pairs, 184 half-sibling pairs, and 122 grandmother–grandchild pairs.

5.2.2 Measurements

Forty-nine skeletal dimensions from 13 bones representing the axial and appendicular postcranial skeleton were measured by one individual (LK) using a Fowler digital caliper and recorded to the nearest 0.01 mm (Table 5.1). Large femurs and

Table 5.1 Traits measured on *Macaca mulata* and *t*, the repeatability of each measurement

Trait	*t*	Measurement definition
SCAP LEN	0.96	Highest point on superior border of scapula to inferior angle
SCAP BR	0.86	Vertebral border to edge of glenoid cavity
SCAP SPL	0.98	Vertebral border to acromial angle
SCAP SUPL	0.98	Edge of vertebral border adjacent to scapular spine to highest point on superior border
SCAP INFLV	0.88	Edge of vertebral border adjacent to scapular spine to inferior angle
SCAP INFA	0.98	Border of glenoid fossa to inferior angle
SCAP ACRL	0.97	Acromial angle to most anterior aspect of acromion
SCAP CORL	0.99	Maximum length of coracoid process
SCAP GLL	0.94	Maximum length of glenoid fossa
SCAP GLW	0.93	Maximum breadth of glenoid fossa
HUM LEN	0.98	Maximum length of humerus
HUM EPI	0.94	Maximum medial-lateral breadth of humerus epicondyle
ULN LEN	0.97	Maximum length of ulna
INN ILL	0.99	Superior iliac crest to center of acetabulum
INN ILB	0.90	Maximum iliac crest breadth, from anterior superior iliac spine to posterior superior iliac spine
INN ILPI	0.72	Posterior superior iliac spine to posterior inferior iliac spine
INN PIAC1	0.98	Posterior inferior iliac spine to edge of acetabulum at union of ilium and ischium
INN PIAC2	0.99	Posterior inferior iliac spine to center of acetabulum
INN PIIT	0.99	Posterior inferior iliac spine to ischial tuberosity
INN ILAI	0.99	Anterior superior iliac crest to anterior inferior iliac crest
INN AIAC	0.99	Anterior inferior iliac spine to center of acetabulum
INN ISL	0.99	Maximum distance from center of acetabulum to ischial tuberosity
INN ACL	0.89	Superior–inferior dimension of acetabulum
INN ACB	0.85	Anterior–posterior dimension of acetabulum
INN PL	0.97	Maximum superior–inferior dimension
SAC BR	0.97	Maximum distance between right and left auricular processes
SAC AUL	0.95	Superior–inferior dimension of auricular surface
SAC S1H	0.97	Maximum height of first sacral vertebral body
SAC S1B	0.91	Maximum breadth (right to left) of first sacral vertebral body
FEM LEN	0.98	Maximum length of femur
FEM EPI	0.97	Maximum medial–lateral breadth of femoral epicondyle
TIB LEN	0.98	Maximum length of tibia
MC5	0.99	Maximum length of fifth metacarpal
MT5	0.99	Maximum length of fifth metatarsal
C1 AP	0.99	Maximum anterior–posterior dimension of first cervical vertebra
C1 ML	0.99	Maximum medial–lateral dimension of first cervical vertebra
C2 AP	0.90	Maximum anterior–posterior dimension of second cervical vertebra

(continued)

Table 5.1 (continued)

Trait	t	Measurement definition
C2 ML	0.84	Maximum medial–lateral dimension of second cervical vertebra
HUM HEL	0.99	Maximum superior–inferior dimension of humerus head
HUM HEB	0.99	Maximum anterior–posterior dimension of humerus head
HUM MID	0.99	Maximum diameter in humerus mid-shaft
FEM HEL	0.97	Maximum superior–inferior dimension of femoral head
FEM HEB	0.98	Maximum anterior–posterior dimension of femoral head
FEM MID	0.99	Maximum diameter in femoral mid-shaft
CAL ARL	0.99	Anterior–posterior length of articular surface of talus on the calcaneus
CAL BR	0.99	Medial–lateral breadth of talus articular surface on calcaneus
CAL BL	0.92	Distal calcaneus to articular surface of talus on calcaneus
TAL TRL	0.99	Anterior–posterior dimension of trochlea on body of talus
TAL NL	0.99	Body to head of talus

tibias were measured using a bone board and recorded to the nearest millimeter. All measurements were taken on the right side of the body unless those elements were broken, diseased, or missing, in which case elements from the left side of the body were substituted. Skeletal elements that were obviously pathological were not included in this study. Thirty-five individuals were measured twice, and repeatability of each measurement was estimated as the proportion of the variance among individuals relative to the total variation (Bailey and Byrnes 1990). There was significant sexual dimorphism in the macaque postcranial skeleton, with males significantly larger than females for most dimensions. The difference between male and female means and standard deviations were adjusted such that

$$Y_{Fi} = (X_{Fi} - \overline{X}_{Fi})(\sigma_{Mi} / \sigma_{Fi}) + \overline{X}_{Mi}, \tag{5.1}$$

where Y_{Fi} is the adjusted value of trait i in females, X_{Fi} is the unadjusted value of trait i in females, $\overline{X}_{Fi}$ is the mean of trait i in females, σ_{Mi} is the standard deviation of trait i in males, σ_{Fi} is the standard deviation of trait i in females, and $\overline{X}_{Mi}$ is the mean of trait i in males (Cheverud 1995).

5.2.3   Quantitative Genetic Methods

Standard quantitative genetic estimates (Falconer and Mackay 1996; Lynch and Walsh 1998) use information from families to decompose the observed phenotypic value (P) into the additive genetic value (A) and the environmental deviations:

$$P = A + E. \tag{5.2}$$

The phenotypic variance (V_P) can be decomposed into the additive genetic variance (V_A) which is due to variability in the separate genes influencing a trait over all loci, and environmental variance (V_E):

$$V_P = V_A + V_E. \tag{5.3}$$

A heritability (h^2) is the proportion of phenotypic variance which is attributable to additive genetic effects:

$$h^2 = V_A / V_P. \tag{5.4}$$

Heritability estimates range from 0, in which there is no heritable variation in the traits, to 1, where all variability is due to inherited factors.

Maximum-likelihood methods that use all available familial relationships were used to estimate genetic parameters (Lange et al. 1976; Hopper and Matthews 1982; Konigsberg and Cheverud 1992; Cheverud 1995) using a program obtained from L. Konigsberg (Konigsberg and Cheverud 1992). These methods were used to estimate additive genetic variance (V_A), phenotypic variance (V_P), and heritabilities (h^2).The effective sample size

$$N_{eff} = \left[2h^4 / V(h^2) \right] + 1, \tag{5.5}$$

is a rough estimate of the number of families used to estimate the genetic statistics (Cheverud 1988, 1995).

5.2.4   Group Differentiation

We analyzed the degree of group differentiation in 1971. This maximized the number of groups that can be analyzed, given the birth years of animals within this sample, and made this study comparable to that of Cheverud (1981) on group differentiation based on cranial metric and nonmetric traits. Animals were assigned to the social group of their matriline as of 1971. Social group histories were presented in Sade et al. (1977) and Chepko-Sade and Sade (1979) and are summarized in Fig. 5.1. Social group membership and population size of each social group in 1971 were obtained from Sade et al. (1985). The skeletal sample size from each group and the 1971 population size for each group are presented in Table 5.2. Groups H and I were formed by fission of group G. Groups G and H would have contained too few individuals, and the groups were combined into group I. Group N was formed by fission from group J, but fused back with the group J 1 year later. Groups N and J were combined into group J. Groups M and O were formed by fission of group F, and they were combined into group F due to small sample sizes of the fission products.

In order to improve our estimates of group differentiation, we used only those postcranial traits that were significantly heritable, and that were estimated with an

| 1956 | 1957 | 1958 | 1959 | 1960 | 1961 | 1962 | 1963 | 1964 | 1965 | 1966 | 1967 | 1968 | 1969 | 1970 | 1971 | 1972 | 1973 | 1974 | 1975 |
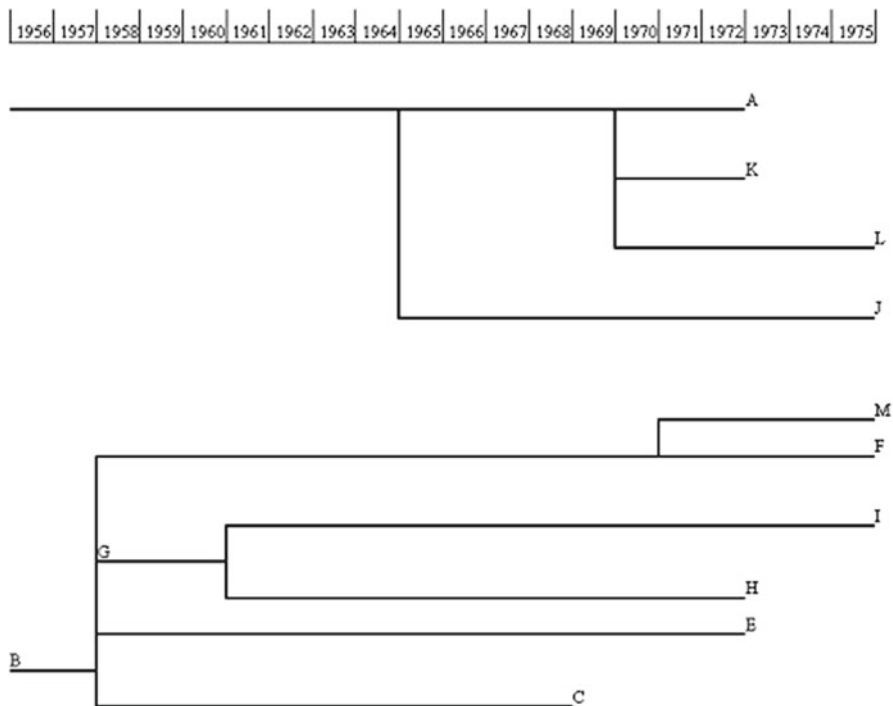
Fig. 5.1 History of social group fission on Cayo Santiago, summarized from Sade et al. (1977) and Chepko-Sade and Sade (1979)

Table 5.2 Sample size and population size of each social group

Group	Sample size	Population size
A	14	177
C	9	126
E	7	117
F (F, M, O)	51	88
I (G, H, I)	26	98
J (J, N)	38	34
K	10	90
L	20	34

effective sample size of at least 10. The estimates of group differentiation were based on the reduced data set of 36 traits. A subset of 177 individuals from the total sample had complete data for all 36 traits and were used to estimate the genetic differences among social groups.

Genetic structure and genetic distances were tested using the methods presented by Williams-Blangero and Blangero (1989), Relethford and Blangero (1990), and Relethford et al. (1997), and the program RMET5.0 provided by Relethford (http://konig.la.utk.edu/relethsoft.html). Relethford (2006) presented additional discussion of the methods. These analyses require an estimate of the population size and an

estimate of the average trait heritability. We used the number of individuals in each social group in 1971 as the population size and the average heritability of the post-cranial traits from this population as the heritability estimate. An R matrix, with the number of rows and columns each equal to the number of groups, was calculated in order to estimate the genetic similarity between pairs of social groups. F_{st} was derived from the R matrix and estimates the degree of population differentiation. The genetic distance, D^2, between social groups was derived from the R matrix.

Of interest is the pattern of group similarity. We tested whether groups formed by fission are more similar to each other than groups that are not formed by fission. A test matrix of relationship was created, in which 1 was entered for group pairs that were related directly by fission and 0 for group pairs that were not related by fission. A Mantel test was used to test if the genetic distance matrix was similar to the test matrix (Cheverud et al. 1989), with 1,000 permutations.

5.3 Results

5.3.1 Repeatability

Measurement repeatability ranged from 72 to 99%, with an average repeatability of 96% (Table 5.1). More than half of the traits (55%) had a repeatability of 98% or higher. Repeatability estimates set an upper limit for heritability estimates, since measurement error is not inherited and would not contribute to heritable variation (Falconer and Mackay 1996). With high measurement repeatability, it is unlikely that measurement error could obscure estimated group differences.

5.3.2 Heritability and Effective Population Size

Heritabilities, mean, variances, and their standard errors are presented in Table 5.3, along with the χ^2 from the maximum-likelihood estimate of heritability. With one degree of freedom, χ^2 values exceeding 2.7 are significant at $P = 0.05$. Heritability of postcranial skeletal traits ranged in value from 13% to 88%, with an average heritability of 52%. Only 5 of the 49 traits were not significantly heritable, including three pelvis traits (INN ACL, INN ACB, and INN PSL) and two sacral traits (SAC AUL and SAC S1H). Heritability estimates are normally distributed, based on the Lillifors test (Systat 2004). There is no significant difference between the mean heritability of traits across regions of upper extremity, lower extremity, and axial skeleton (ANOVA, $F = 1.17$, df = 2, 46; $P = 0.32$). Effective sample size ranged from 2.2 to 85.1, with an average effective sample size of 23.6. Thirteen of the traits had an effective sample size of less than ten. These traits were not included in the estimates of population distance, since these traits were based on less genetic information. The average heritability of the remaining traits was 59%.

Table 5.3 Estimates of heritabilities (h^2), phenotypic variance (V_P), mean, and their standard errors (SE)

Trait	h^2 (SE)	V_P (SE)	Mean (SE)	χ^2	N_{eff}
SCAP LEN	0.49 (0.16)	14.00 (1.29)	83.93 (0.28)	10.29	21.23
SCAP BR	0.55 (0.19)	18.15 (1.73)	73.78 (0.32)	8.33	17.29
SCAP SPL	0.51 (0.16)	19.72 (1.83)	91.36 (0.33)	10.76	21.16
SCAP SUPL	0.61 (0.19)	16.57 (1.60)	35.25 (0.31)	8.74	21.11
SCAP INFLV	0.78 (0.15)	11.69 (1.14)	50.77 (0.27)	19.88	53.67
SCAP INFA	0.29 (0.17)	16.61 (1.51)	87.33 (0.29)	3.00	7.01
SCAP ACRL	0.51 (0.16)	1.96 (0.18)	13.42 (0.11)	9.70	20.44
SCAP CORL	0.65 (0.19)	1.07 (0.10)	15.47 (0.08)	14.55	24.62
SCAP GLL	0.61 (0.16)	0.81 (0.08)	17.95 (0.07)	13.23	31.01
SCAP GLW	0.28 (0.16)	0.81 (0.07)	13.30 (0.06)	3.49	7.07
HUM LEN	0.69 (0.16)	27.14 (2.72)	157.58 (0.43)	17.04	38.16
HUM EPI	0.78 (0.16)	2.49 (0.24)	30.49 (0.12)	21.16	49.99
ULN LEN	0.87 (0.13)	39.35 (3.98)	178.24 (0.52)	29.37	85.11
INN ILL	0.67 (0.15)	14.68 (1.40)	105.29 (0.30)	20.27	40.31
INN ILB	0.60 (0.18)	10.72 (1.03)	40.91 (0.25)	12.10	23.47
INN ILPI	0.32 (0.15)	11.16 (1.02)	59.08 (0.24)	5.24	9.85
INN PIAC1	0.51 (0.17)	9.92 (0.93)	45.09 (0.24)	10.42	20.26
INN PIAC2	0.56 (0.17)	9.84 (0.92)	49.26 (0.24)	10.28	22.91
INN PIIT	0.47 (0.17)	10.02 (0.92)	50.90 (0.23)	8.93	16.45
INN ILAI	0.55 (0.16)	15.46 (1.44)	79.37 (0.30)	13.98	24.76
INN AIAC	0.22 (0.16)	2.60 (0.24)	28.96 (0.12)	2.68	4.86
INN ISL	0.74 (0.15)	7.05 (0.68)	55.41 (0.21)	20.39	52.10
INN ACL	0.22 (0.17)	1.23 (0.11)	21.46 (0.08)	1.91	4.29
INN ACB	0.26 (0.18)	1.04 (0.10)	20.94 (0.07)	2.61	5.16
INN PL	0.16 (0.14)	21.48 (1.95)	42.66 (0.33)	1.78	3.57
SAC BR	0.61 (0.14)	6.28 (0.60)	50.30 (0.19)	19.95	37.36
SAC AUL	0.13 (0.16)	6.50 (0.60)	27.71 (0.17)	0.69	2.23
SAC S1H	0.18 (0.14)	1.64 (0.15)	16.46 (0.09)	2.14	4.44
SAC S1B	0.43 (0.15)	2.35 (0.22)	23.00 (0.11)	9.43	17.74
FEM LEN	0.76 (0.15)	50.88 (4.97)	188.75 (0.57)	27.38	51.94
FEM EPI	0.63 (0.17)	2.07 (0.20)	31.45 (0.11)	14.77	27.41
TIB LEN	0.69 (0.15)	43.34 (4.14)	170.25 (0.52)	24.06	44.85
MC5	0.59 (0.18)	3.18 (0.31)	37.10 (0.14)	11.84	22.75
MT5	0.54 (0.19)	4.93 (0.48)	54.73 (0.17)	9.41	17.62
C1 AP	0.77 (0.15)	1.06 (0.10)	21.70 (0.08)	24.96	56.82
C1 ML	0.36 (0.18)	2.96 (0.28)	37.12 (0.13)	4.57	9.09
C2 AP	0.51 (0.18)	1.20 (0.11)	26.93 (0.08)	7.45	16.37
C2 ML	0.51 (0.18)	2.05 (0.19)	27.11 (0.11)	9.83	17.99
HUM HEL	0.47 (0.20)	0.57 (0.06)	18.06 (0.06)	6.66	12.05
HUM HEB	0.30 (0.19)	0.66 (0.06)	18.80 (0.06)	3.25	5.80
HUM MID	0.47 (0.18)	0.58 (0.05)	12.73 (0.06)	7.03	14.71
FEM HEL	0.55 (0.20)	0.52 (0.05)	17.46 (0.06)	9.87	16.98
FEM HEB	0.50 (0.20)	0.42 (0.04)	17.33 (0.05)	7.53	13.40
FEM MID	0.35 (0.17)	0.62 (0.06)	13.67 (0.06)	4.04	9.73

(continued)

Table 5.3 (continued)

Trait	h^2 (SE)	V_P (SE)	Mean (SE)	χ^2	N_{eff}
CAL ARL	0.88 (0.14)	0.85 (0.08)	22.38 (0.07)	22.58	77.99
CAL BR	0.36 (0.21)	1.03 (0.10)	20.41 (0.07)	3.64	6.75
CAL BL	0.37 (0.20)	0.95 (0.09)	11.43 (0.08)	4.02	7.47
TAL TRL	0.30 (0.20)	0.52 (0.05)	16.44 (0.05)	3.07	5.80
TAL NL	0.61 (0.16)	0.36 (0.03)	13.62 (0.05)	14.17	31.88

The χ^2 tests for heritability significance. The effective population size, N_{eff}, estimates the number of families used to estimate the heritability. *$P<0.05$

Table 5.4 Genetic distance D^2 on lower diagonal, SE on upper diagonal

	A	C	E	F	GHI	J	K	L
A	0.000	0.051	0.046	0.025	0.031	0.032	0.038	0.040
C	0.187*	0.000	0.054	0.030	0.038	0.046	0.051	0.048
E	0.092	0.104	0.000	0.036	0.048	0.051	0.043	0.048
F	0.086*	0.074*	0.075*	0.000	0.021	0.014	0.025	0.021
GHI	0.120*	0.118*	0.164*	0.118*	0.000	0.028	0.033	0.033
J	0.158*	0.236*	0.223*	0.066*	0.204*	0.000	0.034	0.026
K	0.166*	0.229*	0.092*	0.140*	0.192*	0.244*	0.000	0.040
L	0.205*	0.198*	0.141*	0.095*	0.200*	0.136*	0.253*	0.000

*Significant at $P=0.05$

5.3.3 Genetic Differentiation

There is significant genetic differentiation among social groups, with an $F_{st}=0.05$ (standard error$=0.007$; $P<0.01$). With the exception of groups A and E, and groups C and E, there is significant genetic distance between each of the social groups, adjusted for the population size of each group (Table 5.4).

We tested whether groups that were fission products were more similar to each other than the unrelated groups. The correlation between the D^2 matrix and the matrix representing fission products is -0.06 ($P=0.62$), indicating that groups that are fission products are not more similar to their parent group than they are to other groups. This pattern is consistent with multiple significant allelic differences between social groups and reduced gene flow between social groups.

5.4 Discussion

The postcranial skeletal traits in this sample from rhesus macaques from Cayo Santiago were significantly heritable. The average heritability was higher than that observed for cranial traits from this population (Cheverud and Buikstra 1982), and was higher than average morphological heritabilities presented by Mousseau and

Roff (1987). Recent studies on quantitative trait loci associated with mouse skeletal dimensions, representing all regions of the body, found multiple alleles influencing skeletal dimensions (Kenney-Hunt et al. 2008), elucidating the principle behind the assumptions associated with quantitative genetic analyses. While it was not surprising that these postcranial traits are significantly heritable, the confirmation of significant genetic variation is important as we considered the genetic differentiation within this population.

The pattern of social group formation by matrilineal fission resulted in significant genetic differentiation between social groups on Cayo Santiago. We would expect that the male migration between social groups would reduce the level of genetic differentiation. This is consistent with a reduction in gene flow from each social group.

Previous studies that examined genetic differentiation between social group differences, in both baboons (Ober et al. 1978) and rhesus macaques (Buettner-Janusch et al. 1983; Melnick and Kidd 1983; Melnick 1987), were based on observed allele frequencies differences. The F_{st} levels estimated for the postcranial dimensions in this study are less than those observed for carbonic anhydrase II by Ober et al. (1978) and higher than those observed for blood proteins in the Cayo Santiago population (Buettner-Janusch et al. 1983). This study is also consistent with the results of Cheverud (1981), in which genetic differences were observed between social groups from Cayo Santiago for cranial morphology, using different methods.

5.5 Conclusions

These results have important implications for the evolution of morphological traits. Significant genetic differentiation between groups was generated over a relatively short period of time. Formation of groups by matrilineal fission appears to result in allelic differences between groups, probably as a result of founder differences between groups (Templeton 1980). These results illustrate that genetic distance results may not reflect historical events, and interpretation of genetic distance without an understanding of animal behavior or experience may result in misleading conclusions. Additionally, significant genetic distance may be generated over a relatively short period of time. Evolution of morphological traits is a function of natural selection acting on morphological traits that exhibit significant genetic variation and covariation (Lande 1979). While it is unlikely that there are selection differences among the groups on Cayo Santiago, similar group processes in a wild population may establish conditions that enable the evolution of morphological traits.

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Chapter 6
Prenatal Androgenization and Dominance Rank in Female Rhesus Macaques: Evidence from Digit Ratios (2D:4D)

Emma Nelson, Christy L. Hoffman, Martin Voracek, Melissa S. Gerald, and Susanne Shultz

6.1 Introduction

Intrauterine sex hormones, such as the androgen testosterone, program the brain and body tissues at a cellular level according to sex-specific patterns (i.e., neuro-endocrine axes; Fowden and Forhead 2009) and have long-term effects on development (Goy and McEwan 1980; Wallen and Baum 2002; Kaiser and Sachser 2005, 2009). Androgens, in particular, are crucial to programming masculine characteristics in the male phenotype (Wilson et al. 1981) and play an important

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role in female development (Goy 1981; Wallen 1996; Herman et al. 2000; Ostner et al. 2003). For both males and females, these androgenic effects extend not only to the physical development of individuals, but may also have profound effects on social–psychological behavioral traits in primates and other animals (Baron-Cohen et al. 2004; Dloniak et al. 2006; Kaiser and Sachser 2005).

Ethical considerations and the necessity for lab-based analytical techniques make investigating prenatal androgen effects (PAE) in nonhuman primates difficult and also limit the species in which these techniques could be applied (Thornton et al. 2009). However, a convenient biomarker for PAE has been proposed; the second-to-fourth digit ratio (2D:4D) (Manning and Bundred 2000; Manning 2002, 2008). 2D:4D has been widely employed to investigate normal physical and behavioral development in humans (see Voracek and Loibl 2009) and studies are now being extended to nonhuman animals (reviewed in Lombardo and Thorpe 2008).

6.1.1 2D:4D, An Anatomical Marker for Prenatal Androgens Effects

In humans, 2D:4D is sexually dimorphic from 9 weeks of prenatal life (Malas et al. 2006; also see Galis et al. 2010). Lower 2D:4D ratios are associated with higher PAE and 2D:4D tends to be lower in males than females within a population (Manning 2002; McIntyre et al. 2005). 2D:4D has been shown to correlate negatively with direct and indirect measures of prenatal androgens (see Manning et al. 2007a for an overview). For example, females with a male co-twin have lower 2D:4D ratios than females with a same-sex twin, which is possibly the result of intra-uterine hormonal (androgen) transfer between siblings (van Anders et al. 2006; but see Medland et al. 2008). Females with congenital adrenal hyperplasia and polycystic ovary syndrome, conditions which cause the fetus to be exposed to high androgens, have more masculinized (low) 2D:4D ratios, compared to healthy controls (Brown et al. 2002; Ökten et al. 2002; but see Buck et al. 2003; Cattrall et al. 2005; Hönekopp and Watson 2010; but see Lujan et al. 2010). More direct associations with PAE come from a study showing that in men, low 2D:4D is associated with a higher sensitivity androgen receptor gene (Manning et al. 2003; but see Hurd et al. 2010). Additionally, the testosterone-to-estradiol ratio, calculated from hormones assayed from the amniotic fluid, has also been shown to negatively correlate with the 2D:4D of the infants at 2 years of age (Lutchmaya et al. 2004; also see Knickmeyer et al. 2011). Nonhuman animal studies have shown that injecting testosterone into gestating rats masculinizes the digit ratios and the ranging behavior of their adult female offspring (Talarovičová et al. 2008).

The mechanisms underlying these relationships are not clear, but are believed to be linked to common developmental pathways between the fingers and reproductive system. The distal limb buds (digits) and the genital bud are controlled by the same groups of phylogenetically conserved *HOX* genes (Zákány et al. 1997; Kondo et al. 1997; Montavon et al. 2008), and *HOX* gene transcription appears to be sensitive to

sex hormones (Nora et al. 1976; Soto and Sonneschein 1999; but see Carbone et al. 2005). The fourth digit (ring finger) appears to be particularly sensitive to PAE such that individuals exposed to high prenatal androgens have longer fourth digits (4D) relative to their second digits (2D) (McIntyre et al. 2005). It is conjectured that PAE also has a concomitant influence on the reproductive system as a consequence of *HOX* gene pleiotropy between the limb and genital buds (Voracek and Manning 2003). Furthermore, as *HOX* genes are strongly phylogenetically conserved within and between taxonomic groups (Zákány et al. 1997), it has been proposed that genetic associations between 2D:4D and PAE should therefore be common in other four-limbed vertebrates (Manning 2002, p. 17).

Studies of heritability of digit ratios support this contention. Twin studies of 2D:4D have found high heritabilities (narrow sense) for the trait ($h^2 = 50-80\%$) and shared environmental influences (nongenetic effects) on 2D:4D to be small (Paul et al. 2006; Voracek and Dressler 2007; Gobrogge et al. 2008; Medland and Loehlin 2008). Similar results have been found for familial relationships in humans, such as mother–offspring and sibling–sibling comparisons, which yield heritability values of between 41 and 69% (Ramesh and Murty 1977; Marshall 2000; Manning 2002; Voracek and Dressler 2009). High heritability levels have also been calculated for zebra finches ($h^2 = 70-80\%$) (Forstmeier 2005; Forstmeier et al. 2008). These studies, along with the evidence outlined above, have led to 2D:4D being widely employed to study androgenic-programming effects on shaping human sex-linked traits and behaviors (Voracek and Loibl 2009).

In humans, low 2D:4D ratios (high inferred PAE) are associated with dominance-related behaviors in both sexes. Low 2D:4D individuals tend to be more competitive (Manning and Taylor 2001; Manning et al. 2007b), show higher physical strength (Fink et al. 2006; but see van Anders 2007), and exhibit more aggression compared to individuals with higher 2D:4D (Bailey and Hurd 2005; Benderlioglu and Nelson 2004; Millet and Dewitte 2007, 2009). In addition, they exhibit higher drives for social status (Millet and Dewitte 2008; also see Coates et al. 2009), rate themselves as more dominant (Manning and Fink 2008), and are perceived as more dominant than individuals with higher 2D:4D ratios (Neave et al. 2003). In contrast to traits linked with low 2D:4D (high PAE), high ratios (low PAE) have been associated with emotional sensitivity in children (Fink et al. 2007; Williams et al. 2003). Additionally, there is some evidence to suggest that birth order and sex of older siblings may influence PAE/2D:4D relationships (Williams et al. 2000; Saino et al. 2006), possibly via interactions between maternal physiology and parity (Williams et al. 2000; James 2001; Saino et al. 2006).

Studies investigating correlations between 2D:4D and behavior have recently been extended to nonhuman primates. Phylogenetic comparisons demonstrate that 2D:4D ratios covary with social systems and intra-sexual competition across haplorrhine primates, with low 2D:4D ratios associated with competitive social systems (McIntyre et al. 2009; Nelson and Shultz 2010).

Thus, 2D:4D appears to reflect the influence of PAE on social development, and particularly on behaviors linked to intra-sexual competition and sexual selection (see Fink et al. 2006). Based upon the available data, these relationships seem to be broadly stable both within and between primate species (McIntyre et al. 2009;

Nelson and Shultz 2010). Comparisons of 2D:4D between siblings and parent–offspring dyads in both humans and zebra finches also show similar size effects and suggest that heritability of 2D:4D may generalize across taxa (see Voracek and Dressler 2009). The moderate to high heritability levels quoted in studies of 2D:4D suggest that nonshared environmental influences such as maternal effects and epigenetic factors are low to moderate (see Gobrogge et al. 2008).

One approach to understanding the physiological interplay between genetic and gestational effects is to compare 2D:4D within a phylogenetic framework. As the main body of 2D:4D research is in humans, a framework considering species closely related to humans would be the most informative. Haplorrhine primates offer the best comparative model as they reside within the same suborder as humans and will therefore have more similar biological profiles to humans than more distantly related species such as reptiles or birds. Rhesus macaques are a particularly well-studied primate species and the Caribbean Primate Research Centre (CPRC) has facilitated much of this research over a number of decades (see Rawlings and Kessler 1986; Maestripieri 2007). Annual trapping of free-ranging macaques residing on the island of Cayo Santiago (managed and run by the CPRC) made it possible to investigate 2D:4D and female dominance rank, as well as familial resemblance in a group of 60 adult females and their most recent offspring.

6.1.2   Female Dominance Rank in Rhesus Macaques: A Case for Prenatal Androgens?

Rhesus macaques exhibit competitive behaviors at all levels of the social hierarchy (Maestripieri 2007), and females exhibit strong matrilineal bonds that determine dominance relationships within the group (Thierry et al. 2000). A female's position within the hierarchy is established during the juvenile period. Dominance ranks are passed from mother to daughter ("inherited") with younger sisters usually outranking older sisters (Datta 1988; Walters and Seyfarth 1987). Rank acquisition occurs through a gradual process, during which support is provided by the mother and other close kin (Chapias 1992, 2004; Datta 1988; Holekamp and Smale 1991). A female's rank therefore becomes established as a result of her own experiences, by the reactions of others that interact with her and by recognition of her status by other members of the group. These socio-behavioral mechanisms of dominance rank inheritance are widely acknowledged and well understood (Chapias 2004).

Although social processes are the primary mechanism of dominance-rank inheritance, there is some evidence from a number of species to suggest that prenatal androgens may play a role in the ontogeny and maintenance of dominance behaviors in many taxa. For example, exposure to high prenatal androgens has been shown to masculinize social behavior in female rhesus macaques and humans (e.g., Wallen 1996; Thornton et al. 2009; Hall et al. 2004; Kaiser and Sachser 2005). In humans, sex steroids vary with birth order (Bernstein et al. 1986) and may be implicated in competition between siblings (see Saino et al. 2006). In some bird species, yolk androgens (which are allocated by the mother) change with egg-laying order

(Gil et al. 2004) and appear to modify competitive behavior in offspring (Groothuis et al. 2005). In canaries (*Serinus canaria*), yolk androgens have been shown to correlate positively with the social rank of siblings (Schwabl 1993).

The ability to confer signals about the extra-uterine world to a developing fetus, via maternal effects, is adaptive in that it physiologically prepares the individual for life in that environment (Mousseau and Fox 1998). Maternal effects, therefore, vary according to environmental conditions, but the effects on the fetus can be sex specific and transmitted across generations (e.g., Kaiser and Sachser 2005; Matthews and Phillips 2010). Studies have consistently shown that exposing pregnant mammals to specific stressors (i.e., overcrowding or unfamiliar conspecifics), masculinizes–defeminizes daughters and feminizes–demasculinizes sons (Wallen and Baum 2002; Kaiser and Sachser 2005). More recently, the research focus has broadened to understand how maternal effects in mammals adapt offspring under normative (i.e., nonadverse) conditions (Kaiser and Sachser 2005, 2009).

In healthy human individuals, variation in prenatal androgens (assayed from amniotic fluid samples) correlate with differences in behavioral developmental pathways (Knickmeyer and Baron-Cohen 2006). However, it is not known how much of these effects on the fetus are genetic (i.e., androgens secreted by the fetus itself), environmental (i.e., maternal effects), or due to epigenetic combinations of these influences. Nevertheless, these effects may be manifested in the form of different physiologically induced predispositions (Wallen 1996, 2005). The social landscape then acts to adapt these differences, making some behavioral tendencies more prone to develop than others (Wallen 1996). The interaction between physiology and social learning is adaptive in that it provides a means of fine-tuning behavior according to variations (social and physical) in the environment in which the individual is developing (Kaiser and Sachser 2005; Maestripieri 2003).

Research on wild spotted hyenas (*Crocuta crocuta*) suggests a link between prenatal androgens and the transfer of dominance behavior (Dloniak et al. 2006). Spotted hyenas have social systems and mechanisms of rank inheritance that resemble those of cercopithecine primates, particularly the *Macaca* genus (Engh et al. 2000; Holekamp and Smale 1991). In female hyenas, levels of fecal androgens late in pregnancy are positively related to dominance rank (Dloniak et al. 2004). Offspring of mothers with higher levels of fecal androgens are more aggressive and display higher rates of mounting behavior than pups of mothers with lower fecal androgens (Dloniak et al. 2006). The inference is that the levels of prenatal androgens that a pup experiences is, to some extent, governed by maternal effects. Thus, exposure to high PAE primes aggressive behavior in young pups, such that pups of higher-ranking mothers may actually be predisposed to be more confrontational and, therefore, be more adapted to acquiring resources and maintaining their dominant status (via inheritance of social rank). More recently, it has been shown that, in orphaned spotted hyena pups adopted by other females, the dominance rank of the fostered animal was determined by the rank of the surrogate mother (and her social support), not by the rank of the genetic mother (East et al. 2009). It is likely, however, that early life experiences of an individual (i.e., the style of mothering an infant receives as well as the foster mother's dominance rank within the group) will act to modify and adapt prenatally inherited predispositions (see Maestripieri 2003, 2004).

Taken together, evidence from social studies suggests that offspring of high-ranking females are permitted to be more dominant because they inherit their mother's dominance rank, and the biological data indicate that early exposure to high androgens (from higher-ranking mothers) predisposes them to be more confrontational.

6.1.3   Aims of the Study

The aim of this study was twofold: first, to investigate relationships between 2D:4D and dominance rank in female rhesus macaques (Part I) and, second, to use a family-resemblance approach to estimate the heritability of 2D:4D in mother–offspring dyads in the same population (Part II). If female dominance rank is inherited only through socio-physiological effects occurring *after* birth in this species, we would expect to see no relationship with the PAE biomarker, 2D:4D. Alternatively, if female dominance rank is influenced by genetic effects of PAE on predispositions, then higher heritability of 2D:4D should be seen.

6.2   Materials and Methods

6.2.1   Subjects

Data were collected during the 2008 trapping season on Cayo Santiago, a small island (15.2 ha) located 1 km off Puerto Rico's south-eastern coast (see Nelson et al. 2010; Nelson and Voracek 2010). The island's free-ranging rhesus macaque colony was established in 1938, and the present-day population (about 900 individuals) is directly descended from the founder group, originating from the Indian subcontinent (Rawlings and Kessler 1986). Genetic and behavioral analyses indicate no significant inbreeding (McMillan and Duggleby 1981; Mason and Perry 1993; Charpentier et al. 2007), although it is acknowledged that female dispersal patterns might potentially reduce genetic diversity (Chepko-Sade and Sade 1979) which may impact on heritability factors.

Measurements from 60 adult females and 25 of their infants (25 mother–infant pairs; eight females and 17 males) were collected over a 4-week period between January and February. The females in this study were primarily being sampled for a larger, unrelated study. As a result, our sample size was restricted to those females being sedated for that study and, consequently, we could not sample all adult females and their infants within a matriline.

Adult females were between 4 and 24 years of age, and infants were between 1 and 4 months. Individuals came from groups F, R, and S. Females were sampled from two matrilines from social group F (065 and 004) and from social group R (116r and DM) and from one matriline from social group S (116s) (see Table 6.1).

Table 6.1 Social group and matriline variables in Part I (adult females)

Social group	Rank	N	Mean 2D:4D	SD	Age	SD	Weight (kg)	SD	Matriline	Rank	N	Mean 2D:4D	SD	Age	SD	Weight (kg)	SD
F	High	11	0.828	0.03	15.6	5.2	9.6	0.6	065	High	6 (42)	0.838	0.03	16.4	5.2	9.3	2.1
									004	Low	5 (38)	0.824	0.03	14.7	5.6	9.9	2.3
R	Middle	35	0.826	0.04	11.5	5.7	8.5	1.8	116r	Middle	6 (11)	0.833	0.04	10.1	5.3	8.6	1.3
									DM	Low	29 (61)	0.822	0.04	11.9	5.7	8.5	1.9
S	Low	14	0.832	0.04	14.6	4.8	7.8	1.8	116s	Low	14 (31)	0.832	0.04	14.6	4.8	7.8	1.8

Figures in parentheses represent total number of adult females in the matriline (from Nelson et al. 2010)

A matriline is defined as a female kin lineage that can be traced back to the original matriarch of the groups. The matriarchs of groups F and R were born in the 1950s, and the matriarch of group S can be traced to the 1980s, when matriline 116 (originally residing in social group R) split into two lineages, the smaller of which moved out of R to form a new social group – group S (116s).

CRPC staff captured the monkeys in nets or by hand between 08:30 h and 12:00 h inside feeding corrals. Individuals were transferred immediately to standard cages and were held in the cages overnight. Each monkey had access to water and monkey chow during overnight housing, and all infants were kept with their mothers. The following morning, females and their offspring were sedated with ketamine (approximately 10 mg/kg via IM injection). Approximately 5–10 min after ketamine injection, morphometric measures were taken. Following measurements, trained veterinary staff monitored monkeys every 10 min until they had recovered completely.

All data were collected in accordance with the National Institutes of Health Guide for the Care and Use of Laboratory Animals. The study was approved by the School of Archaeology, Classics and Egyptology's Ethics Committee (University of Liverpool, UK) and the Institutional Animal Care and Use Committee (IACUC) of the University of Puerto Rico, Medical Sciences Campus.

6.2.2 Measurement Procedures

While individuals were fully sedated, they were placed on a weigh sling (Detecto™) and weighed to the nearest 0.1 kg. The 2D and 4D of each hand were then measured. Measurements were from the proximal crease at the base of the digit (crease closest to the palm) to the tip of the extended digit without compressing the soft tissues of the fingertip. Procedure followed (as near as possible) was that of Manning (2002). One observer (EN), who was blind to the dominance rank of the individuals, took the digit measurements. All digit measurements were taken twice (to the nearest 0.01 mm), using a Vernier digital caliper (Guo Gen™); the digits of the left hand were measured (2D, then 4D) first, and then the digits of the right hand (2D, then 4D) were measured The second set of measurements was taken immediately after the first, using the same procedure. During the measurement procedure, the hands of most of the sedated adult monkeys remained relaxed, but in the few instances when female's hands became tonic, an assistant gently opened the hand and held the digits in extension to facilitate length measurements. Assistance was also provided to help measure the infants' hands, as the digits were small. Means of the two right-hand (R2D:4D) measurements and the two left-hand (L2D:4D) measurements were averaged to create a mean digit ratio (M2D:4D) value for each individual.

6.2.3 Determination of Dominance Rank

Each female was followed twice a week for a minimum of 16 weeks in the period immediately preceding the trapping period. Female rank within the matriline was

estimated via observation of antagonistic interactions (observations done by the second author). During 30-min focal follows, the initiators and recipients of both aggressive (i.e., threats and chases) and submissive behaviors (i.e., withdrawals, screams, and grimaces) were recorded. Submissive individuals were scored as lower ranking than aggressive individuals, and dominance was only scored when submissive actions were clearly shown. As dominance-rank data were available for all females within matrilines (not just the study sample), it was possible to assign *absolute ranks*. Absolute rank is defined as the rank order of a female in relation to the rank of all other females within the matriline (Nelson et al. 2010). For example, the absolute ranks of the study females in matriline 004 were 21, 22, 25, 26, and 37.

However, as we could only measure the digits of a sample of females within a matriline, we also calculated the *proportional dominance rank in matriline* (see Zehr et al. 2005) as a method of controlling for the large group-size differences between kin lineages. The proportional dominance rank in a matriline was calculated by dividing the absolute rank of the female within the matriline by the total number of mature females in the matriline (Nelson et al. 2010). For example, the absolute ranks of females in matriline 004 were divided by the total number of females in that matrilines ($N=38$; see Table 6.1) yielding proportional ranks of 0.52, 0.58, 0.66, 0.68, and 0.97 – the lower the value, the higher the rank.

Social groups and matrilines within the social groups could be ranked as high, middle, or low (Table 6.1). Social group rank and matriline rank were assessed by observing the direction of displacements at favored sites. For example, if one group displaced another at a feeding patch, the displaced group would be considered lower ranking than the displacing group. Based on observations of individual females and their birth histories, families could also be ranked linearly according to the ranks of the females within them. A family consisted of a matriarch, her daughters, and her granddaughters.

6.2.4   Statistical Methods

6.2.4.1   Part I – Adult Females

2D:4D and age were normally distributed (Kolmogorov–Smirnov tests), but body weight was not; body weight was therefore log-transformed. A general linear model (GLM) was used to investigate relationships between 2D:4D and dominance rank within and between social groups, matrilines, and families (see Nelson et al. 2010). We hypothesized that a female's 2D:4D was influenced by maternal androgens and largely fixed in utero. We therefore assigned 2D:4D as the independent variable and dominance rank as the independent variable. Age and body weight were considered as covariates. For comparisons of dominance rank within social groups, we coded females linearly; the highest-ranking female in the highest-ranking matriline as 1, while the lowest-ranking female in the lowest-ranking matriline (within the same group) was assigned the lowest number (of the total sampled for that social group).

It is important to note that in the regression of 2D:4D and family rank (Table 6.3), we pooled data of families from two social groups (DM and 116s) to increase the

power of the analysis. However, we controlled for social-group differences by assigning "social group" as fixed factor. A paired *t* test (two-tailed) was used to evaluate differences in 2D:4D between left and right hands and younger and older sisters within families. Sample sizes within groups were highly variable (see Table 6.1), but analyses were not weighted since there were no relationships between variances of 2D:4D and sample size.

6.2.4.2   Part II – Mother–Infant Dyads

All data were normally distributed. Data were analyzed using GLM and were used to test across categorical variables and linear regression for continuous variables (see Nelson and Voracek 2010). Cohen's *d* was used to estimate the size effect of 2D:4D between male and female infants. Pearson's correlation coefficient (*r*) was used to examine relationships between 2D:4D, age, and body weight. Paired *t* tests (two-tailed) were used to compare mother and infant 2D:4D ratios. Following standard practice of familial resemblance studies of 2D:4D, heritability (h^2) values for mother–infant dyads were calculated by doubling the Pearson correlation coefficients (Ramesh and Murty 1977; Voracek and Dressler 2009).

6.2.5   Repeatability of Measurements

Intra-observer measurements of repeatabilities were quantified with intra-class correlation coefficients (*ICC*), according to a two-way mixed-effects model with absolute-agreement definition (Voracek et al. 2007b). Adult females ICC's = R2D:4D, 0.895; L2D:4D, 0.942; M2D:4D, 0.955 (all Ps < 0.0001); infants: ICC = R2D:4D, 0.651; L2D:4D, 0.783; M2D:4D, 0.797 (all Ps < 0.02). These results indicated that 2D:4D ratios of infants were somewhat less repeatable than those of their mothers, which is understandable due to the smaller size of infant hands at this age.

6.3   Results

6.3.1   Part I – Adult Females

6.3.1.1   2D:4D, Age, and Weight in Adult Females

Mean 2D:4D (± standard deviation) across the whole sample was 0.827 ± 0.04. L2D:4D and R2D:4D were not significantly different (left: 0.830 ± 0.05; right: 0.825 ± 0.04; t_{59} = 0.776, P = 0.447); as such, our main findings are based on M2D:4D. Mean values for this group of free-living female rhesus macaques are within range of M2D:4D for captive populations (Nelson and Shultz 2010). Age structure differed between social groups ($F_{2,59}$ = 3.37, P = 0.04; Table 6.1).

