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SOCIAL RELATIONSHIPS IN WILD WHITE-FACED CAPUCHIN MONKEYS, *CEBUS CAPUCINUS*

by

Susan Emily Perry

A dissertation submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy
(Anthropology)
in The University of Michigan
1995

Doctoral Committee:

Professor Barbara Smuts, Chair
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For Joe

and Curmudgeon

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ACKNOWLEDGMENTS

I am grateful to the Costa Rican Servicio de Parques Naciónales and the Area de Conservación Tempisque for granting me permission to work in Lomas Barbudal Biological Reserve. In particular, Fernando Cortes and Juan Miguel Sánchez aided me by writing emergency letters to aid in the daunting process of becoming temporary residents of Costa Rica. They, along with ACT directors Wilfran Murillo and Esaú Chavez, and the numerous ACT staff, were patient with my inadequate Spanish during my early days in Costa Rica and kindly explained bureaucratic procedures to me in slow Spanish until I understood what I needed to do. The park guards, particularly Carlos, Freddy and Ania, were amiable and helpful.

Funding for my graduate training at The University of Michigan was provided by a National Science Foundation graduate fellowship, two semesters of TA-ships from the Department of Anthropology, a Rackham Research Partnership Grant (with Barb Smuts), a Rackham predoctoral fellowship, a Rackham one-term dissertation grant, and a block grant. Funding for my research was provided by the EHB program, two Sigma Xi grants, Rackham discretionary funds, a Rackham dissertation improvement grant, a National Geographic Society grant, two L.S.B. Leakey Foundation grants, a University of Michigan Alumnae Society scholarship, and NSF awards (to Barb Smuts and John Mitani).

The University of Michigan's Evolution and Human Behavior Program provided a Utopian atmosphere for my graduate training. The EHB offices, lounge, and computer room provided much-needed work space and were a meeting place for everyone interested in the evolutionary study of social behavior. At all hours of the day and night, graduate

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students and postdocs from the biology, anthropology, and psychology departments were available and eager to discuss theory and methodology problems, listen to practice talks, comment on manuscripts, or swap tales about their study animals. The daily "Lab-O" lunches, frequent EHB brownbag discussions, evening "BarBLabs," the "Darwin Drinking Club," tea time with the British behavioral ecologists, and Café time with the New Yorkers all contributed to my graduate education by exposing me to methods and theories that I would never have encountered in my anthropology courses and were the starting points of numerous friendships. Among the EHB people who provided friendship and inspiration over the years are Dick Alexander, Kate Baker, Laura Betzig, Monique Borgerhoff Mulder, Kari Brandt, Cary Anne Cadman, Tim Caro, Rich Connor, Becky Dowhan, Anne Goldizen, Paula Gros, Julie Gros-Louis, David Gubernick, Alisa Harrigan, Anne Heise, Kim Hill, Warren Holmes, Magdalena Hurtado, Doug Jones, Charles N.W. Keckler, Bobbi Low, Joe Macedonia, Janet Mann, Jill Mateo, Susan McDonald Black, Anne McGuire, John Mitani, Amy Parish, John Pepper, Nancy Peters, Andrew Richards, Jim Rieger, Lars Rodseth, Dan Sellen, Daniela Sieff, Cyndy Sims Parr, Andy Sincoff, Laura Sirot, Holly Smith, Rachel Smolker, Barb Smuts, Craig Stanford, Bev Strassman, Kyle Summers, Michelle Tomaszycki, Paul Turke, John Watanabe, David Watts, Samantha Weber, and Richard Wrangham.

Doug Jones, Barbara Walker, Shelley Smith, and Daniela Sieff were excellent housemates and provided emotional support during some of my more trying moments in graduate school. Susan McDonald and Kurt Black, Becky Dowhan, Julie Gros-Louis, Gamma Alpha Scientific Fraternity, Alisa Harrigan, Janet and Mazi Mann, Nancy Peters, Lars Rodseth, Cyndy Sims Parr, Laura Sirot, Rachel Smolker, and Barb Smuts have frequently provided me with temporary lodging between field seasons, stored all my earthly possessions in their homes for extended periods of time, helped me move from one apartment to another, and/or shuttled me to the airport on numerous occasions. Gillian Haines, Richard Lesure, Roark Miller, Steve Parr, Songy Sohn, Dave and Naomi Tracer,

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and Barbara Walker provided friendship and various forms of assistance over the years, and served as my connection to life outside the walls of EHB. Liz Coscia, my daily "email buddy," shared with me every detail of the trials of graduate school from the day when we co-authored our first conference paper as undergraduates at Washington University, to the final stages of dissertation write-up at our respective universities.