Table 6.2 Mean 2D:4D (M2D:4D) and dominance rank within social groups

Group	Variable	F	P	R^2	df	Power
F	M2D:4D	0.001	0.99	0.09	1,7	0.05
	Age	0.004	0.95		1,7	
	Body weight	0.57	0.47		1,7	
R	M2D:4D	1.28	0.27	0.06	1,30	0.20
	Age	0.35	0.56		1,30	
	Body weight	0.28	0.60		1,30	
S	M2D:4D	6.25	0.03	0.59	1,10	0.64
	Age	8.38	0.02		1,10	
	Body weight	7.53	0.02		1,10	

Rank in social group was assigned as the dependent variable, and M2D:4D was assigned as a covariate along with age and body weight. Note that group S only contains one matriline (116s; Table 6.1) (from Nelson et al. 2010)

There was also a trend for body weight to increase with the increasing dominance rank of social groups ($F_{2,59}=2.79$, $P=0.07$; Table 6.1). We controlled for both of these variables in all analyses to reduce the possibility of type I errors (Grafen and Hails 2002), as age and body weight are known to covary with dominance rank in rhesus macaques (Datta 1988; Zehr et al. 2005).

6.3.1.2   2D:4D and Dominance Rank in Adult Females

Relationships Within and Between Social Groups

We first addressed whether there was a relationship between M2D:4D and dominance rank between social groups. These relationships were not significant ($F_{2,59}=0.10$, $P=0.90$). Next, we investigated relationships within the social group. Analyzing social groups separately there was a significant relationship between M2D:4D and dominance rank for social group S (Table 6.2), which was the only group composed of a single matriline (see Table 6.1). In social group S, significant interactions between dominance rank in social group, age, and body weight were also found ($F_{1,10}=12.05$, $P=0.006$); older and heavier females in this social group tended to be higher ranking.

Relationships Within and Between Matrilines

We found no differences between matrilines in groups F and R, respectively (between matrilines in group F, $F_{1,10}$ 0.10, $P=0.76$; matrilines in group R, $F_{1,33}=0.50$, $P=0.50$). In contrast, within matriline (across all sampled individuals), M2D:4D ratio decreased (higher PAE) significantly, as the proportional dominance rank in matriline increased ($F_{1,55}=6.86$, $P=0.01$, $R^2=0.12$; observed power=0.73); age and body weight were not significantly related to proportional dominance rank (age: $F_{1,55}=0.42$, $P=0.52$; body weight: $F_{1,55}=0.05$, $P=0.82$). Relationships between

Table 6.3 2D:4D and dominance rank of families in matrilines DM and 116s, with family rank assigned as the dependent variable and M2D:4D as a covariate alongside age and body weight

Ranked families	F	P	R^2	df	Power
M2D:4D	6.99	0.01	0.19	6,37	0.73
Social group	0.004	0.95		1,37	
Age	0.92	0.34		1,37	
Body weight	0.56	0.46		1,37	

We pooled data of families from different social groups (R and S; see Sect. 6.2) to increase the power of the analysis, but controlled for social group differences by assigning social group as the fixed factor

M2D:4D and absolute rank within matrilines across the whole group also approached significance ($F_{1,55}=3.48$, $P=0.07$, $R^2=0.06$; Observed power=0.45); again, age and body weight were not significantly related to absolute rank (age: $F_{1,55}=0.09$, $P=0.77$; body weight: $F_{1,55}=0.001$, $P=0.99$). Thus, lower M2D:4D ratios, indexing higher PAE, were more common in higher-ranking females.

Relationships Between Ranked Families Within Matrilines

Small sample sizes for three of the six matrilines (no more than six individuals in matrilines 065, 004, and 116r; see Table 6.1) meant that it was not possible to compare across families in these matrilines in a meaningful way. However, matrilines DM and 116r were larger and contained individuals from seven ranked families within both matrilines; DM: families=7; individuals=27; 116s: families=7; individual=14). As matrilines DM and 116s are from different social groups, R and S, respectively (Table 6.1), we controlled for social group (see Sect. 6.2), and treated age and weight as covariates. 2D:4D ratios and matrilineal family rank were significantly negatively correlated; members of high-ranking families exhibited lower 2D:4D (Table 6.3).

6.3.1.3   2D:4D and Birth-Order Effects in Adult Females

To test for possible birth-order effects, where possible (within families), we compared the 2D:4D ratios of oldest sisters with their youngest sisters ($N=12$ pairs); relationships were not significant (M2D:4D: $t_{11}=-0.39$, $P=0.71$).

6.3.2   Part II – Mother–Infant Dyads

6.3.2.1   Sex Differences in Infant 2D:4D

Male infants did not exhibit significant differences in L2D:4D with female infants (0.833 ± 0.037 for females vs. 0.820 ± 0.025 for males; $t_{23}=1.09$, $P=0.29$, Cohen's $d=-0.45$) or in R2D:4D (0.816 ± 0.034 for females vs. 0.808 ± 0.028 for males;

$t_{23} = 0.58$, $P = 0.57$, Cohen's $d = -0.27$). M2D:4D of male and female infants respectively were 0.814 (±0.022) and 0.824 (±0.027), with an effect size difference of $d = -0.43$. Size effects for the infants are larger than that for a larger sample of adult rhesus macaques from various captive populations (Nelson and Shultz 2010); Cohen's $d = -0.23$.

6.3.2.2   2D:4D, Age, and Weight in Mother–Infant Sample

Comparisons between infants' R2D:4D (mean and *SD*: 0.811±0.03) and L2D:4D (0.824±0.03) were not significant ($r = 0.30$, $P = 0.15$), and infants' R2D:4D was somewhat, but not significantly, lower than their L2D:4D (paired *t* test: $t_{23} = 1.91$, $P = 0.07$). Mother's R2D:4D and L2D:4D were significantly positively related ($r = 0.50$, $P = 0.01$). Digit ratios did not significantly differ between mothers and infants (mother–daughter; L2D:4D, $t_7 = 0.80$, $P = 0.45$; R2D:4D, $t_7 = 2.11$, $P = 0.07$; mother–son; L2D:4D, $t_{16} = -0.91$, $P = 0.38$; R2D:4D, $t_{16} = -1.83$, $P = 0.09$).

Mean body weight for mothers was 8.22 kg (±1.53). Mean body weight for female infants was lower than for males infants (female mean: 0.85 kg, ±0.21; male mean: 1.03 kg, ±0.21), and this difference was significant when age was controlled for ($F_{1,24} = 6.08$, $P = 0.01$; Table 6.4). There was no correlation between maternal body weight and infant body weight ($r = 0.241$, $P = 0.25$). Body weight of individuals did not significantly differ between social groups (mothers, $F_{1,24} = 1.58$, $P = 0.22$; infants, $F_{1,24} = 3.02$, $P = 0.10$) or ranked matrilines (mothers, $F_{1,24} = 1.79$, $P = 0.19$; infants, $F_{1,24} = 1.29$, $P = 0.27$). Mothers' and infants' body weight did not correlate with mothers' absolute rank in matriline (mothers, $F_{1,24} = 0.14$, $P = 0.71$; infants, $F_{1,24} = 1.70$, $P = 0.20$) or proportional rank in matriline (mothers, $F_{1,24} = 0.27$, $P = 0.61$; infants, $F_{1,24} = 0.81$, $P = 0.38$).

Mean age of mothers was 14.6 years (±5.32) and the mean age of infants was 3 months (±0.07; Table 6.4). Female infants had a lower mean age than males (female mean: 73 days, ±0.07; male mean: 83 days, ±0.06), but the ages did not significantly differ ($F_{1,24} = 3.92$, $P = 0.14$). Unlike the larger adult female sample in Part I (see above), mothers' R2D:4D in this study (Part II) significantly increased with age ($r = 0.47$, $P = 0.02$), but not their L2D:4D ($r = 0.20$, $P = 0.34$). Mothers' and infants' age did not significantly differ between social groups (mothers, $F_{1,24} = 2.08$, $P = 0.16$; infants, $F_{1,24} = 0.80$, $P = 0.38$) or ranked matrilines (mothers, $F_{1,24} = 1.73$, $P = 0.20$; infants, $F_{1,24} = 0.27$, $P = 0.61$) and did not correlate with mothers' absolute rank (mothers, $F_{1,24} = 072$, $P = 0.41$; infants, $F_{1,24} = 1.44$, $P = 0.24$) or proportional rank in matriline (mothers, $F_{1,24} = 0.31$, $P = 0.58$; infants, $F_{1,24} = 0.76$, $P = 0.39$).

6.3.2.3   2D:4D and Dominance Rank in Mother–Infant Sample

Unlike the larger, adult sample (Part I; $N = 60$), in this study (Part II; $N = 25$ dyads) there was no relationship between mothers' 2D:4D and absolute rank (M2D:4D, $F_{1,21} = 0.15$, $P = 0.70$, $R^2 = 0.04$, observed power = 0.07) or proportional rank in matriline (M2D:4D, $F_{1,21} = 0.07$, $P = 0.80$, $R^2 = 0.02$, observed power = 0.06;). This was

Table 6.4 Social, physical, and age variables in Part II (mother–infant dyads)

Social groups	Rank	Relatives	Sex	N	Mean 2D:4D	SD	Age	SD	Weight	SD	Matriline	Rank	N
F	High	Mothers	F	8	0.824	0.02	16.2	5.42	8.7	1.7	065	High	5
											004	Low	3
		Infants	F	3	0.821	0.03	0.2	0.04	0.8	0.2	065	High	2
											004	Low	1
			M	5	0.812	0.02	0.2	0.05	1.2	1.0	065	High	3
											004	Low	2
R	Middle	Mothers	F	9	0.822	0.03	15.0	6.49	8.1	1.7	DM	Low	9
		Infants	F	4	0.830	0.03	0.2	0.09	1.2	0.8	DM	Low	4
			M	5	0.802	0.02	0.2	0.09	1.2	1.0	DM	Low	5
S	Low	Mothers	F	8	0.824	0.04	12.5	3.35	7.8	1.1	116s	Low	8
		Infants	F	1	0.804	0.00	0.3	0.00	1.0	0.0	116s	Low	1
			M	7	0.824	0.02	0.4	0.40	1.3	1.1	116s	Low	7
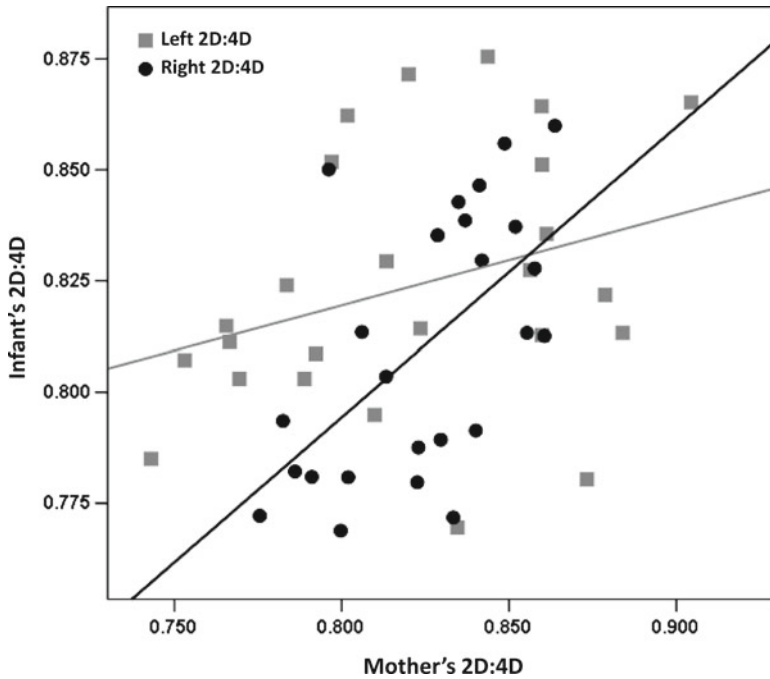
Fig. 6.1 Relationships between mother and infant 2D:4D ratios (*right* 2D:4D, $R^2=0.34$; *left* 2D:4D, $R^2=0.1$). Heritability (h^2) values for mother–infant dyads were calculated by doubling the Pearson correlation coefficients *r*. *Right* 2D:4D ($r=0.58$, $P=0.002$) has higher heritability (off the upper boundary, i.e., $h^2>100\%$) than the *left* hand 2D:4D ($r=0.31$, $P=0.13$, $h^2=62\%$)

also the case for infants, which were assumed to be the same rank as their mothers (absolute rank, M2D:4D, $F_{1,21}=0.02$, $P=0.89$, $R^2=0.07$, observed power$=0.05$; proportional rank, M2D:4D, $F_{1,21}=0.04$, $P=0.84$, $R^2=0.04$, observed power$=0.05$). Age and body weight were factored into each analysis, but were nonsignificant.

6.3.2.4   Heritability of 2D:4D

Mother–infant resemblance (based on 25 dyads, with both sexes of infants combined) was strong and significant for R2D:4D ($r=0.58$, $P=0.002$), but was not significant for L2D:4D ($r=0.31$, $P=0.13$). Hence, the heritability estimate was high, in fact off the upper boundary, for R2D:4D (i.e., $h^2>100\%$), but lower for L2D:4D and $h^2=62\%$ (Fig. 6.1). These findings (higher h^2 for the right hand than for the left) also generally held in separate analyses when accounting for offspring sex. Mother–daughter resemblance (based on eight dyads, R2D:4D: $r=0.53$, $P=0.18$; L2D:4D: $r=-0.12$, $P=0.78$) was not as strong as mother–son resemblance (based on 17 dyads, R2D:4D: $r=0.62$, $P=0.008$; L2D:4D: $r=0.42$, $P=0.09$).

6.4   Discussion

This is the first study to show a relationship between 2D:4D and dominance rank in nonhuman primates. It is also the first to provide heritability values for 2D:4D in a nonhuman primate. We found that lower 2D:4D ratios were associated with high dominance rank, while higher 2D:4D ratios were linked to lower dominance rank in a group of free-ranging adult female rhesus macaques residing on Cayo Santiago. Relationships were most marked between ranked families within matrilines with 2D:4D explaining 19% of variance in family dominance rank (Table 6.3). In contrast, no differences in 2D:4D were found between matrilines or between social groups. Relationships were therefore only evident between related individuals within matrilines (Nelson et al. 2010). These results are similar to relationships between 2D:4D and dominance-linked behaviors in humans (e.g., Hönekopp et al. 2006; Millet and Dewitte 2007; see also Manning and Fink 2008) and between dominance-related behaviors and PAE (inferred from fecal samples) in wild spotted hyenas (Dloniak et al. 2006). Similarities are also shown in the heritability levels of 2D:4D based on mother–infant dyads; values were found to be within the range of human twin and family studies of 2D:4D (Nelson and Voracek 2010).

The life experiences of individuals can differ markedly as a consequence of social rank (Bastian et al. 2003; Sapolsky 2005), and the physiological and psychological factors experienced by a gestating female are known to impact the development of the fetus (Herman et al. 2000; Thornton et al. 2009). We might expect the stable dominance ranks in the Cayo Santiago colony (Stucki et al. 1991) and the pattern by which groups fission along female kin lines (Chepko-Sade and Sade 1979) to provide the potential for differences in 2D:4D to arise between unrelated individuals and groups. However, this was not the case; differences were only detected among related individuals within matrilines. It is possible that the transfer of males leads to gene flow and prevents significant differences in 2D:4D from emerging between longstanding, differently ranked social groups. Female philopatry and the nepotistic social structure (Thierry et al. 2000), on the other hand, provide the substrate for inter-individual differences to emerge within matrilines via maternal effects. Although a females' dominance rank within the social group is likely to influence her overall quality of life, it is her support network of close female kin that she spends most time with (Chauvin and Berman 2004; Datta 1988). Consequently, a female's close kin tend to be her direct competitors. Thus, the levels of competition she experiences will be most strongly linked to her dominance rank within the matriline than her rank within the whole social group.

In rhesus macaques, competition for resources is evident at all levels of the social structure (Maestripieri 2007), and maternal effects represent a mother's ability to maximize the fitness of her offspring before birth. Abnormal conditions, such as extreme maternal stress, have been shown to masculinize and defeminize daughters and adversely affect fertility (Wallen and Baum 2002; Kaiser and Sachser 2005). Kaiser and Sachser (2005, 2009) proposed, however, that prenatal androgenization of females may be adaptive. It is conjectured that when the normal social environment

is highly competitive (i.e., at high population densities), it might be advantageous for female offspring to be androgenized in order to promote dominance traits that equip them to obtain and defend valuable resources. Although high PAE may compromise fertility, androgenized females may still fare better than other females because they can monopolize resources (Kaiser and Sachser 2005, 2009). Similar mechanisms have been proposed for relationships between female dominance rank and PAE in wild spotted hyenas, a species in which resource competition is intense and higher-ranking females have preferential access to food (see Dloniak et al. 2006). We propose that in species, such as rhesus macaques, in which dominance rank is "inherited" and clearly stratified, PAE/2D:4D may be more clearly demarcated than it is in species with more egalitarian and less clearly defined social structures. Effects may be magnified in the Cayo Santiago monkeys because the island setting itself may promote social competition by restricting distances that animals can range in search of new resources as well as restricting their ability to avoid rivals.

In rhesus monkeys, higher-ranking females have preferential access to resources (Silk 2002). When dominance hierarchies are stable, high-ranking females do not need to defend their dominance rank by expressing high levels of aggression (Higley et al. 1996; Westergaard et al. 2003). However, even when social relationships are stable, dominant females tend to show higher rates of low-level aggression toward other females (Higley et al. 1996; Westergaard et al. 2003). Higher-ranking mothers are also quicker than lower-ranking mothers to intervene aggressively on behalf of their offspring (Maestripieri 1994). The social mechanisms that underpin dominance-rank inheritance in rhesus macaque societies permit higher-ranking females to impose their authority down the hierarchy often without threat of retaliation to themselves. However, it is also possible that the physiological profile of higher-ranking adult females (higher PAE) predisposes them to be more aggressive when dealing with potential threats to status (see Millet and Dewitte 2008, 2009) or to be quicker at detecting threats to their status, enabling them to respond faster to those cues (see Coates et al. 2009; Coates 2009). In contrast, for lower-ranking monkeys, inappropriate expression of impulsive or aggressive behavior is more likely to lead to punishment. Exposure to lower PAE (as indexed by higher 2D:4D) in lower-ranking females, in conjunction with the social learning they experience as low-ranking individuals, may predispose them toward more inhibited responses, which would be socially adaptive over the longer term (e.g., winner-and-loser effects: Drummond and Canales 1998; also see Mehta and Josephs 2006).

We speculate that covariation in 2D:4D might therefore indicate different PAE on programming developmental trajectories linked to the formation of predispositions or personality types. The social landscape then provides the potential for some PAE-linked behaviors to be expressed, or reduces the potential for others to emerge during the course of an individual's development (Knickmeyer and Baron-Cohen 2006; Wallen 1996, 2005). If this is the case, these effects may be associated with promoting the development of rank-appropriate behaviors. Certainly, in macaque societies, as in many primate societies, appropriate behavior is adaptive (Bastian et al. 2003; Maestripieri 2003), while rank-inappropriate behavior can be detrimental and may even lead to severe injury and death (Bastian et al. 2003;

Westergaard et al. 2003). An extension of this behavior is that individuals recognize social hierarchies and maintain their position within the pecking order. Thus, while behavioral processes undoubtedly provide the primary mechanism for dominance-rank inheritance in Old World monkeys (e.g., Chapias 1992, 2004; Datta 1988; Holekamp and Smale 1991), physiological processes (i.e., via maternal and genetic effects) may also exert some influence (see Maestripieri 2003). It is possible, therefore, that even small inter-individual rank-related differences in PAE (indexed by 2D:4D) may support female dominance-rank inheritance within and between generations of cercopithecine primates.

In humans, exposure to higher PAE, indexed by low 2D:4D, appears to predispose individuals toward expressions of dominance (i.e., aggression and competitiveness) and these effects have been demonstrated in both sexes (e.g., Bailey and Hurd 2005; Benderlioglu and Nelson 2004; Manning and Fink 2008). Differences in 2D:4D may correlate with different adaptive approaches to situations that increase evolutionary fitness such as avoiding harm or acquiring resources. For example, Millet and Dewitte (2009) have shown that, after exposure to aggressive cues (violent video and aggressive words within written sentences), low 2D:4D individuals tend to respond aggressively under test conditions, while individuals with higher 2D:4D ratios become more prosocial. It is postulated that, individual with low 2D:4D may be predisposed to react strongly in potentially aggressive situations in order to maintain status. Conversely, for individuals with higher 2D:4D, it may be more adaptive to tackle an opponent (who is potentially stronger and more aggressive) by adopting a nonthreatening manner (Millet and Dewitte 2009). These findings might suggest that, in macaques, rank-related differences in 2D:4D could be associated with PAE on the development of rank-appropriate behaviors.

In humans, 2D:4D and digit lengths have been shown to vary with birth order and the sex ratio of older siblings (Williams et al. 2000; Saino et al. 2006). Offspring digit ratios have also been associated with maternal fecundity (Saino et al. 2006). It has been postulated that variation in offspring 2D:4D/PAE could occur via maternal-androgenizing effects that vary according to the mother's physical and social environment (such as those described above; see Kaiser and Sachser 2005). However, maternal effects may also be associated with the *condition* of the mother, such as age and the physiological traces of previous offspring on maternal tissues (i.e., the notion of tissue memory; see Williams et al. 2000). These factors could serve to confer cellular-level signals to the fetus about the extra-uterine environment, such as maternal health or levels of sibling rivalry (see Saino et al. 2006). Although we expected 2D:4D to be lower in younger daughters (PAE increase), we found no birth-order effects on 2D:4D within families: younger, higher-ranking sisters did not have more masculinized (lower) digit ratios than older, lower-ranking sisters. These findings therefore suggest that the pattern of strict youngest daughter ascendancy (within families) in rhesus macaques is not supported by PAE. However, the fact that we see associations between dominance ranks within matrilines (which are rank-ordered by the youngest daughter ascendancy rule) suggests that we should see a relationship. This leads us to conclude that the sample size used in this test ($N=12$ sister–sister dyads) is too low to test this hypothesis and may be obscuring real relationships.

Do individuals with low 2D:4D have higher circulating androgen levels? Relationships between 2D:4D and serum androgens have been shown in male, but not in female guinea baboons (*Papio papio*; Roney et al. 2004). Associations in humans are also inconsistent (see Hönekopp et al. 2007 for an overview), although parallels are evident between the behavioral responses of individuals with low 2D:4D (high inferred PAE) and individuals with high testosterone levels (Mazur and Booth 1998; Grant and France 2001). It is possible that 2D:4D could be reflecting PAE on programming neuroendocrine pathways (i.e., hypothalamic–pituitary–gonadal axis; see Fowden and Forhead 2009) and/or genetic sensitivity to circulating androgens. For example, in mammals (guinea pigs), masculinization of female offspring is associated with male-typical patterning and upregulation of androgen receptors in certain brain regions (Kaiser and Sachser 2005). In humans, low 2D:4D ratios in males (females were not tested) have been associated with more sensitive androgen receptor gene expression (Manning et al. 2003; but see Hurd et al. 2011). If higher-ranking female rhesus macaques with lower 2D:4D are more sensitive to androgens compared to lower-ranking females, these effects could lead to different responses to androgen-inducing situations in adulthood, even though absolute levels of the hormone may not vary significantly between individuals.

This study provides the first opportunity to investigate sex differences in 2D:4D in a cohort of nonhuman primate individuals that have been only minimally influenced by postnatal influences (mean age 3 months). Among infant monkeys, males had lower 2D:4D than females. Although these sex differences were not significant, they were in the expected direction; males are normally exposed to higher PAE and will therefore generally have lower 2D:4D than females. Mean 2D:4D values in this infant sample were similar to published values for captive, adult rhesus macaques (Nelson and Shultz 2010), and size effects between male and female infant ratios were also in the range of those presented for humans (see Voracek et al. 2007b). If, as suggested by our results, interactions do exist between maternal-androgenizing effects and female dominance rank in rhesus monkeys, then it is possible that these rank-related mechanisms may act to blur sex differences in 2D:4D ratios in this species (e.g., higher-ranking females having more male-like 2D:4D ratios).

The heritability values are based upon mothers and very young infants. This study design might be advantageous in that the potential impact on 2D:4D from possible postnatal growth and environmental influences can be considered minimal. However, the disadvantage of this approach is that heritability can be inflated due to the exclusion of possible nonshared environmental effects on the digit ratio occurring through growth (Nelson and Voracek 2010). For example, we found that right 2D:4D increased with age among adult females in Part II, but not in Part I (Part II females formed part of the Part I sample). Age effects were not observed in infant monkeys, which could be attributable to this group's narrow age range. In adult chimpanzees, sex differences in 2D:4D have been shown to increase with age (McIntyre et al. 2009). Humans differ from this pattern in that 2D:4D increases slightly during childhood while sexual dimorphism remains consistent (McIntyre et al. 2005; Trivers et al. 2006). By adulthood, 2D:4D appears stable (Manning 2002; Gillam et al. 2008). Changes in 2D:4D through life (within and between species) are

likely to confound heritability estimates based upon familial resemblance, and this should be considered in future analyses.

Familial resemblance of 2D:4D between mothers and their infants yielded high heritability values (Fig. 6.1). This suggests that genetic and prenatal contributions to the expression of 2D:4D are substantial and strengthens the conjecture that relationships between 2D:4D and PAE may generalize across taxa (Manning 2002; Nelson and Voracek 2010). Heritability values were higher in the right hand compared to the left (Fig. 6.1). These estimates, particularly the lower correlation for left 2D:4D and the high heritability estimate for right 2D:4D, may stabilize in larger samples. The differences in heritability between hands in this study (higher for the right side than for the left) are concordant with results from another familial study (Voracek and Dressler 2009), but differ from twin studies that show higher heritability values for left hands than for right hands (Gobrogge et al. 2008; Medland and Loehlin 2008). Some of these contradictory findings may be associated with environmental factors that are reported to have a stronger influence on one side of the body than the other (see Flegr et al. 2008).

Heritability of 2D:4D was higher between mothers and sons than between mothers and daughters. A familial resemblance study in humans, however, showed stronger heritability through the male line (i.e., father–son and brother–brother; Voracek and Dressler 2009), which suggests that 2D:4D may be inherited though Y-linked genes (i.e., *Sry*, sex-determining gene). Inheritance of 2D:4D via the Y-chromosome conflicts with the idea of X-linked associations (i.e., via the androgen receptor gene; see Manning et al. 2003) and the findings of no evidence of sex-linked inheritance in a recent study of twins (see Medland and Loehlin 2008). However, given the general conformity of high heritability estimates for 2D:4D from this study, several human studies (twin and family), and two parent–offspring studies of zebra finches, it seems unlikely that mechanisms of genetic inheritance differ between macaques and other taxa. It is possible that our results (higher heritability between mothers and sons) may be a consequence of low sample size ($N=25$ mother–offspring dyads), particularly for females ($N=8$ mother–daughter dyads), which makes the results prone to error (types I and II). Additionally, the application of different measurement methodologies may also impact heritability estimates. The digit ratios in this study are based on direct measurements of finger lengths, whereas heritability studies use measurements taken from hand images such as photocopies (e.g., Gobrogge et al. 2008; Medland and Loehlin 2008; Voracek and Dressler 2009). It is now recognized that the imaging process can distort finger lengths in sex-specific ways (Manning et al. 2005; Caswell and Manning 2009; Hönekopp and Watson 2010); so, when possible, direct measurements of hands should be used (Manning and Hill 2009). In addition, it is known that soft-tissue changes occur in response to cyclical and short-term changes in hormonal concentrations in males and females (Scutt and Manning 1996; Manning et al. 2002). These factors, along with age-related changes (see above), are likely to impact heritability estimates of 2D:4D and confound cross-study comparisons.

The results of this small familial study clearly need to be supported by further research before firm conclusions can be drawn. Future studies may consider using

callitrichids, the only family of primates that consistently produce twins (Goldizen 2003) or, alternatively, a study design that includes pedigree relationships (see Kruuk 2004). Incorporating sire–offspring dyads in a family study design would also enable maternal effects to be estimated and would provide an opportunity to explore and resolve conflicts in the human 2D:4D literature regarding sex-liked genetic inheritance pathways. Importantly, studies of heritability should aim for much larger samples and address possible founder effects (see Chepko-Sade and Sade 1979) and, when possible, any potential influence of consanguinity and assortative mating (see Voracek et al. 2007a; Voracek and Dressler 2009), as well as other potentially relevant developmental influences on 2D:4D such as growth (see Manning 2010).

6.5   Conclusions

Social processes undoubtedly provide the primary mechanism by which dominance rank is attained in cercopithecine primates; however, the preliminary results presented in this study support the idea that PAE, indexed by 2D:4D, might also contribute to maintaining dominance hierarchies. We found that the 2D:4D ratios of adult female rhesus monkeys were positively related to dominance rank, with effects being most evident between related individuals. Familial resemblance of 2D:4D indicates that heritability is high in this population. The rank-associated patterns shown in the larger study suggest that a proportion of this familial resemblance may be linked to prenatal maternal effects, which may occur via physiological responses to competition between relatives within matrilines. We further speculate that variation in PAE between ranked individuals may influence whether individuals react to social situations in a rank-appropriate manner. If correct, these effects are likely to be highly adaptive in strongly bonded hierarchical social systems, as even small differences in an individual's abilities to dominate and confront others appropriately are likely to impact fitness.

More research on nonhuman primate 2D:4D is needed to understand how genetic and nongenetic components of PAE may influence behavior and how these might vary within and between populations. In primatological research, however, obtaining data from many individuals (even captive species) is rarely achievable. Refining the study design may therefore be the most practical approach to primate 2D:4D research. For example, a better understanding of maternal and genetic effects on 2D:4D could be achieved by introducing other familial dyads such as sibling–sibling, half-sibling, or sire–offspring data and by incorporating birth order and sibling sex ratio. Unfortunately, in many colonies (wild and captive), even this approach is not possible due to uncertainties about sires. The Caribbean Primate Research Center can, however, support this kind of research since all monkeys are known on an individual basis and matrilineal records have been maintained and, for some cohorts, information of sires is also available. The CPRC therefore provides a unique potential to investigate inter-individual differences in nonhuman primate 2D:4D, which will add to our knowledge of the

biological underpinnings, evolutionary variation, and potential usefulness of digit ratios as a convenient research tool.

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Chapter 7
Ontogeny of Anatomical Mechanical Advantage of the *Biceps Brachii* Muscle in Macaques

Connie D. Fellmann

7.1 Introduction

Compared to adults, young primates experience a unique set of social and ecological pressures. Specifically, young primates tend to be slower, weaker, and less agile than adults due to smaller muscle mass and lack of complete integration between their central nervous and motor systems (Bradley and Bekoff 1989; Thelen 1989; Stehouwer 1992; Assaiante and Amblard 1993; Carrier 1996). These limitations can increase juvenile risk, defined as the ecological risk of death in individuals between weaning and sexual maturity (Janson and van Schaik 1993). Such risk can occur from predators which target younger weaker animals and adult conspecifics that displace juveniles from or more quickly secure prime feeding locals. Janson and van Schaik (1993) suggested two alternate strategies that may effectively counter these limitations and positively influence fitness: (1) rapid growth, minimizing the duration of the juvenile stage, or (2) slow growth, allowing juveniles time to acquire the social and life skills necessary to become successful adults. The second strategy is facilitated by a suite of age-dependent morphological and social attributes selected to decrease juvenile risk, maximize survivorship, and reach reproductive maturity.

In the extended juvenile life-history phase of primates, dramatic postcranial changes occur that influence locomotion in ways that can distinguish their behavior from adults or allow adult behavior despite smaller size. These changes can include (1) the shifting of muscle limb mass from a distal to a proximal placement, (2) attainment of adult body proportions or segments but not adult mass, and (3) epiphyseal growth and fusion (Cheverud 1981; DeRousseau et al. 1983; Turnquist and Wells 1994; Wells and Turnquist 2001; Raichlen 2005b). Shifting muscle mass placement in young primates, such as rhesus (Turnquist and Wells 1994), Japanese macaques

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(Hamada 1983), and yellow baboons, results in lower stride frequencies, longer stride lengths, and longer stance durations as documented in *Papio cynocephalus* (Raichlen 2005a, b, 2006). The increased distal limb mass concentration in young baboons suggests that the juvenile gait may be selected to increase stability. Such stabilization may be a selective advantage to overcoming the clumsiness of youth.

The negative allometric growth of skeletal elements has also been suggested as an adaptive response to counter ontogenetic limits on locomotor performance (Hamada 1983; Young 2005; Lawler 2006). For example, negative allometric growth is documented in the distal limb elements (Jungers 1985), particularly in the hands and feet. Thus, individuals have relatively large hands and feet early in ontogeny. These elements decrease in their growth velocity relative to overall body mass after the attainment of locomotor independence and is documented in *Macaca* (Hamada 1983; Grand 1977; Cheverud et al. 1992; Turnquist and Wells 1994), *Cebus* (Jungers and Fleagle 1980), *Ateles* and *Saimiri* (Ford and Corruccini 1985), and *Propithecus* (Ravosa et al. 1993; Lawler 2006). The relatively large hands and feet of juveniles allows for the use of "adult-sized" substrates, facilitating "adult-like" locomotor behavior despite not having attained adult body mass (Lawler 2006).

Ontogenetic allometric scaling is also documented in other skeletal element. In capuchin monkeys (*Cebus apella* and *C. albifrons*), for example, the distal forelimb segment increases with extreme positive allometry, resulting in the negative growth allometry of muscle mechanical advantage in *biceps* and *triceps brachii* muscles. As a result, young capuchin monkeys have relatively higher muscle mechanical advantage compared to older conspecifics despite smaller muscle and body sizes (Young 2005).

7.1.1 Evolutionary Implications for Increased Muscle Mechanical Advantage in Juveniles

Higher muscle mechanical advantage in the limb skeleton of juveniles might be under strong selective pressure. This is because higher muscle mechanical advantage provides increased muscle and propulsive power to smaller muscle mass which (1) may facilitate access to alternative locomotor substrates and (2) increases predator avoidance response times. Juvenile primates in several taxa including Barbary (Mernard 1985) and Japanese macaques (Chatani 2002, 2003), mountain gorillas (Fossey and Harcourt 1977; Fossey 1979), and chimpanzees (Doran 1992, 1997) are documented to use the arboreal substrate at much higher frequencies than adult conspecifics. Juvenile rhesus macaques, for example, spend nearly half of their activity budget in arboreal substrates compared to just over a third of the adult budget increasing body mass from ~1.60 kg in infants to ~10.60 kg in adults (Grand 1977). Further, they have a more varied locomotor repertoire with higher frequencies of climbing, leaping, galloping, trotting, running, hopping, and clambering and much lower frequencies of quadrupedal walking compared to adults (~33% vs. ~71% in adults, Wells and Turnquist 2001). As such, Wells and Turnquist (2001) described the locomotor behavior of young macaques as one that involves high

frequencies of climbing and "rapid propulsive quadrupedal modes." Higher muscle mechanical advantage would also be beneficial to less vigilant juveniles by increasing their response time in evading predators by increasing the propulsive power of their limbs despite slower running speeds (Carrier 1983, 1995, 1996).

To test for changes in muscle mechanical advantage with ontogeny, the skeletal growth allometry in the forearm of three Old World Monkeys is examined following previously established methods by Carrier (1983) and Young (2005), and the hypothesis that muscle mechanical advantage is relatively high in young macaques decreasing with age through negative allometric scaling of the forelimb skeleton is tested.

7.1.2 Changes in Effective Mechanical Advantage with Body Size and Growth

Locomotor function, performance, and postural stability are directly related to muscle mechanical advantage. High mechanical advantage is obtained through relatively high ratios of lever to load arm values, while low mechanical advantage is obtained through low ratios. Functionally, higher mechanical advantage (longer lever arm to load arm length) increases the propulsive power of the associated muscle group, improving the ability to accelerate and decelerate rapidly. Conversely, low mechanical advantage (relatively short lever arm to load arm length) creates greater limb angular excursion, emphasizing speed rather than power (Gregory 1912; Stern 1974; Carrier 1983; Anemone 1993; Lieber and Friden 2001).

The *effective mechanical advantage* (EMA) of a given muscle (F_m) is defined as the ratio (r/R) of the agonist muscle lever arm (r) to the load arm or moment arm (R) of the substrate reaction force (F_s) acting about a joint (Fig. 7.1). EMA is proportional to the force necessary to maintain body posture against the force of gravity. Several factors influence EMA, including the scaling relationships between body and muscle mass and limb posture (Biewener 1989b, 1990). Biomechanically, as an animal increases in size, peak stresses (ratio of force to muscle physiological cross-sectional area) should increase, producing greater joint moments at a given mass-specific force (Alexander et al. 1981; Biewener 1982a, b). However, this increase in mass-specific force is mitigated by limb joint posture whereby larger animals adopt more extended limb postures, thus aligning their joints more closely with the substrate reaction force (F_s) (Gray 1968; Biewener 1989a, b). By so doing, the associated load arm (R) is effectively shortened. The combination of longer lever arms (r) and shorter load arms (R) increases the effective mechanical advantage (r/R) of the limb muscles and decreases the muscle force needed to support the body's mass against gravity. Several studies indicate that as muscle moment arms increase, the torque production increases while shorter muscle moment arm allows greater distal limb displacement through greater angular velocity (Gregory 1912; Stern 1974; Anemone 1993; Lieber and Friden 2001). In other words, high EMA decreases the magnitude of muscle force needed to counter the torque acting on a joint (Biewener 1989a, b, 1990, 2003, 2005; Polk 2002, 2004). According to Biewener (1989a, b, 1990), the increase in EMA is a significant factor in the locomotor behavior of
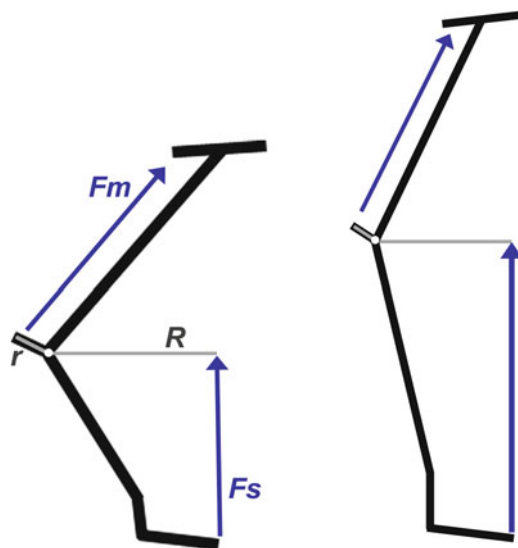
Fig. 7.1 Here a primate forelimb is shown in mid-stance for flexed (*left*) and extended limb postures (*right*). The animals head would be to the right. Effective mechanical advantage (EMA) is the ratio of **r** (the lever arm of the agonistic muscle) to **R** (the moment or load arm of the substrate reaction force). If the force of the agonistic muscle (F_m) acting on the joint lever (*r*) is equal to the torque produced by the substrate reaction force (F_s) acting on its moment arm (*R*), then postural stability is maintained. The moment arm (*R*) of the substrate reaction force is dependent on the length and posture of the limb

mammals. For example, a 0.3-kg squirrel has an EMA of ~0.2 compared to ~1.0 for a 300-kg horse, which exerts only 17% of the mass-specific force of a squirrel, thus decreasing its joint force by ~85% (Biewener 1989a, b).

The positive scaling relationship between body mass and EMA has been documented within primates (Polk 2002, 2004). Polk focused on the effects of differing limb length and body mass on muscle mechanical advantage in closely related cercopithecine monkeys with similar locomotor modes: *Chlorocebus aethiops* (vervet monkey), *Erythrocebus patas* (patas monkey), and *Papio anubis* (olive baboon). Polk's results showed that (1) *within* similarly sized taxa, those with longer limbs used more extended limb postures and (2) *across* these taxa, larger animals used more extended limb postures, had lower joint moments, and higher extensor muscle EMA. Thus, Biewener's predictions concerning the positive allometric scaling relationship between EMA and body size and negative allometric relationship between joint moment and limb posture are supported within the primates.

Following Biewener's (1989a, b, 1990) model, I expect the growing musculoskeletal system to place those same forces on an individual throughout growth if increases in body mass cause a concomitant increase in joint torque. Thus, allometric increases in muscle mass, lever arm length, and extended joint postures will allow an animal to overcome increases in joint moments. Currently, data examining the scaling relationship between muscle mass and body weight is lacking. But, there is some suggestion that muscle groups scale independently of one another, and that

muscles of the hands and feet may scale with negative allometry, while those of the arm increase with slight positive allometry relative to body mass (Grand 1977; Rodman 1979; Hamada 1983; Turnquist and Wells 1994). In terms of limb posture, both young rhesus (Wells and Turnquist 2001) and Japanese macaques (Chatani 2002) are observed to use fairly flexed limb postures compared to adult conspecifics. However, as with data on muscle mass, data measuring ontogenetic changes in limb posture are rare. Several studies addressing quadrupedal ontogeny and limb mass distribution found that young baboons used longer strides and lower stride frequencies due to more distally concentrated limb mass distribution and estimated that the changes in limb flexion with age in yellow baboons (*Papio cynocephalus*) could reduce the natural pendular period of the limb by as much as 12% (Raichlen 2004, 2005a, b). The decrease in the natural pendular period resulted in infants with relatively lower internal power outputs but higher external power outputs. Ontogenetically, total power outputs remained the same, suggesting that ontogenetic changes in kinematics help to maintain energy costs (Raichlen 2006).

Two studies have found that EMA scales with negative allometry during growth in mammals (Carrier 1983 and Young 2005). In these studies, Carrier and Young used *anatomical mechanical advantage* (AMA) as a proxy for EMA, dividing the length of the *anatomical* lever arms by their associated *anatomical* load arms. For example, to measure the AMA of the *triceps brachii* muscle, Carrier (1983) divided the olecranon process by forelimb length (the sum of the forearm and hand). He found that during growth in black-tailed jackrabbits (*Lepus californicus*) and domestic cats (*Felis domesticus*) lever arm lengths for the *triceps brachii*, *triceps surae*, and *gastrocnemius* scaled to body mass with negative allometry. Further, juveniles had relatively stronger *gastrocnemius* muscles giving them greater forces around their joints, allowing them to accelerate more rapidly when jumping than did adults despite being 25–30% of adult size (Carrier 1995, 1996). Young (2005) obtained similar results in capuchin monkeys (*Cebus albifrons* and *Cebus apaella*). Specifically, Young found that while lever arm length of the *m. biceps brachii* and *m. triceps brachii* scaled to body mass with positive allometry, the ratio of lever to load arm length (AMA) scaled with negative allometry due to the extreme positive scaling of the associated anatomical load arm. Thus, young capuchin monkeys had greater muscle mechanical advantage compared to older conspecifics, possibly helping younger animals overcome relatively weak extensor muscles.

In the context of these previous studies, I suggest that the rapid and propulsive quadrupedal modes of juvenile macaques are facilitated, morphologically, through increased muscle mechanical advantage. Here, I test for changes in muscle mechanical advantage by examining the ontogenetic scaling relationships between body mass and the *biceps brachii* muscle of the forelimb in three species of Old World Monkeys (*Macaca fuscata*, *M. fascicularis*, and *M. mulatta*) that differ in body size and frequency of substrate use. Changes in lever arm scaling are analyzed across an ontogenetic sample of infants, juveniles, and adults by regressing (1) *anatomical* lever arm length onto *anatomical* load arm length and (2) AMA on body mass. The hypothesis will be supported if (1) the *anatomical* lever arm length scales to the *anatomical* load arm length with negative allometry and (2) *anatomical* mechanical advantage (AMA) scales to body mass with negative allometry.

7.2   Materials and Methods

7.2.1   Macaques Used in this Study

In this study, changes in anatomical lever arm scaling with age are evaluated in an ontogenetic sample of known body mass of three species of macaques: *Macaca mulatta* (Zimmermann 1780), *Macaca fuscata* (Gray 1870), and *Macaca fascicularis* (Raffles 1821), all of the *fascicularis* group of macaques (Fooden 2006). The macaques used in this study have similar intermembral indices (93 in *M. fascicularis* and *M. mulatta*; 91 in *M. fuscata*) and are considered semi-terrestrial quadrupeds (Fleagle 1999; Kurita et al. 2002). However, they differ in body mass and frequency of use of the terrestrial substrate, suggesting difference in the scaling relationship of key muscle groups. The smaller *M. fascicularis* (3.6–5.4 kg) is the least terrestrial, occupying the terrestrial substrate about 30% of the time compared to the larger *M. mulatta* (5.3–7.7 kg), and *M. fuscata* (8.5–11.2 kg) which are about 70% terrestrial (Cant 1988; Fleagle 1999; Wells and Turnquist 2001; Chatani 2003; Fooden 2006). Female Japanese macaques, however, exhibit similar frequencies of arboreal behavior as *M. fascicularis* (Chatani 2003). These differences in body mass and substrate use are important for identifying whether differences in scaling are the result of body mass or locomotor behavior.

7.2.2   Dental Age Comparisons

Samples of *Macaca mulatta* are from the Cayo Santiago research colony of the Caribbean Primate Research Center (CPRC) in San Juan, Puerto Rico. Rhesus macaques from the CPRC are Indian derived and partially provisioned (Rawlins and Kessler 1986). *Macaca fuscata* and *M. fascicularis* are housed at the Kyoto University Primate Research Institute (Inuyama, Japan). Both samples are from wild-caught populations (Dr. Yuzuru Hamada, personal communication). Samples include male and female infants, juveniles, and adults (Table 7.1). Individual specimen age is determined by dental crown eruption and subdivided into age classes (modified from: Shea 1981; Smith 1989; Smith et al. 1994; Taylor 1997): infant (partial to full eruption of deciduous dentition), juvenile (all deciduous dentition erupted plus any combination of M^1 or M^2 partially or fully erupted or M^3 partially erupted), and adult (M^3 fully erupted with minimal to moderate wear). Individuals with heavy wear on the M^3 are excluded to control for age-related bone loss.

7.2.3   Measuring Anatomical Mechanical Advantage

In order to facilitate comparison with previous studies (i.e., Carrier 1983 and Young 2005), I follow previous established methods and measurements to test for changes in muscle mechanical advantage with age in the *biceps brachii* muscle through the

Table 7.1 Sample sizes for specimens by developmental stage

	Infant	Juvenile	Adult
Load arm length			
M. fascicularis	15	79	74
M. fuscata	49	68	87
M. mulatta	33	68	85
Biceps brachii lever arm			
M. fascicularis	18	79	74
M. fuscata	53	68	87
M. mulatta	73	73	88
Body mass			
M. fascicularis	10	46	43
M. fuscata	40	67	74
M. mulatta	7	26	10

Fig. 7.2 Measurements used in this study shown in the right radius of a macaque: (*r*) the *biceps brachii* lever arm length (*dashed line*) and (*R*) the anatomical load arm length (*solid line*)

use of a skeletal proxy. All measurements were taken with digital sliding calipers and an osteometric board. Anatomical mechanical advantage (AMA) is used as a proxy for effective mechanical advantage (EMA) with the assumption that anatomical load arm length is proportional to but not equal to substrate reaction force load arm (Young 2005). Body mass (kg) measurements were available for most individuals and had been taken at the time of death.

The anatomical lever arm (*r*) for the *biceps brachii* muscle is measured from the most proximal point on the radial head to the midpoint of the radial tuberosity (Fig. 7.2). The more distal the insertion for the muscle, the longer the lever arm for the muscle and the greater the increase in force the muscle can produce (Swartz 1993). The *biceps brachii* muscle is an elbow flexor during forearm supination (Naito 2004). Its associated anatomical load arm (*R*) is forearm (radius) length (modified from Young 2005). The measured anatomical load arm length serves as a proxy and is assumed to be proportional but not identical to actual load arm length (Young 2005). A more accurate measure of anatomical lever arm length would include a measure from the center of joint rotation (i.e., the humeral trochlea); however, this element was generally lacking in availability within the samples. Given that trochlear length is not included in any individual measured here, the difference is presumed to be proportional across all age classes. Only elements with associated epiphyses were included in this study.

7.2.4   Bivariate Ontogenetic Allometric Analyses

Changes in the rate of growth between lever and load arm are measured as the degree of allometric scaling. There are several methods for allometric analysis: (1) ontogenetic/growth allometry, (2) intraspecific allometry, and (3) interspecific allometry. Here, I use ontogenetic growth allometry where individuals under comparison are growth stages within a single species (from infancy to adulthood) and size differences are age differences (Shea 1983; Fleagle 1985). In growth allometry, a line of best fit across all data points represents the ontogenetic pathway transversed by all normal individuals of that species (Fleagle 1985).

Using mode II reduced major axis regression (Sokal and Rohlf 1995), all growth data are log transformed whereby X and Y are related by the allometric power equation: $Y = ax^b$ (Huxley 1932). Where X (body mass or load arm length) relates to parameter Y (AMA or lever arm length) by the exponent b. Log transforming the data gives the linear equation $\log Y = \log b + a \log X$. The power function of the exponent (b) is equal to the slope of the fitted line and shows whether parameter Y is increasing at a faster rate (positive allometry), slower rate (negative allometry), or at the same rate (isometry) as parameter X (Huxley 1932; Gould 1966; Carrier 1983; Warton et al. 2006). The value of the allometric exponent (b) that determines isometry is dependent on the units of X and Y. When the units are the linear, isometry is recognized when $b = 1$; when a linear measurement is regressed onto mass, isometry is recognized when $b = 0.33$ (Gould 1966). When regressing AMA onto body mass, isometry is recognized when $b = 0$; this is because anatomical mechanical advantage (length/length) is a dimensionless ratio (Young 2005).

Reduced major axis regression slopes, for each species, were calculated, compared, and tested for isometry using SMATR (Warton et al. 2006; Table 7.2). SMATR is analogous to tests made in ANCOVA. If a common slope was found where $p > 0.05$, residual scores (R) and fitted scores (F) were compared to test for shifts in elevation and shifts along the common slope. If no common slope was found (i.e., $p < 0.05$, slopes differed across taxa), post-hoc multiple comparisons were run to determine which group differed (Table 7.3). In tests of slope heterogeneity (i.e., pair-wise comparisons), the probability of type I error increases; thus, a Bonferroni adjustment was made by lowering the significant critical p value of 0.05–0.0167 and the highly significant p value of 0.01–0.003 ($p = \alpha/n$ test) (Hill and Lewicki 2007). All statistical procedures were performed in the program SMATR – Standardised Major Axis Tests & Routines Version 2.0 (Falster et al. 2006; Warton et al. 2006) and R v2.10 (R, 2008).

7.2.5   Predictions for Anatomical Mechanical Advantage

In all macaques, body size and limb length increase with ontogeny (Grand 1977; Hamada 1983; Turnquist and Wells 1994). The increase in mass and length should create an increase in joint moments as suggested by Biewener (1982a, b).

Table 7.2 Ontogenetic scaling of variables

	n	Slope[a]	F[b]	Scale[c]	R^2	Low CI	Upp CI	Intercept
Radius on body mass								
M. fascicularis	98	0.3739**	3.975*	+	0.69	0.333	0.419	0.774
M. fuscata	178	0.4117**	117.75**	+	0.937	0.396	0.428	0.562
M. mulatta	40	0.335**	0.032	=	0.929	0.307	0.366	0.740
Biceps brachii lever (BLA) on body mass								
M. fascicularis	99	0.445**	29.117**	+	0.702	0.3947	0.4916	−0.350
M. fuscata	180	0.4578**	149.30**	+	0.869	0.4339	0.4829	−0.502
M. mulatta	43	0.4737**	48.179**	+	0.890	0.42167	0.5259	−0.535
Biceps brachii lever (BLA) on radius (load arm)								
M. fascicularis	168	1.150**	20.948**	+	0.845	1.082	1.21	−1.204
M. fuscata	203	1.115**	44.945**	+	0.947	1.080	1.151	−1.209
M. mulatta	184	1.222**	95.748**	+	0.923	1.173	1.272	−1.448
Biceps brachii AMA on body mass								
M. fascicularis	98	0.184*	–	+	0.043	0.151	0.223	−1.505
M. fuscata	178	0.120**	–	+	0.048	0.103	0.138	−1.404
M. mulatta	40	0.175**	–	+	0.39	0.135	0.225	−1.687

[a]$p_{crit}=0.05$ (*$p \leq 0.05$; **$p \leq 0.01$)
[b]F-statistic for the estimated RMA slope tested against the expected isometric value
[c]Direction of ontogenetic scaling: positive allometry (+), isometry (=) based on test of isometry F-statistic

Table 7.3 Test of heterogeneity of RMA slopes

	p[a]	*M. fascicularis* vs. *M. fuscata*[b]	*M. fascicularis* vs. *M. mulatta*	*M. fuscata* vs. *M. mulatta*	F[c]	R
Radius on body mass	0.001	0.119	0.134	0.001	–	–
BLA on body mass	0.631	–	–	–	98.89**	101.39**
BLA on radius	0.002	0.385	0.094	0.001	–	–
AMA on body mass	0.003	0.001	0.770	0.012	–	–

[a]Test for heterogeneity in slope across all three taxa. Slopes are significantly different if $p \leq 0.05$
[b]p values for test for heterogeneity between two taxa (i.e., pair-wise comparisons), slopes are significantly different if $p \leq 0.01$
[c]Comparison of lines with common slope. Wald test for shifts of fitted axis scores along the axis (F) and residual axis scores for shifts in elevation (R), *$p<0.05$, **$p<0.01$

In order to compensate for the increasing joint moments with age, these primates could increase muscle cross-sectional areas, thus giving muscles more force to overcome joint moments, use more extended limb postures, or increase the mechanical advantage of the associated muscle group (Young 2005). The EMA of a muscle to generate a given force against the ground is calculated as the ratio of r/R, where r is the product of the muscle lever arm weighted against the muscle fiber cross-sectional area (a measure of muscle force) and R is a measure of the ground reaction force vector (Biewener 1991, 1989b; Biewener et al. 2004). Currently, no data are available that address the ontogenetic scaling of muscle

fiber cross-sectional area. However, there are data suggesting that muscle mass of the *biceps brachii* muscle increases proportionally with growth in macaques (Grand 1977; Hamada 1983) and limb posture becomes increasingly extended with age (Hamada 1983; Wells and Turnquist 2001), suggesting that EMA should scale with allometry. The following prediction regarding AMA is tested based on the assumption that muscle mass increases isometrically with growth and limb postures become more extended: P1: AMA should increase with positive allometry or isometry to counter increased joint moments due to increased body mass and longer limbs. Under this expectation, both lever arm and load arm length, relative to body mass increase at a similar rate or lever arm length, increase at a slightly faster rate than its associated load arm. The larger *M. fuscata* should have faster rates of AMA growth due to larger lever arm length to counter larger body mass and increased terrestriality. *M. fascicularis* should have the slowest rate of growth given its smaller size.

7.3   Results

Radius (load arm) length grows with significant positive allometry when scaled to body mass in *M. fascicularis* ($b = 0.373$, $F = 3.975$, $p = 0.049$) and *M. fuscata* ($b = 0.412$, $F = 134.54$, $p < 0.001$); however, *M. mulatta* scales with isometry (Table 7.2; Fig. 7.3). With a critical p value set to 0.01, there were no significant differences in scaling between any taxa (Table 7.3). Similarly, *biceps brachii* lever arm length scaled to body mass with significant positive allometry and was significantly different from the expected isometric slope of $b = 0.33$ in all three taxa: *M. fascicularis* ($b = 0.44$, $F = 29.11$, $p < 0.001$), *M. fuscata* ($b = 0.45$, $F = 149.30$, $p < 0.001$), and *M. mulatta* ($b = 0.47$, $F = 48.19$, $p < 0.01$). Moreover, interspecific rates of scaling did not differ significantly across taxa ($p = 0.631$, Table 7.3). Even though all slope values increased with positive allometry (with the exception of radius length in *M. mulatta*), slope values for lever arm lengths were much higher than those for the associated load arm length. In both *M. fascicularis* and *M. mulatta*, larger and older individuals have longer forearms relative to their body mass, and across all taxa, larger and older individuals had much longer lever arm lengths than expected for their body mass.

Changes in anatomical mechanical advantage (AMA) were calculated (1) by regressing anatomical lever arm onto anatomical load arm length and (2) by regressing AMA directly onto body mass (Fig. 7.4). By regressing lever arm length onto load arm length, the relative growth of lever arm to load arm could be assessed. Regression of the ratio of lever arm to load arm length (AMA) onto body mass allows for a more direct relationship between AMA and size to be assessed (Fig. 7.4). The *biceps brachii* lever arm length on load arm length (*biceps brachii* AMA) scales with significant positive allometry and is significantly different from an isometric slope of $b = 1.00$ in all taxa (Table 7.2, Fig. 7.4). Results indicate that with age and
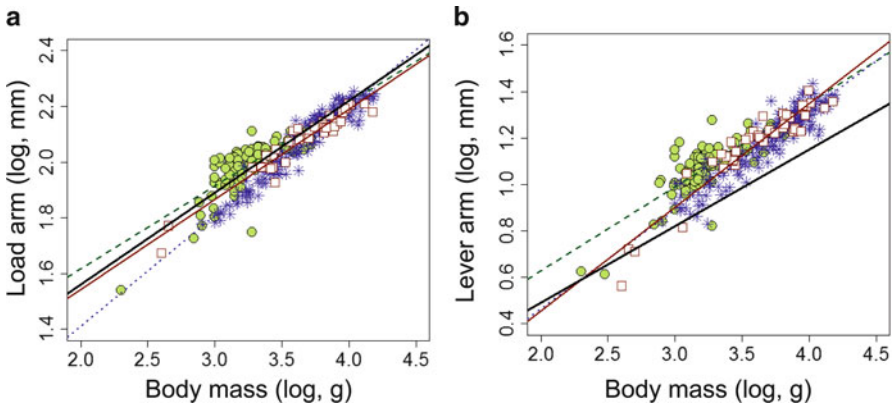
Fig. 7.3 Relative growth of (**a**) the *biceps brachii* load arm (radius) and (**b**) the *biceps brachii* lever arm scaled to known body mass. *Macaca fascicularis* (*green circles*), *M. fuscata* (*blue stars*), and *M. mulatta* (*squares*). *Black line* represents isometry. For radius length, *M. fascicularis* and *M. mulatta* scaled with isometry. *M. fuscata* scaled with significant positive allometry and was significantly different from *M. mulatta*. For *biceps brachii* lever arm length, all taxa scaled with significant positive allometry
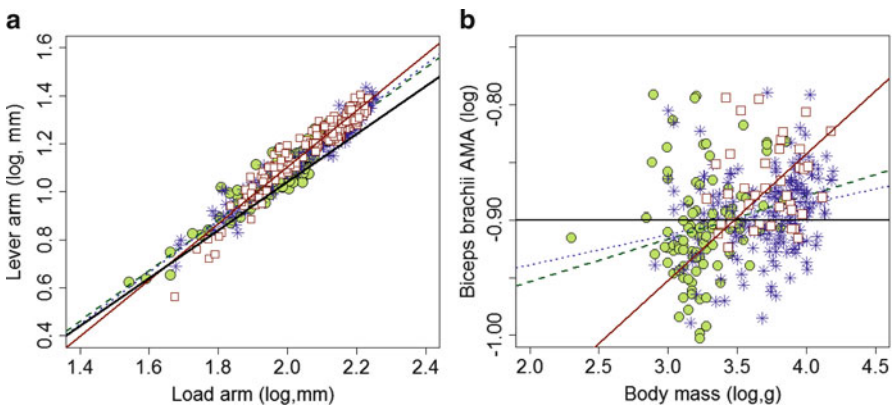
Fig. 7.4 Relative growth of (**a**) the *biceps brachii* lever arm scaled to its load arm length and (**b**) *biceps brachii* AMA scaled to body mass. *M. fascicularis* (*green circles*), *M. fuscata* (*blue stars*), and *M. mulatta* (*squares*). *Black line* represents isometry. *Biceps brachii* lever arm length scales to load arm length with significant positive allometry across taxa. *Biceps brachii* AMA on body mass scales with significant positive allometry, although the relationship is weak

longer load arm lengths, the anatomical lever arm is longer than expected in all taxa. *Macaca mulatta* has the fastest rate of growth ($b = 1.222$, $p < 0.001$), while *M. fuscata* increases with the slowest rate ($b = 1.115$, $p < 0.001$). There are significant differences across taxa in the scaling of lever arm to load arm length ($p = 0.002$, Table 7.3). In pair-wise comparisons of slope, *M. fuscata* and *M. mulatta* significantly differ ($p = 0.001$).

Ontogenetic scaling of *biceps brachii* AMA (i.e., *r/R*) onto body mass increases with significant positive allometry in all taxa (Table 7.2, Fig. 7.4). However, the scaling relationship is weak. These results indicate that with increased body mass and age, larger individuals have slightly higher AMA. Interspecific slope comparisons for AMA on body mass across taxa show a significant difference ($p = 0.003$). In pair-wise slope comparisons, values are significantly higher in *M. fascicularis* ($b = 0.184$, $p < 0.05$) than in *M. fuscata* ($b = 0.120$, $p < 0.001$). This bolsters the values above, indicating that *M. fuscata* has the lowest slope values and the least difference in AMA between adult and nonadult individuals.

7.4 Discussion

The general results presented here do not support the hypothesis that the rapid propulsive quadrupedal modes observed in juvenile macaques are the result of increased muscle mechanical advantage in the forelimb. Conversely, results indicate that ontogenetically, with increasing size and age, macaques disproportionately increase the length of their anatomical lever arm. Thus, younger individuals have relatively shorter lever arm lengths compared to adult conspecifics when scaled to anatomical load arm length and body mass, suggesting that lever arm growth of the *biceps brachii* muscle may be responding to mechanical pressures from increased body weight following Biewener's model (1989a, b, 1990). Previous research on muscle mass growth in *M. mulatta* and *M. fuscata* indicates that there are no differences in the percentage of arm muscle mass with age (Grand 1977; Hamada 1983). In *M. mulatta*, upper arm muscle mass increases from 2.2% of total body weight in prenatal individuals to 3.1% in postnatal individuals up to three kilograms (infants and juveniles) to 3.3% in adults (Grand 1977). Similarly in *M. fuscata*, Hamada (1983) showed that there is no significant change in the percentage of *biceps brachii* muscle mass to total body mass with age and muscle mass increases with isometric growth. The ontogenetic results here follow the interspecific scaling trends in other mammalian taxa (Biewener 1983, 1989a, b, 1990, 1991, 2003, 2005; Biewener and Betram 1993; Polk 2002, 2004).

In all taxa examined here, when lever arm length of the *biceps brachii* muscle is scaled onto its anatomical load arm length, lever arm length scales with positive allometry. This scaling relationship is counter to that seen in the *biceps brachii* in capuchin monkeys (*Cebus apella* and *C. albifons*). The difference in scaling between *Cebus* and *Macaca* is unexpected, given the similarity in scaling between *Cebus* and *Lepus* in the *triceps brachii* muscle. There may be several explanations for scaling differences between *Cebus* and *Macaca*, including differences in the timing of the shift from forelimb to hind limb dominance, generalized locomotor type (i.e., arboreal versus terrestrial habitat), and limb posture.

During growth, the hind limb skeleton in macaques increases in length and mass at a faster rate than the forelimb (Turnquist and Wells 1994). At birth, the length of the hind limb is longer than the forelimb and throughout ontogeny has greater

relative growth than the forelimb. However, by 1 year of age, hind limb and body length (crown-rump length) are approximately equal in length (Turnquist and Wells 1994). The increase in hind limb length is concurrent with a shift in the locomotor repertoire of rhesus macaques from a newborn dependence on forelimb musculature for clinging to one that is dominated by hind limb propulsion at locomotor independence (Turnquist and Wells 1994; Kimura et al. 1979; Demes et al. 1994; Hanna et al. 2006). Rhesus macaques attain locomotor independence by 4–6 months (Turnquist and Wells 1994) while young capuchins reach locomotor independence around 2–3 months (Oppenheimer 1968; Levy and Bodini 1986; Robinson 1986; Mitchell 1989; Byrne and Suomi 1995). Earlier attainment of locomotor independence in young capuchins may partially explain their higher AMA values as they need to effectively inhabit the adult locomotor niche earlier.

The difference in the timing of the transition to hind limb dominant locomotion and attainment of locomotor independence between *Cebus* and *Macaca* are most likely facilitated by scaling difference in the limb. Here, lever arm length of the *biceps brachii* scaled with positive allometry in both *Cebus* and *Macaca* with little difference in the rate of scaling between taxa (*C. albifrons*: $b = 0.45$; *C. apella*: $b = 0.41$; *M. fascicularis*: $b = 0.445$; *M. fuscata*: $b = 0.45$; *M. mulatta*: $b = 0.473$). However, there are differences in the rate of scaling of the anatomical load arm length between the two taxonomic groups. In macaques, the associated load arm length (the radius) relative to body mass, scaled with isometry in *M. mulatta* ($b = 0.335$, $p < 0.001$) and with positive allometry in *M. fascicularis* ($b = 0.3739$, $p < 0.001$) and *M. fuscata* ($b = 0.4117$, $p < 0.001$). However, in *Cebus*, when load arm length is expressed as a function of body mass, it scales with extreme positive allometry ($b = 0.67$ in *C. albifrons*; $b = 0.53$ in *C. apella*). The extreme positive scaling of the anatomical load arm length increases at a much faster rate than its associated lever arm length in capuchins, resulting in relatively high ratios of AMA in younger individuals (Young 2005). Conversely, in the macaques, when lever arm length is scaled to load arm length, the rate of change is not as dramatic due to slower rate of growth, resulting in positive scaling of AMA.

Differences in the rate of scaling in the forearm between *Cebus* and *Macaca* are also related to differences in their overall locomotor repertoires. Macaques are, generally, terrestrial with long limbs and a relatively high intermembral index (93) (Fleagle 1999). Conversely, Cebus monkeys are largely arboreal and spend significant amounts of time in the middle and upper canopy (Fleagle and Mittermeier 1980). Their relatively short limbs and low intermembral index (81) (Fleagle 1999) reflect the increased need of the forelimb to be mobile rather than act as a stabilizing platform, particularly on smaller rounder substrates (Reynolds 1985a, b). While *Cebus* prefer larger diameter substrates, they often employ small branches, lianas, and palm fronds, and use high frequencies of climbing, clambering, and leaping across branches occasionally greater than three meters (Freese and Oppenheimer 1981; Youlatos 1998; Garber and Rehg 1999; Gebo 1992; Fragaszy et al. 2004). If arboreal locomotion is more costly than terrestrial locomotion for mammals, as argued by Studel (2000), young capuchins may be under greater selection to effectively use the adult locomotor niche by obtaining higher AMA values early in

ontogeny compared to young macaques which might be under decreased selective pressures. Additionally, it may be these differences in substrate and locomotor niche that are driving differences in load arm scaling across taxa.

Results here run counter to previous hypotheses regarding the negative scaling relationships between AMA and body mass found in *Lepus*, *Felis* (Carrier 1983), and *Cebus* (Young 2005), indicating that negative allometric growth of the forelimb is not a pattern shared by all young mammals. Assuming that AMA is a valid proxy for effective mechanical advantage, Beiwener's model is supported in the sense that within macaques, larger animals have relatively higher mechanical advantage of the limbs. However, the positive ontogenetic scaling relationship observed cannot be ruled out as an adaptation. When the ratio of lever to load arm length is low, greater limb angular excursion is emphasized resulting in increased speed about the fulcrum as opposed to increased power (Carrier 1983). Thus, the relatively low mechanical advantage observed in this study in younger, smaller macaques may facilitate increased acceleration through a faster response time. This type of adaptation could be critical to predator avoidance by decreasing the time necessary to accelerate, particularly in young individuals who are less vigilant than older conspecifics. Future research is needed to test this by measuring ontogenetic changes in live individuals particularly in gait speed and take-off velocity.

7.5   Conclusions

This study examined patterns of relative muscle lever arm growth in the elbow of three Old World Monkeys: *Macaca fascicularis*, *M. fuscata*, and *M. mulatta*. The positive ontogenetic scaling relationship for the anatomical lever arm length, found here, follows scaling patterns predicted by Biewener's interspecific model in which larger taxa increase leverage of muscle groups to compensate for increased joint moments associated with larger body mass (Biewener 1983, 1989a, b, 1990, 2003, 2005). As in previous studies which examined lever arm scaling in *Cebus*, lever arm lengths and load arm lengths scaled to body mass with positive allometry in all taxa. The resultant scaling relationships led to positive scaling of the *biceps brachii* AMA, again supporting Biewener's model of increased muscle mechanical advantage with increased size.

The results of this study suggest that young macaques do not use higher anatomical mechanical advantage to overcome ontogenetic limits on their locomotor performance. On the contrary, young macaques appear to have relatively low mechanical advantage associated with this muscle group despite having proportionally smaller muscle mass and more flexed limb postures. Given the differences in scaling between the macaques used in this study and the Capuchin monkeys used in previous studies (Young 2005), it is essential to examine the relationships between muscle growth and locomotion in other taxa with similar locomotor modes. Capuchins and macaques exploit different locomotor substrates and behaviors and the differences in scaling found here may be a reflection of these differences. Further, because this

study focuses entirely on skeletal changes with age, difference in posture, gait, speed, and muscle fiber physiological cross-sectional area cannot be controlled. Thus, examinations of the ontogenetic relationships between these variables in other arboreal and terrestrial taxa are required to verify these hypotheses and clarify the role that selection places on juvenile primates.

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Chapter 8
Dental Maturity and the Ontogeny of Sex-Based Differences in the Dentofacial Complex of Rhesus Macaques from Cayo Santiago

Qian Wang

8.1   Introduction

The dentofacial complex has important functions related to vision, sound, and nutrition (Lieberman 2011). In addition to traditional attempts to estimate age in lieu of birth records in forensic and anthropological studies (i.e., Relethford et al 1982; Nuzzolese and Di Vella 2008), investigations of dental eruption in various past and present primates have revealed important information on ontogeny, phylogeny, evolution, diet, living conditions, physiology, and life history patterns (i.e., Zuckerman 1928; Schultz 1935; Hurme and Van Wagenen 1961; Nissen and Riesen 1964; Cheverud 1981; Mann 1988; Phillips-Conroy and Jolly 1988; Smith 1989, 1994; Anemone et al. 1991, 1996; Kuykendall et al. 1992; Kuykendall and Conroy 1993; Smith et al. 1994; Harvati 2000; Dirks et al. 2002; Godfrey et al. 2001; Swindler 2002; Kelley and Smith 2003; Liversidge 2003; Zihlman et al. 2004; Nargolwalla et al. 2005; Schwartz et al. 2006; Smith et al. 2010). The facial skeleton of primates, being affected structurally and functionally by the dental component, responds and adapts to the biomechanical environment induced by the presence or absence of teeth (i.e., Hylander 1977; Anton 1990; Rak 1983; Spencer and Demes 1993; Ravosa et al. 2000; Wright 2005; Wang et al. 2008; Dechow et al. 2010; Ross et al. 2011). Thus, that the primate facial skeleton and teeth should have a similar ontogenetic tempo (i.e., developmental changes in the facial skeleton that correlate with tooth eruption, resulting in their simultaneous maturation) would seem to be a reasonable expectation. Evidence exists, however, that the developmental pattern of the facial skeleton in primates differs between the sexes. Studies of rhesus macaques

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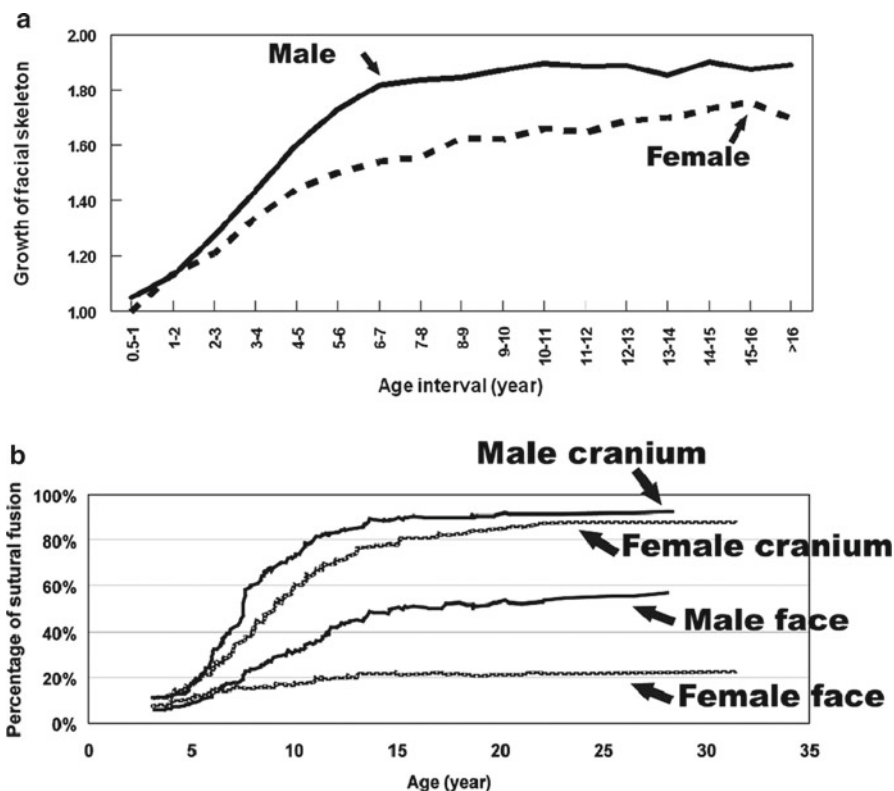
Fig. 8.1 (**a**) Ontogeny of sex difference in the size of the facial skeleton in rhesus macaques from Cayo Santiago, based on Euclidean Distance Matrix Analysis (EDMA) (Adapted from Wang et al. 2007:354–355). Growth of facial skeleton in males and females are compared using female size initially at 6–12 months of age (0.5–1 year) and over subsequent yearly intervals. (**b**) Sex differences in fusion patterns of craniofacial sutures (Adapted from Wang et al. 2006b: 481). Most sutures eventually fused in both male and female cranial skeletons, but sutures commonly did not fuse in the facial skeleton, especially in females

(Macaca mulatta) from Cayo Santiago, for example, reveal that females retain patent craniofacial sutures longer than males, demonstrating that the ontogeny of the female facial skeleton is actually of greater duration than that of the male (Fig. 8.1) (Wang et al. 2006b, 2007). In light of this sexually dimorphic feature, female rhesus macaques are predicted to have a prolonged dental ontogeny to match the prolonged facial ontogeny. Differing life histories between males and females are complicating our understanding of sexually dimorphic developmental differences. Cayo Santiago rhesus females reach sexual maturity at 3 years, 2 years earlier than males (Rawlins et al. 1984; Bercovitch and Nurnberg 1996; Bercovitch et al. 1998; Bercovitch and Harvey 2004; Blomquist 2009; Blomquist and Turnquist 2011;

Blomquist et al. 2011). Despite adult rhesus macaques being sexually dimorphic for body mass (Smith and Jungers 1997; Plavcan 2001; Rawlins et al. 1984; Delson et al. 2000), both sexes apparently must attain a comparable minimal body mass before reproductive maturity can be achieved. Multiple studies of the Cayo Santiago population indicate that this body mass threshold is approximately 5 kg (Rawlins et al. 1984; Bercovitch and Nurnberg 1996; Bercovitch et al. 1998). Thus, females must be reaching the 5 kg threshold 2 years earlier than males. One possible means by which females can attain this body mass threshold more quickly than males is to have a higher food-processing capacity for increased nutritional intake. Thus, prior to sexual maturity, dental development and functional capability in females is predicted to be more advanced than in males of the same age; that is, female dental eruption may be accelerated. Therefore, if dental ontogeny can be used to gauge maturation rate (Smith et al. 1994) and maturation rates differ between the sexes, then predictions can be generated for maturation differences between males and females, depending upon whether dental development is based on development of the facial skeleton or life history. Accordingly, two conflicting hypotheses on sex-based differences in dental ontogeny are proposed, one based on facial skeleton maturity and the other based on sexual maturity.

Hypothesis # 1 predicts that female teeth mature at a *slower* rate than male teeth. This hypothesis anticipates that the female dental complex matures at a rate comparable to the relatively slower developing female facial skeleton, resulting in the fully functional adult female dental complex emerging later than in males.

Hypothesis # 2 by contrast, predicts that female teeth mature at a *faster* rate than male teeth. This hypothesis anticipates that the fully adult female dental complex must emerge earlier in life than in males in order to enable the processing of an adequate volume of food to meet the increased energy requirements for achieving sexual maturity at an earlier age.

By building upon previous investigations (Wang et al. 2006b, 2007), and by testing the two hypotheses above, this study attempts to reveal differences between male and female rhesus macaques in the eruption sequence of their permanent teeth. Additional insights are provided into sex-based differences in, and the biomechanical consequences of, dentofacial complex development, and into the ontogeny of sexual maturity and life expectancy in general.

8.2   Materials and Methods

Information was collected and analyzed on functional tooth eruption in 427 (223 male, 204 female) rhesus monkey crania from the Cayo Santiago skeletal collection of the Caribbean Primate Research Center (CPRC), which is housed in the Laboratory of Primate Morphology and Genetics on the University of Puerto Rico Medical Sciences Campus (Table 8.1). The cross-sectional sample represented an initial 6-month to 1-year age group and yearly age groups extending to 16+ years. This long-standing collection, consisting of individuals of known age and sex,

Table 8.1 Cayo Santiago sample

Age interval (year)	Female	Male	Total
0.500–0.999	9	14	23
1.000–1.999	14	14	28
2.000–2.999	15	13	28
3.000–3.999	16	15	31
4.000–4.999	15	14	29
5.000–5.999	15	15	30
6.000–6.999	12	16	28
7.000–7.999	11	15	26
8.000–8.999	14	14	28
9.000–9.999	13	9	22
10.000–10.999	9	11	20
11.000–11.999	10	14	24
12.000–12.999	9	9	18
13.000–13.999	9	8	17
14.000–14.999	5	8	13
15.000–15.999	4	7	11
>16.000	24	27	51
Sum	204	223	427

provides an excellent opportunity to examine the ontogeny of sexual dimorphism in a primate population with an extended life history. A longitudinal population study revealed an annual mortality rate among Cayo Santiago rhesus macaques of approximately 6.8% (Rawlins et al. 1984). In this paper, survival curves and life expectancies were determined for males ($N=337$) and females ($N=269$) of known age. Hazard ratios between males and females were then generated or calculated, based on the skeletal collection and using the Kaplan–Meier survival analysis with GraphPad Prism 4.00 (GraphPad Software Inc, San Diego, CA, USA). In this study, "hazard ratio," which is defined as the slope of the survival curve, was used to measure (1) how rapidly individuals are dying and (2) how rapidly teeth are erupting. The hazard ratio compares these trends between treatment groups. For example, if the hazard ratio is 1.0, then the rate of dental eruption (or deaths) in one treatment group (e.g., males) is at the same rate as in the other group (e.g., females). If the hazard ratio for this same comparison is 2.0, then the rate of dental eruption (or deaths) in males is twice the rate in females. The Cochran-Maentel-Haenzel Logrank Chi-Square test reports a chi-square value with one degree of freedom, and the computed P value tests the difference between the survival trends of the two groups, or whether or not the hazard ratio differs from (1). A low P value ($\alpha=0.05$) indicates that there is a significant difference between the trends of the two groups, or that the hazard ratio is not 1.

The point of complete occlusal eruption, termed "functional eruption," was used in this study as a key developmental event, along with sexual maturation and the end of ontogeny of the craniofacial skeleton. Different definitions of tooth eruption, however, have been used by others. The first sign of tooth eruption, for example, has been defined as gum eruption (i.e., emergence from the gingivae) (i.e., Phillips-Conroy and Jolly 1988) or as alveolar eruption (i.e., emergence from the bone, as

seen in dry bones and X-ray images) (Schultz 1935; Kuykendall et al. 1992). "Functional eruption," by contrast, occurs when a tooth in the lower jaw can occlude with a comparable tooth in the upper jaw, transferring load energy to both the mandible and maxilla. Thus, whether or not individual teeth or the entire dental rows have achieved functional eruption is important because both in vitro and in vivo experiments, as well as finite element analysis, have demonstrated that loadings on different teeth will induce different strain patterns in the facial skeleton (Hylander et al. 1991; Ravosa et al. 2000; Wang et al. 2008; 2010c; Kupczik et al. 2009; Strait et al. 2009).

The condition of individual upper (or maxillary) and lower (or mandibular) permanent teeth were recorded using a five-stage ordinal scale:

Stage (0): No alveolar eruption or opening is present in the alveolar bone
Stage (1): Window in the alveolar bone is open, and the cusp(s) is (are) visible, but the tooth is not erupting
Stage (2): Tooth cusp(s) has (have) emerged above the level of alveolar bone
Stage (3): Tooth crown has emerged to half its mature height and Stage
Stage (4): Tooth crown has achieved its full height, it has reached the occlusal plane, and, therefore, is functionally mature

Patterns of functional dental eruption were also analyzed with the widely used (Kuykendall et al. 1992; Holman and Jones 1998) Kaplan–Meier survival analysis, which "provides a number of advantages for estimating parameters of tooth emergence, incorporates a variety of messy data, and provides efficient and complete statistical estimates" (Holman and Jones 1998:226). The analogies between survival and death of an individual on the one hand, and erupting (coded as 0 for Stages 0–3) and fully erupted teeth (coded as 1 for Stage 4) on the other hand, allow the same analytical methods to be applied in both cases. Sex-based differences in functional dental eruption can also be demonstrated with the "hazard ratio."

The trend analyses used in this study were sufficient to demonstrate sex-based differences in the patterns of functional dental eruption. Nevertheless, a caveat should be raised, in that age structure and sample size can influence the accuracy and precision in reflecting true age variation, and can thereby impact the statistical results (Foote 1993; Konigsberg and Frankenberg 2002; Konigsberg et al. 2002; Steadman et al. 2006; Wang et al. 2006b, 2007). The influences of age structure and sample size on the final results, however, were likely to be minimal. A relatively balanced skeletal sample size for each sex at early ages was randomly chosen from the skeletal population, as enough specimens were usually available. In addition, as will be revealed in this study, the entire tooth eruption process was completed at relatively early ages (Table 8.1).

Even though the sequence of functional eruption is slightly different from that of alveolar eruption (Smith 1989), maturation of the maxillary and mandibular teeth is synchronized in both males and females, indicating an inherent functional relationship (Nissen and Riesen 1964; Kuykendall et al. 1992; Reid et al. 1998).

The overall sex-based differences in dental ontogeny were further examined in terms of the following three types of dental maturity, and were then compared to the ages of sexual maturity and facial skeletal maturity.

1. *Material maturity*: the age at which all teeth are functionally erupted. This stage represents the end of dental ontogeny.
2. *Functional maturity*: the age at which all premolars and the first and second molars are fully erupted. The third molars are less functionally important than the other post-canine teeth. In humans, the third molars are the last to develop in ontogeny and the first to disappear in phylogeny (Cartmill and Smith 2009). Thus, a tooth row without the third molars is nevertheless functionally mature.
3. *Canine maturity*: the age at which the canines are fully erupted. Among rhesus macaques, adult males have much larger canines than adult females (Plavcan 2001). In light of this sexually dimorphic feature, it was predicted that female canines would fully erupt *earlier* than male canines.

Finally, dental, facial-skeletal, and dentofacial maturity were quantified as follows. Sex differences in the dentofacial complex throughout ontogeny were summarized by combining two separate patterns: tooth eruption and facial skeleton size. The total number of upper and lower teeth of one side ($N = 16$) and facial skeleton size at the end of ontogeny (i.e., maturity) were scaled to 1. The ontogenetic process was described in terms of the "dental maturity index" and the "facial maturity index," which are cumulative percentile values ranging from 0.0 to 100%. Specifically, the dental maturity index is the number of teeth that have functionally erupted at the point of interest, divided by 16, and multiplied by 100%. The facial skeletal maturity index is the facial skeletal size at the point of interest, divided by the facial skeletal size at the end of facial ontogeny, and multiplied by 100%. The combined dentofacial maturity index was defined as the sum of ½ the dental maturity value and ½ the facial maturity value. Sex differences were defined as the difference between males and females, in terms of degree of maturity. Specifically, the sex difference in dental maturity at a point of interest is calculated as the male dental maturity index minus the female dental maturity index, and the sex difference in dentofacial maturity is calculated as the male dentofacial maturity index minus the female dentofacial maturity index. Sexual dimorphism in facial skeleton size is diachronic, with fluctuations in the degree of sex-based size differences. Furthermore, dental eruption changes both the morphological and functional properties of the dentofacial complex. Thus, the combined scenario of dental maturation and skeletal maturation of the face in males and females is proposed to demonstrate how sex-based differences become manifested, and to offer insights into the structural and biomechanical impact of these differences on the craniofacial skeleton. Therefore, sex-based, diachronic maturation of the dentofacial complex is predicted.

8.3 Results

8.3.1 Survival Analysis

The Kaplan–Meier survival analysis for Cayo Santiago rhesus monkeys revealed that the overall survival curves for males and females did not differ significantly

Table 8.2 Kaplan–Meier survival plots for rhesus monkeys on Cayo Santiago

	Total N=606	Male N=337	Female N=269
Daily survival rate (%)	99.964 (99.961–99.969)	99.966 (99.963–99.970)	99.961 (99.565–99.658)
Annual survival rate (%)	87.7 (86.8–88.6)	88.4 (87.3–89.6)	86.8 (85.3–88.3)
Life expectancy (year)	7.646 (7.073–8.295)	8.123 (7.339–9.094)	7.055 (6.293–8.004)
Median age (year)	6.118 (5.600–6.636)	6.595 (5.829–7.361)	5.132 (4.278–5.986)
Longevity/maximum age (year)	31.444	28.301	31.444
Female vs. male		Log-rank Chi-square test: $\chi^2=3.822$; P=0.0506	Hazard ratio: 1.172; (0.9996–1.3850)

among individuals living to only 6 months of age (Table 8.2). As predicted, the overall effect of age and sample size was diminished by using a balanced number of skeletons for each sex in each age group.

8.3.2   Patterns of Functional Tooth Eruption

Functional tooth eruption sequences were similar between Cayo Santiago rhesus males and females (Table 8.3, Fig. 8.2). Functional eruption of the upper and lower teeth was highly synchronized, the maxillary teeth reaching maturity either at the same time as, or slightly earlier than, the mandibular teeth, attesting to the inherent developmental and functional relationships between corresponding maxillary and mandibular teeth. The upper and lower first molars in both sexes were the first to functionally erupt. A 1.5-year period of delay then occurred before the incisors and most of the remaining teeth were also fully erupted.

Sex differences for each of the three types of dental maturation were nevertheless present (Table 8.3, Fig. 8.2). *Material maturity* was reached at 6 years in males, but not until 6 months later (i.e., 6.5 years) in females. This sex-based difference was attributed largely to the delay (2.4 years in males, 3.3 years in females) in maturation of the third molar, following that of the second molar. *Functional maturity*, by contrast, was achieved in females (3.4 years) earlier than in males (3.9 years). Thus, compared to males, females had a slower material maturity rate, as predicted by Hypothesis #1, but a faster functional maturation rate, as predicted by *Hypothesis #2*. C*anine maturity* also occurred earlier in females (3.95 years) than in males (5.98 years) as predicted (Table 8.4).