Judy Maas (EHB administrative assistant) and the numerous staff of the anthropology department of University of Michigan -- particularly Margie Greenman and Debra Graddick -- guided me through the daunting bureaucracy of registration, grant applications, and financial aid applications during my eight years at Michigan. I am particularly indebted to Michelle Tomaszycki, who, with the help of Nancy Peters, solved the majority of the bureaucratic problems that arose during my final year, when I was living in Los Angeles. The staff of the UCLA Department of Anthropology were extremely kind and helpful in providing me with office space and logistical aid during the writing of my dissertation. Several members of the UCLA anthropology department helped make UCLA a "home away from home" while I was completing my dissertation, by providing friendship and/or commenting on my work: Rob Boyd, Betsey Caldor, Lynne Fairbanks, Melissa Gerald, Jake Lusis, Marguerete Mehrabian, Monica Olsen, Tom and Wahida Plummer, and Joan Silk.

Data transcription and computer entry of data are unquestionably the two most excruciating phases of behavioral research, and I was delighted to have assistance in both of these tasks. Laura Sirot nobly suffered through 3 notebooks of transcription on my behalf. Meta Landys, Sarah Newman, and Michelle Tomaszycki all aided me with the only slightly less odious task of computerizing the data. Barb Smuts provided the funding necessary to hire research assistants for these tasks. Nancy Peters jollied me out of many a "transcription depression" by distracting me with her phenomenal silliness, and it is likely that I would have gone insane without the aid of her remarkable sense of humor.

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I am exceedingly grateful to all my committee members for being so cooperative at every stage of my dissertation work, and in particular for their willingness to give me rapid feedback during my frenzied final months of write-up while I was living in Los Angeles.

Barb Smuts has been a source of inspiration to me ever since my undergraduate days, when her book *Sex and Friendship in Baboons* caused me to choose a career studying social relationships in nonhuman primates. Barb's course, "Behavioral Biology of Women," was my first exposure to primate sociobiology and gender issues, and was therefore the most influential course I have taken. Whereas most scientists seek to stay in the mainstream, Barb is always looking outside the discipline for new insights. I am continually impressed by her ability to cut across interdisciplinary boundaries, to integrate in innovative and profound ways ideas from sources as diverse as evolutionary biology, feminism, and pop psychology. Throughout my graduate career, Barb has been an ideal advisor, giving me free rein to choose my own research topics. I appreciate the effort she made to visit me in the field and meet my monkeys in person; this shared experience allowed her to fully enjoy the endless stream of monkey stories with which I bombarded her upon my return. Another extremely important way in which Barb shaped my life is by introducing me to my husband, Joe Manson. If she had not assigned us to be officemates during my first semester of graduate school, the course of my life might have been quite different.

John Mitani gave me excellent grant-writing tips during his first year at Michigan and encouraged me to pay more attention to vocal behavior. Both he and Barb loaned me sound-recording equipment to use in the field, and John helped me do some preliminary analyses of acoustic data during my visit from the field in 1992, which sharpened my ear to the subtleties of capuchin vocalizations in the remainder of my fieldwork. John also contributed funds to vehicle maintenance in the field, which were absolutely essential but could not be covered by other grants. John gave me prompt and thorough feedback on all of my dissertation chapters, as well as advice on how to convert chapters to publications. I

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deeply appreciate John's open-door policy for advising graduate students, which permitted us to pester him at any time of day. I hope we didn't abuse the privilege. I am also grateful to John for hosting some of the most memorable parties at U of M. Sorry about the rubber bands.

Warren Holmes has been generous with his time throughout my graduate career, giving me prompt and thorough comments on all of my dissertation chapters, as well as grant proposals and manuscripts. He has always encouraged methodological rigor and has done his best to steer me away from primate-centrism. The humorous remarks which he sprinkled throughout his comments on my thesis made the process of revising it much more enjoyable.

Bobbi Low saved the day by joining my committee at the last minute to replace Kim Hill when he left Michigan. I deeply appreciate her willingness to take on yet another major time commitment when her schedule was already more hectic than seemed humanly possible. Her enthusiasm about my research during lunchtime chats and her cheery email messages improved my morale considerably.

Although he was not officially on my committee, Frans de Waal gave me helpful comments on some chapters and has been very supportive of my research. I particularly appreciate his permission to let me visit his capuchin colony in 1990. This experience was helpful to me in designing my ethogram and methods prior to fieldwork.

I am indebted to my mother, Linda Perry, for encouraging all of my eccentric interests and career plans over the years. Because she never pressured me to be a "normal child," and because she devoted endless hours to bring together odd children with interests similar to my own, I was a happy nerd throughout childhood. I appreciate the time she has taken to meet all of my monkeys in person (both at Cayo Santiago and Lomas Barbudal), go hiking in all of my favorite habitats, and read all of my favorite books. She, in turn, has taught me to share her passion for playing chamber music, and this hobby has been an outlet for me throughout graduate school. The astonishing speed with which my mom

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completed her doctoral program while holding down a job was a source of inspiration to me while I struggled to keep my own dissertation on schedule. David "Beast" Perry's and Nancy Lutes' senses of humor and George Wagoner's proofreading abilities were also of assistance in completing my dissertation.