8.3.3   Dental Maturation Events in Life History

Early life events of the Cayo Santiago rhesus specimens revealed a mosaic pattern of development, producing sex-based differences in their life histories. In females,

Table 8.3 Tooth functional eruption patterns in male and female rhesus macaques from Cayo Santiago

Tooth	Female			Male			Median age of maturity[a]		Log-rank test	
	Earliest alveolar eruption[b]	Earliest functional eruption[b]	Latest functional eruption[b]	Earliest alveolar eruption[b]	Earliest functional eruption[b]	Latest functional eruption[b]	Female	Male	Hazard ratio[c] (F vs. M)	P
M_1	>0.912	1.575	1.575	<0.912	0.912	1.542	1.575	1.542	1	NS
M^1	<1.200	1.200	>3.093	<0.912	0.912	>2.033	1.575	1.899	1	NS
I^1	<2.101	2.101	>2.945	<2.841	2.841	3.093	2.789	2.956	2.76	NS
I_1	<2.468	2.468	3.005	<2.811	2.811	3.112	3.005	3.112	3.95	0.028
I_2	<2.468	2.468	>3.156	<2.811	2.811	3.112	3.005	3.112	3.95	0.028
I^2	2.468	2.770	>3.165	<2.841	2.811	3.093	3.085	3.093	1	NS
P_4	<3.085	3.085	>4.063	3.112	3.616	>3.967	3.216	3.795	7.35	0.002
P_3	<3.085	3.085	3.882	3.112	3.795	>5.148	3.216	3.795	7.26	0.002
M_2	<2.770	2.770	>4.063	3.093	3.112	>4.726	3.216	3.616	7.67	0.002
M^2	<3.011	3.145	>9.318	2.956	3.112	4.726	3.216	3.616	1	NS
P^3	<3.085	3.085	>3.882	3.795	3.795	>3.953	3.216	3.936	7.59	0.002
P^4	<2.770	3.047	>3.882	<3.616	3.616	3.953	3.411	3.858	3.68	0.014
C_1	<3.085	3.085	3.948	>3.795	4.726	>5.688	3.948	5.455	8.79	<0.001
C^1	2.770	3.216	>3.882	3.079	4.726	6.501	3.948	5.978	12.32	<0.001
M^3	4.748	5.534	>9.836	<5.096	5.334	<7.855	6.391	6.019	0.348	0.018
M_3	3.216	5.534	10.501	4.962	5.334	>6.419	6.529	5.921	0.602	0.039

[a]The median age of functional eruption was considered to be when a tooth is fully erupted and functional. A smaller median age indicates that a tooth tends to be fully erupted at an earlier point in time. Differences in the median ages between the sexes may indicate the sequence of functional dental eruption at a given ontogenetic stage

[b]The study sample is cross-sectional or pseudo-longitudinal. Thus, the earliest alveolar or functional eruption time was determined by the age of the youngest specimen to have the tooth just emerge from the alveolar bone or reach the occlusal plane. Likewise, the latest functional eruption time was the age of the oldest specimen to have the tooth just reaching the occlusal plane

[c]The "Hazard Ratio" was interpreted as a measure of differences in the age of functional eruption between the two sexes
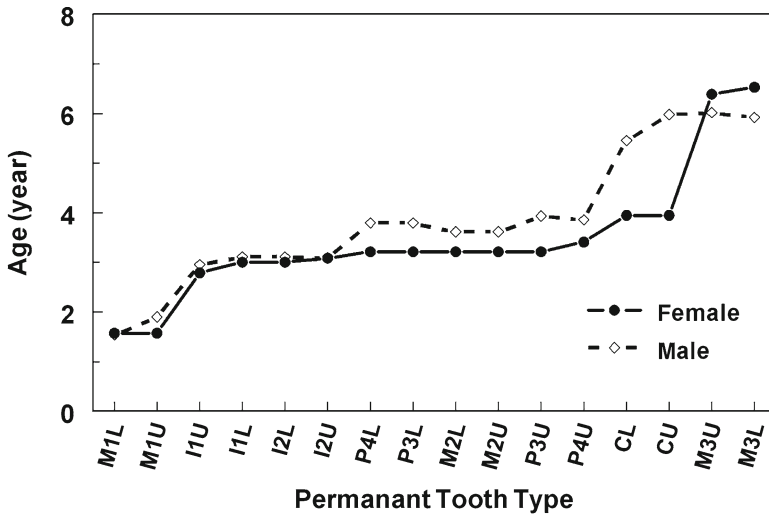
Fig. 8.2 Sequence of tooth maturity in rhesus macaques from Cayo Santiago. The tooth sequence along the *X*-axis is based on the female eruption pattern. Male and female rhesus macaques had similar functional tooth eruption sequences, yet females reached earlier dental maturity in the premolars. *Abbreviations*: *I* incisor; *P* premolar; *M* molar; *U* upper or maxillary teeth; *L* lower or mandibular teeth

Table 8.4 Survival rates at different developmental stages for rhesus macaques on Cayo Santiago

	Female		Male	
	Age (years)	Survival rate (%)[a]	Age (years)	Survival rate (%)[a]
Dental material maturity[b]	6.5	41.3	6.0	56.1
Dental functional maturity[b]	3.41	67.3	3.94	78.3
Canine maturity[b]	3.95	62.8	5.98	56.7
Sexual maturity[c]	3	73.0	5	67.4
Facial skeletal maturity[d]	15	10.8	8	39.2

[a]Survival rates are those collected from the survival curves in Fig. 8.2
[b]The ages of dental total maturity are based on the median ages of fully functional eruption or maturation of the upper and lower third molars (M[3] and M₃ in Table 8.3). The age of dental functional maturity was based on the median ages of the fully functional eruption or maturation of all post-canine teeth, with the exception of the third molars. The age of canine maturity is based on the median ages of the fully functional eruption or maturation of all four canine teeth
[c]Among Cayo Santiago rhesus monkeys, the canines reach sexual maturity at around 3 years in females and around 5 years in males (Rawlins et al. 1984; Bercovitch et al. 1998; Blomquist et al. 2011)
[d]The age of facial skeletal maturity is based on the age at which facial skeletal growth or ontogeny ended (Wang et al. 2007)

functional maturity of the dentition occurred at around 0.4 years *after* sexual maturity, whereas in males it occurred approximately 1 year *before* sexual maturity. Relative to functional maturity, however, *material maturity* followed a different pattern. Specifically, material maturity occurred 3.1 years after functional maturity
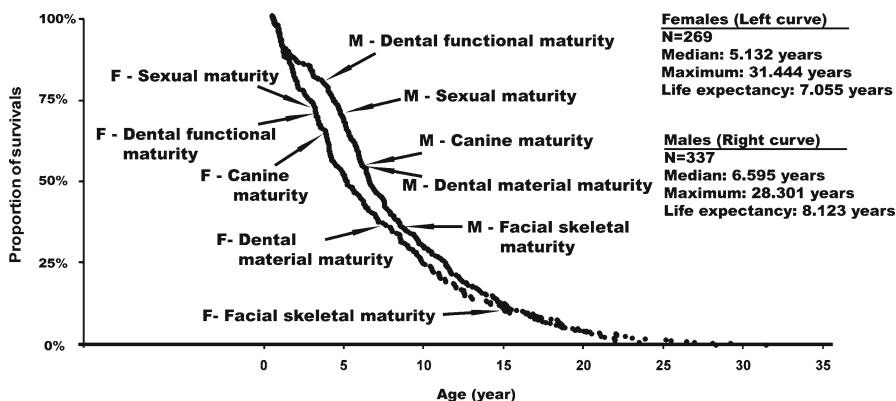
Fig. 8.3 Early life events in rhesus macaques from Cayo Santiago projected onto survival curves. Among rhesus monkeys, in general, reproductive maturity is reached at 2.5–3 years in females, but not until 4.5–7 years in males (Nowak 1990). Among Cayo Santiago rhesus monkeys, this age is around 3 years in females and around age 5 years in males (Rawlins et al. 1984; Bercovitch et al. 1998; Blomquist et al. 2011). The ages of facial skeletal maturity for females ($N=15$) and males ($N=8$) are derived from Wang and colleagues (2007) (see also Fig. 8.1). The ages at which three dental maturity events occur are summarized in Table 8.3

(or 3.5 years after sexual maturity) in females, but only 2 years after functional maturity (or 1 year after sexual maturity) in males. *Canine maturity* occurred approximately 1 year later than sexual maturity in both males and females. Compared to functional maturity, by contrast, canine maturity was delayed 3–4 times longer in males (2 years) than in females (0.6 years) (Table 8.4).

Projecting survival curves beyond 6 months, fewer females reached either functional (females 67.3% vs. males 78.3%) or material (females 41.3% vs. males 56.1%) maturity than males; but more females (62.8%) attained canine maturity than males (56.7%) (Table 8.4, Fig. 8.3). Thus, in terms of early life events, females had relatively earlier functional maturity and sexual maturity, later material maturity, and lower survival rates than males.

8.3.4   Sex-Based Differences in Structural Maturation of the Dentofacial Complex

Males reached dentofacial maturity approximately 5 years earlier than females (Fig. 8.4a). Whereas only a small proportion of females lived to the end of dentofacial ontogeny, males had a fourfold greater chance of surviving long enough to achieve full dentofacial maturity (females 10.8% vs. males 39.2%) (Table 8.4, Figs. 8.3).

When the maturation patterns of the teeth and facial skeleton were combined (Fig. 8.4b), the dentofacial complex of males was found to have a relatively shorter ontogeny than that of females, which was attributed primarily to the shorter ontog-
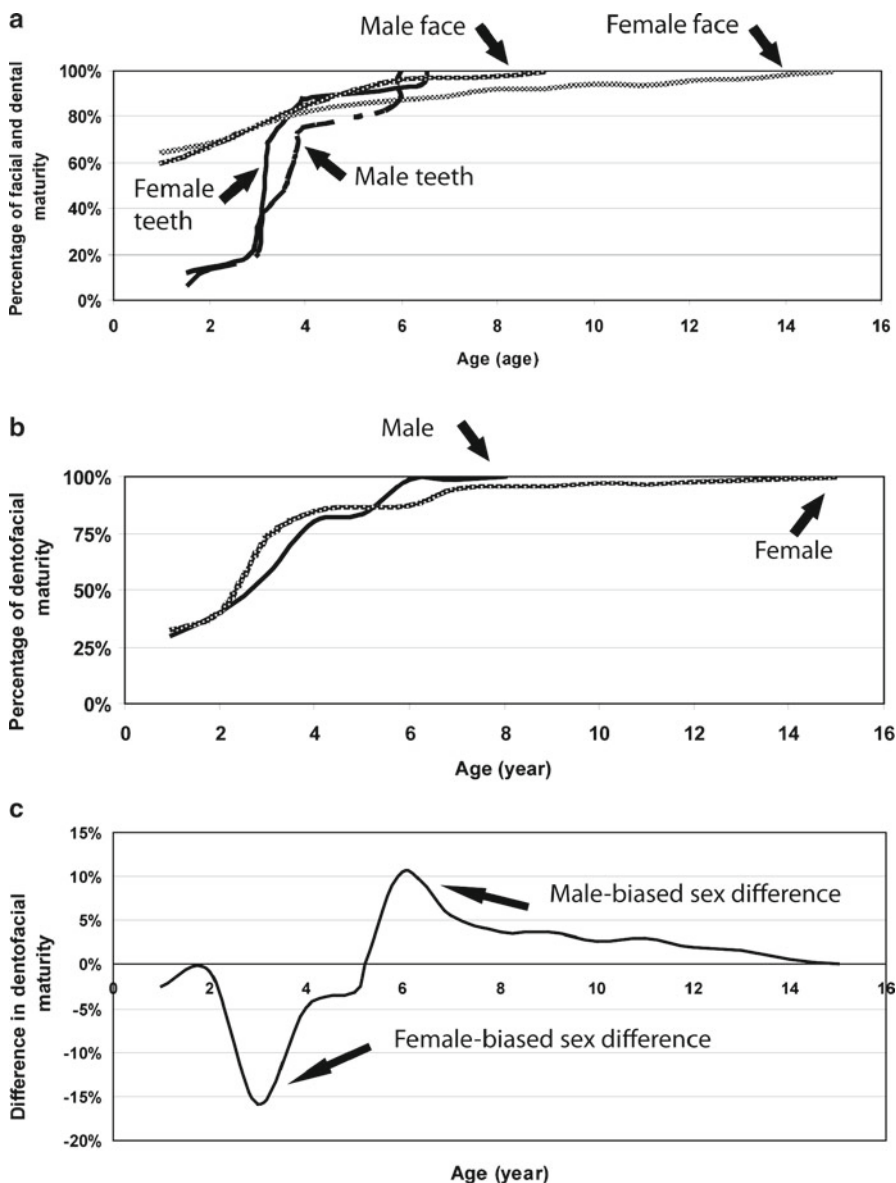
Fig. 8.4 Ontogeny of sex differences in the dentofacial complex of Cayo Santiago rhesus macaques. (**a**) Patterns of facial (data from Wang et al. 2007) and dental maturity in males and females. The full tooth number and skull size at the end of ontogeny were scaled to 1, and the process of ontogeny was characterized in terms of accumulative percentile values or the "dental and facial skeletal maturity index." (**b**) Ontogeny of the dentofacial complex, based on tooth eruption and growth of the facial skeleton. Combined dentofacial maturity = ½ Facial maturity + ½ Dental maturity × 0.5). (**c**) Ontogeny of sex differences in the dentofacial complex. These values are derived from (**b**) in that Y values were the difference (male minus female) in the degree of skull maturity at any given age. Before full eruption of the post-canine teeth (with the exception of the third molar in males), sex differences in the dentofacial complex are female-biased (the difference value was negative, with a peak at around 3 years of age). After 3 years, this sex difference is male-biased (the difference value was positive, with a peak at around 6 years of age)

eny of the male facial skeleton. The period between sexual maturity and facial skeleton maturity was 12 years in females, but only 3 years in males; similarly, the period between dental functional maturity and facial skeleton maturity was over 11.5 years in females, but only 4 years in males (Table 8.4, Fig. 8.3). Owing to their later functional maturity, however, 2–5-year-old males had slower maturation rates for the dentofacial complex than females at the same ages. The male developmental rate for the complex subsequently elevated, however, because of their relatively early material maturation and their ability to reach the end of facial skeleton ontogeny. Thus, the dentofacial complex in females was more mature (female-biased sex difference) than that in males before 5 years of age, with its peak at around 3 years (Fig. 8.4c). After 5 years of age, by contrast, the male dentofacial complex was more mature (male-biased sex difference), peaking at around 6 years. Subsequently, the dentofacial complex remained male-biased, but the magnitude of the maturational differences between the sexes gradually decreased, reflecting the long growth duration of the female facial skeleton.

8.4   Discussion

The dentition of female rhesus macaques reaches functional maturity *earlier* than that of males, but reaches material maturity *later*. As with dental material maturity, facial suture fusion and facial skeleton maturity also occur later in rhesus females. Thus, female tooth eruption is diachronic, correlating with sexual maturity and skeletal ontogeny. In a true age-based profile, sex differences will be either female-biased (i.e., females larger or more mature) or male-biased (i.e., males larger or more mature), depending upon the particular age and developmental stage selected. Thus, there is no uniform pattern of sex differences in craniofacial dimensions or the resultant biomechanical environments.

The significant differences between rhesus males and females in survival rate at comparable developmental stages indicate a necessary relationship among morphology, early life traits, functional adaptation, and survival. The ontogenetic strategy of the dentofacial complex may be closely related to energy intake and the cost of sexual maturity. Free-ranging rhesus macaques have the ability to flourish in a wide diversity of environments, largely due to their omnivorous diet (Lutz and Novak 2005). They have been observed to consume over 100 species of plants (shoots, fruits, and seeds) and occasionally eggs, insects, and small animals (Lindberg 1971). Free-ranging rhesus macaques in rural areas spend nearly 50% of their time moving from one food site to another for foraging, whereas urban populations can reduce this time to 16% or less (Teas et al. 1980; Malik 1986; Seth and Seth 1986; Goldstein and Richard 1989; Marriott 1988; Marriott et al 1989; Lutz and Novak 2005). On Cayo Santiago, the monkeys can select various foods from the fauna and flora on the island and from the surrounding ocean. In addition, each animal is provisioned with approximately 0.23 kg of commercial chow each day (Marriott et al. 1989). This relative abundance of food enables the Cayo Santiago

macaques to spend less time on food foraging, compared to wild populations. For example, animals in group L spend 10.8% of their time eating (Marriott et al. 1989), the overall time being divided more or less equally between provisioned and natural resources. Although their eating bouts are of comparable duration to those of other sex-age groups, lactating females consume a larger volume of food per bout. This high level of consumption suggests that, like young adolescent females who must reach a minimal body mass to achieve sexual maturity at an earlier age than males, lactating females must take in more food to meet higher energetic demands or metabolic requirements (Marriott et al. 1989).

In multimale–multifemale societies, such as those of macaques and chimpanzees, the developmental events in the life history of females are complicated by menarche, first ovulation, first offspring, and other reproduction-related life traits. For example, mortality is especially high in females at around 3 years of age. During the period between 2.5 and 3.5 years, female survival rate drops by 10%, double the drop rate for males (Fig. 8.3). By slowing down growth rate, the energy cost can be minimized, and the saved energy can be re-directed to the cost of reproduction, which is beyond the cost of survival. In this regard, a prolongation of female growth may be an evolutionary response to high levels of intrasexual competition (Leigh and Shea 1995), and delayed female facial development may be an adaptive measure for survival and reproductive success (Jones et al. 1995).

Rapid functional maturation of the dentition, by contrast, is necessary for females to adequately process food in order to attain the minimum body size necessary for effective sexual maturity (Rawlins et al. 1984; Bercovitch and Nurnberg 1996; Bercovitch et al. 1998). This cross-over pattern of slow and fast growth rates may indicate a tradeoff, possibly regulated by sex hormones, between the functional needs of the dentofacial complex versus the reproductive necessity of achieving a minimal overall body mass. For a greater understanding of these diachronic changes in sexual dimorphism, studies need to be conducted on the ontogeny of the postcranial skeleton, particularly in regard to changes in body mass and the potential role of sex hormones that are comparable to those on the craniofacial skeleton (Wang et al. 2007; Blomquist and Turnquist 2011). However, whereas a minimal body mass appears to be essential for sexual maturity, body mass in excess of this minimum does not. Among baboons, at least, there is no evidence that females with a greater body mass than other sexually mature females have greater reproductive success (Johnson 2003).

These complex sex-based differences in the development of skull components may indicate differences in reproductive and survival strategies between males and females. For females, heavy investment in producing offspring early in life imposes an energy cost and a cost on life expectancy (Blomquist 2009). Thus, whereas females have a longer period of ontogeny, they may have a shorter life expectancy, due to the cost of bearing offspring. The impact of childbirth is not directly apparent from the skeleton, but a high mortality rate among females does occur at around 3 years of age when they normally reach sexual maturity (Fig. 8.3). Furthermore, females remain in their maternal group throughout life, but most adolescent males must leave their natal group before reaching sexual maturity. The delayed sexual maturation of males

enables them to develop the social skills necessary for mating success (Bercovitch and Harvey 2004), although adolescent males are often in significant danger from dominant males during this period of social transition (Berard 1989).

Sexual dimorphism of the rhesus skull raises interesting questions about functional differences in craniofacial performance throughout ontogeny. The structural and material properties of skulls (Wang and Dechow 2006; Wang et al. 2006a, b, 2010a, b), the morphological consequences of heterochrony and phylogentic affinity (Ravosa 2007), and dietary and nondietary behavioral effects (Strait et al. 2009; Kupczik et al. 2009; Wang et al. 2010c) have been studied. Thus, armed with this knowledge of how dentofacial morphology affects skull geometrics, kinematics, and kinetics, we can now address how the biomechanics of the skulls of males and females differ across the life span. Furthermore, whereas the functional significance of teeth, jaws, masticatory muscles, and food material properties is frequently studied for testing hypotheses related to primate adaptation and evolution, further investigations on sex-based differences in ontogeny, food intake patterns, locomotor patterns, social interactions (e.g., grooming), early life traits, and reproductive success are essential for understanding primate and human adaptation and evolution.

8.5 Conclusion

Comparisons of the patterns of tooth eruption in male and female Cayo Santiago rhesus macaques reveal that females reach functional dental maturity at an earlier age than males. Combined with the delayed fusion of facial sutures and later maturity of the female facial skeleton, these data demonstrate that ontogenetic differences exist between the dentofacial complexes of rhesus male and females, suggesting a tradeoff between growth of the dentofacial complex and achieving the minimal body mass that is necessary for female reproductive success.

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Chapter 9
Female Age of First Reproduction at Cayo Santiago: Heritability and Shared Environments

Gregory E. Blomquist

9.1 Introduction

The timing of female sexual maturation or age of first reproduction (AFR) is one of the most frequently studied life history variables by primatologists (Kappeler and Pereira 2003; Charnov and Berrigan 1993; Ross 1988). Within population variation in AFR has been a particular focus of research on the fitness benefits and costs of social status in cercopithecine primates (especially macaques, baboons, and vervets) with strong, stable dominance hierarchies and female philopatry (Whitten 1983; Harcourt 1987; Silk 1987; Altmann et al. 1988; Cheney et al. 1988; Sade 1990; Stucki et al. 1991; Bercovitch and Berard 1993; Ellis 1995; Packer et al. 1995; van Noordwijk and van Schaik 1999). Female philopatry is important because the formation of cooperative coalitions within matrilines (sets of females descended from a single founding female ancestor) is instrumental in maintaining and acquiring rank (Chapais 2004; Datta and Beauchamp 1991; Datta 1983a, b). Rank affects health by providing priority of access to limited resources (Koenig 2002) and shelter from stress induced by aggressive interactions (Sapolsky 2005). Females of higher rank tend to have earlier AFR which, all things being equal, provides a fitness advantage (Stearns 1992; Sibly and Calow 1986).

Pioneering research on Cayo Santiago macaques provided some of the earliest demonstrations of rank-related life history benefits for female primates (Drickamer 1974; Sade et al. 1976), and unraveled the typical patterning of social dominance in rhesus macaques and their closest relatives within the genus (Sade 1967; Missakian 1972; Kawai 1965; Kawamura 1965; Thierry et al. 2004). Females form a linear dominance hierarchy with daughters ranked just below their mothers. As younger

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sisters reach maturity, they displace their older sisters and occupy the rank immediately below their mother (Schulmann and Chapis 1980). Matriline members thus form blocks within the dominance hierarchy of roughly similar status.

This chapter builds on this remarkable foundation of research to present the results of several quantitative genetic studies on phenotypic variation in AFR at Cayo Santiago. Previous quantitative genetic work with the Cayo Santiago macaques primarily dealt with morphology (e.g., Cheverud 1981, 1982; Cheverud and Buikstra 1981a, b; McGrath et al. 1984; Cheverud et al. 1990; Hallgrímsson et al. 2002). There remains relatively little published quantitative genetic information on the life history traits of non-human primates (Martin et al. 2002; Jaquish et al. 1996; Williams-Blangero and Blangero 1995; Cheverud et al. 1994). Though developed by animal breeders (Kruuk 2004; Lynch and Walsh 1998; Postma 2006), the methods of quantitative genetics are increasingly being employed to answer questions about variation in wild and free-ranging populations, such as "How much of the variation in AFR is due to genetic variation?" and "Do high ranking females mature earlier because they share a common beneficial environment or because they have genes that promote more rapid maturation than their lower-ranking peers?"

9.1.1   Genetic, Cohort, and Maternal Effects

In this chapter, I use quantitative genetic methods to address two major questions about female AFR at Cayo Santiago. The first involves the estimation of underlying variance components that contribute to the phenotypic variation in AFR. I explore three main sources: additive genetics, cohort effects, and maternal effects. Additive genetic variance is that due to differences among population members in their breeding values. Breeding values can be thought of as a multilocus genotype for AFR, or how much the alleles an individual carries causes it to depart from the population mean for AFR. Additive genetic variation for a trait is often reported as a heritability, the ratio of additive to phenotypic variance ($h^2 = V_A/V_P$). Because relatives share genes according to the rules of Mendelian inheritance, the resemblance among relatives can be used to separate this genetic source of variation from environmental causes (Lynch and Walsh 1998). Cohort effects are the result of temporal variation in a variety of factors that may affect AFR, such as group or total population density, food abundance, or disease prevalence. Animals born in the same cohort are likely to be more similar to one another because of these shared aspects of their environment. Finally, maternal effects are caused by offspring sharing the special, intimate environment provided by their mothers, pre- and postnatally (Maestripieri and Mateo 2009; Cheverud and Wolf 2009; Wolf and Wade 2009).

Maternal effects have received increased attention from primatologists, often focused on the intergenerational transmission of behavior. Because mothers transmit their social rank as well as their genes to offspring, the patterning of social dominance in female macaques has been explained as a possible maternal effect on offspring life history traits (e.g., Maestripieri 2009; Charpentier et al. 2008; Altmann and Alberts 2005; Setchell et al. 2001; Hrdy 1999). High-ranking females are born

with a "silver spoon" of a benign social environment while lower-ranked females have to make the best of their bad situation (Grafen 1988). Such studies use a straightforward route to identify maternal effects either by exploiting variation among the offspring of a single female and relating it to some known difference among the offspring (e.g. birth order) or comparing the offspring of different mothers and relating outcomes to a measurable maternal characteristic (e.g., dominance rank). For example, Altmann and Alberts (2005) found higher-ranking baboons at Amboseli had offspring that were relatively larger for offspring age, and primiparous mothers had relatively smaller juveniles. Similar birth order effects have also been documented in captive macaques (Broadhurst and Jinks 1965).

An alternative approach borrowed from animal breeders (Wilham 1963; Bijma 2006) that has been used successfully with wild populations of birds and mammals is the estimation of a maternal variance component (V_M) or maternal effect ($m = V_M/V_P$) within a quantitative genetic model (Kruuk and Hadfield 2007; Kruuk 2004; Kruuk et al. 2000; Wilson et al. 2005; Keller et al. 2001; Cheverud and Moore 1994). This is identical to household effects identified in studies of humans (e.g., Pettay et al. 2005; Towne et al. 2005). For example, Kruuk et al. (2000) found that birth weight in female red deer had a maternal effect of about 0.20 and the heritability of 0.25, meaning that the identity of a mother (a proxy for the environment she provides) explained an additional 20% of phenotypic variation beyond the additive genetic effects gauged by the heritability. This quantitative genetic method only partially overlaps with the phenotypic approaches discussed earlier. For example, the rank effects on baboon mass could contribute to m, but the primiparity effect on mass would reduce m because it causes offspring of the same female to *differ* from one another. The analysis presented in this chapter is intended to help clarify the influence of maternal effects on primate life histories by taking both approaches to unpack variation in female AFR at Cayo Santiago – identifying maternal characteristics that influence AFR similar to Altmann and Alberts (2005) through phenotypic regressions and deploying quantitative genetic techniques to estimate m.

9.1.2 Rank-Related Trends in AFR: Genes or Environment?

The second major topic of this chapter is highlighting and providing a tentative answer to an often-overlooked problem in comparing the life history traits of female macaques of different rank. Strictly phenotypic comparisons suffer from an important shortcoming. Because matriline members share similar rank and are also genetic relatives, and AFR is known to be heritable at Cayo Santiago (Blomquist 2009a, b), it is unclear to what extent the environment provided by social rank or potential genetic differences among matrilines contribute to these regularly observed life history disparities (Silk 1984).

Genetic and rank-related environmental differences are confounded in simple phenotypic comparisons. However, techniques used by animal breeders can be applied to resolve this question by separating genetic and environmental contributions to phenotypes of pedigree members (Postma 2006; Postma and Charmantier 2007).

This requires paternal genealogical links or cases of change in female rank, both of which provide genetic linkages between rank environments. The resulting predicted breeding value (PBV) is an estimate of the additive genetic value of an individual for a given trait, or how much the alleles an individual carries cause it to depart from the population average for the trait (Kruuk 2004; Mrode 1996).

9.2 Explaining Phenotypic Variation in AFR

Quantitative genetic techniques are essentially statistical models that exploit resemblance among relatives and rules of Mendelian inheritance to break down phenotypic variation. In the past, this meant comparisons of a few kinds of relatives in standard statistical designs, such as mother–daughter regression or sibling ANOVAs (Lynch and Walsh 1998; Roff 1997). More recently, evolutionary-minded ecologists and anthropologists have applied the "animal model" to decompose phenotypic variation (Kruuk 2004; Cheverud and Dittus 1992). This method offers two important advantages over its predecessors. First, it easily allows the incorporation of known environmental factors that may affect phenotypes, such as age, birth cohort, or social group membership. Second, it functions well in highly unbalanced cases where animals are not related as standard mother–daughter or sibling pairs, and instead exploits of all the known genealogical relationships among individuals there is phenotypic information on. The animal model is thus more flexible and statistically more powerful.

The animal model is a linear mixed model (9.1) where $\mathbf{y}$ is a vector of phenotypic data (e.g., AFRs), $\mathbf{X}$ a design matrix for fixed effects, $\mathbf{b}$ a vector of fixed effects used for controlling known variation among individuals, $\mathbf{Z}_a$ a design matrix for random effects, $\mathbf{a}$ a vector of random effects such as individual breeding values, and $\mathbf{e}$ the residual error (Kruuk 2004; Lynch and Walsh 1998). Additional random effects, such as maternal effects, can be accommodated by adding another vector and design matrix to the model (e.g., $\mathbf{Z}_m\mathbf{m}$):

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Z}_a\mathbf{a} + \mathbf{e} \tag{9.1}$$

I used phenotypic data on 975 females born on Cayo Santiago between the 1965 and 1999 birth cohort, derived from the Cayo Santiago ACCESS demographic database. AFR was treated as an ordinal variable taking only the integer values of

Table 9.1 Descriptive statistics for female age of first reproduction (AFR) and linear model terms, $N = 975$

Variable	Minimum	Maximum	$\bar{x}$	SD
AFR (cohort years)	3	6	4.270	0.586
Age in cohort (days)	100	346	201.607	41.522
Mother's age at birth (years)	3.05	22.86	7.861	3.495
Matriline rank at birth[a]	1	3	1.997	0.805
Birth cohort (calendar year)	1965	1999	1983.807	8.624

[a]Coded as high = 1, middle = 2, low = 3

three to six and was calculated as the difference between a female's birth cohort and that of her first offspring regardless of the offspring's sex or survival.

Several other variables were selected or calculated for use as fixed effects in the animal model and exploration of the influence of maternal characteristics on AFR Table 9.1. These were birth cohort, the age of a maturing female within her birth cohort in days after the beginning of the cohort (August 1), and the age of a maturing female's mother when she gave birth to her. Several other variables were explored but dropped from the final analysis because they had very little explanatory value (presence of a maturing female's mother when she was three years old, whether the maturing female was the product of her mother's first reproduction, and the presence of an older sibling born in the birth cohort prior to the one a maturing female was born in to six months of age).

In addition to these variables, annual matriline rank information was shared by John Berard and Donald Sade. I used the matriline rank of a maturing female within her birth group in the year of her birth coded ordinally as high = 1, middle = 2, or low = 3 rank. In most cases, the matrilines of a group were divided into thirds and assigned to these categories. In situations where a social group had two matrilines, they were scored as high and low. If there were four matrilines, the middle-ranking two matrilines were both scored as middle. Females in groups with only one matriline were excluded from analysis.

Pedigree information, or the patterns of relatedness, came from maternal records in the demographic database and genetic paternity determination via microsatellites sampled through the end of 2000 (Nurnberg et al. 1998). While the demographic database contained records for nearly 8,000 individuals at the time of this study most were not informative for the quantitative genetic analysis. A reduced pedigree file containing 1,192 individuals was used to indicate relatedness among the 975 females with AFR records analyzed (Fig. 9.1). While 1,162 of them had known mothers, only 221 had known fathers, such that maternities outnumber paternities by about five to one. There are 30 matrilines represented in the pedigree file but many are linked by paternities such that there are only 14 separate "families." Nearly all of the individuals (95.6%) are contained within one large pedigree of 1,140 members, while the remaining individuals are in linked in smaller groupings with only three to nine members each. The mean coefficient of relatedness between females with the AFR records used in analysis was 0.0050 ($SD = 0.0299$).

Fixed effects were explored in using a general linear model in R (R Development Core Team 2007) prior to running the animal model. Age in cohort, matriline rank at birth, and birth cohort were all highly significant predictors ($P < 0.01$). Mother's age at birth was not significant ($P = 0.218$) but was retained to remove potential variation that might complicate the quantitative genetic estimates. The model R^2 indicates that this set of variables explains about 24% of the variation in AFR, with birth cohort making the largest contribution (SS in Table 9.2). Regression slopes for age in cohort and maternal age were positive indicating later AFR resulted from being born late within a cohort or being born to an older mother (age in cohort $\beta = 0.0030 \pm 0.0005$; maternal age at birth $\beta = 0.0062 \pm 0.0050$). The well-known pattern of higher matriline rank yielding earlier maturation is also illustrated in Fig. 9.2.
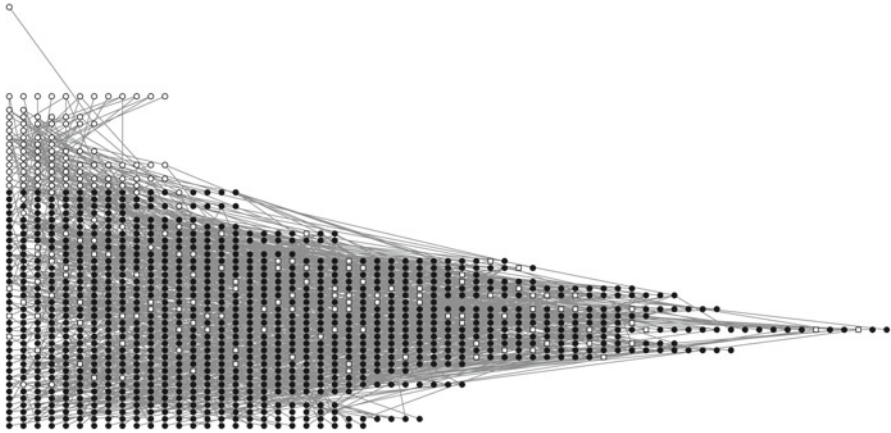
Fig. 9.1 Pedigree(s) of 1,192 Cayo Santiago macaques used in quantitative genetic analysis. *Circles* indicate females and squares males. *Filled symbols* identify AFR records used in the analysis. *Open symbols* are individuals providing pedigree links but phenotypic information was not applicable or not available for them. Each row gives the members of a birth cohort starting with one individual from 1938 at the *top*, followed in larger numbers after 1951, and finishing at 1999 on the bottom *row*

Table 9.2 Linear model analysis of variance table predicting female AFR at Cayo Santiago ($R^2 = 0.242$)

	SS	df	F	P
Age in cohort	9.56	1	35.32	<0.001
Mother's age at birth	0.41	1	1.52	0.218
Matriline rank at birth	3.09	2	5.71	0.003
Birth cohort	69.24	34	7.52	<0.001
Residuals	253.35	936		
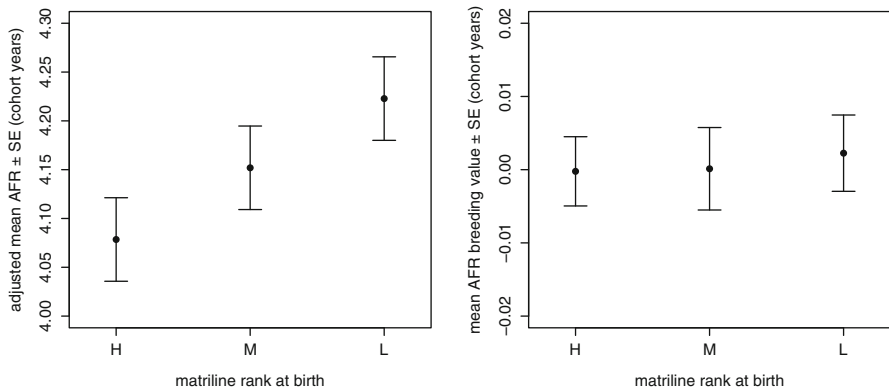
Fig. 9.2 Phenotypic (*left*) and breeding value (*right*) mean differences in female AFR among matriline rank levels at Cayo Santiago. Phenotypic values are adjusted means from the linear model evaluated for a maturing female who was born 200 days into the 1965 birth cohort to a 10-year-old mother

Variance components were computed running the animal model in WOMBAT (Meyer 2007). Age in cohort and mother's age at birth were used as linear covariates while matriline rank at birth and birth cohort were entered as multi-level fixed effects. Three random effects in the model were animal identity to account for additive genetic variation, maternal identity to estimate any maternal effects, and unexplained residual error. These sources are assumed to be uncorrelated such that the phenotypic variance is the sum of its variance components ($V^P = V_A + V_M + V_R$).

9.3 Results

The reduction in phenotypic variance by accounting for the fixed effects variables was about 21% of the total (0.343–0.270), consistent with the general linear model R_2 (Tables 9.2 and 9.3). Additive genetic variation accounted for about 15% of the remaining phenotypic variation ($h^2_{anim} = 0.159 \pm 0.065$; $t_{975} = 2.293, P = 0.011$, $P = 0.011$) or 12% of the total phenotypic variance (h^2_{total}). Wilson (2008) proposed h^2_{total} is better for comparisons among published heritability estimates because it does not depend on the fixed effects used in the animal model. The maternal effect was estimated to be zero, leaving about 67% of the total phenotypic variance unexplained (Table 9.3). Dropping matriline rank at birth as a fixed effect caused a very minor increase in the heritability estimate but did not change the maternal effect. Unfortunately, the small number of paternities in the pedigrees used does not allow for very good separation of additive genetic and maternal variance in this data set (Fig. 9.1) and this result of $m = 0$ could be regard with some suspicion.

9.4 Genetic vs. Environmental Causes of AFR Differences by Matriline Rank

An additional result of running the animal model just described is the generation of predicted breeding values (PBVs: Kruuk 2004; Mrode 1996). These are estimates of how much the alleles each individual carries caused its AFR to depart from what

Table 9.3 Variance components and ratios for female AFR at Cayo Santiago

Variance component $\pm SE$		Ratio $\pm SE$
V_A	0.040±0.018	$h^2_{anim} = 0.149 \pm 0.065$
V_M	0.000±0.010	$m = 0.000 \pm 0.036$
V_R	0.230±0.019	$r = 0.851 \pm 0.065$
V_{Panim} [a]	0.270±0.013	
V_{Ptotal} [b]	0.343	$h^2_{total} = 0.117$
		Fixed effects = 0.211

[a]Phenotypic variance after fixed effects are removed
[b]Total phenotypic variance including fixed effects

would be expected given the fixed effects used in the model (age in cohort, maternal age, matriline rank, and birth cohort) and the known variance components. While rank-related differences in AFR are well documented phenotypically, using PBVs could identify genetic causes for those phenotypic trends.

Postma (2006) argued that exploration of breeding values must be done with a full understanding of the reliability of predicted breeding values and clear statement of null hypotheses when testing for trends within them. When individuals are not randomized among environments, a predicted breeding value is not equivalent to the true breeding values and will continue to reflect the environmental component of an individual's phenotype. Reliability (r^2) is a measure of how well predicted breeding values reflect true breeding values. Technically, reliability indicates how much information is contributed to breeding values by records on related individuals beyond the individual's own phenotype and the trait heritability. It is calculated as the ratio of the variance in the predicted breeding values to the additive genetic variance ($r^2 = V_{PBV}/V_A$). The range of the reliability spans from the heritability where relatives contribute nothing to the breeding values, to one, where predicted values are equivalent to true breeding values. Reliabilities much larger than heritabilities indicate the predicted breeding values are accurate reflections of the true breeding value.

Once generated, predicted breeding values can be analyzed like phenotypic data using standard statistical software (Kruuk 2004). As just noted, however, interpretation of trends in the breeding values depends on the quality of the pedigrees used (Postma 2006; Postma and Charmantier 2007). Small numbers of pedigree links across rank categories, a situation known as low connectedness (Kennedy and Trus 1993), will cause low trait reliability and limit power for detecting or rejecting trends in the predicted breeding values. To demonstrate AFR records in the Cayo Santiago pedigree are well-connected, I calculated the percentage of close relatives (coefficient of relatedness ≥ 0.125) in matriline rank categories different from the rank category of each individual (Garant et al. 2005). Pair-wise coefficients of relatedness were determined by the makeA() function in R's pedigree package (Coster 2008).

9.5 Results

The predicted breeding values show no rank-related trends (ANOVA $F_{2,972} = 0.064$, $P > 0.93$; Fig. 9.2). This implies that the additive genetic variation previously noted for AFR is essentially randomly distributed among the different rank levels, and, importantly, that the well-known phenotypic differences are simply the result of the beneficial environment shared by females of higher social rank.

The AFR reliability and connectivity among rank categories both suggest that the lack of trend in the PBVs is trustworthy. The reliability is 0.221 (0.009 / 0.040) which is 48% greater than the heritability. Furthermore, about 25–30% of a female's close relatives come from different matriline rank categories, suggesting high amounts of connectivity between the rank levels (Table 9.4).

Table 9.4 Connectivity between rank categories where the coefficient of relatedness between individuals was 0.125 or more

	High	Middle	Low	Total pairs	Different (%)
High	1,759	458	214	2,431	27.64
Middle		2,290	358	3,106	26.27
Low			1,498	2,070	27.63

9.6 Discussion

The general picture of female maturation from these results is one of great environmental responsiveness, with a small but significant genetic component. The heritability estimate for AFR for the Cayo Santiago females differs from the one previous estimate for a nonhuman primate population. It is much higher in captive baboons that live in a much more controlled environment at the Southwest Foundation for Biomedical Research ($h^2 = 0.87$, Williams-Blangero and Blangero 1995). Quantitative genetic studies on living and historical human populations indicate that a wide range of heritabilities can be found for menarcheal age and AFR (e.g., Towne et al. 2005; Pettay et al. 2005; Kirk et al. 2001). This suggests that these are largely population-level rather than interspecific differences. Heritabilities of life history traits such as AFR are generally expected to be low either because past selection has eroded additive genetic variation (Roff and Mouseau 1987) or because there are more physiological and environmental factors that determine life history traits than morphology – increasing their residual variation (Price and Schluter 1991). A low heritability for AFR at Cayo Santiago is unsurprising. Additional sources of variation will be contained in the residual variance (V_R) for AFR. These include genetic sources such as dominance and epistasis and other environmental factors beyond the fixed effects used in the animal model. For example, individual rank differences within matrilines might also explain some variance.

The larger cohort effects on AFR incorporate a wide variety of potential inter-annual differences between 1965 and 1999. Population and group size or age structure may be among the most important of these (Bercovitch and Berard 1993) while climatic factors or changes in population management may play a role as well (Rawlins and Kessler 1985, 1986; Sade et al. 1985). A small amount of additive genetic variance also might be mistakenly contained within the cohort variance here, which would depress the heritability. This would be caused by the concentration of paternity among few sires within birth cohorts (Widdig et al. 2003). However, because cohorts have multiple sires and sires typically produce offspring in multiple cohorts, it is unlikely that this effect is very large.

Maternal effects on AFR are even less clear and require care to communicate the manner in which there are or are not maternal effects on this life history trait. Several variables that could be interpreted as maternal characteristics (e.g., mother's age, matriline rank at birth, and perhaps even age within cohort) systematically contribute to advance or delay in AFR. However, maternal age and age in cohort are transient phenomena that will not contribute to similarity among a mother's offspring.

The stability of matriline rank should increase similarity among offspring. However, the intergenerational stability of rank also suggests that rank could be interpreted as a direct effect of offspring environment rather than a maternal effect (Cheverud and Wolf 2009). Regardless of the strength of the relationships or interpretation of these variables, the animal model estimate for $m = 0$ implies that maternal identity does not contribute to resemblance among maturing females any more than is already expected by Mendelian inheritance. This is consistent with studies of domesticated or lab animals on morphology where maternal effects commonly decline with offspring age such that AFR may be at the terminal age limit of their detectable strength (Wilson and Réale 2006; Atchley 1984). However, the interpretation of this result should also be cautious because of the low number of paternities in the pedigrees that limit the separation of additive and maternal variance. Increasing the number of paternities, especially if adequate tissue samples for individuals born in the 1950s–1970s were available to be genotyped, could resolve this question.

The lack of breeding value differences among rank categories is important for at least two reasons (Blomquist 2009a). First, it verifies the long-assumed position that matriline differences in life history traits are due to the environment provided by rank and not genetic differences among the matrilines (Silk 1984). This is encouraging for field observers who may never have access to rich genealogical or genetic information on their study populations but can document the environmental factors that cause rank to influence life history traits by predicting priority of access to limited resources and shelter from stress (Koenig 2002; Sapolsky 2005). Second, it implies some aspects of the evolutionary dynamics of female age of first reproduction at Cayo Santiago and perhaps more generally among female cercopithecines with strong, nepotistic dominance hierarchies. Because breeding values are essentially randomly distributed among rank categories, predicting response to selection will not be complicated by gene-environment covariance (van Tienderen and de Jong 1994). Furthermore, the accurate prediction of response requires an estimate of the heritability that is unpolluted by shared environments among relatives, which is provided by the animal model (Kruuk 2004). Nevertheless, selection on age of first reproduction in female primates is likely complex, involving trade-offs with infant survival and maternal survival or future reproduction (Bercovitch et al. 1998; 2000; Bercovitch and Berard 1993) that may be genetically correlated and strongly influence evolutionary response (Stearns 1989; Pettay et al. 2005; Blomquist 2009c).

Like many studies carried out at Cayo Santiago, this one would likely have been impossible in a field setting. Sufficient pedigree information and life history data are simply not currently available at most primate field sites. Cayo Santiago is exceptional for its temporal depth and topical breadth of information ranging from behavior, demography, and genetics through morphology, immunology, and endocrinology. The potential synergy of the ever-expanding data set on this thoroughly studied population is exciting.

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Chapter 10
Costs of Reproduction Among Rhesus Macaque Females on Cayo Santiago

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10.1   Introduction

Reproduction is energetically costly for mammalian females during the periods of gestation and lactation and, consequently, is likely to be associated with reduced survival (Stearns 1989, 1992; Roff 2002), particularly when maternal condition is poor. Higher mortality may be associated with birth-related complications, but it also may be the consequence of elevated circulating levels of cortisol suppressing immune function (see McEwen et al. 1997, for a review). If the hypothalamic–pituitary–adrenal (HPA) axis is hyperactivated in post-partum females during prolonged periods as a result of either the energetic demands of lactation or the associated psychosocial stressors, immune function may become impaired, potentially making females more vulnerable to diseases and to increased risk of mortality.

Survival costs of reproduction have been documented for a few mammalian species. Among seasonally breeding Columbian and Richardson's ground squirrels (*Spermophilus columbianus* and *Spermophilus richardsonii*), adult female mortality is highest in the birth season and during the period of lactation (Michener and Locklear 1990; Michener 1998; Neuhaus and Pelletier 2001). Among baboons (*Papio* spp.), mortality rates are highest among lactating and pregnant females (e.g., Cheney et al. 2004).

The terminal investment and senescence hypotheses both predict that the costs of reproduction should increase with age. According to the senescence hypothesis,

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physical and physiological deterioration lead to declining reproductive output (Weladji et al. 2002). Evidence for this hypothesis has been documented in many animal populations (e.g., *Parus major*, Bouwhuis et al. 2009; *Arctocephalus tropicalis*, Beauplet et al. 2006; *Ovis canadensis*, Berube et al. 1999). According to the terminal investment hypothesis (Williams 1966), a female's reproductive strategies should change depending upon her likelihood of conceiving and surviving until her offspring reach independence. When she is in poor physical condition or in advanced age, her reproductive effort should increase. This hypothesis has been supported by studies of several avian and mammalian species (e.g., *Passer domesticus*: Bonneaud et al. 2004; *Sula nebouxii*: Velando et al. 2006; *Kobus megaceros*: Bercovitch et al. 2009). Although reproductive output should decrease with age according to the senescence hypothesis, and reproductive effort should increase with age according to the terminal investment hypothesis, these two hypotheses are not mutually exclusive (Weladji et al. 2010). Compared to younger females, older females, for example, may have fewer resources to provide for offspring due to senescence, but they may invest a greater proportion of their available resources in their offspring. Even with such increased investment, however, offspring mass and survival may still decline with maternal age if the effects of senescence outweigh the consequences of increased maternal investment.

Primates are ideal subjects for examining the costs of gestation and lactation and for testing the senescence and terminal investment hypotheses because they tend to be long-lived and their offspring have a prolonged period of dependency, requiring months and sometimes years of maternal care. Although the process of senescence has been documented for primates (Walker and Herndon 2008), evidence for the terminal investment hypothesis is mixed. Studies of several species have demonstrated that interbirth intervals increase with maternal age (e.g., Gagliardi et al. 2007; Robbins et al. 2006), which may suggest slowed reproduction due to senescence or to increased maternal investment. Furthermore, some studies have reported that infants born to older mothers have greater birth weights and survival rates (Dolhinow 1979; Silk et al. 1993; Paul et al. 1993), but this relationship has not been found in other studies (Borries and Koenig 2008; Wright et al. 2008; Fessler et al. 2005). Few studies have taken multiple measures from mothers and their infants to test both hypotheses simultaneously.

The goals of this study are to assess the costs of reproduction for rhesus macaque females and to investigate possible age-related changes in female reproductive strategies and offspring survival, such as those predicted by the senescence and terminal investment hypotheses. Rhesus macaques are an interesting species for studying female reproductive strategies because females have long life spans and infant survival is entirely dependent upon maternal care. Furthermore, dominance ranks are stable for female rhesus macaques (Melnick and Pearl 1987), and studies have generally reported higher cortisol levels in low-ranking than in high-ranking females (e.g., Gust et al. 1993; Maestripieri et al. 2008). Chronic activation of the HPA axis, as evidenced by high levels of cortisol, can impair immune function (Sapolsky 2005) and may contribute to life history differences.

The rhesus macaques on Cayo Santiago comprise an ideal population for investigating the survival costs of reproduction because colony records spanning more than 50 years exist that include birth and death dates of all females and their offspring who have resided on the island. There is also the opportunity to collect blood samples and morphometric data from this population during the annual trapping period. Blood samples can be assayed for cortisol levels, and morphometric data can be used to characterize the physical conditions of mothers and their infants. Age-related effects on interbirth intervals and infant survival rates can be determined using the long-term database, and age-related changes in maternal care can be studied readily since individuals are tattooed and well-habituated. Given that the rhesus macaques on Cayo Santiago are food-provisioned and reside in a predator-free environment, there may be limitations regarding the generalizability of findings obtained in this population (Maestripieri and Hoffman 2011). If, however, we find variability in maternal physiology, behavior, or survival in relation to reproduction, we can conclude that reproduction is costly even when food is abundant and predators are absent.

In our study, we show that:

1. Breeding on Cayo Santiago is seasonal, and reproduction is influenced by climatic factors, such as rainfall.
2. Female deaths are more likely to occur in the birth season than in the mating season.
3. Plasma cortisol is higher for lactating females than for cycling females.
4. Female body condition and activity levels decline with age in accordance with the senescence hypothesis.
5. Interbirth intervals increase as a function of age in accordance with the terminal investment and senescence hypotheses.
6. Older females, in accordance with the terminal investment hypothesis, invest more resources in their infants even though offspring survival does not necessarily improve with such increases.

10.2   Methods

Cayo Santiago is a 15.2 ha island located 1 km off the southeastern coast of Puerto Rico. The rhesus macaque colony on this island was established in 1938, with free-ranging individuals captured in India (Rawlins and Kessler 1986). Since then, no new individuals have been introduced into the population, except through births. To maintain a stable population size, a fraction of the yearlings and 2-year olds are transferred off the island each year. Monkeys living on Cayo Santiago forage on vegetation and are provisioned with commercial monkey chow. The data for this study came from two different data sets, which will be referred to as "long-term data" and "short-term data," respectively.

10.2.1 Long-Term Data

This data set is comprised of records maintained in the Cayo Santiago database, which includes information on each animal's genealogy and dates of birth and death, as well as a history of each individual's group membership and reproduction. Throughout the periods of interest to this study (1957–2005 for analyses related to female mortality and reproductive seasonality; 1957–2007 for analyses related to maternal age, interbirth intervals, and infant survival), Cayo Santiago staff updated colony records with daily censuses of all animals.

To determine whether there were seasonal effects on reproduction and female mortality, we included in our sample adult females who were born on Cayo Santiago in the period 1957–2001 and died on the island in the period 1961–2005. Only sexually mature females that were at least 4 years old at their time of death were included in the sample. To determine whether rainfall patterns affected the timing of seasonal reproduction, we obtained data on daily precipitations from 1963 to 1996 from the National Oceanic and Atmospheric Administration (NOAA) of the US Department of Commerce station in Humacao, PR (approximately 6 miles from Cayo Santiago). The onset of the spring rainy season was identified as the first day since January 1st in which precipitation was equal to or greater than 1 in.

We calculated median life span, interbirth intervals, and infant survival rates for all reproductively mature females who were born in or after 1957, lived their entire lives on the island, and died prior to May 1, 2007 ($n = 637$). For every age at which a female gave birth to a live infant, we assessed the number of days between that birth and her previous birth. Additionally, we used the long-term database to determine whether or not the female had given birth in the previous birth season. After rounding female ages at birth to the nearest year, we calculated the average interbirth interval for females at each age. We included females between 4 and 24 years in these analyses.

We measured the effects of maternal age and offspring sex on average offspring life span and on rates of infant mortality during the first 30 days and 1 year of life. The Cayo Santiago database does not contain accurate information about the animals' dominance ranks; therefore, this variable was not included in analyses using the long-term data set.

10.2.2 Short-Term Data

Approximately 850 animals distributed among six naturally formed social groups resided on Cayo Santiago when the short-term data were collected. This data set is comprised of plasma cortisol samples, morphometric measures, and behavioral data. Between January and March 2007, we collected morphometric measurements and blood samples from females from six social groups who were between 15 and 26 years of age ($\overline{X} = 18.3\,\text{years}$). Between January and February 2008, we collected

morphometric data and blood samples from adult females from four social groups who were between 7 and 26 years of age ($\overline{X} = 15.8$ years). We collected behavioral data between April and December 2007, from subjects ranging between 6 and 22 years of age ($\overline{X} = 15.0$ years).

In order to collect blood samples and to take morphometric measurements, trained staff members captured adult females and their infants in a feeding corral, approximately 100 m², which was provisioned daily with monkey chow. Infants remained with their mothers during the entire trapping and data-collection process. Trapping generally occurred between 8:30 and 12:00. The staff members netted or captured the monkeys by hand in one of three feeding corrals, transferred them to a holding cage ($0.62 \times 0.42 \times 0.62$ m), and moved them to a small field laboratory. The monkeys remained in a standard squeeze cage with their infants for overnight housing. The following morning, veterinary technicians anesthetized the adult females and their infants with ketamine (approximately 10 mg/kg via IM injection).

Veterinary technicians drew blood from the femoral vein of anesthetized females between 7:15 and 10:40 (average time of day: $8:18 \pm 5.0$ min) and, on average, 66.5 ± 5.5 min after the door of the laboratory was first opened (range: 7–213 min) and 22.1 ± 2.7 min after ketamine administration (range 0–127 min). All blood samples were collected into heparin-treated Vacutainer tubes. We refrigerated samples for 20 min and then centrifuged them for 20 min. Following centrifugation, we aliquotted the plasma into microcentrifuge tubes, and stored the tubes at −80°C until we shipped them to the Biomarker Assay Core Lab of the Yerkes National Primate Research Center, where they were assayed for cortisol by radioimmunoassay using a commercially available kit (Diagnostic Systems Laboratories, Webster, TX, USA). The samples collected in 2007 were assayed in April 2007 (see Maestripieri et al. 2008, for some of these data), while the samples collected in 2008 were assayed in July 2008. The assay used has an intra-assay coefficient of variation of 4.90%. Measures of inter-assay variation, assessed by adding low and high concentration standards to each assay, were 15.6% (low) and 13.5% (high). Cortisol concentrations measured the morning after capture presumably reflect the cumulative stressful effects of capture and overnight housing (see Laudenslager et al. 1999; Maestripieri et al. 2008).

To take morphometric measurements, we weighed the anesthetized females and infants separately in a standard hanging scale. We used a large anthropometer (Lafayette Instruments, Lafayette, IN) to measure crown-rump length of each anesthetized adult female while she was placed in a standardized position with her back fully straight. We collected morphometric measurements from 53 adult females from six social groups in 2007 and from 40 adult females and 26 infants from four social groups in 2008. We calculated body mass index (BMI) for each adult female by dividing mass (kg) by the square of crown-rump length (m²) (Campbell and Gerald 2004).

We collected behavioral data during pre-birth observations (those occurring from April 1, 2007 until a female gave birth) and post-birth observations (occurring from the date a focal female gave birth until mid-December 2007). We determined the proportion of time focal animals spent feeding, resting, traveling, and engaging in grooming interactions by conducting instantaneous sampling at 1-min intervals

during 30-min focal follows. The grooming measure combined grooming given to and received from social partners who were 3 years old and above. During the first month post-birth, we recorded the amount of time mothers and infants were in ventro-ventral contact during 30-min focal follows.

Behavioral data collection initially included 28 females. Each subject was multiparous and belonged to one of three social groups. All 28 females gave birth during the birth season, and we collected behavioral data post-birth on those females that gave birth prior to the termination of behavioral data collection ($n = 23$). We conducted focal follows on three additional females, beginning with the week they gave birth. Dominance ranks were assigned on the basis of behavioral data on aggressive and submissive interactions collected by trained observers. Subjects were classified as high-, middle-, or low-ranking depending on whether their rank fell within the top, middle, or bottom third of the dominance hierarchy within their social group.

10.2.3 Data analysis

Seasonality of reproduction and climatic factors affecting seasonality – The first and the last birth in the birth season of any given year were identified as the earliest and the latest birth that occurred within two standard deviations below and above the mean for that year, respectively. Since pregnancy in rhesus macaques lasts about 165 days (Ardito 1976), the beginning and the end of the mating season were identified by counting backward 165 days from the date of the first and the last birth (see also Rawlins and Kessler 1985). We ran Pearson's correlation tests to determine if there was a relationship between birth season year and birth season start date, and if there was a relationship between the onset of the birth season and the onset of the rainy season.

Seasonality of adult female deaths – The monthly mortality probability for adult females was calculated by dividing the number of females that died in a given month by the number of adult females present in the population that month (i.e., all the adult females that could potentially die). To test statistically for seasonality in the probability of mortality of females, we used Poisson regression analysis. Our model included a linear trend in year to capture long-term changes in probability of mortality between 1961 and 2005. Seasonality over the course of the year was captured via a single harmonic sine wave. This was entered in the model using a sine and a cosine term to allow for different phases (timing of the peak), yielding a test for seasonality with 2 df.

Plasma cortisol in relation to reproductive state – We used general linear mixed models (GLMMs) to assess the effects of three categorical variables and three continuous variables on cortisol levels. Dominance rank, social group, and reproductive condition were fixed factors in the models, and female age, female mass, and infant age were continuous factors. We included individual identity and year of sample collection as random factors in the models. One female was excluded from analyses because her cortisol level was more than 2.5 standard deviations below the group average.

To conduct within-subjects comparisons of 2007 and 2008 cortisol values, we transformed raw cortisol values into *z*-scores because 2007 and 2008 average values differed significantly (for a more detailed explanation see Hoffman et al. 2010a). We used restricted maximum likelihood methods for model estimation and Sattherwaite's *F* tests to gauge fixed effects. We chose the best model using Akaike's information criterion (AIC), starting with all main effects and interactions between each main effect and the random factors "identity" and "year." None of the interactions with identity or year were included in the final model.

Age-related physical and behavioral change – Using the short-term data, we employed general linear modeling (GLM) to test the effects of female age, social rank, and reproductive condition (fixed factors) on BMI (dependent variable). We also used GLM to determine the effects of age and social rank on the proportion of time females spent resting or grooming pre-birth (i.e., when cycling or pregnant) and during the first month post-birth.

Age-related changes in interbirth interval – We performed linear and quadratic regression analyses on data from the long-term data set to determine the influence of female age on interbirth intervals. We conducted linear regression analyses to determine relationships between maternal age and the proportion of offspring surviving to 30 days and 1 year in the long-term database, and we used Chi square analyses to determine if offspring sex influenced offspring survival to these time points.

Age-related changes in maternal behavioral investment and offspring survival – We employed GLM to test the effects of maternal age and social rank on the average number of minutes mother–infant pairs spent in ventro-ventral contact per hour during each infant's first month. We performed linear regression analysis to determine whether infant birth date influenced time in ventro-ventral contact.

For analyses involving infant mass, we excluded infants younger than 60 days at the time of measurement because rhesus growth is linear only between 2 months and 11 months (Smith and Small 1982). We used GLMM to determine the relationship between infant mass and maternal age, infant age, and infant sex. To determine whether offspring sex ratio changes with age, we calculated from the long-term data set the proportion of offspring that were male born to females at each year of life (years 4–24) and then ran linear and quadratic regressions to determine whether sex ratio changed with maternal age.

Unless otherwise noted, we conducted two-tailed tests. We considered $p < 0.05$ as significant. We conducted data analyses in SPSS 17.0.

10.3   Results

For females in the long-term data set spanning 1957–2007 who survived to at least 4 years of age ($n = 631$), median life span was 15.0 years and maximum life span was 31.4 years. The oldest female to give birth did so at 24.2 years.

10.3.1 Seasonality of Reproduction and Climatic Factors Affecting Seasonality

Although the rhesus macaques on Cayo Santiago have year-round access to food and water, they continue to breed seasonally, with 86% of births occurring between November and March. Birth records collected between 1961 and 2005, however, indicate that the birth season has commenced increasingly earlier over time ($r = -0.89$; $p < 0.001$; $n = 42$). The shift in the onset of the birth season over the years has corresponded with a shift in the onset of the spring rainy season ($r = 0.43$, $n = 34$; $p = 0.01$), which has begun increasingly earlier in the year over the period of time for which data were available.

10.3.2 Seasonality of Female Deaths

A total of 396 female deaths was included in these analyses. Female mortality probability peaked in February and March (Fig. 10.1a). There was a smaller peak in female mortality in September, but this peak was not statistically significant. The 2-df test for seasonality in the probability of female mortality according to calendar year was significant ($X^2 = 24.91$, $p < 0.0001$). Mortality probability is generally higher in the birth season than in the mating season, but it appears to be more evenly distributed across the first 4 months of the birth season than it is across the first 4 months of the calendar year (Fig. 10.1b). More females died in the birth season than in the mating season (no. of birth season deaths = 198; no. of mating season deaths = 114; $X^2 = 22.08$, df = 1, $p < 0.001$).

10.3.3 Plasma Cortisol in Relation to Reproductive State

Our final model included only female reproductive state as a predictor of cortisol levels (GLMM: $F_{1,58} = 7.86$, $p = 0.007$). Female age, female mass, infant age, dominance rank, and social group were not included in the final model because they were not significant predictors of cortisol concentrations. The model indicated that cortisol levels were significantly higher for lactating females than for cycling females ($t = -2.80$, df = 19, $p = 0.007$).

Among the females who provided plasma samples both years, 12 were lactating one year and cycling the other. Within-subjects comparisons revealed that cortisol was significantly higher when females were lactating than when they were cycling (lactating: 0.44 ± 0.29; cycling: -0.26 ± 0.32; $t = 2.98$, df = 11, $p = 0.01$). For the eight females who were in the same reproductive state when trapped in 2007 and 2008, there were no differences in 2007 and 2008 cortisol values (2007: 0.39 ± 0.35; 2008: 0.47 ± 0.36; $t = -0.19$, df = 7, $p = 0.86$). Age did not affect the increase in cortisol
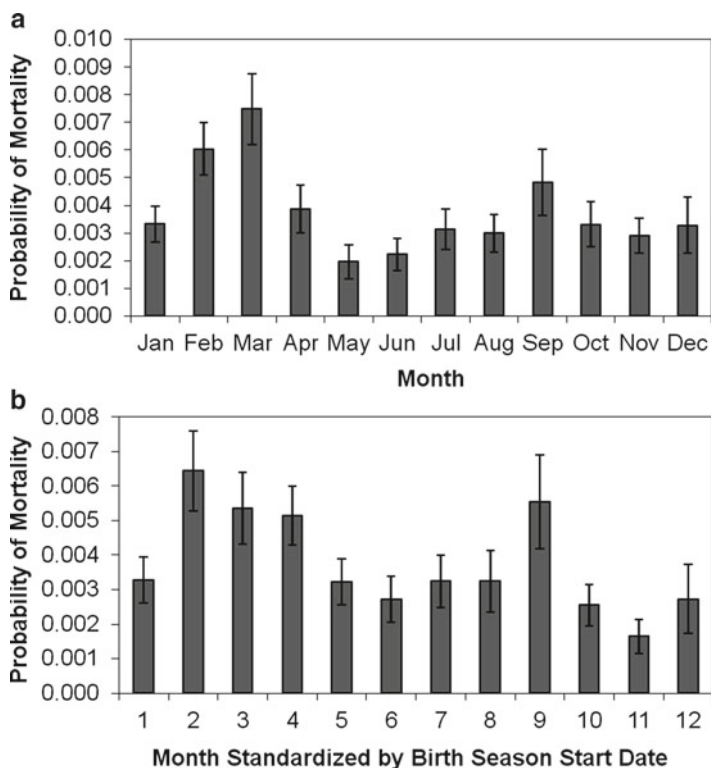
Fig. 10.1 The probability of adult female mortality based on (**a**) the number of months into the calendar year and (**b**) the number of months into the birth season. Modified after Fig. 2a, b in Hoffman et al. (2008)

from the cycling condition to the lactating condition ($n=12$, $r=-0.36$, $p=0.25$), but dominance rank did: low-ranking females had greater increases in cortisol from the cycling condition to the lactating condition than did middle- or high-ranking females ($F_{2,9}=6.99$, $p=0.02$) (Fig. 10.2).

10.3.4   Age-Related Physical and Behavioral Changes

Although we found no association between maternal age and cortisol, we did find age-associated declines in body condition and changes in behavior. In both 2007 and 2008 samples, there was a significant relationship between female age and BMI (2007: $F_{1,51}=5.90$, $p=0.02$; 2008: $F_{1,38}=4.90$, $p=0.03$), with BMI decreasing with increasing maternal age. Social rank and reproductive condition were not significant predictors of BMI. No age-related behavioral differences were observed during the
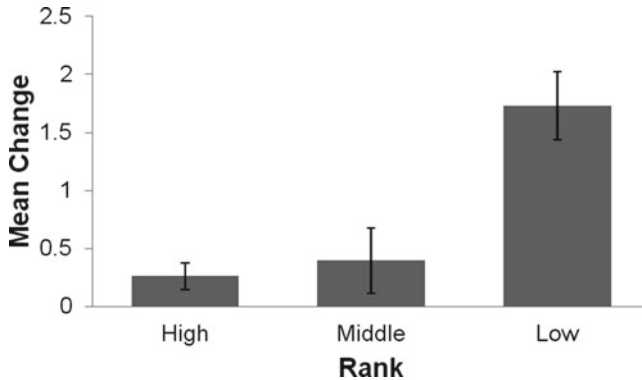
Fig. 10.2 Relationship between social rank and mean change in cortisol from the cycling condition to the lactating condition. *z*-Scores are used here because, as described in the text, mean cortisol values for 2007 and 2008 differed significantly. Modified after Fig. 2 in Hoffman et al. (2010a)

pre-birth period of observation, but differences emerged during the first month post-birth. Female age did not affect the proportion of time females spent resting or grooming pre-birth (resting: $F_{1,26}=0.79$, $p=0.38$; grooming: $F_{1,26}=0.26$, $p=0.61$), but during the first month post-birth, the proportion of time females spent resting increased with maternal age ($F_{1,24}=6.24$, $p=0.02$). Furthermore, the proportion of time females engaged in grooming during that month decreased with maternal age ($F_{1,24}=4.24$, $p=0.05$).

10.3.5 Age-Related Changes in Interbirth Interval

We found age-related changes in the frequency of reproduction. The interbirth intervals for the 631 females who lived their entire lives on Cayo Santiago ranged from 300 to 2,591 days ($\overline{X}=431.6$days, SD$=147.4$, $n=1,800$ births) and increased significantly with increasing maternal age ($F_{2,18}=66.93$, $p<0.001$) (Fig. 10.3). Average interbirth intervals of females between 4 and 18 years of age ranged between 392 and 463 days, but the average interbirth interval rose to 541 days at 19 years and was 607 for females 19 years and older.

10.3.6 Age-Related Changes in Maternal Investment and Offspring Survival

Compared to younger mothers, older mothers spent more time in ventro-ventral contact with their infants during the first month post-birth ($F_{1,24}=10.02$, $p=0.004$). Even though we observed age-associated behavioral changes, these changes did not result in greater infant body condition or survival rates. There was no relationship
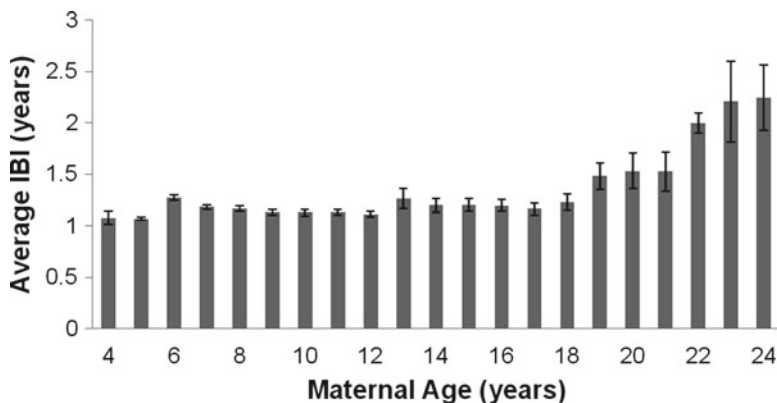
Fig. 10.3 Relationship between female age and interbirth interval. Modified after Fig. 6 in Hoffman et al. (2010b)
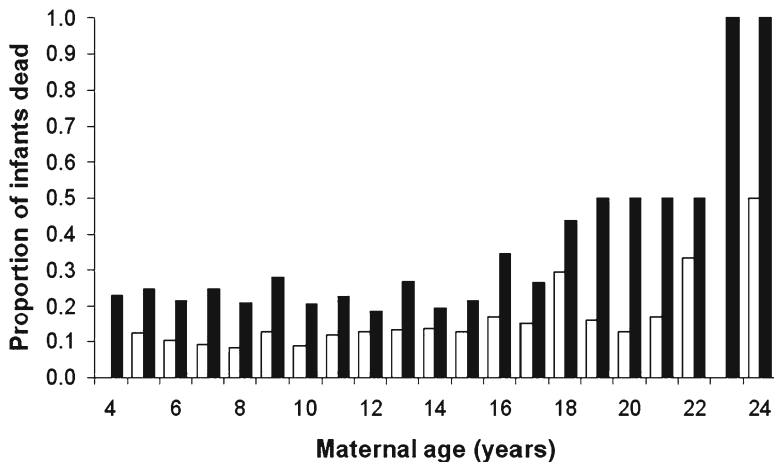
Fig. 10.4 Relationship between maternal age and probability of infant death by 30 days (*white bars*) and 1 year (*black bars*). Modified after Fig. 5 in Hoffman et al. (2010b)

between infant mass and infant age or sex (for both $p>0.10$), but there was a relationship between infant mass and maternal age ($F_{1,17.82}=6.94$, $p=0.02$). Infant mass was lower for those infants born to older mothers. In the long-term data, we found no relationship between maternal age and sex ratio (linear: $F_{1,19}=0.71$, $p=0.41$; quadratic: $F_{2,18}=1.74$, $p=0.20$).

Based on analysis of the long-term data, early offspring survival was not affected by infant sex but decreased as a function of increasing maternal age. The proportion of infants dying by 30 days and 1 year post-birth was greater for older females, even when mothers dying prior to these time points were excluded from analyses (30 days: $F_{2,18}=4.65$, $p=0.02$; 1 year: $F_{2,18}=57.61$, $p<0.001$) (Fig. 10.4).

10.4 Discussion

Even though the Cayo Santiago rhesus macaques are food-provisioned year-round, their reproduction remains seasonal and has significant fitness costs for adult females. Most conceptions in the period 1961–2005 occurred between May and October, and most births occurred between November and April (see also Carpenter 1942; Koford 1965; Rawlins and Kessler 1985, 1986). We confirmed and extended Rawlins and Kessler's (1985) finding that the onset of spring rainfall is a seasonal predictor of reproduction by showing that a gradual shift in the onset of the spring rainy season over the period 1963–1996 was accompanied by a parallel shift in the beginning of the mating and birth seasons.

Our study also provides evidence that not only births but also deaths show significant seasonal fluctuations. Specifically, the probability of mortality for adult females is significantly higher during the birth season than during the mating season. It is possible, especially in wild primate populations, that annual changes in climatic factors may result in seasonal patterns of deaths as a result of changes in food or water availability, but it is unlikely that climatic factors are the direct cause of the observed mortality patterns on Cayo Santiago since this population is food-provisioned year-round and free of predators.

Although our study does not provide direct evidence for a causal relation between reproduction and mortality, the most reasonable interpretation of our results is that mature females are most likely to die when they give birth and rear offspring. Suggestive evidence of a causal link between reproduction and adult female mortality was provided by the finding that as the onset of the birth season shifted gradually over the 45-year period of this study, so too did the pattern of mortality for adult females. Furthermore, our finding that plasma cortisol levels were elevated during the period of lactation also indicates that the period of lactation is energetically taxing for females. Although higher levels of cortisol among mothers may be an artifact of increased glucose production during lactation (Gittleman and Thompson 1988; Bell and Bauman 1997), it is unlikely that the metabolic costs of lactation accounted for the observed differences in cortisol levels since we found no relationships between reproductive condition and body mass or between cortisol and body mass.

The higher cortisol responses to stress exhibited by lactating females may have been the result of concerns about infant safety. Consistent with this explanation, we found that the amount of increase in cortisol from the cycling reproductive state to the lactating reproductive state for females sampled in 2007 and 2008 was significantly higher in low-ranking females than in middle- or high-ranking females. Compared to middle- and high-ranking mothers, low-ranking mothers may perceive their infants to be at greater risk of mistreatment from other group members, and these mothers experience greater constraints in their ability to provide protection for offspring (Maestripieri 1995). Since infant rhesus macaques born to low-ranking females have a lower probability of surviving their first year than infants born to high-ranking females (Drickamer 1974), motherhood may be particularly challenging for low-ranking females. Thus, in addition to the energetic demands of pregnancy

and lactation, the psychosocial stress associated with motherhood can be a significant cost of reproduction for rhesus macaque females. Sustained hyperactivation of the HPA axis during lactation may impair immune function (Sapolsky 2005), increasing the risk of mortality.

By integrating demographic data on survival and reproduction from the Cayo Santiago long-term data set with new morphometric and behavioral data collected from a sample of mothers and infants, we found that older females may increase investment in their offspring, but the increased effort does not result in increased offspring survival. In accordance with the senescence hypothesis, older females had lower body mass indices, were less active post-birth, and had infants with lower masses and survival rates than younger females. Age-associated increases in inter-birth intervals and time in ventro-ventral contact with infants, however, suggest that older females may invest more in their offspring than younger females, providing evidence for the terminal investment hypothesis. Thus, we found strong evidence for senescence and only weak evidence for terminal investment.

As previously observed in a captive rhesus macaque population (Gagliardi et al. 2007), infant survival on Cayo Santiago decreased sharply as females entered their late teens. Our data highlight at least two factors that may lead to this: maternal social behavior and maternal body condition. Though there were no age-related differences in grooming or resting pre-birth, older mothers were involved in less grooming interactions following their infant birth than younger mothers were. Unfortunately, previous studies that have characterized rhesus behavior in wild habitats have not included female age, rank, or infant presence in their analyses (e.g., Teas et al. 1980), preventing comparison of these results with wild populations. Given that cercopithecine non-mothers and mothers with young infants tend to be attracted to females with young infants (e.g., *Papio anubis*: Frank and Silk 2009; *Papio cynocephalus ursinus*: Silk et al. 2003; *Macaca mulatta*: Whitham et al. 2007), this reduced grooming time may mean that the offspring of older rhesus females are less attractive to other females. The observed decrease in sociality may affect the likelihood of infant survival, given the potential links between social support and survivorship in primates (Silk et al. 2006). Strong social bonds may increase infant survival and benefit infants by providing mothers with support in agonistic interactions, lowering mother's basal cortisol levels, increasing infant protection from harassment, or making more resources accessible to mother–infant dyads (Silk et al. 2003).

The low body mass of the older females' infants likely reflects old mothers' diminished abilities to invest energetically in offspring during pregnancy and lactation due to their poor body condition. Although a previous study failed to document direct relationships between maternal body composition or age and lactation performance in captive rhesus monkeys (Hinde et al. 2009), the effects of female age, body composition, and access to resources on lactation performance should be explored on Cayo Santiago due to the amount of variation present within this population. Free-ranging, rhesus females in poor physical condition are expected to produce milk in low quantities or of lower quality since relationships between maternal condition and lactation performance have been reported from studies of human populations (Ettyang et al. 2005; Villalpando et al. 1992). The infants' low masses

also suggest that infants of older mothers may develop more slowly than those born to younger mothers. Slower infant growth rates have also been observed in offspring born to older chacma baboon mothers (*Papio ursinus*, Johnson 2006), and low infant mass is predictive of infant mortality in common marmosets (*Callithrix jacchus*; Tardif et al. 2002). Low body mass may be a major factor contributing to high mortality rates for rhesus infants born to older mothers.

According to the terminal investment hypothesis, increasing interbirth intervals and suckling time may increase infant survival for older females, but this is not the case for females in our study. Consistent with a vast body of literature on primate life history (e.g., Higham et al. 2009; Okamoto et al. 2000; Malik et al. 1992), we might expect interbirth intervals to be shorter for females whose infants die, but we see no evidence of this; whereas infant survival was lower for the older females in our study, their interbirth intervals were longer. These patterns are consistent with general reproductive senescence in these females. Additional data are needed to determine if lengthening interbirth intervals are associated with hormonal or behavioral changes. Hormonal data would indicate whether the increasing interbirth intervals are associated with increasingly irregular ovulatory patterns, as they are in captive rhesus populations (Gilardi et al. 1997). Furthermore, behavioral data collected from mothers and infants between 2 and 8 months post-parturition would reveal whether age-related differences in suckling intensity affect time between parturition and the resumption of mating (see Johnson et al. 1998). If extended interbirth intervals among older females are clearly related to increased lactational effort, this would be consistent with a terminal investment interpretation for longer interbirth intervals. Conversely, if extended interbirth intervals occur among older females even though overall lactational effort is consistent across the adult life span, this would support a senescence interpretation of the effect.

10.5   Conclusion

The rhesus macaques on Cayo Santiago reside in a provisioned, predator-free environment, but they continue to breed seasonally. Furthermore, the population appears to remain sensitive to climatic factors since the onset of the birth season closely tracks the onset of the rainy season. Our findings show that although rhesus macaque females on Cayo Santiago have the physical and physiological ability to conceive and give birth virtually until the end of their life span, they experience increased HPA axis activation during the period of lactation and, perhaps as a consequence, elevated mortality risks. The costs of reproduction increase with female age whereas the benefits diminish since a female's ability to sustain pregnancy and lactation and guarantee infant survival decreases steadily and dramatically in her last 5–10 years of life due to senescence. Extremely old females would fare better if they ceased reproducing and, instead, invested their resources in their existing offspring because even when they increase their investment in new offspring, the probability of their

offspring surviving beyond infancy is low. In wild populations of macaques, predators, disease, and unpredictable food sources make it unlikely that adult females will survive into their third decade (Johnson et al. 1991; Jones-Engel 2006), such that selective pressures for early termination of reproduction are probably negligible or nonexistent in the wild. Thus, our findings regarding the changes in female reproduction and maternal care observed within the oldest residents in the Cayo Santiago population may not generalize to wild populations.

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Chapter 11
Variation Over Time in Grooming Kin Bias Among Cayo Santiago Rhesus Macaques Supports Time Constraints

Carol M. Berman and Ellen Kapsalis

11.1 Introduction and Background

In the early days of primatology, studies of rhesus (*Macaca mulatta*) and Japanese macaques (*M. fuscata*) launched the topic of kinship by describing the central importance of strong female kin preferences (kin bias) in shaping affiliation, aggression, dominance, maternal behavior, and other aspects of social structure (e.g., Kawai 1958; Kawamura 1958; Sade 1965, 1967). Although studies of additional primate taxa have expanded, modified, and refined our knowledge of kin-related behavior (Chapais and Berman 2004; Silk 2006; Strier 2008; Berman 2010), macaques remain central to efforts to understand the nature and origins of kin bias in female philopatric species. Because all macaque species display a similar basic social structure (female philopatry, male dispersal, and linear hierarchies) but vary widely in tendencies to favor kin and to display a set of associated social characteristics (tolerance to subordinates, intensity of aggression, conflict management, and tolerance of infant handling) (Thierry 2007), they provide unique opportunities to investigate the nature and origins of kin bias in a closely related group of species. However, research results so far have not produced a consensus. One set of findings has given rise to the hypothesis that the degree to which female macaques express kin preferences is tightly constrained by evolutionary history(Thierry 2000), and it predicts that the intensity of kin bias displayed by females should vary consistently between species but relatively modestly within

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species. Another set of findings suggests that female kin bias may be highly responsive to current social, demographic, and/or ecological conditions (Dunbar 1988, 1992; Sterck et al. 1997; Chapais and Berman 2004). Hence, variation within species could be substantial and associated with current conditions. It is also possible that variation in kin bias is attributable to both current conditions and inherent species differences in attraction to kin, but at present, we have little information on the ranges of flexibility in kin bias for different species and individuals. This is partly because few data are available on variation in kin bias for a given type of interaction within species across different groups or over time. A recent study of female grooming kin bias among wild Tibetan macaques (*M. thibetana*) (Berman et al. 2008) found that the intensity of kin bias varied markedly over time within the same social group and that patterns of variation were largely consistent with Dunbar's time constraints model (Dunbar 1988, 1992), a model based on responses to current conditions.

In this chapter, we examine female grooming patterns in Cayo Santiago rhesus monkeys from 1983 to 1986 in group I and in its fission products. We ask whether female grooming kin bias also varies substantially over time and across groups, and if so, whether time constraints also provide a viable explanation for a species that typically displays female kin bias more consistently and more intensely than Tibetan macaques. Finally, we examine the extent to which the marked differences in female kin bias between the two macaque species may be due to differences in current conditions, inherent differences in attraction to kin, or both.

11.1.1   Evolutionary Constraints

Phylogenetic views on the origins of kin-related behavior view kin bias primarily as a species characteristic, pointing to both consistent differences in the intensity of kin bias in affiliation, support, and reconciliation among a variety of macaque species housed under similar captive conditions (e.g., Butovskaya 1993; review in Thierry 2000) and to a small body of evidence showing consistency between captive and wild groups of the same species (Aureli 1992; Balcomb et al. 1993; Judge and de Waal 1997; Kutsukake and Castles 2001). This evidence, along with findings of species-level covariation of kin bias with other traits related to aggressive behavior, tolerance, conflict management and maternal style (Thierry 2000), has led to the hypothesis that female kin bias is part of a highly integrated, self-organized, tightly constrained set of social characteristics sometimes referred to as dominance style (de Waal and Luttrell 1989) or social style (Thierry 1990). Consistent with this view, some core characteristics of dominance style display phylogenetic signals within the macaque genus (Thierry et al. 2008). Although strong phylogenetic signals can be the result of historically stable environmental conditions and/or conditions that constrain adaptation to current conditions (Bloomberg and Garland 2002), advocates of the phylogenetic view favor the idea of evolutionary constraints, citing evidence that dominance style is often unrelated to current ecological conditions at a species level (Menard 2004). Specifically, they hypothesize that ecological factors

played a role in the early origins of kin bias and other aspects of dominance style but that subsequent evolutionary constraints produced disconnects between dominance styles and current ecological conditions (Matsumura and Kobayashi 1998; Matsumura 1999; Thierry et al. 2000). This hypothesis is challenged, however, by weak evidence for a phylogenetic signal in kin bias *per se* (Thierry et al. 2000, 2008) and by growing evidence of substantial within-species variation in kin bias and other aspects of dominance style. For example, a group of wild Tibetan macaque females showed no evidence of kin bias in some years and levels comparable to those of rhesus monkey groups of the same size in other years (Berman et al. 2004, 2008). In this study and in two others – a study of grooming in capuchin monkeys (*Cebus capucinus*) (Perry et al. 2008) and a study of proximity in Cayo Santiago rhesus infants (Berman et al. 1997) – kin bias increased with group size, suggesting that some forms of kin bias respond to changes in current social/demographic circumstances.

11.1.2   Time Constraints

The time constraints model (Dunbar 1988, 1992) is an extension of the socioecological model of Sterck et al. (1997). Briefly, their model is based on the idea that kin-biased female social networks in female philopatric species are shaped primarily by within-group contest competition for monopolizable food resources. In general, females that experience high within-group contest competition (WGC) are expected to form within-group coalitions with kin and with high-ranking individuals to increase their access to food. Alliances with kin are expected given both long-term familiarity and potential inclusive fitness gains, whereas high-ranking individuals make particularly powerful allies. Since alliances are widely believed to be maintained by grooming (Schino 2007; but see Henzi and Barrett 1999), females are expected to display strong tendencies to support and affiliate with kin. Thus, the model predicts that the intensity of grooming and supportive kin bias should be directly related to levels of WGC, except when groups experience both high WGC and high between-group competition (BGC). In these cases, females should show greater tolerance toward nonkin and subordinates than they do in groups with only high WGC in order to insure group-level cohesion and cooperation. Some aspects of the model have been usefully tested by comparing closely related primate species or groups of the same species that experience different levels of WGC and BGC (reviewed in Koenig 2002). While some of these studies have demonstrated links between within-group contest feeding competition and tendencies for females to affiliate and form coalitions with one another (e.g., Mitchell et al. 1991; Barton et al. 1996; Hill 1999, 2004), others have found no such links (e.g., Boinski 1999; Koenig 2002). Similarly, little empirical support has been found across primate species for the idea that high BGC moderates the influence of high WGC via increased group cohesion or reduced kin bias (Cheney 1992). Among macaques specifically, researchers have found little correspondence between intensity of kin bias and competitive regimes in either qualitative cross-species analyses (Menard 2004; Okamoto

and Matsumura 2002) or a quantitative study of a single social group of Tibetan macaques over time (Berman et al. 2008).

Dunbar (1988, 1992) proposed the time constraints model to address these sorts of discrepancies. Like the Sterck et al. (1997) model, the time constraints model assumes that grooming is necessary for maintaining alliances that are needed in turn for competing over monopolizable food resources in groups with high WGC. However, Dunbar noted that when groups are small, WGC is likely to be moderate, and females may be able to groom nearly all female group members long enough to insure their cooperation over food. In such cases, kin bias would be expected to be weak or absent. However, as groups increase in size, WGC is expected to increase (Sterck et al. 1997), and along with it, the need for large within-group coalitions. Thus, as groups grow, the socioecological model predicts that both the size of grooming networks and rates of within-group support should increase. However, as Dunbar (1984) pointed out, when grooming time is limited, as it is likely to be in groups with substantial competition for food, females may have limited abilities to maintain increasing numbers of strong grooming relationships. This is in spite of the fact that females in larger groups are likely to have a larger pool of potential allies. Under these circumstances, females should benefit from focusing their limited grooming time on a subset of potential partners, because spreading grooming out thinly would not ensure support. For reasons of inclusive fitness and long-term familiarity, this subset should be increasingly composed of close kin (Altmann 1979; Chapais 2001). In this way, grooming networks may be more directly shaped by time constraints than by levels of within-group competition per se, and there should not necessarily be a close association between grooming kin bias and indicators of within-group competition. Several studies of baboons have found evidence that grooming time is indeed constrained and that grooming networks become increasingly focused on a subset of potential partners in large groups (Dunbar 1984, 1988; Sambrook et al. 1995; Henzi et al. 1997; Silk et al. 1999). However, these studies have not examined kin bias. So far, only the Berman et al. (2008) study of wild Tibetan macaques has done so and found evidence that time constraints also appear to shape the intensity of grooming kin bias (see also Berman and Thierry, 2010).

11.1.3   Predictions

A major prediction of both Sterck and coworkers' socioecological model and Dunbar's time constraints model, but not of the phylogenetic model, is that female grooming kin bias should be strongly and positively related to group size, or more specifically numbers of potential adult female grooming partners (prediction 1). We test this prediction and then test additional predictions (see below) related to two questions: (1) Is grooming actually constrained by time? (2) If so, do time constraints specifically shape grooming kin bias? Positive answers to both questions would be consistent with the time constraints model but would not be expected by Sterck and coworkers' socioecological model.

11.1.3.1 Is Grooming Constrained by Time?

If females have a finite amount of time to groom, the total amount that a given female grooms should reach a limit as groups increase in size, and then no longer be related to group size or numbers of females (potential grooming partners) in the group. Thus, in all but the smallest groups, there should be no relationship between total amounts of time spent grooming and either group size or numbers of females in the group (prediction 2). In addition, if females have limited amounts of time to groom, the mean amount of grooming that a given female can theoretically distribute to each potential partner should decrease with group size and numbers of females (prediction 3). If females are unable to maintain strong grooming relationships with increasing numbers of partners, and if they respond by focusing their grooming on a subset of potential partners, the number of grooming partners each female has should reach a limit as group size increases and then remain similar. Thus there should be no overall relationship between numbers of grooming partners and either group size or numbers of females in the group (prediction 4). Finally, if females increasingly focus grooming on a subset of partners as groups enlarge, there should be a negative relationship between percentage of potential partners actually groomed and both group size and numbers of females in the group (prediction 5).

11.1.3.2 Are Time Constraints Associated with Intensity of Grooming Kin Bias?

If time constraints shape variation in grooming kin bias, we predict that when females focus down their grooming networks, they focus specifically on close kin. Thus, the intensity of kin bias should be negatively correlated with the percentage of potential partners that are actually groomed (prediction 6). In addition, lower-ranking females should show more intense kin bias than others, because they are likely to have less time to spare from other essential activities (foraging, resting, and traveling) than others (prediction 7). Finally, if females have limited amounts of time to groom and focus on close kin, females with many close kin should display less intense kin bias than females with only a few close kin, because they have a finite amount of time to spread out among a larger number of close kin. Thus, there should be a negative relationship between grooming kin bias and numbers of close kin (prediction 8).

11.2 Methods

11.2.1 Study Groups and Subjects

We examined grooming data for females living on Cayo Santiago in group I and its fission products R, S, and Q between 1983 and 1986. All the females in 1983 and

Table 11.1 Group size, numbers of females, and numbers of subjects in each group-year analyzed

Group-year	Group size	Number of adult females	Number of subjects
I-83	268	54	21
I-84	282	71	22
I-85	293	66	21
Q-85	61	14	2
I-86	182	50	14
Q-86	87	19	4
R-86	94	24	2
S-86	39	8	1

1984 were members of group I. Group Q fissioned from group I in 1985, followed by groups R and S in 1986. As such, our observations covered a total of eight group-years (group I in 1983–1986, group Q in 1985 and 1986, and groups R and S in 1986) and 87 female-years. The sizes of the groups varied from 39 to nearly 300 individuals and contained from eight to 71 adult females (Table 11.1).

Our sample included 33 adult females that were part of a larger longitudinal study of parent–infant relationships. The sample of females (all mothers with infants) was drawn from all three lineages in group I in 1983 and represented a wide range of dominance ranks. In subsequent years, we observed the same females again, provided they had an infant that year. Data for 80 (92.0%) female-years were for multipares and 43 (49.4 %) were for mothers with infant daughters. We excluded data from mothers whose infants were less than 13 weeks of age to eliminate grooming that may have been due to the presence of an attractive young infant.

11.2.2 Data Collection, Measures, and Data Analysis

We used 2-min point-time sampling to record proximity within 5 m and grooming between the female subjects and other group members during focal-animal observation sessions that generally lasted 30 min and took place once per week for a mean $\pm$ SE of 27.4 ± 0.8 weeks per female-year. Full details of data collection are in Berman et al. (1997). We calculated the percentage of time each focal female groomed with each other adult female group member (4 years or older) in each group-year as the number of point-time samples observed grooming or being groomed divided by the number of point-time samples observed. We used partial Kr row-wise matrix correlation tests (Hemelrijk 1990) with 2,000 permutations to detect significant kin preferences in the percentage of time spent grooming within each group-year, controlling for rank distance. In all group-years except group S in 1986, we used rectangular matrices in which we listed focal animals in the rows and nonfocal females in the columns of the matrices. When the number of focal subjects was four or more, we also used square matrices in which we listed the focal animals in both the rows and columns. In all the matrix correlation tests, we classified kin by degree of relatedness (r) through maternal lines: mother–offspring $= 0.50$;

grandmother–grandoffspring, siblings = 0.25; aunt–niece = 0.125; first cousin, great aunt–great niece = 0.063; others = 0. Since group S contained only one focal female in 1986, we simply correlated this female's grooming time with her degree of relatedness to her eight potential grooming partners, using a Spearman correlation test.

We measured the intensity of kin bias (KBI) as the ratio of observed to expected percentage of time spent grooming between each focal female and her close female kin during each group-year. Close female kin were related maternally by at least $r = 0.25$ (mothers, daughters, grandmothers, granddaughters, and maternal sisters). We based expected frequencies on the null hypothesis that grooming was distributed evenly among adult females. Thus, we calculated the expected amounts as total amounts of grooming given and received by a female multiplied by the proportion of females in the group who were related by at least 0.25. We preferred this method to the calculation of regression coefficients (slopes) between amounts of interaction and degree of relatedness (Berman et al. 1997) because most females groomed partners in only one or two kin categories. As a result, slopes could have been greatly affected by total amounts of grooming. For example, if two females groomed their close kin exclusively (as many did), but one groomed ten times more than the other, the more active groomer would display a much higher slope than the less active groomer. Also, evidence for kin preferences in macaques and baboons beyond $r = 0.25$ are inconsistent (Chapais and Belisle 2004). With one exception, all females had at least one close female kin within the group in all years. We excluded the exceptional female-year from the analysis, reducing the sample of female-years to 86. Mean ± SE numbers of close kin were 4.3 ± 0.3 (range = 1–18).

We examined possible relationships between group-level variables (group size and numbers of adult females in the group) and mean grooming KBI, mean total amounts of grooming, mean percentage of time grooming per potential partner, mean numbers of grooming partners, and mean percentage of potential partners actually groomed across group-years ($n = 8$), using Spearman correlation tests. We examined the relationship between grooming KBI and the availability of close kin (numbers of kin related by at least 0.25 through maternal lines) at the level of individual female-periods, using a Pearson correlation test. One-way ANOVA tests were used to detect significant differences in KBI scores for individual female-years across group-years and as a function of the percentage of females dominated within the group. The parametric tests were weighted to equalize the contributions of individual females and were carried out on subset of female-years that did not include six outlying scores for KBI. Eliminating the outliers reduced kurtosis and skewness to acceptable levels (z scores for skewness were reduced from 8.0 to 0.33 and z scores for kurtosis were reduced from 20.6 to 1.4) and produced a distribution that did not vary significantly from normal (Kolmogorov–Smirnov one-sample test: $Z = 0.717$, $n = 80$, $p = 0.682$).

Finally, to investigate whether differences in current conditions could explain differences in grooming kin bias between Cayo Santiago rhesus and wild Tibetan macaques, we used ANCOVA methods to compare KBI scores for the two species while controlling for group size and numbers of females in the group. We used published values of KBI for Tibetan macaque females for seven data analysis periods

recorded over 15 years (1991–2004) in a single social group of Tibetan macaques in Huangshan, China (Berman et al. 2008). Over the 15 years, the group grew and fissioned, varying in size from 21 to about 52 members and from 8 to 14 adult females. Our data included 16 adult females and 63 female-periods. Complete details are in Berman et al. (2008). Although we derived the KBI scores for Tibetan macaques from measures of bout rates rather than point-time samples, we found virtually identical values using either approach with the same data (unpublished data). In all statistical analyses, we used two-tailed tests and considered probabilities of 0.05 or smaller to be significant.

11.3   Results

Females displayed significant preferences for grooming female kin within all group-years except group S in 1986. Partial Kr correlation coefficients between percentage of time spent grooming and degree of relatedness were highly significant for all matrix correlation tests, using either rectangular or square matrices (Table 11.2). In group S in 1986, however, there was no evidence that the single focal subject preferentially groomed kin over nonkin ($r_s = 0.12$, $n = 8$ potential partners, NS, Spearman correlation test).

Values for grooming kin bias intensity (KBI) varied significantly across group-years ($F = 2.8$, df $= 7,72$, $p = 0.014$, one-way ANOVA). Mean values ranged from 1.1 in group S in 1986, indicating that the female groomed kin as much as nonkin, to 13.1 in group I in 1984, indicating that kin groomed each other on average about 13 times more than expected by chance (Fig. 11.1).

Table 11.2 Presence of grooming kin bias among adult females: partial Kr matrix correlation coefficients between percent time spent grooming and degree of relatedness, controlling for rank distance

Group-year	Focals with focals[a]	Focals with nonfocals[b]
I-83	0.32***	0.40***
I-84	0.27***	0.33***
I-85	0.33***	0.35***
Q-85	---[c]	0.41*
I-86	0.48***	0.41***
Q-86	0.89**	0.40***
R-86	---	0.39***
S-86	---	---

*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$
[a]Kr test was done with square matrices examining grooming between different focal subjects
[b]Kr test was done with rectangular matrices examining grooming between focal subjects and other nonfocal partners
[c]--- indicates insufficient sample size for the Kr test
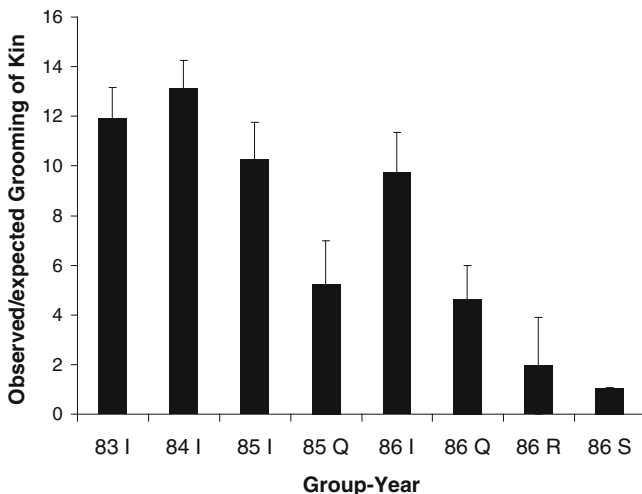
Fig. 11.1 Mean ± SE for intensity of grooming kin bias among females in each group-year studied. Intensity of grooming kin bias was measured as the ratio of observed to expected percentages of time spent grooming close kin through maternal lines (degree of relatedness ≥ 0.25)
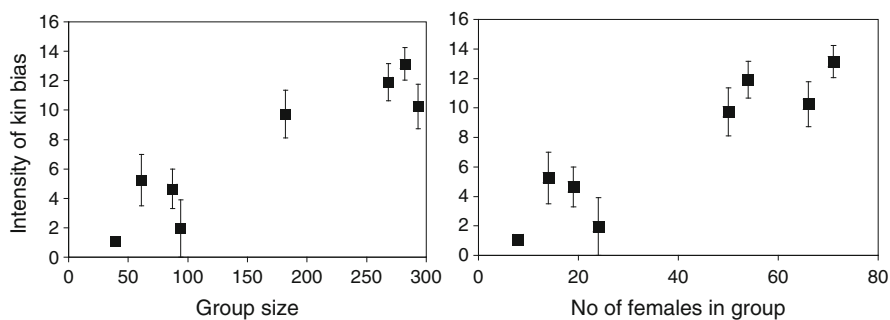
Fig. 11.2 Mean ± SE for intensity of grooming kin bias among females as a function of group size (*left*) and numbers of females in each group-year (*right*)

As predicted (prediction 1), mean values for KBI were positively related to both group size ($r_s = 0.88$, $n = 8$ group-years, $p = 0.01$, Spearman correlation test) and to numbers of females in the group ($r_s = 0.91$, $n = 8$ group-years, $p < 0.001$) (Fig. 11.2).

11.3.1 Grooming and Time Constraints

The results supported the prediction that, if females had a limited amount of time for grooming, the total amount of time females would groom would be unrelated to group size and numbers of potential partners (prediction 2); mean values for
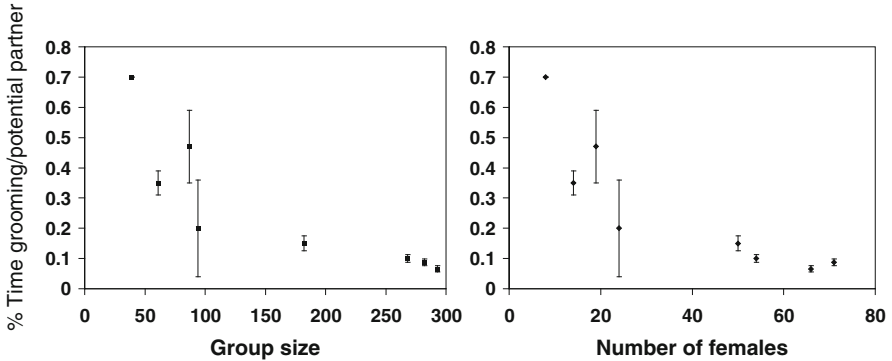
Fig. 11.3 Mean±SE for percentage of time spent grooming per potential partner as a function of group size (*left*) and numbers of females in each group-year (*right*)

total amounts of grooming for each group-year were unrelated to either group size ($r_s=-0.19$, $n=8$ group-years, NS) or numbers of females in the group ($r_s=-0.07$, $n=8$ group-years, NS). The prediction that the mean amount of time that a female could theoretically distribute to each potential female partner in a group would decrease with group size and numbers of potential partners (prediction 3) was also supported; mean percentages of grooming per potential partner were negatively correlated with both group size ($r_s=-0.98$, $n=8$ group-years, $p<0.001$) and numbers of females in the group ($r_s=-0.95$, $n=8$ group-years, $p<0.001$) (Fig. 11.3).

The results also supported the prediction that the number of grooming partners should be similar, regardless of group size or numbers of potential partners (prediction 4); mean numbers of grooming partners were unrelated to either group size ($r_s=-0.10$, $n=8$ group-years, NS) or numbers of females in the group ($r_s=-0.05$, $n=8$ group-years, NS). In addition, as predicted, we found negative correlations between the mean percentages of potential partners actually groomed and group size ($r_s=-0.83$, $n=8$ group-years, $p=0.007$) and numbers of females in the group ($r_s=-0.86$, $n=8$ group-years, $p=0.01$) (prediction 5) (Fig. 11.4). Taken together, these findings support the presence of time constraints and suggest that females in larger groups respond to them by limiting the number of partners they groom rather than by distributing grooming evenly among all potential partners. This response does not appear to be a by-product of greater interindividual distances between females in larger groups; females in larger groups were observed within 5 m of larger numbers of adult females at any one time than females in smaller groups ($r_s=0.74$, $n=8$ group-years, $p=0.018$).
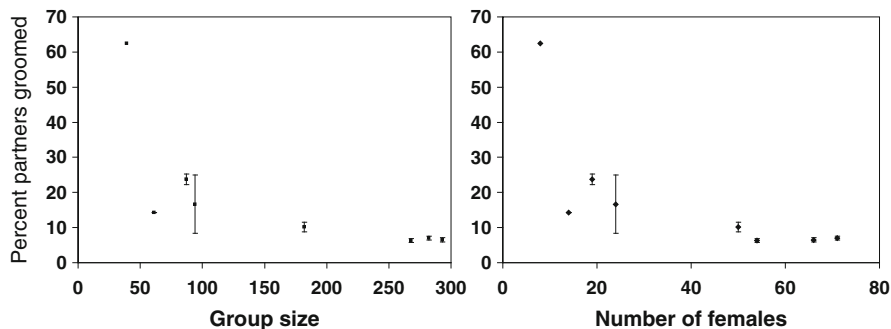
Fig. 11.4 Mean ± SE percentage of potential partners actually groomed as a function of group size (*left*) and numbers of females in each group-year (*right*)

Fig. 11.5 Intensity of grooming kin bias among females as a function of the percentage of potential partners actually groomed
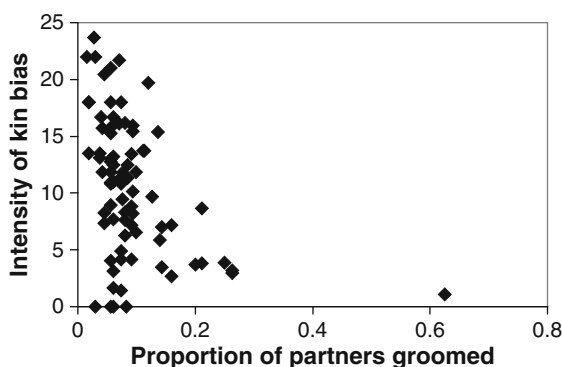
11.3.2 Time Constraints and Kin Bias

If time constraints lead to grooming kin bias, we predict that, when females focus their networks, they focus specifically on close kin. Consistent with this prediction (6), the percentage of potential partners actually groomed was negatively correlated with the intensity of kin bias ($r_s = -0.36$, $n = 80$ female years, $p = 0.001$, Pearson correlation test) (Fig. 11.5). In addition, low-ranking females displayed lower intensities of kin bias than higher-ranking females, as expected if they had less time to spare for grooming than high-ranking females. KBI varied significantly with rank ($F = 2.89$, df = 3,76, $p = 0.041$) (Fig. 11.6), and contrast tests confirmed that females in the bottom quartile of the dominance hierarchy displayed significantly higher scores than those in higher quartiles. Finally, the results supported the prediction that, if females have limited amounts of time to groom and favor close kin, females with many close kin should show less intense grooming kin bias than those with only a few (prediction 7); there was a negative correlation between grooming KBI and numbers of close kin (degree of relatedness ≥0.25) ($r = -0.344$, $n = 80$, $p = 0.002$) (Fig. 11.7).

Fig. 11.6 Intensity of
grooming kin bias among
females as a function of
dominance status (percentage
of females dominated)
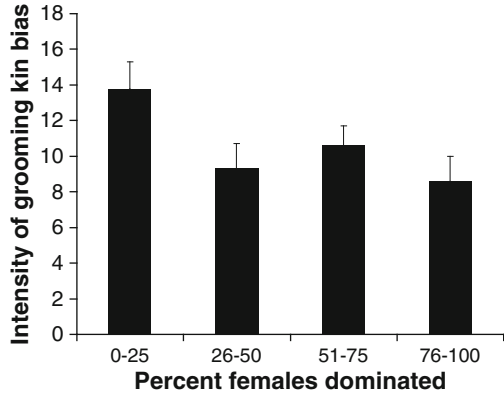
Fig. 11.7 Intensity of
grooming kin bias among
females as a function of the
availability of close kin
(numbers of female kin
related through maternal lines
by at least 0.25)
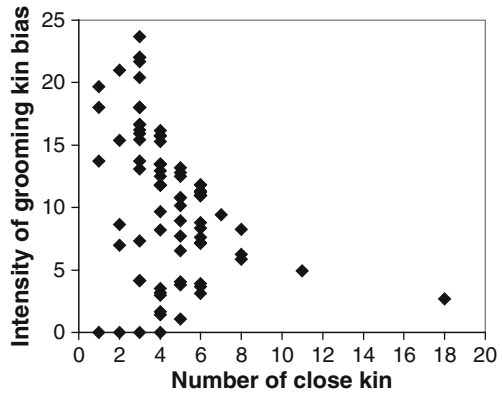
11.3.3 *Cayo Santiago Rhesus vs. Tibetan Macaques*

Cayo Santiago rhesus females displayed significantly higher scores for grooming
KBI than did Tibetan macaque females when group size and numbers of potential
partners were not considered (mean $\pm$ SE $= 7.2 \pm 1.6$, $n = 8$ group years for Cayo
Santiago rhesus vs. 1.9 ± 0.2, $n = 7$ periods for Tibetan macaques, $T = 3.26$, df $= 13$,
$p = 0.013$, T-test for independent samples). However, significant species differ-
ences were not sustained when we used ANCOVA methods to control the effects of
group size ($F = 0.19$, df $= 1,12$, ns) and numbers of females in the group ($F = 0.28$,
df $= 1,12$, ns). Thus, the two species displayed similar intensities of grooming kin
bias when group size or numbers of females were taken into consideration
(Fig. 11.8).
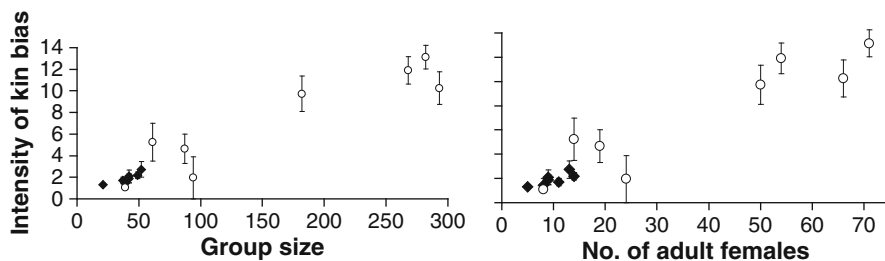
Fig. 11.8 Mean ± SE intensity of grooming kin bias among females as a function of group size (*left*) and numbers of females (*right*). *Open circles* represent data for Cayo Santiago rhesus. *Closed triangles* represent data for Tibetan macaques (Berman et al. 2008)

11.4   Discussion

The results of this study confirm that grooming kin bias among Cayo Santiago females is a flexible characteristic that responds to changes in individuals' current circumstances. Intensities of grooming kin bias varied significantly across years in the same social group and in its fission products. The findings that KBI (1) varied markedly across group-years from 1.1 (indicating little or no kin bias) to 13.1 (indicating that females groomed kin 13 about times more than expected by chance), (2) was strongly and positively related to two group-level social/demographic factors (group size and numbers of females), and (3) further varied with individual social circumstances (female status and availability of kin) are not consistent with views of kin bias as highly constrained on a species level. Although they do not rule out phylogenetic influences, they strongly support an important role for current social/demographic conditions. Similar relationships between grooming KBI and group size were also found over a 15-year period in a group of wild Tibetan macaques (Berman et al. 2008) a 7-year period in Ton kean macaques (Berman and Thierry, 2010), and over a 10-year period in a group of wild capuchin monkeys (Perry et al. 2008), raising the possibility that these findings may apply to a wide range of female philopatric species. In contrast, Majolo et al. (2009) reported less intense grooming kin bias in the larger of two Japanese macaque groups. However, this result was probably due to the fact that they used mtDNA analysis to identify maternal kin, a method that does not distinguish close kin from distant kin. Since larger groups are likely to contain larger proportions of distant kin/close kin than small groups, and female macaques tend not to favor distant kin over unrelated individuals (Kapsalis and Berman 1996a; Chapais and Belisle 2004), the inclusion of distant kin in calculations of kin bias could artificially reduce values relative to small groups.

11.4.1 Time Constraints

When we examined patterns of grooming more closely in relation to group size and numbers of potential grooming partners, we found that our results, like those for Tibetan macaques (Berman et al. 2008) and baboons (Dunbar 1984, 1988; Sambrook et al. 1995; Henzi et al. 1997; Silk et al. 1999), were consistent with several predictions for Dunbar's time constraints model (Dunbar 1988, 1992) –that grooming networks are shaped at least in part by time constraints on grooming time. First, females spent similar total amounts of time grooming, regardless of group size or numbers of females in the group, rather than increasing their grooming time as more potential partners became available. As such, mean amounts of time spent grooming per potential partner decreased with increasing group size and numbers of potential partners. These findings are consistent with the presence of time constraints on grooming and suggest that females in larger groups did not have sufficient time to maintain strong grooming relationships with all potential partners (see Lehmann et al. 2007 for a cross-species analysis).

In addition, females groomed similar numbers of partners regardless of group size or numbers of potential partners, and as a result, they groomed progressively smaller percentages of potential partners as groups enlarged and included more females. This suggests that females in larger groups responded to limitations on grooming time by focusing their grooming on a subset of potential partners rather than by spreading their grooming out evenly among all potential partners. They did so in spite of the fact that females in larger groups found themselves near (within 5 m) larger numbers of female group members at any one time. By focusing their networks, it was possible for females to maintain strong grooming relationships with the subset of partners but at the expense of other potential relationships. Both the presence of time constraints on grooming and these female responses to them cannot be accounted for by the Sterck et al. (1997) socioecological model, because their model predicts both increased amounts of grooming and larger grooming networks in larger groups.

Finally, our results support the hypothesis that time constraints specifically shape grooming kin bias. When females in larger groups focused their networks, they concentrated specifically on close kin, as indicated by a significant negative correlation between kin bias and the percentage of potential partners actually groomed. It is unlikely that this was due simply to having fewer distant kin and unrelated individuals nearby. A previous analysis of the composition of neighbors within 5 m of the subjects' infants indicated that those in larger groups were surrounded not only by larger numbers of neighbors but also by larger proportions of distant kin and unrelated individuals than those in smaller groups (Berman et al. 1997). Given the close proximity of mothers and infants, this was most likely the case for their mothers as well. In addition, low-ranking females displayed more intense kin bias than others, as expected if they had less time to spare for grooming. Finally, females with many close kin displayed less kin bias than those with only a few, as expected if they had finite amounts of time to devote to each of their close kin. Thus, individual

females responded to time constraints not simply as members of a group of a particular size but also according to their particular social circumstances within their group.

What benefits, if any, females receive by focusing their grooming on a few partners when groups are large is not clear. Among some populations of baboons, females that form strong social bonds with a few other females (Silk et al. 2003) and particularly with close kin (Silk et al. 2009) have offspring that live significantly longer than females with weaker social bonds, although proximate explanations for such a link are not yet clear. Dunbar's model emphasizes the need to maintain strong grooming relationships in order to receive agonistic support in conflicts with other females. However, findings by Henzi et al. (1997) suggest that female mountain baboons display progressively more focused grooming networks in larger groups even in the absence of alliances. They suggest instead that focused networks are simply by-products of great interindividual distances between females in larger groups. However, neither explanation appears to be appropriate for Cayo Santiago rhesus females. First, although females regularly form agonistic alliances, alliances are not more common among strong grooming partners (Kapsalis and Berman 1996b). Second, the fact that mean numbers of adult females found near females at any given time actually increase with group size raises the possibility that focused networks may be a response to the stress of high group densities and the social risk they entail (cf. Berman et al. 1997; Berman and Kapsalis 1999). Such an explanation would be consistent with links between highly focused grooming networks and reduced glucocorticoid levels found in baboons both during baseline conditions (Crockford et al. 2007) and in response to stressful events (Wittig et al. 2008). Another possibility is that Cayo Santiago females focus their grooming networks as a means to gain access to water, given that dominant females show more tolerance at drinking fountains toward subordinates that groom them frequently (Kapsalis and Berman 1996b).

11.4.2   Species Compared

All the predictions we tested for Cayo Santiago females were also supported in a study of wild Tibetan macaques (Berman et al. 2008), suggesting that the influence of time constraints on grooming kin bias is not confined to rhesus macaques or species that typically display extreme kin bias. Indeed, the finding that differences in grooming kin bias between rhesus and Tibetan macaques could be attributed to differences in group size and/or numbers of potential partners suggests that time constraints affect both species in very much the same manner. These results were surprising given that rhesus macaques, but not Tibetan macaques, are generally considered to be among the most kin-biased primate species. Studies of Tibetan macaques from the early 1990s (Ogawa and Takahashi 2003; Ogawa 2006) found little or no evidence of kin bias in grooming, huddling, or other affiliative behavior, whereas studies of the same social group a decade later (Berman et al. 2004, 2008)

found clear evidence of kin preferences in grooming, proximity, and tolerance but at intensities that were still modest compared with most Cayo Santiago groups. Thus, the results of this study suggest that even marked species differences in kin bias can have more to do with the particular social/demographic conditions they experience (and with the processes producing them) than with differences in inherent species-specific tendencies to prefer kin.

The finding that time constraints appear to influence grooming kin bias in the same way in both species also has implications about the extent to which species differences in kin bias among macaques in general may be due to evolutionarily constrained species-level tendencies to prefer kin vs. individual level responses to kin based on current conditions. Clearly, our results indicate that species variation in grooming kin bias cannot be attributed solely to evolutionary constraints. Nor is it possible to rule them out, given findings of consistent differences in at least some forms of kin bias between captive macaque species housed under similar conditions (e.g., de Waal and Luttrell 1989; Butovskaya 1993; reviewed in Thierry 2000). Thus the evidence so far leads us to favor the suggestion that variation in kin bias is influenced by both a species' evolutionary history and its members' current conditions, with each species displaying an inherent range of potential responses to particular current conditions, i.e., a social reaction norm (cf. Kappeler and van Schaik 2002).

Although dominance style in general has been found to vary both among species and among individuals within species (e.g., Richter et al. 2009), reference to dominance styles at the species level may be heuristic in examining this idea. If, as hypothesized, phylogenetic influences on kin bias are associated with species' dominance styles (Thierry 2000), phylogenetic influences may be apparent only when species with different dominance styles are compared. Conversely, one would expect species with similar dominance styles to show few differences when current conditions are similar or controlled statistically. Data on the dominance styles of rhesus and Tibetan macaques are consistent with this hypothesis. Researchers generally agree that rhesus macaques display among the most extreme despotic dominance styles. Although early assessments of dominance style in Tibetan macaques placed them among the relaxed macaques (Thierry 2000), additional data indicate that they are more appropriately considered despotic (Berman et al. 2004). Similar comparisons between relatively relaxed and despotic macaque species are also needed to test this hypothesis but have yet to be carried out.

To fully explore the relative contributions of phylogeny and current conditions on kin bias on the species and individual levels, additional comparative research is needed on a broad range of macaques that live in groups of varying sizes and numbers of females and that display a variety of social styles. Because captive groups are generally confined to small areas and provided with generous amounts of food by humans, it would be preferable to use groups that are unprovisioned or only partly provisioned, so that females experience more nearly normal constraints on their time. Several forms of kin bias should be examined, since it has been suggested that kin bias in reconciliation may be more phylogenetically constrained than kin bias in other kinds of behavior.

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Chapter 12
Behavior and Social Dynamics of Rhesus Macaques on Cayo Santiago

Dario Maestripieri and Christy L. Hoffman

12.1 Introduction

Rhesus macaques are Asian primates with a current geographic distribution that encompasses many countries such as Afghanistan, India, Thailand, China, Pakistan, Bhutan, Burma, Nepal, Bangladesh, Laos, and Vietnam. They thrive in almost any type of habitat, including tropical forests, dry and semidesert regions, swamps, and mountains up to 4,000 m high. In some countries such as India, free-ranging rhesus macaques also live in highly populated urban areas including villages, towns, temples, and railway stations. Although rhesus macaques can be found in large numbers and, in many cases, are easily accessible for observations, studies of free-ranging rhesus macaques in Asia have mainly focused on population biology, demography, and geographic distribution and much less on behavior and ecology (e.g., Southwick and Siddiqi 1994).

Much of our knowledge of the behavior, life history, and social dynamics of rhesus macaques comes from studies of the population on Cayo Santiago, a small island off the coast of Puerto Rico. Clarence Ray Carpenter, an American biologist who established the rhesus monkey colony on Cayo Santiago in 1938, began studies of social and sexual behavior soon after the monkeys were transplanted onto the island (Carpenter 1942a, b), but such studies were suspended during World War II. Stuart Altmann, a Harvard graduate student supervised by E. O. Wilson, is credited with the resumption of behavioral studies on Cayo Santiago in the late 1950s and

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early 1960s. Studies by Altmann and later by Conaway, Koford, and Sade provided the first systematic description of rhesus macaque behavior and social organization (Altmann 1962; Conaway and Koford 1965; Koford 1965; Sade 1972). These researchers began to recognize and track individual monkeys to gather information on births, deaths, and migration and on patterns of spatial association, affiliation, and aggression. By identifying and studying individuals, they learned that rhesus macaque society was organized around male dispersal, female kinship, and dominance relationships. Continued observations of rhesus macaques on Cayo Santiago up to the present day have provided a detailed understanding of their behavior and social dynamics. The information provided by research conducted with this population has generally been confirmed and supplemented by behavioral studies conducted in other research facilities as well as by studies of free-ranging rhesus macaques in India, Nepal, Pakistan, and other Asian countries (e.g., Southwick et al. 1965, 1982, 1996; Neville 1968a, b; Mukherjee 1969; Teas et al. 1980, 1982; Pearl and Schulman 1983; Marriott 1988; Goldstein and Richard 1989).

   The rhesus macaque population on Cayo Santiago, however, differs from other captive and free-ranging populations in some aspects of its structure and internal dynamics. Whether the unique characteristics of the Cayo Santiago population translate into differences in the behavior of individuals, or in within-group or between-group behavioral dynamics, is an issue that has not been systematically addressed.

   In this chapter, we will first review and summarize our knowledge of the species-typical social organization and behavior of rhesus macaques, using information that appears to be consistent across different populations, environments, and geographic areas where rhesus macaques have been studied (see Maestripieri 2007, 2010). We will then examine the unique ecological and demographic characteristics of the Cayo Santiago population and discuss how these characteristics may result in differences in social dynamics and behavior between the Cayo Santiago macaques and their wild counterparts.

12.2 Species-Typical Social and Behavioral Characteristics of Rhesus Macaques

12.2.1 Social Organization and Life History

Rhesus macaques live in social groups composed of a few adult males and many adult females and their offspring. The adult females and immature individuals within a group belong to several different matrilines, i.e., families of individuals related through the maternal line. The matrilineal structure of rhesus groups results from sex-specific patterns of dispersal and philopatry: males emigrate from their natal group at puberty and join a new group, whereas females remain in their natal groups throughout their lives (e.g., Lindburg 1971; Sade 1972). Within a matriline, there can be four to six overlapping generations of individuals. For example,

a 10-year-old female's mother, grandmother, great-grandmother, offspring, and grand offspring may simultaneously be present in a group. The adult males in the group are generally unrelated to all other adults because they immigrated by themselves from another group.

Males emigrate from their natal group around the time they reach puberty. In their natal group, young males receive increasing amounts of aggression from both resident adult males and adult females, particularly when they attempt to mate with females (e.g., Colvin 1986). Aggression and lack of opportunities for mating eventually result in emigration. Young males may also be sexually attracted to females from other groups. By emigrating from their natal group, rhesus males minimize the risk of inbreeding and maximize their chances of mating success. When rhesus males emigrate, they usually do so alone, although in some cases two brothers may emigrate together (e.g., Meikle and Vessey 1981). After spending several months, or even years, alone or as part of a small all-male group, rhesus males join a new group. They can stay in the new group for several years, after which they may leave and try to join another group (e.g., Drickamer and Vessey 1973).

The size and demographic composition of a rhesus macaque group are influenced by rates at which infants are born, their age-specific patterns of survival and mortality, the ages at which individuals begin and cease reproducing, how frequently they reproduce, and patterns of immigration and emigration. Male and female infants are generally born in equal numbers, although small deviations in the birth sex ratios can occasionally arise in relation to variations in local environmental conditions (Rawlins and Kessler 1986; Berman 1988). Infant mortality is generally high, especially for males (Hoffman et al. 2010). If infants survive their first year, however, their probability of mortality drops dramatically (Hoffman et al. 2010). Females reach puberty at 3–4 years of age, while males do so 6–12 months later. Both females and males continue growing after puberty, and adult body size is typically reached between 5 and 6 years of age. Post-pubertal females can reproduce once every year, every other year, or less frequently. Female reproductive rates typically decline with old age, but it is unclear whether menopause occurs (Hoffman et al. 2010). Males, at least in theory, can reproduce multiple times every year. Mating activity is concentrated in a 5–6 month period (mating season), while infants are born and raised by their mothers in a subsequent 5–6 month period (birth season) (Hoffman et al. 2008).

The maximum life span for rhesus macaques in captivity is 35 or 40 years but is much lower in free-ranging populations (see below). As with other mammals, males have higher mortality rates than females at any age (e.g., Sade 1980). Adult mortality is significantly affected by reproduction. In general, adult males are more likely to die during the mating season, whereas adult females are more likely to die during the birth season (Hoffman et al. 2008). Sex differences in seasonal patterns of mortality reflect the survival costs of reproduction, which differ for males and females in a sexually promiscuous species such as the rhesus macaque. Mating effort is the most costly aspect of reproduction for males, and pregnancy and lactation are the most costly aspects for females. Increased male mortality during the mating season likely results from high vulnerability to infectious diseases due to mating-related male–male aggression and wounding in conjunction with testosterone-induced suppression of the immune system (Hoffman et al. 2008). Increased female mortality

during the birth season may be the result of pregnancy or delivery complications, or due to pregnancy- and lactation-related energetic stress, psychosocial stress, and stress-related immunosuppression (Hoffman et al. 2008).

12.2.2 Dominance

Rhesus macaques are aggressive and xenophobic primates, who have a strong tendency to attack unfamiliar conspecifics (Maestripieri 2007). In general, the first fight between two individuals can establish a stable dominance relationship between them: the winner of the fight will be dominant and the loser will be subordinate. After dominance is established, the subordinate individual generally avoids the dominant or expresses fear and submission in his/her presence. The dominant attacks the subordinate occasionally, and this will maintain or reinforce the dominance relationship between them. In many cases, the dominant's aggression consists of ritualized threats, to which the subordinate responds with submissive signals (e.g., Bernstein and Ehardt 1985).

Every rhesus macaque has hierarchical relationships with every other individual in the group, and such relationships are generally transitive; that is, if individual A is dominant over B, and B is dominant over C, A is also dominant over C. As a result of these dominance relationships, all individuals within a group are ranked on a linear hierarchy, and the individual's position in the hierarchy is called dominance rank. The highest-ranking male and female are called the alpha male and the alpha female, respectively. The alpha male outranks all other individuals in the group, and the alpha female outranks all of the females and most of the males with the exception of the alpha male (e.g., Bernstein and Williams 1983).

Females maintain stable dominance ranks within their natal groups throughout their lives, whereas males lose their original rank when they leave their natal group at puberty and acquire a new rank when they join a new group. Males who have joined a new group are typically lower ranking than the other adult male residents in the group. They gradually work their way up the hierarchy by making alliances with powerful males and females (Manson 1998). Females who belong to the same matriline have similar dominance ranks. In particular, closely related females, such as mothers and daughters or pairs of sisters, occupy adjacent positions in the dominance hierarchy. Mothers typically remain dominant over all of their daughters throughout their lives, while sisters rank in reverse order of their age, such that young females dominate their old sisters and a female's youngest daughter typically is the most dominant of her female offspring (Chikazawa et al. 1979). In addition to individual ranks within a matriline, dominance relationships also exist between matrilines. Each group of rhesus macaques has a top-ranking matriline, a bottom-ranking matriline, and other matrilines that rank between them. High-ranking matrilines tend to be larger than low-ranking matrilines (e.g., Ehardt and Bernstein 1986).

The hierarchical relationships between individuals and between matrilines are ultimately determined by the mechanisms through which dominance rank is transmitted

across generations. These transmission mechanisms are not genetic, but social, and involve agonistic support given by mothers to their offspring (e.g., Bernstein and Williams 1983; Bernstein and Ehardt 1986; Datta 1986). Natal males acquire ranks from their mothers just as females do. Mothers consistently intervene on behalf of their immature offspring when offspring get into fights with other group members. When pairs of juveniles fight, the mothers of both juveniles intervene to support their offspring, and the outcome of the fight is ultimately determined by the relative ranks of the mothers. Since this process is repeated many times and with different individuals, offspring eventually acquire a dominance rank just below that of their mother (Datta 1986). Although juveniles are initially lower ranking than all adults within the group, juveniles will challenge every adult that ranks lower than their mother. With their mother's support, they will eventually outrank these individuals. Dominance relationships between sisters are also settled by maternal intervention, as mothers always support their younger daughters against their older sisters (Datta 1986). More specifically, young females are initially subordinate to their older sisters but, around the time of puberty, they outrank them with their mother's help (Datta 1986). Rank reversals between mothers and daughters, or between adult sisters, are possible but rare (Chikazawa et al. 1979). They are likely to occur between sisters if their mother dies before the youngest sister reaches maturity.

Agonistic support between relatives is used not only to transfer dominance rank to juveniles but also to help females maintain their rank in adulthood. Agonistic support between nonrelatives is less frequent but plays an important role in social dynamics, particularly for males. Adult males rise in rank through the formation of coalitions with unrelated males or females (Datta 1986; Manson 1998; Higham and Maestripieri 2011). Furthermore, both adult males and females maintain and reinforce their status by intervening on behalf of unrelated individuals whenever these individuals attack males or females that are lower ranking than themselves. Agonistic support is solicited with scream vocalizations, particular facial expressions (raised eyebrows and eye movements), and body postures (tail raising and hindquarter presentation) (Gouzoules et al. 1984). Agonistic support is also obtained in exchange for grooming behavior, as grooming a higher-ranking individual for extended periods of time increases the probability of receiving tolerance and agonistic support from this individual (Schino 2007).

12.2.3 Affiliation

The strength of social bonds between individuals in a rhesus macaque group is generally predicted by their kinship, sex, and age (e.g., Lindburg 1971). Measures of the strength of social bonds include the amount of time spent in close proximity, physical contact, or engaged in grooming behavior. The strongest social bonds are between mothers and infants. Mothers and juvenile daughters also have strong bonds, as do sisters and other closely related adult females. Males are strongly bonded to their mothers as infants and to other young or adult males as juveniles or

subadults. Adult males who have no family members in their group form temporary social bonds with females in estrus, in which spatial association and affiliation are accompanied by mating (Lindburg 1971). Adult males generally do not associate with their offspring or show paternal behavior.

Social grooming, or allogrooming, is the main affiliative behavior used by rhesus macaques to establish and cement social relationships with one another. Grooming involves slowly brushing the coat of another individual and removing skin parasites and other particles with the fingertips. Grooming serves a hygienic function and also relaxes the recipient. A rhesus macaque can request grooming from another individual by lip smacking to encourage the other individual to approach and then by lying down in front of the other, often exposing the part of the body that needs to be groomed. Grooming can last a few seconds, minutes, or, occasionally, over an hour. Compared to males, rhesus macaque females generally give and receive more grooming (Drickamer 1976). Infants receive a great deal of grooming from their mothers beginning on their first day of life, but they rarely groom their mothers or other individuals in the first 6–8 months of life. Rates of grooming performed increase with age in both males and females, but sex differences emerge during the first year of life when females start performing more grooming than males (Drickamer 1976). Juvenile females increasingly groom both older females and younger individuals, and grooming of males increases dramatically after puberty. Females continue to groom their female relatives, particularly their mothers and sisters, at high rates into adulthood, but after they give birth, a large fraction of their grooming is directed to their offspring. At 3–4 years of age, juvenile males seek out adult males and maintain one-sided grooming relationships with them (Drickamer 1976). Young males shift from grooming older males to grooming females after puberty and around the time of emigration; in other words, they mostly groom males prior to departure from their natal group, and they mostly groom females after immigration into a new group. Prior to emigration, males receive grooming mostly from their mothers, and after immigration they receive grooming from unrelated females that are potentially their sexual partners. Grooming between adult males is much less frequent than grooming between adult females, particularly during the mating season (Drickamer 1976).

12.2.4   Mating

During the mating season, females have estrus periods, which usually last 5–10 days, around the time of ovulation. Adolescent females exhibit exaggerated sexual swellings during estrus periods, whereas adult females advertise their fertility through a reddening of the facial and anogenital skin and through behavioral solicitations of copulation. During female estrus periods, male and female macaques form temporary social bonds called consortships, which include proximity maintenance, grooming, and repeated copulations (Gordon 1981; Wilson et al. 1982). The male and female follow each other around and spend a lot of time sitting next to and grooming each other; the female frequently solicits copulation by presenting her hindquarter

to the male and the male responds by mounting her. Consortships may last from several hours to a few days. Rhesus males need multiple mounts (about ten or more) to achieve ejaculation, although subordinate males can occasionally ejaculate after a single, very brief mount. During consortships, dominant males guard female partners to prevent other males from approaching and mounting them (Gordon 1981; Wilson et al. 1982). The alpha male, however, often disrupts the consortships of other males. When a consortship ends, a female can begin consorting with a different male. Females may consort and copulate with several different males within an estrus period or even on the same day. Males are sexually promiscuous as well, and adult males and females mate, on average, with a similar number of partners (Gordon 1981).

Despite this promiscuity, rhesus macaques do not mate indiscriminately, and pairings are not simply the result of intrasexual competition for mates. Instead, it is very likely that partner choice plays an important role in the formation of consort-ships and more generally in the occurrence of all mating activities. Mate choice, however, is a poorly understood phenomenon in rhesus macaques (Manson 1995). Kinship and familiarity are the variables whose effects on mate choice are perhaps best understood. Neither males nor females tend to be sexually attracted to geneti-cally related individuals or to unrelated individuals who are very familiar to them. Young males who have not yet left their natal group become increasingly attracted to females from other groups and attempt to follow them. Similarly, females are attracted to novel males and may leave their group temporarily to consort with peripheral or extra-group males. Although females also mate with the alpha male and other unrelated males within their group, they typically do not mate with males with whom they have a strong affiliative relationship ("friendship"; Manson 1995). Furthermore, females seem to develop a sexual aversion for males that have been in their group for 3–4 years or longer. This could be a proximate factor promoting male departure from the natal group at puberty and further migration after a few years of residence in a group. Attraction to novel individuals and aversion to mating with relatives and friends are behavioral adaptations that function to minimize the risk of inbreeding (Manson and Perry 1993).

Another variable whose effects on mate choice are relatively well understood is age. In rhesus macaques, both males and females tend to mate preferentially with middle-aged individuals in their reproductive prime rather than with sexually mature adolescents or very old but still fertile individuals (Manson 1995). Effects of domi-nance rank on female or male mate choice are generally weaker than those of famil-iarity and age. Although in some cases both males and females have been observed to mate more frequently or have longer consortships with high-ranking partners, in other cases there seemed to be proximity and mating preferences for low-ranking individuals (Manson 1995).

12.2.5   Maternal Care and Life Span Development

Pregnancy in rhesus macaques lasts about 5.5 months. Females typically give birth to a single infant; twins are rare and their probability of survival is very low. Mothers

are the main caretakers of their offspring, receiving no help from the offspring's father or other family members (e.g., Hinde and Spencer-Booth 1967). Newborn infants spend a great deal of time nursing or sleeping on their mother's chest. For the first several months post-birth, mothers carry their infants ventrally or dorsally while they travel. During the time devoted to resting or social activities, however, infants spend increasing amounts of time out of physical contact with but in close proximity to their mothers. During this time, young infants explore the environment or play with other infants. Young infants also receive much attention and grooming from juvenile and adult females. Mothers may restrict and control their infants' activities by physically restraining them and by making contact with them frequently (e.g., Hinde and Spencer-Booth 1967).

During the first few weeks of infant life, mothers are almost entirely responsible for maintaining contact and proximity with their infants. For example, infants tend to break contact and walk away from their mothers, while mothers follow them and reestablish contact. During the second or third month of infant life, however, responsibility for maintaining contact and proximity shifts to infants (Hinde and Spencer-Booth 1967). Therefore, mothers frequently break contact and walk away from their infants, while infants follow their mothers and make contact with them. In addition to breaking contact with infants more and more often, mothers also increasingly reject their infants' attempts to make contact and gain access to the nipples (Hinde and Spencer-Booth 1967). In doing so, mothers encourage their infants' independence and reduce the energetic costs involved in carrying them around.

Although changes in maternal behavior in relation to infant age are observed in all mothers, individual mothers differ from one another in the frequency with which they cradle or groom their infants, make or break contact with them, or restrain or reject them. Individual differences in maternal behavior are consistent over time and across different infants (Hinde and Spencer-Booth 1971). These differences are accounted for by characteristics of the mothers (e.g., their age, previous maternal experience, dominance rank, and personality), those of their infants (e.g., age and sex), and those of the surrounding environment (e.g., availability of food, risk of predation, risk of aggression, and risk of infant kidnapping by conspecifics) (Hinde and Spencer-Booth 1971).

Infants begin eating solid food in the first few months of life and are generally weaned by the end of the first year. Six months after giving birth, mothers may resume their menstrual cyclicity, mate, and conceive again. Infants actively resist weaning by responding to maternal rejection with screams and tantrums. They also interfere with their mother's mating activity and, in some cases, successfully delay conception and the birth of a sibling (Simpson et al. 1981). High-ranking mothers often produce an infant every year, while low-ranking mothers may give birth only every other year (e.g., Gomendio 1990). These differences in reproductive rates may result from differences in maternal behavior, as high-ranking mothers generally reject their infants earlier and at higher rates than low-ranking mothers (Gomendio 1990). Limitation of suckling activity through maternal rejection reduces the length of lactational amenorrhea and increases the probability that the mother will conceive again during the mating season. The birth of a sibling accelerates

the acquisition of independence for a 1-year-old rhesus monkey. As they become more independent, young males spend increasing amounts of time in rough-and-tumble play with their peers, while young females become increasingly interested in exchanging grooming with older female relatives or in playing with infants.

The sex differences in behavior that emerge at the end of the first year of life, or earlier, become more marked in the second and third years of life, when young males affiliate mostly with same-age or older males, while females become more embedded in the social networks of their matrilines (Hinde and Spencer-Booth 1967). In adulthood, male and female behavior is strongly affected by the alternation of the mating and the birth seasons. During the mating season, males have competitive and aggressive interactions with other males, while attempting to consort with estrous females. During the birth season, adult males spend much of their time alone, or occasionally affiliate with other males (Chapais 1986). Females maintain strong bonds with their female relatives throughout the year. During the mating season, they also spend time consorting with males, while during the birth season their attention is primarily focused on their own and other females' infants. As males get older, they experience a sharp decline in their mating and social activities and spend more and more time alone (Corr 2000). Old females become less attractive as mating and social partners, the size of their social networks becomes smaller, and they focus most of their attention on their closest relatives, particularly their immature offspring (Corr 2000).

12.3 Unique (or Potentially Unique) Characteristics of the Rhesus Macaque Population on Cayo Santiago Relative to Other Rhesus Populations

The description of rhesus macaque social organization, life history, and behavior provided in the previous sections of this chapter can be considered species typical and applies to rhesus groups and populations living in different geographic areas and environments. Particular populations of rhesus macaques, however, can exhibit unique social and behavioral characteristics as a result of the ecological characteristics of the habitat in which they live and their own particular demographic structure. Although the rhesus macaque population on Cayo Santiago probably shares some demographic similarities with the rhesus macaque populations that live in urban areas in Asia (e.g., in terms of size of groups and the impact of food provisioning on behavior; Singh 1969), the Cayo Santiago macaques probably differ from the forest-dwelling rhesus macaques in Asia in a number of ecological and demographic variables. Such differences can potentially translate into differences in social behavior at the individual and group level.

Assuming that the forests of India, Nepal, Pakistan, and other Asian countries in which rhesus macaques currently live represent the closest representation of the habitat in which these primates evolved, Cayo Santiago differs from this environment in three major ecological variables: food provisioning, absence of predators,

and restricted home ranges. Food provisioning and absence of predators are associated with reduced risk of mortality and increased longevity in the Cayo Santiago population. Although no data are available for wild rhesus macaques, studies of other wild cercopithecine monkeys have suggested that it is rare for adults to live beyond 10–15 years. Among the free-ranging rhesus macaques on Cayo Santiago, half of adult females die between 15 and 25 years of age, with the maximum life span being around 31 years (Hoffman et al. 2010; Maestripieri and Hoffman 2011). Although adult males on Cayo do not live as long as adult females, when compared to wild rhesus populations, the effects of food provisioning and the absence of predators on adult survival (Hill 1999) are likely to be even stronger for males than for females. In macaques and other cercopithecine monkeys, risk of mortality is especially high when males spend time alone, either while they migrate from one group to another in adolescence or when they are evicted from their new group later in life (e.g., Sugiyama 1976). Being alone is risky because of the difficulty of finding food and the increasing vulnerability to predation. On Cayo Santiago, where these risks are nonexistent, there are many more adult males in the population than there would be in the wild, and many more of these males spend time alone without a permanent affiliation with a group (Berard 1990). Even though many more males than females are culled from the Cayo Santiago population every year, the presence of supernumerary males still represents a significant alteration in the demographic structure of the population and exerts a potentially important influence on behavior (see below).

In addition to affecting mortality and demography, lack of predation and food provisioning, along with restricted home ranges, can also have more direct influences on behavior. In the wild, vigilance for predators is crucial for survival and may represent an important constraint on social activities (Cords 1995). The rhesus macaques on Cayo Santiago are probably much less vigilant for predators than their wild counterparts, and their social activities are much less disrupted by anti-predator alarm calls and the need for quick dispersion. Therefore, reduced vigilance associated with lack of predators on Cayo Santiago may result in greater amounts of time available for social interactions and, therefore, higher frequencies and longer durations of such interactions (e.g., Marriott 1988).

The rhesus macaque groups on Cayo Santiago have distinct home ranges on the island and travel along particular paths within these areas on a daily basis, just as wild macaques do. The home ranges of the Cayo Santiago macaques are much smaller than in the wild. Because of food provisioning and restricted home ranges, the Cayo Santiago macaques spend much less time traveling and foraging and more time resting and engaging in social interactions than their wild counterparts (Marriott 1988). Food provisioning and restricted home ranges on Cayo Santiago also result in more frequent encounters and displacements between groups and more frequent aggression (see also Hill 1999, for Japanese macaques).

Increased aggression, both between and within groups, is especially frequent during feeding times, inside and around the feeding corrals where the food is distributed. Although feeding times and locations can be excluded from

behavioral data collection, it has been suggested that feeding-related aggression in food-provisioned macaque populations affects the social interactions between group members outside of the feeding context (Hill 1999). For example, social relationships between adult males in food-provisioned macaque populations may generally be more tense and competitive (with low frequencies of affiliation and high frequencies of aggressive and submissive behavior) than in wild populations (Hill 1999). Although adult males on Cayo Santiago occasionally affiliate with one another, especially during the birth season (Chapais 1986; Hill 1986), it is possible that male–male affiliation is less prominent in this population than in wild rhesus populations. Tense and competitive relationships between adult males on Cayo Santiago may also explain why these males form coalitions against other males or females less often than is observed in wild populations of other macaque species (e.g., Barbary macaques; Widdig et al. 2000; but see Higham and Maestripieri 2011, for recent observations of male–male revolutionary coalitions on Cayo Santiago).

The behavior of adult males on Cayo Santiago may be different from that of their wild counterparts not only because of the high number of males and their competitive relationships but also because of differences in migration patterns. On Cayo Santiago, opportunities for male dispersal are limited, and some males remain and mate in their natal groups or return to their natal groups later in life. As a result, all groups in the population contain a few natal adult males, some of which belong to the dominant matriline and are therefore themselves high ranking (Chapais 1983). Although some studies have reported that mating between close kin, such as mothers and their adult sons, may occur, it is rare and generally less than expected by chance (Sade 1968; Manson and Perry 1993). As previously mentioned, females show strong sexual aversions to related males based on familiarity cues such as proximity, and these aversions are effective in preventing incest even in groups in which the natal adult males are sexually active.

Regardless of the occurrence of incestuous mating, the presence of some natal males within a group can potentially alter the social dynamics and the rank relationships between males and females, particularly in cases in which natal males are high ranking (Chapais 1983; but see Manson 1993). Since high-ranking natal males continue to receive support from their mothers and other family members, opportunities for other non-natal males to achieve high rank may be lower than if no natal males had been present. If high-ranking natal males support their mothers and other close relatives against others, this can also result in significant alterations in social dynamics within their matriline as well as in the dominance relations between matrilines. One possible difference between the Cayo Santiago and wild populations concerns the acquisition of alpha male status. Studies of wild populations of long-tailed macaques have shown that adult males who have recently immigrated into a new group pursue one of two different strategies to try to achieve alpha status (van Noordwijk and van Schaik 1985, 1988, 2001). Some males challenge the alpha male directly at the time of immigration; if they defeat him, they inherit his status and take over the group. Males who pursue the second strategy enter the male dominance hierarchy in the new group at the bottom and slowly work their way up the

ranks. These two different strategies have been reported also for wild rhesus macaques in Asia (Neville 1968b; Lindburg 1971), although they are not as well documented in rhesus as in other species. In the Cayo Santiago rhesus population, however, there is no evidence of males pursuing the first strategy; males generally join the group at the bottom of the hierarchy and accept a "seniority system" in which a male's rank is a function of how long he has resided in the group (Berard 1990; Manson 1998). Recently, however, middle-ranking rhesus males on Cayo Santiago have been observed to form multi-male coalitions that resulted in significant changes in the dominance hierarchy including the eviction of the alpha male from a group (Higham and Maestripieri 2011).

Differences in group and matriline size between the Cayo Santiago and other rhesus populations may be the source of potential differences in female social behavior. In the period 2005–2010, the Cayo Santiago population has consisted of 900–100 individuals divided into only six groups, which range in size from 70 to 300 individuals. In addition, these groups contain only a few, very large matrilines (e.g., group R, $n = 280$, currently contains only three matrilines). Clearly, groups and matrilines are much larger on Cayo Santiago than in the wild, and this may have consequences for female behavior. For example, the influence of matrilineal kinship on the distribution female grooming and agonistic support within the group may be greater on Cayo Santiago than in other wild populations. Early studies in Cayo Santiago evidenced differences in maternal behavior and in early social development in relation to matriline and group size (Berman 1983; Berman et al. 1997; see also Blomquist 2009). Mothers may be more or less permissive of their infants' social interactions, depending on the extent to which they are surrounded by kin and enjoy their protection and support. Infants' social interactions with others, in turn, may differ in the extent to which they are biased toward their kin, depending on maternal care received and the size of the matriline and group to which they belong.

Although the processes of rank acquisition and maintenance are likely to be similar in all rhesus macaque populations, the benefits and costs of being high ranking versus low ranking may differ in relation to demographic variables. In a group of 20–30 individuals with several small matrilines, a female belonging to the second-highest-ranking matriline may have only three or four females above her in the hierarchy and receive relatively low rates of aggression. In a group of 120 individuals and only three matrilines, however, a female belonging to the middle-ranking matriline may be outranked by 30 or 40 other females and receive as much aggression as a low-ranking female. In this group, rank can be beneficial only to females in the top-ranking matriline. Accordingly, on Cayo Santiago, middle- and low-ranking females have equally high cortisol responses to stress when compared to high-ranking females (Maestripieri and Hoffman 2011), suggesting that both middle- and low-ranking females experience chronic social stress due to the aggression received. Rank-related chronic stress results in accumulation of allostatic load especially during aging, suggesting that social variables can have potentially important effects on longevity, health, and reproduction toward the end of the life span (Maestripieri and Hoffman 2011).

12.4   Conclusions

Differences in ecological variables such as food provisioning, absence of predators, and restricted home ranges between the Cayo Santiago macaques and their wild counterparts are associated with differences in the demographic structure of the populations, which in turn, may affect social dynamics and behavior. In addition, the ecological characteristics of the Cayo Santiago population affect the time budgets of rhesus macaques and increase the time available for social activities with conspecifics. Consequently, the frequencies of affiliation, aggression, and other social interactions, both within and between groups, may be much higher on Cayo Santiago than among macaques living in Asian forests. Food provisioning in itself can be associated with increased between- and within-group aggression. The presence of supernumerary adult males on Cayo Santiago, their limited opportunities for dispersal, and the tense and competitive nature of male–male relationships may result in potential alterations in the patterns of mating behavior within groups and in the mechanisms by which adult males rise in rank. Finally, the large size of groups and matrilines on Cayo Santiago may be associated with differences in female social networks, the benefits and costs of high versus low rank, and differences in maternal behavior and social development. Although Cayo Santiago represents in many ways an ideal site for studies of social dynamics and behavior, the unique ecological and demographic characteristics found on this island suggest that caution should be used when extrapolating findings from this population to other populations of the same or other primate species. The same caution should also be used in studies of other primate species, as differences between populations in predation pressure, food availability, or demographic structure could result in significant differences in behavior and social dynamics.

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Chapter 13
Natural History of the Self

Donald S. Sade

13.1 Introduction and Background

For a generation, a dominant theme in behavioral primatology has been the interpretation of social interactions as fitness strategies. This approach seeks the ultimate causes of sociality in adaptation through natural selection. Studies from Cayo Santiago have contributed to this approach in a number of studies of fitness consequences of agonistic status of females, most recently and extensively by Blomquist (2007, 2009) and Blomquist et al. (2011), and of males (Berard et al. 1993, 1994). Here a second, yet complementary, approach, which seeks the proximate causes of behavior in the organization of the neural mechanisms of perception and action, is taken. Each approach makes inferences about processes that are not directly observable, in the first case natural selection, in the second the activity of neural networks in the brain.

A fascinating synthesis of ethology, human psychology, neurology, and evolutionary biology has developed, called evolutionary psychiatry by Stevens and Price (2000). As a clinical science, it largely emphasizes the second approach. Evolutionary psychiatry developed from connections between the psychoanalysis of Carl Jung, especially as practiced by Anthony Stevens (2003), the attachment theory of Bowlby (1969), and social ethology, beginning especially with Tinbergen (1951), Maslow (1937), Harlow and Harlow (1965), and John Price (1967).

The direction of influence so far has been from ethology to psychiatry. It is believed by the author that the concepts and findings of evolutionary psychiatry usually applied only to humans can, with care, also be used in behavioral primatology.

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Of course, language, the medium of psychoanalysis is not available to us in the study of nonhuman primates. We are limited to observations of the occurrence and orientation of expressive behaviors and the spacing and movements of the monkeys with respect to each other.

Cayo Santiago has been an ideal facility for constructing the detailed life histories of individuals from consistent observation over periods of years. These provide the detailed descriptions, in near-clinical detail, of individual lives upon which a natural history of the self must be based. The rhesus monkey is only one species among a number of similar species that vary in the details of social life (Kaplan 1987; Thierry et al. 2000). A comparative biology of the "self" requires a terminology that applies both to humans and to nonhuman primates and thus avoids implying self-consciousness. It is hoped that through the comparative method, one can eventually identify the phylogenetic substrate out of which self-consciousness evolved in humans.

13.1.1 Definitions

The terms "self," "ego," "autos," and "identity" have been used in many ways, sometimes overlapping in meaning, and sometimes mutually exclusive, depending on whether inner or outer aspects are emphasized by the writer and how he wants to slice up the conceptual pie. The self-reflexive consciousness of humans, and its linguistic construction, dominates discussion in the literature. But self-consciousness is a new development, depending upon the most recently evolved features of the human brain (Feinberg 2005; Stamenov 2005). For the comparative approach compelled upon us by evolutionary psychiatry, a definition broad enough to apply generally across species is needed: Explicit or implicit in most discussions of the self is the relation of the individual to what is external to the individual (Churchland 2002). For instance, Barkow (1980: p. 322) writes that:

> "The self functions in part as an evaluation device, monitoring both the internal state of the organism and its position in the physical and social environments. It evaluates the state of the organism in terms of the goals and goal-states built into it by biological evolution."

In an unpublished summary of his *Studies in Comparative Vertebrate Sociology* (c. 1986) Earl Count outlined the topic of "The Vertebrate Ego:"

> "…there is at work among vertebrate 'personalities' a self-conditioning process … whereby the individual seeks some center of reference which gives orientation to his behavior. It gives a dimension of context to all his acts. Territorialism, orientation to whatever or whoever may stand as a parent, dominance/subordinance determinations, are vertebrate matters which appear to shed light upon the human personality's 'search for identity'. The reverse of the coin shows in the *déraciné*."

In this paper, "self" and related terms are defined as follows: The "self" is the neural process that relates the inner state of the individual to its place or status in the external world. The "inner state" means the neural representation of internal processes

including the body schema and motivational and emotional states. Substitute "biological" for "neural" and the above definition applies to any organism.

By "external world" is not meant the actual environment, but rather its neural representation, greatly abstracted by the selective action of the perceptual filters (the Merkwelt: von Uexküll 1909), by inherited propensities to attend to particular features that have value, and not to others, by experiences of sufficient emotional importance to be retained as memories, all underlain by ontogenetic programs that predispose, even compel, the individual to acquire specific information and form specific attachments at specific stages in the life cycle.

Attachments (Bowlby 1969) are the individual's connections of especial emotional value to features of the external world. The attachments formed, whether to a particular habitat, a territorial center, a set of social companions, and, in humans, to the purely imaginary, symbolic systems of mythologies, are the identity of the individual. The identity is the inner experience of the individual. Viewed from the outside by an observer or a conspecific, the attachments and their qualities are the status of the individual. A well-established identity results in the emotional state of well-being called self-esteem, which is expressed outwardly as confidence, to a degree that varies widely across individuals. Leary (1999) elaborated Barkow's (1980) ethological approach to "self" and "self-esteem" into the "sociometer theory:" the self uses the emotional consequences of self-esteem to track the state of the individual's own status in the social network.

A component of self-esteem in humans is the self-perceived status compared with the desired, expected, or targeted status of an individual. Durkheim (1897 [1951]) proposed that when the social environment fails to limit aspirations to achievable goals, desires become unbounded and goals unreachable. Individuals in such a state of *anomie* despair of pursuing unachievable goals and turn to suicide.

Could a monkey's identity include expectations and evaluations in any comparable sense to that discussed above? Walters (1980), based on his own observations of baboons and a review of several macaque species, suggested that the predictability of adult statuses in female monkeys in fact implied that, during development, they acquire a knowledge of the statuses among others in the group, that they develop an expectation of their own adult status within it, and that they target specific individuals in agonistic interactions to achieve that status. Berman's exquisitely precise studies of infant social maturation at Cayo Santiago suggest that such expectations may develop, as maturing infants broaden their attachments to wider circles within the social group (Berman 1980; Berman 1982; Berman and Kapsalis 1999; Berman et al. 1997).

How pretension to a particular status could be represented in a brain lacking self-consciousness and language remains unexplored. However, one might think of the appetitive–consummatory action chains described by the early ethologists (Craig 1918) as indicating hard-wired "expectations" of a sort, even in vertebrates lacking cerebral cortices. Developmental programs, such as the archetypes discussed below, anticipate the presence of appropriate objects of attachment at later stages of maturation. It seems not unreasonable to suggest that a monkey could develop specific expectations in regard to other recognized individuals, that achieving or failing to

satisfy such expectations could affect the degree of his self-esteem, and that a mismatch of expectation and achievement could be equivalent to loss of an established status.

Can monkeys recognize relations among other individuals? The intuitive answer for the naturalist steeped in familiarity with his subjects may be "yes." But there is also some experimental evidence in favor of that intuition: Dasser (1988) found that two female Java monkeys identified mother–offspring pairs from pictures, suggesting a concept of the mother–infant relation. Chase's (1982) study on the origin of transitive dominance hierarchies suggested that if one of a pair of animals of established rank observed the other fight with a stranger, the observing animal would himself become subordinate or dominant to the stranger, depending on the outcome of the observed fight. This implies that the observing animal can recognize the relation between the other two. Mendoza and Barchas (1983) experimentally showed that dominance hierarchies in rhesus monkeys can form according to Chase's suggestion. Seyfarth and his colleagues (Bergman et al. 2003) interpreted the response of baboons to recorded calls combined to mimic fights between known group members as showing that baboons recognize both kinship and dominance rank among other individuals.

13.1.2 Dissection and Phylogeny of the Self

The use of the singular nouns "self" and "process" above obscures the fact that clinical studies of humans with neural diseases, noninvasive imaging techniques, and noninvasive techniques that interfere with neural activity in specific areas of the brain during cognitive experiments, show that the "self," however defined, can be dissected into component processes that depend upon different regions of the brain. Seeley and Miller (2005) offer a phylogenetic and ontogenetic scheme of the levels of self-representation that characterized the human "self," the age at which they appear in development, and their occurrence among the vertebrates. These authors discuss the neuroanatomical components of each level (in humans) and the dementia that disrupt them. This topic will return in the final results' section.

13.1.3 Archetypes

Carl Jung gave the name "archetypes" to the inherited neural processes that "initiate, control, and mediate the common behavioral characteristics and typical experiences of all human beings" (Stevens and Price 2000, page 279). The archetypes include the "deep structures" that predispose the developing individual to form specific attachments at the appropriate stage. The familial attachments, between mother and infant, between siblings, between the young of each sex and an associated adult male, and, at puberty, between sexual consorts, are central in understanding human societies as well as individual psychology and pathologies. Jung's concept of archetypes has proven to be of enormous explanatory power in understanding the essential

similarities of human beings, not only in social relations, but in the symbolic content of dreams (Stevens and Price 2000, Chapter 18), the structure of mythologies (Campbell 1949, 1959), and the plots of folk tales and literature (Booker 2004).

Although mythological motifs and stories may seem to be purely symbolic constructions, the underlying archetypes, as neural systems, are biological traits that are part of the evolutionary heritage of the species. As such, we should expect the anatomical structures of the archetypes, and their functional correlates, to be similar across species in proportion to phylogenetic closeness. Thierry et al. (2000) compared a variety of measures of social behavior across 16 species of macaques and concluded that many features were conservative, suggesting phylogenetic inertia rather than environmental adaptation as the explanation of similarity. At greater phylogenetic distances, one should still expect to find homologies in structure. The expression of the archetypes and the behavior of the species should be more variable as a correlate of the social ecology of each species. The locomotor skeleton offers an illustration: We can easily recognize the homologies between the bones of the extremities of horses and humans, while still admiring the perfect adaptive modifications each species has achieved to fit it to a unique mode of life. The fundamental attachments discussed above are an ethological "skeleton" of the anatomy of the self. Description of social relations and organization in terms of the frameworks of archetypes (in the phylogenetic sense rather than the literary sense) is an alternative to, but not in contradiction with, the modeling of social relations as fitness strategies. Rather, the archetypes are part of the context of constraints within which and upon which selection operates. These matters are discussed at much greater length and with much greater eloquence in Stevens (2003).

13.1.4   Application to Rhesus Monkey Social Relations

Suomi (2005) argued for the phylogenetic similarity between the mother–infant attachments of rhesus monkeys and humans. He reviewed aspects of Bowlby's attachment theory, and Harlow's theory of affectional systems, as well as more recent work on the development of social relations in monkeys, including studies from Cayo Santiago. This work shows there is considerable variation in the development of relations according to birth order, group size, and rank of mother. Nevertheless, the variations seem to be centered on specific sets of relations that are distinct in quality and can be usefully named.

Bowlby, following Harlow, suggested that five "affectional systems" condition the maturation of social attachment in monkeys and in humans: the maternal, the infant–mother, the peer, heterosexual, and paternal (cited in Stevens 2003, p. 176), but a slightly simpler scheme for monkeys is adequate, outlined as follows: (1) The mother's attachment to the infant and the infant's attachment to the mother are obvious and well-documented in rhesus monkeys and can persist into adult life for both females and males. (2) Sibling attachment's form next, especially between sibs of similar age. There may be a component of the maternal system active in the relation

between elder and younger siblings. It is suggested that the sibling system underlies the formation of attachment with peers other than siblings ("friendships": Strum 1987). Forming later, and lacking the common identity of attachment to the same mother, attachment to peers is less strong and persistent. (3) With maturation, a new system becomes active during a variable interval centered on puberty. It compels the revision of the individual's identity, which we observe as a reorganization of status. Among females, younger sisters rise in rank over elder sisters (Sade 1972; Datta 1983, 1988). Males usually migrate from the social group during this stage. Among males who remain for a time (usually sons of higher-ranking females), younger brothers may rise in rank over elder ones, and sons may rise in rank over their mothers (Sade 1968). Human societies celebrate this stage with initiation ceremonies ("rites of passage") and symbolize it in myths and literature in the "call to adventure," which compels the hero or heroine to embark upon a quest. Whatever the consequences of this stage in monkeys in relation to population genetics (dispersal), or in relation to individual reproductive strategy, in terms of identity we might call it the "stage of passage." (4) In rhesus monkeys, the heterosexual attachments are controlled by the estrous cycles of the females (Conaway and Koford 1964; Loy 1971). Consorts of a few days' duration may form between a male and female and temporarily override all other attachments, except the maternal: females will usually carry their infant even if the consorts leave the social group.

It is believed that the above systems, or combinations of them, motivate all other attachments. Smuts (1985) referred to nonmating associations between adult males and females as "friendships." Strum (1987) applied the term to all attachments other than mother–infant, sibling, and consort between mates, a useful broadening of the meaning, which is followed in this paper. Friendships are probably based on the same affectional system that underlies sibling attachments. "Paternal" behavior is likely maternal behavior expressed in the male, combined with "friendship," itself derived from the sibling attachment system. Adult male rhesus monkeys can carry, groom, lip smack at, and defend infants and juveniles using the same expressive behaviors more often thought of as being maternal, suggesting a shared repertory of caregiving, although not as strongly developed as in tamarins. Count (1968) pointed out that among vertebrates the behavioral repertory that characterizes one sex is also largely present in the other, although it may remain latent under normal circumstances.

Because the above terms refer to potentially discoverable neural processes and to observable characteristics of behavior, they can be used for both humans and, at least, nonhuman primates without recourse to metaphor. Suomi (2005) makes a similar argument, although less recklessly.

13.1.5   Natural History and Personal Knowledge

Anthony Stevens' earlier work "The Natural History of the Self" (Stevens 2003) exhorted his colleagues to abandon the notion of the "tabula rasa" in human development, in favor of the ethological approach implied by Jung's concept of archetypes. By "natural history," he meant the biological and evolutionary bases of the human psyche.

In this paper Stevens (2003) is accepted as axiomatic. By "natural history," however, in this paper, is meant the accumulative descriptive and inferential processes by which the biologist acquires an understanding of the subject. Good science depends on the foundation of good natural history. Natural history proceeds by an accumulation of knowledge of descriptive examples, like the case histories of the clinician. From these, patterns may eventually be recognized that can become the building blocks of theories and eventually lead to the deductive practice of hypothesis testing. The natural history stage of the science must be well developed for theoretical deductions to be based in reality. Otherwise, what results is philosophy, or mythology.

The study of the self is still very much in the natural history stage. Paleontologist Ruben Stirton once stated that the extensive collection of mammalian fossils at the University of California, Berkeley, were part of his personal knowledge of mammalian evolution. By this he meant that he related every new specimen or idea to his lifelong experience of this collection for comparison, description, or evaluation. Every naturalist has a similar accumulated fund of personal knowledge of his subject. For example, the sociometric and demographic observations that the author and colleagues made at Cayo Santiago, and on a colony of tamarins at Northwestern University (Knox and Sade 1991), are the major parts of the personal knowledge of primate ethology of the author and how the ideas outlined above relate to the origin and nature of the self.

13.2 Materials and Methods

13.2.1 Cayo Santiago

The Cayo Santiago colony of free-ranging rhesus monkeys, its history, management, and characteristics through the mid-1970s, and the history of the study from which this chapter derived, are given in detail in a previous publication (Sade et al. 1985). All demographic information regarding the individual monkeys mentioned in this chapter is abstracted from that work.

13.2.2 Seasonality

During these years, mating and births were strongly seasonal, with copulation occurring mostly from July through December and births occurring from January through June. In later years, the breeding season gradually shifted earlier by nearly 5 months (Blomquist 2007; Hoffman et al. 2008). Strong estrous cycles and consorts between adult males and females were largely confined to the mating season. Migrations of males between social groups are more frequent during the mating season, especially at the start. Adult males showed a corresponding increase in testis size and levels of circulating testosterone at the start of the mating season (Conaway and Sade 1965; Sade 1964; Sade et al. 1977; Zamboni et al. 1974). In adult males,

Table 13.1 Group J observers for the period covered in this chapter

Observer	Period of observation
Kathy Cushing	January 1, 1973–August 16, 1973
Kathy Cushing	January 1, 1975–July 30, 1975
Kathy Wilson	July 3, 1973–August 31, 1973
C. Jean De Rousseau	August 30, 1973–September 11, 1973
Donald Sade	September 12, 1973–October 28, 1973
Peter Cushing	October 25, 1973–July 23, 1974
Terry Morse	July 2, 1974–December 20, 1974

Kathy Cushing and Donald Sade made incidental observations on group J throughout the study

the annual physiological cycle reactivates the stage of passage each year but perhaps less profoundly than at its initial activation at puberty. Count (1973) referred to an animal's changed attitude toward familiar surroundings at the start of a breeding cycle as a "psychological migration," even if there is no geographic movement. Serious wounds are more frequent during the mating season than during the rest of the year (Wilson and Boelkins 1970) and male mortality is higher (Hoffman et al. 2008). Some degree of sexual attraction may persist during the nonmating season. Loy (1971) found a cyclical pattern of grooming between adult males and females during the nonmating season, suggesting a persistence of low intensity estrous periods. The division of group J outlined below occurred during the more volatile time of the mating season. The fusion of the two daughter groups occurred during the subsequent nonmating season.

13.2.3 Descriptive Field Notes

As part of a larger longitudinal study, a series of observers observed group J under my direction from 1 January 1973 through 30 July 1975 (Table 13.1). Observations were carried out almost daily. All observed episodes of grooming and agonistic interactions, as well as a variety of other kinds of information, were noted in descriptive field notes.

13.2.4 Interaction Matrices

Computer text files of all dyadic grooming and agonistic interactions were prepared from the handwritten field notes preserving the date, time, names of the monkeys, and the direction of the behavior between them. The interaction matrices of grooming and of agonistic interactions from these files for each desired interval of dates were tabulated using a computer program (D. Sade: MacMatrix6v2a). Then the matrices were transferred to programs for social network analysis (Borgatti 2002; Borgatti et al. 2002).

13.2.5   Quotations from Field Notes

All quotations from the descriptive field notes are paraphrases of the abbreviated English used for recording observations.

13.2.6   Social Networks

A social network is a description of the relations among a group of individuals. As applied to human affairs, "relations" may include events far removed from interindividual interactions, such as transfer of funds between bank accounts in money-laundering schemes, patterns of telephone exchanges suggesting terrorist connections, and the distribution of attitudes toward superiors in a business organization. Many other applications are found in social psychology and the social sciences (Wasserman and Galaskiewicz 1994). Studies of animal social networks are becoming more common and varied in their application (Sade and Dow 1994; Sueur and King 2011). A recent and lucid introduction to the use of social network methods for animal behaviorists should stimulate many new studies (Croft et al. 2008).

   Human social networks are often based either on interviews of subjects who state their attitudes toward other individuals or on the passage of materials for the flow of information between them. These measures are not possible for most primate species (except food sharing in chimpanzees?). Rather we must observe the display of expressive behavior exchanged between individuals. Grooming and agonistic displays are considered in this chapter. Descriptions of the displays are found in previous publications (for example Sade 1965, 1967, 1973).

13.2.7   The Grooming Network

Although a monkey can solicit grooming from another, it is useful to think of the groomer as orienting to or being attracted to the groomee. Grooming indicates a link from the groomer to the groomee and is an indication of attachment.

13.2.8   Agonism and the Agonistic Network

Agonistic displays in rhesus monkeys seem to derive from behaviors of attack and flight seen in fights with physical contact (Sade 1967). In this species, they are highly asymmetrical, with very few or no reversals of the direction of threat and subordination seen between the pair, except when status is being established. The status within the pair can remain stable over years Sade 1967, 1972). The subordination displays (the cower, grimace, and shriek) indicate acknowledgment of a status within the relation. A monkey can end an interaction by backing or running away without

showing any of these distinctive displays. This is often seen in fights between members of different social groups (Hausfater 1972). Thus, the subordination display indicates a connection or a link from the subordinate to the dominant, not merely an avoidance of aggression. Subordination is sometimes referred to as "dependence" in studies of human groups. In the present study, subordination is used as another indication of attachment. De Waal (1988, 1996, Chapter 3) and Rowell (1974) discuss this and other aspects of the integrative function of dominance and subordination relations. In this paper, the term "agonistic network" (Knox and Sade 1991) was used rather than "dominance hierarchy," as the former emphasizes the connections in the dominance/subordination relation. Also, it does not imply transitivity of the relations, as does the latter term. Although the agonistic networks of rhesus monkeys are strongly transitive, those of other species may not be.

13.2.9   Matrices and Diagrams

In the diagrams of the grooming network (Figs. 13.1a–13.6a), the arrows point from the groomer to the groomee. The strength of the link, as might be proportional to the number of episodes tabulated in the cells of the matrix, is not shown in the diagrams, to avoid excessive visual clutter. The matrices of grooming interactions upon which the figures are based are available from the author as UCINET data files.

In the matrices of agonistic display (Tables 13.4 through 13.7), the row monkey is the dominant, and the column monkey is the subordinate. In the diagrams of the agonistic network (Figs. 13.1b–13.6b), the arrows point from the subordinate to the dominant, indicating the direction of attachment in the agonistic network. This is the opposite direction from the usual way in which a "dominance hierarchy" is drawn. The complete matrices of agonistic interactions upon which these figures are based are available from the author as UCINET files.

The diagrams of the attachments of the individuals in the grooming and agonistic networks are an overview of the patterns of statuses from which we infer the identities (in the sense discussed above) of the members of the group.

13.2.10   Geodesic Distance

Monkeys may be linked to other monkeys indirectly through intermediaries rather than directly. The maximum number of links that can lead to an individual is $N-1$, where N is the number of monkeys in the group. If a monkey has no links to others he is an isolate, with respect to that network. The minimum number of links that connects two individuals, which can vary between 1 and $N-1$, is the geodesic distance between them. In preparing the diagrams, geodesic distance was used to plot the position of the individuals relative to one another, using multidimensional scaling (MDS). In the agonistic network, the geodesic distance between two monkeys is equivalent to "rank distance" (de Waal 1991). It does not depend upon transitivity in the network.

13.2.11 Multidimensional Scaling

MDS is an iterative routine that plots the position of each individual in relation to each other individual in proportion to their closeness on some measure, in the present case geodesic distance. If tried manually with a small number of individuals, it can be seen that there is not one unique solution. It is a problem of taking an $N-1$ dimensional diagram and projecting it onto the two-dimensional space on the page (in the present instance). It is a heuristic device of considerable utility in the natural history stage of research.

13.2.12 Centrality

An individual's central or peripheral status in the monkey group has usually been based on impressions of his spatial relations with the other monkeys. Centrality status in the social network, however, is some measure of the degree of attention paid to an individual, as in the attention–structure correlated with dominance rank proposed by Chance (1967), or the number of pathways of length *N* directed toward a monkey (Sade 1989). Clique size, as used by Kudo and Dunbar (2001) as a correlate of size of the neocortex, is a nondirectional measure of grooming partners and thus related to the measure of centrality used below. Some measures of centrality used in studies of human social networks, such as "betweenness," implying that something, such as a message, passes along a chain of individuals, may be harder to interpret when applied to nonhumans. "Information centrality" (McDonald 2007), "betweenness" (Lehmann et al. 2010), and "embeddedness" (Blumstein et al. 2009) may represent more the structure of a group than the status of an individual, when applied to animals.

The measures of centrality used in the diagrams of the grooming and agonistic networks in the present study are respectively the number of monkeys who groom an individual and the number of monkeys who display subordination to an individual. This measure is called in-degree centrality of pathways of length 1. This measure was chosen so as to stay as close to the actual observations as possible in the descriptions.

13.3 Results

This section provides detailed descriptions of changes in the statuses of individuals that occurred at Cayo Santiago (1) spontaneously during a group division and fusion, (2) in a noninvasive experiment, and (3) as a result of a brain lesion study (Myers and Swett 1970; Myers et al. (1973). In Sect. 13.4, these changes will be interpreted in terms of the archetypes discussed in Sect. 13.1.

13.3.1 Group J Division and Fusion 1973–1975

The following provides an overview of the division and subsequent refusion of group J. A much finer-grained analysis is possible but beyond the scope of this chapter.

Group J formed in late 1964 when female 092 and her descendants, and female 031 and her descendants, except for her eldest daughter and her offspring, left group A. These females and offspring, along with a few unrelated males, formed an independent social group (Koford 1966; Chepko-Sade and Sade 1979).

Margaret Varley (unpublished) made the first systematic observations of social interactions in group J in 1968 and 1969. Varley found that the dominant male of the group was 056, who had been with the group from its formation, and that the females of 092's genealogy were dominant to those of 031's genealogy. The next systematic observations on group J began in January 1973 and continued through July 1975. During this period, group J split into two groups, J and N, during the mating season. During the subsequent nonmating season, the groups fused again into a single group, J. The females of the former dominant genealogy, 092, were now subordinate to the females of the former subordinate genealogy. These events are described below in six stages.

Figures 13.1 through 13.6 illustrate the grooming and agonistic networks during each stage. In each figure, males are shown by triangles and females by circles. The size of each symbol is proportional to the individual's in-degree centrality in the interaction network. Light gray symbols are non-natal monkeys (all males). Dark gray symbols are descendants of 092. White symbols are descendants of 031. Labels are the names of the monkeys in the colony records. The location of each symbol was determined by the MDS routine, not subjectively by the author.

The present study includes only monkeys born 1971 or before, and so excludes 61 juveniles. Tables 13.2 and 13.3 list the included monkeys, their mothers, genealogies, age, and deaths that occurred during the study. The monkeys are sorted by genealogy and within genealogy by age (cohort) to facilitate locating a monkey of interest. Further details on each monkey's biography are found in Sade et al. (1985). Migrations of males to and from groups J and N are mentioned in the text. The complete migration history of each male is included in Sade et al. (1985). Most of the non-natal males who joined groups J and N were either born in group F or joined group F before moving to group J or N.

13.3.2 Stages of Division and Fusion

Consult the figures frequently while reading the following descriptions. Matrices of agonistic networks are included only for the predivision and post-fusion intervals due to limitations of space. Complete grooming and agonistic matrices for all the intervals are available as UCINET data files from the author (donaldssade@earth-link.net).

Table 13.2 Biographical abstract of females of groups J and N 1 January 1973–30 July 1975

Name	Mother	Genealogy	Cohort	Birth group	Death date
031	Unknown	031	55	Unknown	1–12 Apr 1973
XJ	031	031	63	A	
WF	031	031	64	A	
A6	031	031	65	J	
Z1	XJ	031	67	J	
9H	JP	031	68	J	
7H	031	031	68	J	
240	031	031	69	J	1 Apr 1974
238	WF	031	69	J	
375	XJ	031	70	J	
320	031	031	70	J	
420	031	031	71	J	
417	XJ	031	71	J	
416	Z1	031	71	J	
LA	S009	092	61	A	
XQ	S009	092	63	A	14 Jun 1973
TN	092	092	62	A	
Z4	XQ	092	67	J	
9K	TN	092	68	J	
8K	XQ	092	68	J	
327	TN	092	70	J	
458	Z4	092	71	J	
447	XQ	092	71	J	

13.3.2.1 Stage 1: January–August 1973 (Fig. 13.1a, b)

Females: The agonistic interactions among the females are tabulated in Table 13.4. (1) As Varley (unpublished) found, the older females of 092's genealogy were dominant to the females of 031's genealogy. Within each genealogy, younger adult sisters were dominant to older adult sisters, as predicted by other studies (Sade 1972; Datta 1983). (2) However, 9H was higher ranking than her predicted status. 9H should have ranked below XJ and Z1 because 9H's mother was the elder sister of XJ (Sade et al. 1985, plate 43; Datta 1988). Here 9H is placed in the matrices at her actual rather than her predicted rank. (3) The ranks of the sisters 7H, 240, 320, and 420 vary from the rule over the course of the study, as discussed below. (4) TN is the highest-ranking female and was dominant to her adult son 248 as well as to several non-natal males.

Non-natal males: Males living apart from any heterosexual group, whether solitary or in small all-male groups, are referred to as extra-group males (EGMs). (1) Male 056 was still with group J nearly 9 years after it formed but lost rank to WK (see below). He received much more grooming from females of 031's genealogy than from females of 092's genealogy. (2) OV joined group J by August 1972, leaving the

Table 13.3 Biographical abstract of males of groups J and N 1 January 1973–30 July 1975

Name	Mother	Genealogy	Cohort	Birth group	Death date
OV	004	004	65	F	
UD	031	031	62	A	
249	JP	031	69	J	
459	A6	031	71	J	
056	Unknown	056	55	Unknown	
JS	065	065	61	F	
TD	065	065	62	F	2 Nov 1973
WK	065	065	63	F	
7P	065	065	68	F	
JG	EK	073	61	F	
D7	EK	073	65	F	
FD	EK	073	64	F	
8T	YB	073	68	F	
303	OT	073	69	F	
304	WX	076	69	F	
381	WX	076	70	F	
JV	R010	081	61	A	
M6	AS	090	66	A	
F7	092	092	65	J	10 Oct 1973
K7	TN	092	66	J	
7E	092	092	68	J	
248	TN	092	69	J	
319	XQ	092	70	J	
448	TN	092	71	J	
418	LA	092	71	J	
LT	CG	DM	61	I	
ZW	CP	DM	64	I	

second-ranking genealogy of group F. (3) TD joined group J from group F in September 1972, and shortly after, his brother WK, the dominant male of group F, also joined. WK became the new high-ranking male within group J. TD's status with respect to 056 remained unknown. Their older brother JS, also once the dominant male of group F, joined group J from EGM status in March 1973. (4) JG joined only briefly by March 1973 from group I but left for group L within a month. His younger brother D7 also joined by March, from EGM status. (5) FD, another brother, joined group J from EGM status by June 1973. Groups L and J were often near each other. JG's only connection in the grooming network was to FD, and occurred after he had left group J. 8T, who was FD's, D7's, and JG's sister's son, joined group J by August 1973. (6) 304 joined group J by April 1973 after several migrations during the past year. His younger brother, 381, joined group J by May 1973, after several months in EGM status. Figure 13.1a shows that these sets of brothers and former associates from group F form a loose grouping on the periphery of the grooming network, and through TD and OV to WK and the center of group J. 056 is positioned among the females with whom he associated when the group formed.
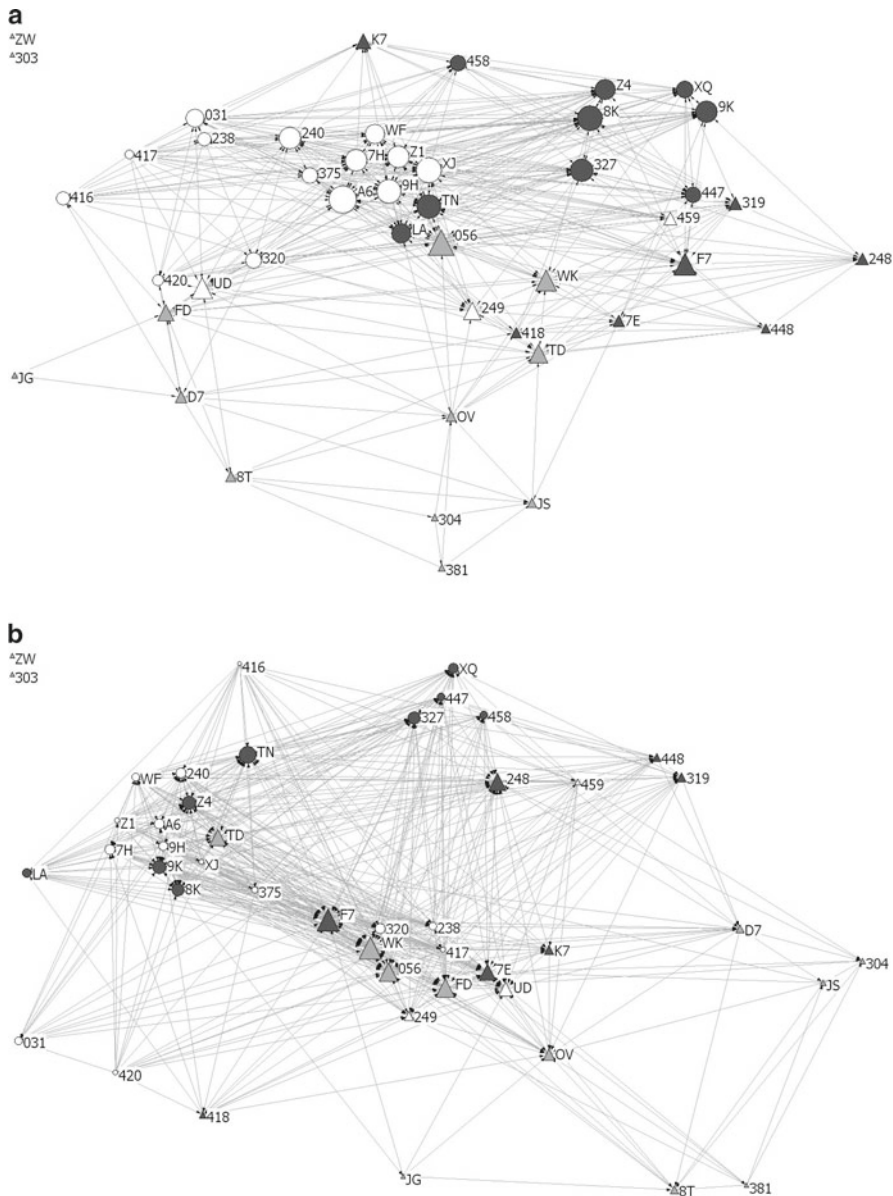
Fig. 13.1 Group J grooming and agonistic networks January 1–August 31, 1973. See text for explanation of symbols. *Observers*: K. Cushing January 1–August 16; K. Wilson August 17–30. (**a**) Group J grooming network 1 Jan 1973–31 Aug 1973. (**b**) Group J agonistic network 1 Jan 1973–31 Aug 1973

Table 13.4 Agonistic interactions of group J females January 1 through August 31, 1973

	TN	32	9K	XQ	44	8K	Z4	45	LA	03	32	24	7H	42	A6	WF	23	9H	XJ	41	37	Z1	41
TN		14	10	6	3	12	8	2	3	0	4	4	5	1	3	5	0	13	5	0	4	19	2
327	0		10	2	3	12	3	1	1	0	8	2	0	0	3	2	3	2	0	0	4	5	0
9K	0	0		2	3	18	9	0	2	5	3	6	4	0	5	6	3	10	5	2	6	9	0
XQ	0	0	0		5	2	0	1	0	0	1	0	1	0	4	1	1	0	0	0	1	4	0
447	0	0	0	0		2	0	3	0	0	5	0	0	1	0	0	2	0	0	4	0	2	0
8K	0	0	0	0	0		4	3	1	0	6	8	5	1	3	3	3	6	2	2	4	5	2
Z4	0	0	0	0	5	0		2	1	2	3	5	8	4	3	3	1	6	2	5	3	6	4
458	0	0	0	0	0	0	0		0	0	4	0	0	0	0	0	2	0	0	2	1	1	0
LA	0	0	0	0	0	0	0	1		0	0	0	2	0	3	0	0	1	3	2	2	5	1
031	0	0	0	0	0	0	0	0	0		1	1	1	1	0	3	0	1	0	0	1	0	0
320	0	0	0	0	0	0	0	0	0	0		8	5	2	1	0	3	2	0	5	5	1	1
240	0	0	0	0	1	0	0	0	0	0	0		10	0	4	4	10	9	2	2	7	7	1
7H	0	0	0	0	0	0	0	0	0	0	0	0		2	6	1	2	7	2	2	6	4	1
420	0	0	0	0	0	0	0	0	0	0	0	0	0		0	0	1	0	0	2	0	0	0
A6	0	0	0	0	0	0	0	0	0	0	1	0	0	0		1	10	3	3	0	3	7	2
WF	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0		5	4	4	1	0	4	0
238	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0		3	2	1	1	4	3
9H	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0		2	7	11	11	4
XJ	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		1	3	1	0
417	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		12	0	3
375	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0		12	1
Z1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0		0
416	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	

Row monkey is the dominant, column monkey is the subordinate. Some column labels are truncated. Observations by Kathy Cushing January 1–August 16, 1973 and by Kathy Wilson August 17 through August 31, 1973

Natal males: (1) TN's son K7 had migrated from group J to group H in September 1972, to EGM status in October, and back to group J in November 1972. Over the next year, he moved back and forth between J, EGM, and N (after the division), and finally to group F in October 1974. As son of the dominant female, he would be predicted to become the dominant male of group J (Chapais 1983; Koford 1963; Sade et al. 1988). Perhaps the sudden arrival of TD and WK prevented that. By 1973, he was subordinate to his younger brother 248. His most frequent grooming episodes while with group J in 1973 were with his mother TN and sister 9K. During this interval, he was still subordinate to his mother TN, as was his brother 248. (2) TN's younger brothers 7E and F7 were well connected in the grooming and agonistic networks, especially F7. F7 ranked just below 056 in agonistic status, and his central position played a role in the division described below. Like 056, he received more grooming from females of 031's genealogy than from females of his own. (3) UD, a male of 031's genealogy, had migrated to other groups 5 years before he rejoined group J in April 1972. He was mostly connected to the females of 031's genealogy. His most frequent grooming partners were his sisters 7H and 240 (this is obscured by XJ's position in the MDS output but is clear from the grooming matrix (not shown). (4) XQ, the mother of 319, died in June 1973. 319 was located more with the males on the periphery than with his sisters in the interaction networks, but his elder sister 8K groomed him twice as much as did 249, his next most frequent grooming partner. (5) 249 and UD moved to group M by September. The agonistic interactions among all the males during this period are tabulated in Table 13.5.

Table 13.5 Agonistic interactions of group J males January 1 through August 31, 1973

	WK	TD	05	F7	24	7E	UD	FD	8T	OV	31	24	JS	K7	30	JG	D7	ZW	30	38	44	41	45
WK	0	3	10	15	8	4	2	2	1	5	0	5	0	2	0	0	2	0	0	0	2	1	0
TD	0	0	0	2	3	3	0	0	0	0	0	0	1	0	0	0	0	0	0	0	3	0	3
056	0	0	0	4	0	1	2	3	1	0	1	1	0	1	0	0	0	0	0	0	1	0	0
F7	0	0	0	0	2	6	4	8	0	3	7	2	0	0	0	1	1	0	0	0	3	5	2
248	0	0	0	0	0	2	0	2	0	3	5	3	0	1	2	0	1	0	0	0	2	0	2
7E	0	0	0	0	0	0	2	4	0	2	6	8	2	0	1	0	0	0	0	1	0	3	4
UD	0	0	0	0	0	0	0	3	2	2	1	1	0	2	0	1	1	0	0	0	0	2	2
FD	0	0	0	0	2	1	0	0	3	5	0	3	0	5	1	0	1	0	0	0	1	0	0
8T	0	0	0	0	0	0	0	0	0	2	0	0	1	0	2	2	4	0	0	2	0	0	0
OV	0	0	0	0	0	0	0	0	1	0	1	8	1	2	0	1	3	0	0	2	0	1	2
319	0	0	0	0	0	1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1	0	3
249	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	2	0	1	3
JS	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	6	0	0	2	0	0	0	0
K7	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	1
304	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	1	0	0	2
JG	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
D7	0	0	0	0	0	0	0	0	0	1	0	0	3	0	0	0	0	0	0	0	1	0	0
ZW	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
303	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
381	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
448	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
418	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
459	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Row monkey is the dominant, column monkey is the subordinate. Some column labels are truncated. Observations by Kathy Cushing January 1–August 16, 1973 and by Kathy Wilson August 17 through August 31, 1973

13.3.2.2 Stage 2: September–October 1973 (Fig. 13.2a, b)

Several males who migrated are still shown on the interaction networks because of an occasional continued interaction. During this interval, two subgroups formed within group J. This was first recognized in the field by consistent spatial separation and independence of movement. The division is apparent in Fig. 13.2a, in fact more apparent than to observers in the field at the time. Both the grooming and agonistic networks show the separation of the two genealogies. (1) Males WK, TD, and OV are more connected to 092's genealogy, while 056, F7, 7E, and K7 are even more connected to 031's genealogy, the latter three moving with this subgroup rather than with their relatives in the other subgroup. Field-note entries such as "the monkeys who have been following 056," "the monkeys who have been moving with F7," and "WK's subgroup" are common. Eventually, the name "J" was retained for the part centered on WK and 092's genealogy and "N" for the other part. Some shifting back and forth between groups occurred, especially by the sisters A6, 7H, 320, and 420, all of the highest-ranking family within 031's genealogy. (2) 056, however, was seen more and more with group F during September 1973 and by October had essentially migrated. In late September, F7 was seriously wounded (assailant unknown), became more and more solitary, and died on 10 October. Also, by October K7 had left group J and again was of EGM status. 7E moved to group F and D7 to EGM status by October. These departures left subgroup "N" with no adult males.

a

b

Fig. 13.2 Group J grooming and agonistic networks September 1–October 31, 1973. See text for explanation of symbols. Group J grooming and agonistic networks. *Observers*: J. DeRousseau August 30–September 11, 1973; Donald Sade September 12–October 28, 1973. (**a**) Group J grooming network 1 September–31 October 1973. (**b**) Group J agonistic network 1 September–31 October 1973

There still were some grooming and agonistic interactions between the subgroups, as well as some mating activity, especially around the feeding stations. (3) Meanwhile, several males joined the other subgroup "J" and others departed: 303 and ZW joined subgroup J, while 381, 8T, FD, and JS moved to group L. (4) Several interactions between the subgroups "N" and "J" were seen that exactly resembled the aggressive encounters between established social groups, as described in detail by Hausfater (1972). One example follows from D. Sade's field notes:

> 15Sep73 1631 hours
>   … 248 suddenly peers south from inside corral, then stalks bob-peering south towards White House. I see F7, 416, 9H and other group N monkeys between White House and Lower Corral. 248, 304, 319 20 – 50 feet apart from each other but more or less in line stalk toward F7 and others. Group N immediately grows compact, moves quickly south to woods behind White House. I follow group N. It was a perfectly typical group withdrawal, just as if the two groups were completely distinct.

(5) In late October, TD was seriously wounded (assailant unknown), disappeared, and was found dead on November 2, 1973. This left subgroup J with only males WK, OV, and 4-year-old 248, still subordinate to his mother TN, as was OV.

13.3.2.3   Stage 3: October 25–December 6, 1973 (Fig. 13.3a, b)

By November 1973, the two groups were sufficiently distinct that in the census they were named J (092's genealogy and associate males) and N (031's genealogy and associate males). Group N soon acquired new males, all from group F: (1) LT was seen with female Z1 on September 22, and by early October was clearly in consort with her. By October 12, 056 was mostly with group F, but on October 12, when LT and Z1 were near group F, 056 threatened LT, who cowered, grimaced, and moved aside: LT did not force 056 out of group N. After this date, LT was regularly with group N. (2) JV was seen mounting 375 on October 30 and, although he was chased away by other group N females, he stayed in consort with 375 into early November and remained with group N after that. (3) M6 remained within group F through September and October but was noted in several agonistic interactions with monkeys from both groups N and J. On November 6, M6 approached Z1, XJ, and 320, who responded with subordination displays. From then on, M6 was regularly with group N. (4) 7P, the dominant male of group F, lost rank to an older, non-natal male (E2) August 14, 1973, but remained with group F and was active in mating. E2 died on September 29, leaving 7P again the dominant male of group F. On November 7, however, 7P was seen following 375 of group N and was in consort with her for several days. On November 12, 7P copulated with XJ and on November 13 with 416. After that, 7P remained with group N. (5) These four males became the central adult males of group N. The agonistic ranking was 7P > M6 > JV > LT, the inverse of the order in which they joined group N, and contrary to the usual observation that non-natal males rank in order of joining a new group. In this case, their relative positions may have been retained from their ranking within group F. (6) 303 moved from group F to J by October, to low rank and peripheral status. His only connection
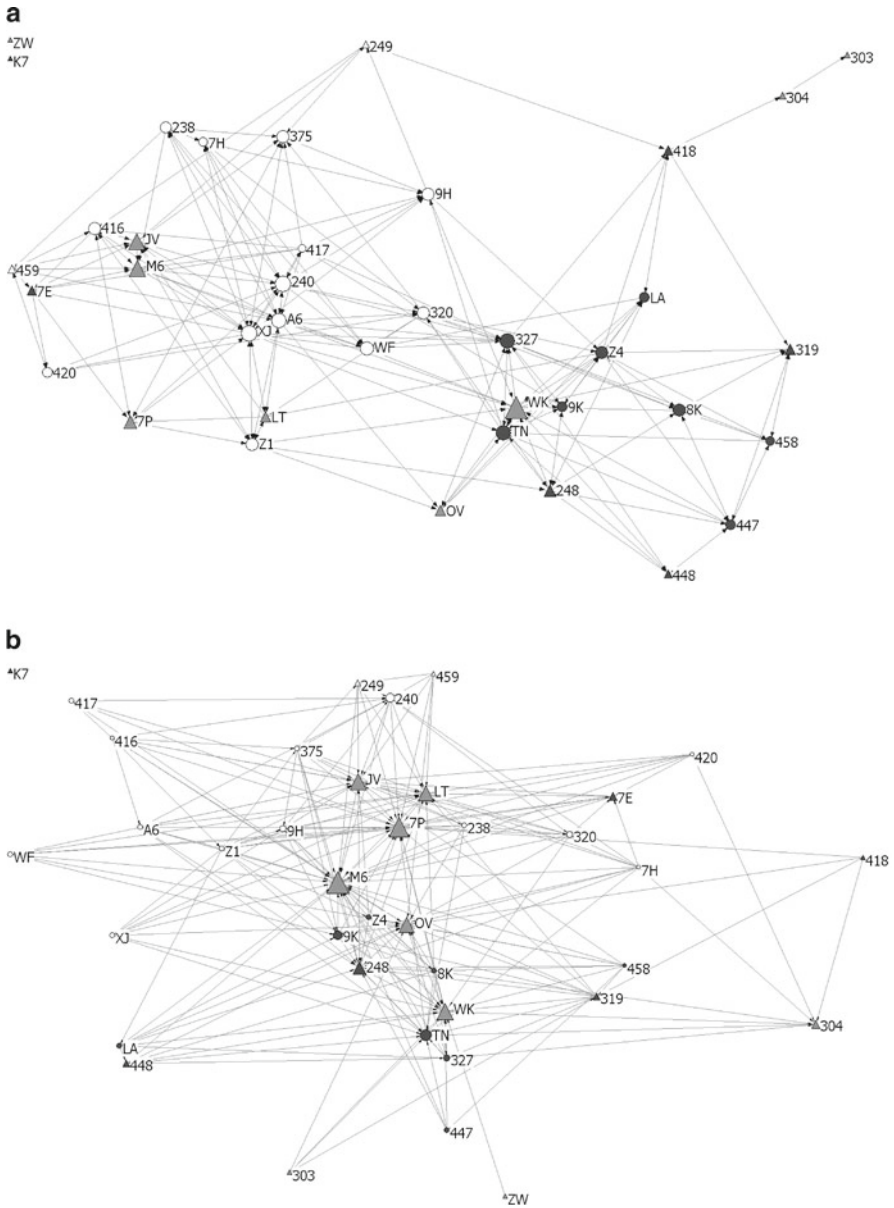
Fig. 13.3 Groups J and N grooming and agonistic networks October 25–December 6, 1973. See text for explanation of symbols. *Observer*: Peter Cushing. (**a**) Groups J and N grooming network 25 October 1973–6 December 1973. (**b**) Groups J and N agonistic network 25 October 1973–6 December 1973

in the grooming network was to 304, an same-aged peer from group F who had migrated earlier. (7) By November 7E, TN's brother, had returned, but to group N, not to group J and his own relatives.

The grooming network (Fig. 13.3a) clearly shows the separation of the groups and the association with each of its respective males. Among the females within each group, the agonistic relations remained unchanged. Between-group grooming and agonistic exchanges continue. Females of group J were still dominant in all agonistic interactions with females of group N save one: 8K cowered to 9H in one interaction. Many of the between-group interactions occurred near feeding stations.

Group N now wins most intergroup encounters (11 out of 12), which are typical of the interactions between established groups. An example follows from Peter Cushing's field notes:

> 30Nov73 1650 hours
> OV hoarse grunts at group N. JV, LT, 238, and others of group N hoarse grunt at group J. Group J runs into mangroves. Group N chases group J. Later, LA, 9K, 319, 8K, 248, Z4, and others of group J line fight with LT, JV, WF, 238, 249, 7E, 320, and others of group N, including occasionally 7P, 240, M6, and 7H. Fight lasts for approximately 16 minutes, during which group J is pushed all the way through the north mangroves almost to the isthmus. [Note that 7E actively participates against his relatives in the other group.]

13.3.2.4 Stage 4: December 7, 1973–March 13, 1974 (Fig. 13.4a, b)

During this interval, the separation between the groups in the interaction networks was at its greatest. K7 rejoined group N by January 1974. No grooming or dyadic agonistic episodes were seen between the females of the two genealogies. A few grooming episodes show connections between three males of group N and three males of group J, including between K7 in group N and his brother 248 in group J. These are the only between-group grooming ties.

The agonistic network shows much more connection between the two groups, prominently through the males M6, JV, LT, K7, and 7E, but not 7P, the dominant male. Some of the interactions occurred when the groups were close together, such as at feeding stations. Most were initiated by a male of group N approaching a male, including WK, or less often a female, of group J. In most instances, the group N male was dominant. Although few in comparison to intra-group agonistic interactions, these interactions may have established the connections upon which the subsequent fusion of the groups was based. In all intergroup encounters during this period, group N displaced group J. K7 and 7E were both active against their relatives in group J. During this period, TN first grimaced and cowered to her son K7. TN remained dominant to her son 248 and to male OV within group J.

No change in agonistic status among the females of group J occurred during this period. Within group N, however, 420 rose in rank over her elder sister 7H, as predicted by the usual rule. But in contrast, 240, who had been subordinate to 320 as predicted, unexpectedly reversed their agonistic status in a lengthy series of interactions.
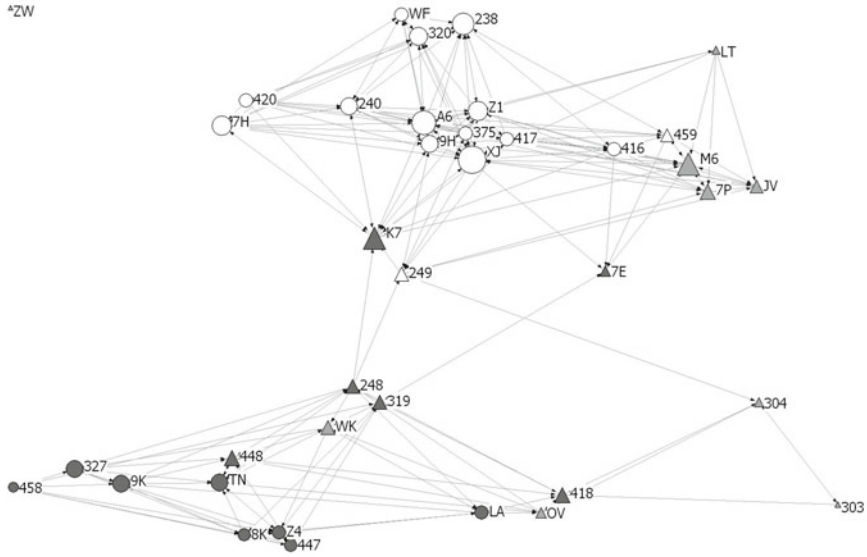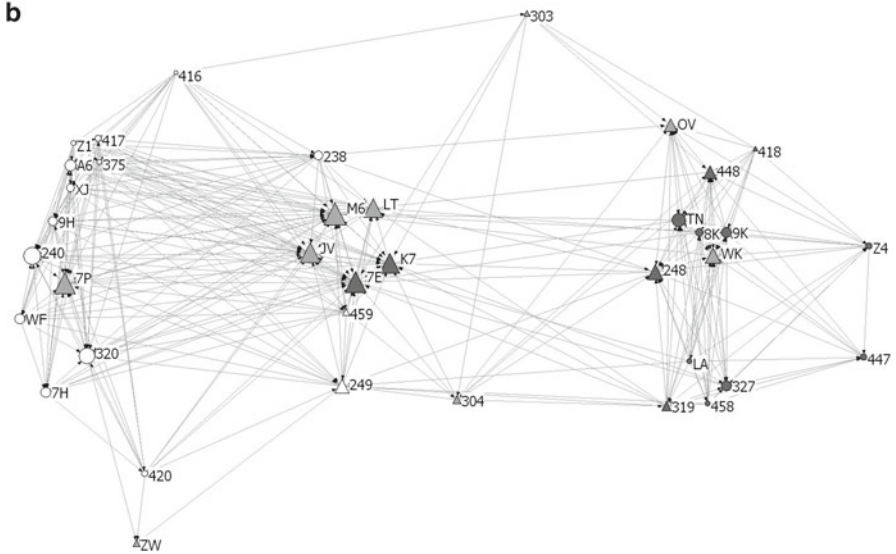
Fig. 13.4 Groups J and N grooming and agonistic networks December 7, 1973–March 13, 1974. See text for explanation of symbols. *Observer*: Peter Cushing. (**a**) Groups J and N grooming network 7 December 1973–13 March 1974. (**b**) Groups J and N agonistic network 7 December 1973–13 March 1974

320 had been dominant female of group N since it formed. Unfortunately, 240 died early during the next interval, terminating the history of this unusual case. These changes occurred a year after 031, the mother of these sisters, died. A more detailed study of the records of this event might suggest its cause.

13.3.2.5 Stage 5: March 14–July 23, 1974 (Fig. 13.5a, b)

The first reversal of agonistic status between the females of the two genealogies was a single episode in which 8K displayed subordination to 9H on November 22, 1973. No further case of a dyadic reversal was seen until March 14, 1974, on which date TN approached 9H and cowered to her. Over the next 12 days TN was seen displaying subordination 17 times to formerly subordinate females of 031's genealogy.

Here are the descriptions from Peter Cushing's field notes of the first two instances:

14Mar74 0930 hours
… Group N approaches Upper Corral. Group J is at the Upper Corral. … At 0940 hours 9H carrying her infant and 555 [9H's infant of 1973 – DSS] approach TN and her infant. TN and 9H sit girn-grunting [a non-agonistic vocalization – DSS] at each other. Soon TN, carrying her infant, moves towards 555. 555 mews at TN. TN scans slightly towards 9H and cowers from 9H. Soon TN walks northeast out of view.

15Mar74 1705 hours
… TN carrying her infant approaches group N. TN approaches 7H and her infant and 490 [7H's 1972 infant – DSS], and sits about 3 feet from 7H. 7H glances towards TN. TN cowers from 7H. TN open-mouth- faces and head raises at 490. 7H groom's 7H's infant. TN sits scanning. Later, at 1712 hours 7H carrying her infant runs past TN and her infant, TN cowers from 7H. 7H runs out of sight. TN open mouth faces at 490. 490 cowers and jumps back from TN. 490 screams and scream-faces at TN. TN scans area. 555 sits touching K7 [TN's son – DSS].TN open mouth faces at 555. K7 glances towards TN. TN cowers from K7, and open-mouth-faces at 490. K7 looks away from TN. 490 screams and scream-faces at TN. TN glances towards 555. 555 fear-grimaces at TN. TN runs at 555 and bats 555 with hand. 555 cowers from TN and screams and scream-faces at TN. TN sits scanning rapidly.

These episodes show TN's approach, her spontaneous display of subordination to a former subordinate, followed (in the second episode) by her threats toward juveniles closely associated with the dominant in the interaction, an example of redirected aggression. There were no interventions in these episodes, although TN seemed to expect interference from her son, K7, in the second.

Over the next several months, the other females of 092's genealogy were seen displaying subordination in dyadic interactions with the females of 031's genealogy, showing that the agonistic status between the two groups had completely reversed (Table 13.6.) The only exception was that TN was still dominant to 416 until June 6, 1974, when 416 rose in rank above TN.

Within each genealogy, agonistic statuses among the females remained unchanged. 320 was again the dominant female, now of the entire group, following 240's death. TN remained dominant to her son, 248, and to male OV. Among the males, all the males of group N except 3-year-old 459 were now dominant to WK

Fig. 13.5 Groups J and N grooming and agonistic networks March 14–July 23, 1974. See text for explanation of symbols. *Observer*: Peter Cushing. (**a**) Groups J and N grooming network 14 March 1974–23 July 1974. (**b**) Groups J and N agonistic network 14 Mar 1974–23 July 1974

Table 13.6 Agonistic interactions of group J females July 2 1974 through July 30, 1975

	32	42	7H	A6	WF	23	9H	XJ	41	37	Z1	41	TN	32	9K	44	8K	Z4	45	LA
320		21	34	6	14	8	6	6	4	3	3	1	1	0	0	1	1	1	1	0
420	0		7	2	2	3	3	0	7	1	0	3	5	1	0	0	1	0	1	0
7H	21	1		10	11	7	4	3	5	3	7	7	3	3	3	0	1	2	1	0
A6	0	0	0		0	1	2	0	1	1	0	3	5	1	0	2	2	2	1	0
WF	0	0	0	0		1	7	2	0	0	2	0	1	1	0	0	0	1	1	0
238	0	0	0	0	0		3	0	1	1	5	2	4	0	2	0	0	1	2	0
9H	0	0	0	0	0	0		6	8	3	6	8	1	2	0	2	2	1	1	0
XJ	0	0	0	0	0	0	0		0	5	3	2	0	1	1	0	0	1	1	2
417	0	0	0	0	0	0	1	0		5	5	1	3	0	1	0	3	1	1	0
375	0	0	0	0	0	0	0	0	0		8	2	12	6	2	0	3	2	1	1
Z1	0	0	0	0	0	0	0	0	0	0		4	6	1	3	0	4	1	1	0
416	0	0	0	0	0	0	0	0	0	0	0		5	1	1	4	1	3	6	0
TN	0	0	0	0	0	0	0	0	0	0	0	0		3	2	2	5	5	1	2
327	0	0	0	0	0	0	0	0	0	0	0	0	0		1	4	3	0	3	1
9K	0	0	0	0	0	0	0	0	0	0	0	0	0	0		2	2	4	2	0
447	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		4	4	4	0
8K	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		1	4	0
Z4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		3	0
458	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		0
LA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	

Row monkey is the dominant, column monkey is the subordinate. Some column labels are truncated. Observations by Terry Morse July 2 through December 20, 1974, by Kathy Cushing January 1 through July 30, 1975

Table 13.7 Agonistic interactions of group J and group N males March 14 through July 23, 1974

	7P	M6	JV	LT	7E	K7	24	45	WK	24	OV	31	30	30	44	41
7P		0	4	3	1	2	1	2	4	0	1	0	1	1	0	0
M6	0		1	2	4	1	4	7	14	2	4	0	0	0	1	0
JV	0	0		7	1	7	0	3	4	1	3	0	0	0	1	1
LT	0	0	0		2	2	3	7	5	1	4	1	0	0	1	0
7E	0	0	0	0		1	5	2	3	4	1	2	0	0	4	0
K7	0	0	0	0	0		2	2	12	6	2	0	1	1	1	2
249	0	0	0	0	0	0		4	4	5	2	1	0	0	5	1
459	0	0	0	0	0	0	0		0	0	0	0	0	1	0	0
WK	0	0	0	0	0	0	0	1		20	4	2	1	1	11	0
248	0	0	0	0	0	0	0	0	0		16	7	2	3	2	2
OV	0	0	0	0	0	0	0	0	0	0		0	0	0	0	4
319	0	0	0	0	0	0	0	0	0	0	0		2	1	0	4
304	0	0	0	0	0	0	0	0	0	0	0	0		2	0	0
303	0	0	0	0	0	0	0	0	0	0	0	0	0		0	0
448	0	0	0	0	0	0	0	0	0	0	0	1	0	0		3
418	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	

Row monkey is the dominant, column monkey is the subordinate. Some column labels are truncated. Observations by Peter Cushing

and the other males of group J (Table 13.7.) The ranking of the former males of group J remain unchanged among themselves. By July 1, 1974 the two groups had merged sufficiently for the census to consider them a single group, for which the name group J was retained.

13.3.2.6 Stage 6: July 2, 1974–July 30, 1975 (Fig. 13.6a, b)

Four males that joined peripherally during this interval are omitted: D2, 309, 407, and 414. For information on these, consult Sade et al. (1985). Following the fusion of the two groups, there were only a few noteworthy changes: (1) 418 and 319 become EGM by August; (2) 248 and 7E move to group M by October, but 248 returns to group J again by November 1974; and 248 remained subordinate to his mother TN following his return. (3) Although WK did not lose rank further, he became marginal in both the grooming and agonistic networks and by September 1974 had moved to group M. Subsequently, he vacillated etween EGM status, group L, and group J without ever gaining prominence again. (4) K7 moved to group F by October 1974.

Between and within the two genealogies, the agonistic relations remained the same, except among the sisters 7H, 320, and 420. Beginning on September 23, 1974, 7H becomes dominant to 320 in an extended series of interactions. On October 10, 420 cowered to 7H.

However, by January 1975, 320 was again dominant to 7H; 420 later also reversed her status with 7H; and 420 did not rise in rank above 320 during the study. Datta (1983) later observed the same ranking among these sisters. This case deserves a more detailed analysis beyond the scope of the present chapter.

13.3.3 Removal and Return of a Dominant Male of Group I

The strength and specificity of attachment of even adult males to their current social group is evaluated by a study of physical growth in 1960 through 1961, an opportunity to monitor the effects of removal of monkeys from their social groups, retaining them for several days, then releasing them and observing any resulting changes in affiliation or status. Upon release, individuals invariably returned to the group from which they had been removed, often calling and clearly searching until locating it. Usually, an intense period of vocalization and grooming followed, but no change in affiliation or status was observed (Sade 1966).

Jim Loy and Donald Sade wondered what would be the effect on group affiliation and agonistic status of removing a dominant male for a longer period. Would he return to his former group and status, or return at a lower rank, or migrate? The dominant male of group I in early 1968 was 096. He was a 13- or 14-year-old male of unknown parentage. He was with group G when it split into groups H and I in 1960 and remained with group I. The second-ranking male was LT (yes, the same LT discussed above), who was natal to group I. Loy trapped 096 on February 3, 1968 and placed him in a large retraining cage where he was held until March 19, 1968 when he was released, as described in Sade's field notes:

> 19Mar68 1624 hours
> I release 096, he runs from retaining cage, climbs half way up palm tree, climbs down, runs to mangrove swamp and disappears.
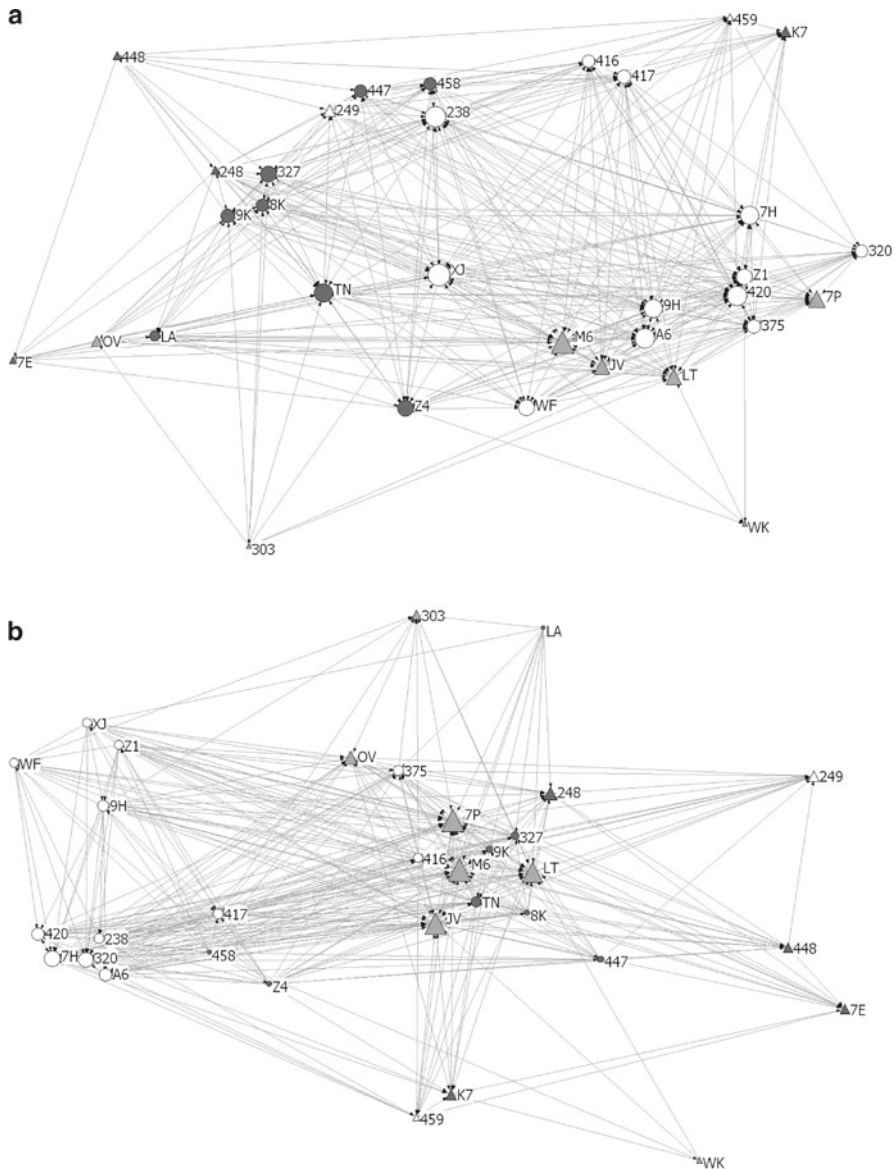
Fig. 13.6 Group J grooming and agonistic networks July 2, 1974–July 30, 1975. See text for explanation of symbols. *Observers*: Terry Morse July 2–December 20, 1974; Kathy Cushing January 1–July 30, 1975. (**a**) Group J grooming network 2 July 1974–30 July 1975. (**b**) Group J agonistic network 2 July 1974–30 July 1975

1700 hours

I return to group I …

1828 hours

[Group I is at] Catchment Point and East Cliffs [of Big Cay]. Considerable rapid hoarse grunting sound from group I. I see 096 stalk through group I, 096 grunting-open-mouth charges JG [the same JG discussed above –DSS]. LT grunting-open-mouth charges 096, 096 runs, LT follows: the chase is long but not particularly fast, from Catchment Point to shore under East Cliffs north to under Lab Point, then south to South-East Point. All of group I lope after chase, many vocalizing. …(096 followed LT during part of chase). On reaching South-East Point 096 was ahead, ran up cliffs alone ahead of LT. LT others moved up cliffs, 096 drops behind at 1836 hours. At one point during chase 096 sat calmly on the shore among group I monkeys, his hands folded, forearms resting on knees, then ran ahead as LT charged him and chase continued. At one point during chase 096 was sitting, LT ran toward him, then close past him, LT grunting-open-mouth facing ahead of 096. 096 cowered aside as LT charged past, then 096 ran grunting-open-mouth face at side of LT briefly. Then LT chases 096 again, but again slowly.

The impression during the record at the time was that the chase was more typical of the excitement when a monkey returns to the group rather than an aggressive encounter. The chase seemed more like an excited greeting ritual rather than an aggressive chase, particularly since neither LT nor the other monkeys tried to catch 096. Nevertheless, from then on, 096 was second ranking to LT. Margaret Varley (unpublished) observed group I in 1969 and 1970 and found that this status had persisted. Instead of migrating, 096 remained with group I until his death in February 1971. This was the only change in status following a removal and return that I documented.

13.3.4   Brain Lesion Studies

I do not advocate invasive experiments involving brain lesions at Cayo Santiago; yet one such study was done and should be mentioned here (Myers and Swett 1970; Myers et al. 1973) Several types of cortical ablations were performed, and the monkeys were released back onto Cayo Santiago after brief periods of recovery. Most of the animals disappeared or died shortly after release, before useful information could be acquired. The monkeys are listed in Sade et al. (1985). A few survived long enough for the authors to draw conclusion on the effects of the lesions. Two findings are relevant to the topic of this chapter: (1) Two females with reported bilateral anterior temporal lobectomies did not rejoin their social groups, but remained solitary, as did several monkeys with prefrontal cortical resections. (2) Two of the latter were females with infants and were observed to reject their infants completely while being held for recovery.

Opportunistic observations on the two monkeys with temporal lobectomies were recorded. In each case, it was witnessed by the author that they interacted briefly with monkeys of social groups other than their own or with humans. In each case, the operated monkeys responded to threat gestures with typical subordination displays: grimace and cower, the form, temporal patterning, orientation, and appearance in an

appropriate context seeming identical with the behavior of normal monkeys. In one individual, the intensity of the displays was so reduced that they were barely observable, although typical in pattern, as if the arousal of the motor engrams was partly suppressed. The communication system remained intact while the identity of the individual as indicated by attachment to social companions was destroyed. These studies suggest to me the possibility of isolating various neural components of the attachment processes discussed above, should advancing technology make that possible in a social context with noninvasive techniques.

13.4 Interpretation of Results

The events described above are here interpreted, not in terms of strategies, but in terms of identities. Although speculative, these interpretations could be the bases of further studies. Of the archetypical systems discussed above, the "passage stage," in which an identity is disrupted, or abandoned, and a new one established, is the least studied, and will be emphasized here.

13.4.1 Males

The loss of 056's established identity as dominant male of group J near the end of the mating season of 1972, when he lost rank to WK, precipitated the division of group J at the start of the following mating season, when rising testosterone levels reactivated the archetype of the passage stage, and he began to migrate from the group. The females of genealogy 031 followed him for a while, maintaining their close ties with him, while the females of 092's genealogy stayed with WK, with whom they had developed closer ties as shown by his position in the grooming network.

Berard et al. (1993, 1994) show that the relation of rank to reproductive success in males is not a simple one at Cayo Santiago. However, the departure of 056 makes no sense in terms of reproductive strategy: he departed the subgroup with the most females, in which there was little competition to join a group with many males in which he could only assume low status. Perhaps once activated, the passage stage requires a more radical rebuilding of identity than possible with long associates. (1) F7, brother of the dominant female TN, ranking just below 056, and still with his natal group years after the usual age of first migration, might have been expected to become dominant male but was prevented by the arrival of WK and TD. The frequent agonistic interactions between F7 and WK suggest targeting of this status, but F7 failed to achieve it. F7's frequent grooming associations with females of 031's genealogy may indicate the start of his migration from the natal group. 056's departure to group F left F7 as the dominant male of the subgroup N briefly before he died. (2) 7P also left his (natal) group after losing his established position as dominant male. The loss was temporary due the death of E2, but sufficiently disrupted

7P's identity that he left during the mating season, as did 056 (and WK later). (3) WK lost his established status as dominant male of group J when the groups N and J merged in March 1974, even though his status among the members of his subgroup remained unchanged. This was a sufficient disruption of his identity that when the mating season began, he migrated. (4) The history of the other males who joined group N at this time (LT, JV, and M6) has not yet been studied. However, they, and 7P, established their new identities as central males of group N through the heterosexual attachments of consort relations with females of that group. There may have been "friendships" among them within group F, and certainly they were linked by agonistic interactions. (5) As noted earlier, the males who joined at various times peripherally and with low rank tended to renew connections with siblings, other relatives, or "friends" from their natal group, sometimes after a hiatus of several years. This shows the persistence of the earliest established attachments despite the disruption of early relations through the passage stage. But these did not result in stable or persistent relations with the core of females of the group. (6) Note however, no grooming was seen between the brothers 7P and WK, even after the two groups merged. (7) The reconstruction of the individual's identity during the passage stage is most dramatically illustrated in intergroup encounters, when migrants defend their new group against members of their old, including their own relatives, as described above for 7E. (8) The return of 096 to group I after his release and the subsequent reestablishment of an agonistic relation with LT (albeit reversed) indicates the strength of the attachment between these two, as well as 096's attachment to group I. The fact that 096 did not migrate from group I following loss of rank, unlike the males in the examples given above, needs explanation. Loy (1971) referred to the cementing of attachments through agonistic interactions among unrelated males as "dominance bonding." This may be also the explanation as to why the association of 096 and LT persisted in spite of change of status. It is also presumed that the rank change was experimentally induced rather than resulting from changes in attitude originating within the individuals. Experimental manipulation of ranks (Chance et al. 1977; Chapais and Larose 1988; Marsden 1968) is very informative with regard to possibilities but does not necessarily mimic spontaneous changes as seen in normal groups. This matter merits more attention.

13.4.2   Females

The separation of the females of group J into their respective daughter groups, each with its associated males, follows the pattern described for several other group divisions at Cayo Santiago (Chepko-Sade and Sade 1979). Mothers and offspring, sisters, and more distant relatives, are nested sets of decreasing degree of attachment that underlie the coherent associations that we name a "group" ("network" is a better term: it suggests that the boundary of the group is a matter of degree).

The reversal of agonistic status between the two genealogies likely began in intergroup encounters during the period of maximum separation. The presence of

the new males in group N likely accounts for the displacement of group J in these encounters. Although intergroup encounters are usually not ended with displays of subordination, they likely established the expectation of defeat among the monkeys of group J and the expectation of victory among the monkeys of group N. Perhaps the process was similar to the way in which expectations of future rank are shaped among young juveniles, as described by Berman (1980).

The expectations were reinforced by dyadic agonistic interactions between the males of group N and both the males and females of group J. WK and TN, the dominant male and female of group J, respectively, were particularly targeted. In these interactions, the monkeys of group J were usually subordinate. Dyadic agonistic interactions between the females of the two groups came later as the groups began to merge.

TN, the dominant female of group J, initiated the merger by approaching females of group N. She displayed subordination to them without being threatened. Interventions in these interactions by other monkeys were not apparent. There were no contests over status, as would be indicated by doubtful outcomes, severe fighting, or periods during with the dominant and subordinate changed back and forth. Rather, the new identities had already become fixed, and now were being affirmed. After TN had shown subordination to a number of the females of 031's genealogy, her daughters and other female relatives began to do so also, as if simply following her into their new position in the reunited group. Gouzoules (1980) describes in detail the rise in rank of a female over the former dominant female in a group of Japanese monkeys. In this case, the subordinate female targeted the dominant, the reverse of the example of TN and 092's genealogy. Following her rise in rank, the other members of her genealogy followed her into new ranks above the former dominant genealogy. Ehardt and Bernstein (1985) also describe four reversals of rank between matrilines in a captive colony of rhesus monkeys. In these reversals, subordinate females targeted and rose above formerly dominant families. Interestingly, these authors report that interventions by high-ranking adult males had little influence.

Returning to the group J division: Following the merger of the two daughter groups, TN's son, K7, and her brother 7E, who had joined group N, were now her most frequent grooming partners among the males, and she was now subordinate to each of them. As discussed above, the agonistic ties between the new males of group N and several members of group J during the period of greatest separation, as well as the kinship ties between her and her son and brother, may have been the attraction that led to the merger.

The unusual dominance reversals between 240 and 320, and later between 7H and 320 probably had a complex cause. During the period of greatest separation, these three suddenly found themselves the top-ranking females of the group. When males suddenly become high ranking, they can go through a period of increased activity and exuberance that suggests a release from inhibition (D. Sade, unpublished observations). The females may have experienced a similar excitement. Kathy Cushing (unpublished) suggested that 240's recent consort with the new dominant male 7P may have played a role in her rise over 320. 7P was in consort

with 240 from November 28 through December 7, 1973, and again from December 30 through 31, 1973. The first observed display of subordination from 320 to 240 was on January 2, 1974. From Peter Cushing's field notes:

2Jan74 0939 hours
    240 approaches 320 and XJ. XJ cowers from 320 as 320 glances towards XJ. 7P runs at 320 and chases 320. I did not see 320 cower. XJ runs from area. 240 stands facing in the direction that XJ went. D. Sade says that 240 climbs tree. 320 climbs tree and approaches 240. 240 stares at 320. 320 cowers from 240. 240 grooms 320.

This was not an intervention on behalf of 240 against 320. But could the recent association with the dominant male and her recent sudden climb in rank have raised 240's self-esteem, while the attack by 7P on 320 may have lowered hers sufficiently to reverse the agonistic status between the two sisters?

During the next mating season, 7P was in consort with 7H from August 28 through September 10, 1974. 7H was first seen dominant to 320 September 23, 1974. In this case, there was no intervention, but 7P (with his eyes closed) was 3 ft away from where 320 was grooming 7H. 320 cowered at 7H when the latter moved suddenly, then grimaced when 7H shook a tree nearby (Terry Morse's field notes of September 23, 1974).

7P was in consort with 320 from November 14 through 25, 1974 and again from December 5 through 13, 1974. On December 16, 1974, Terry Morse saw 320 approach A6 who was grooming 7H. 7H turned away and grimaced and cowered at 320. A6 then groomed 320, who groomed 7H. After this episode, 7H remained subordinate to 320.

If 7P influenced these interactions, it was through indirectly affecting the relative self-esteem of these two sisters by his recent association with each, not through direct intervention in their agonistic interactions. A detailed look at every case of rise in rank of females might show whether association with a high-ranking male is a common feature.

13.5   Conclusions

The concepts adapted from evolutionary psychiatry and the terminology suggested above prove useful in directing attention to and interpreting aspects of rhesus monkey life history and social relations. They also suggest further studies:

Are attachments among siblings and those among nonrelatives derived from the same affectional archetype? Observations modeled on Berman's studies of mother–infant and peer relations might be directed at distinguishing the quality of these relations. If distinct qualities were found that were unique to sibling relations, absent from the relations between other peers, a distinction in archetype might be implied. Human patients with right hemisphere lesions suffering from Capgras syndrome can suffer delusions about the identity of intimate associates, places, and objects, while still able to normally recognize less familiar individuals (Feinberg 2001). This author suggests that the emotional attachments to close individuals depend on

limbic cortical connections separate from the circuits upon which recognition of individuals depends.

Does the quality of an individual's attachment to siblings reverberate into adult relations, as does the mother–infant relation (Count 1967; Sade 1968). Comparison of the history of relations of the eldest sibling, and especially the eldest daughter, with the history of relations of younger siblings might suggest contrasts. During the "passage stage" whom, if anyone, does the eldest daughter target, since she lacks an elder sister? If no one, are there consequences from the frustration of the underlying archetype?

The psychology of the "passage stage" in the life cycle deserves much more attention directed at the mechanisms underlying loss and reorganization of identity. Perhaps existing descriptions of changes in status could be examined from this point of view, as a start.

The role of interventions (Berman 1980; Chance et al. 1977; Datta 1983, 1988; Kaplan 1977, 1978; Marsden 1968; Walters 1980) in the acquisition of status should be carefully re-examined to suggest the mechanism through which interventions operate. My impression from the literature is that status acquisition is like a pool game, the balls driven from without, bouncing off one another until they fall into a hole. My impression from the monkeys, however, is that change in status originates within the self, rather than being imposed from without. Related to this is the issue, mentioned above, of how experimentally induced changes in status compare with spontaneous changes.

It is hoped that neuroscientists who are active in the study of human cognition and neuropathology would continue to devote some attention to the broader, more ancient, aspects of the self. Human self-consciousness is unique, yet nevertheless operates within and upon a more ancient set of constraints and potentials.

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