Capuchin researchers Aimee Campbell, Linda Fedigan, J. Feuerstein, J. Johnson, Katie Mackinnon, Megan Matheson, and Lisa Rose have allowed me to cite their unpublished observations. I have benefitted from conversation with them, as well as with Filippo Aureli, Sue Boinski, Rosie Bolen, Beth Dettmer, Frans de Waal, Larry Fedigan, Doree Fragaszy, Paul Garber, Kellen Gilbert, Bob Harding, Bill Hopkins, Charlie Janson, Matt Jorgensen, Lynne Miller, Rodrigo Morera Avila, John Oetting, Lisa Parr, Kim Phillips, Georgina Slavoff, Alex Skolnick, David Watts, Annie Weaver and Elisabetta Visalberghi. Lisa Rose has been an exemplary collaborator, and I look forward to more joint projects with her. Visits with the Santa Rosa monkey researchers, at both Santa Rosa and Lomas Barbudal, have helped me understand which aspects of my monkeys' behavior are potentially "capuchin universals" and which are apparently idiosyncrasies of my study group.

Several people gave me logistical aid in setting up a field site. Colin and Lauren Chapman first told me about Lomas Barbudal, after their census of the primates there in 1988. Colin helped me make the contacts necessary for doing a pilot study at Lomas in 1990. Ken Glander generously donated his time during our first months in Costa Rica to helping us find a place to live in Bagaces and guiding us through the bureaucracy involved in obtaining permits. He also loaned us walkie talkies for use in data collection, which immeasurably improved our ability to find and follow the monkeys. We greatly enjoyed our weekly visits to La Pacifica to visit Ken and his assistants, during which we swapped monkey stories. Evening potlucks with the La Pacifica crowd became a tradition, and although there were too many howling monkey researchers to thank everyone individually, I would like to thank in particular Erin Boydston, Nancy Feinstein, Holly Ferrette,

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Susanne Gfeller, Karen Richardson, Isa Salas, and Sharon Savage for providing us with excellent cuisine and companionship in spite of the fact that the capuchins beat up the howling monkeys on a regular basis. Isa also helped me identify many of the plants used by capuchins.

Gordon and Jutta Frankie aided us in innumerable ways. Their tireless campaign to heighten environmental awareness in the vicinity of Lomas Barbudal has no doubt contributed to the maintenance of good monkey habitats, particularly in the San Ramon de Bagaces area where I did my research. They provided logistical aid by renting us a house, arranging for us to use a research vehicle, and loaning us equipment on various occasions. We and numerous other people benefited from the use of public facilities (e.g. the Centro Patrimonial and the Amigos de Lomas Barbudal Center in Bagaces), which were constructed by their conservation organization, Friends of Lomas Barbudal. Gordon and Jutta gave us lots of advice on matters as diverse as plant identification, auto maintenance, and fire-fighting techniques. Their friends Ladina and Verena were also helpful in providing advice and assistance. Innumerable residents of Bagaces and the communities surrounding Lomas Barbudal were involved in Amigos de Lomas Barbudal's efforts to preserve local wildlife, and I am exceedingly grateful to them for their cooperation and foresight. Some of these people, including the Stewarts, Manuel Gonzalez, the people of Rancho Jojoba, and numerous residents of San Ramon de Bagaces, were also helpful to us in locating monkey groups and in granting permission to work on their property.

Numerous people helped Joe and me adjust to Costa Rican life during our first months, when our Spanish was inadequate. Ken Jones, Carol Koury, Brian Wisenden, Miles and Hilda Keenleyside, Magda Campos, and Gillian de Gannes helped us by translating and explaining which stores in Bagaces sold which objects. Karen Richardson and Holly Ferrette aided us in obtaining permits and in finding monkey troops. Bill Eberhard and Mary Jane West Eberhard provided hospitality and welcome academic discussion during some of our trips to the Central Valley. The residents of Bagaces were

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exceedingly kind and patient with our Spanish. Fermin and his taxista friends transported us to the reserve during the pilot study. Our neighbor Dennis Guido kept our car running, and we enjoyed long conversations with his wife Virginia and her daughters while we waited for the car to be fixed. In particular, Cynthia Guido became a close friend. Our next-door neighbor on the other side, Nidia Lippi Zuniga, also became a good friend, and she and her relatives taught us a lot about Costa Rican cooking. Yami and Nela Jiménez Rodríguez aided us in establishing a household by teaching us tropical housekeeping tricks, caring for our infamous guard dog Yogi Perra, and creating wonderful monkey decor for our walls and wardrobes. Myrna Rivera Carballo and Lilliam Lopez provided able logistical assistance and lively conversation whenever I visited the NUPLAN center. Jeff Christie, Hillary Duffy and Bee Wisenden offered us their friendship and the opportunity to speak English on occasion. Elisa Ruiz Luna rented us her lovely home and loaned us her ferocious but lovable dog, Yogi Perra, who ably protected our data and equipment from theft. Rosan Chavez entertained us with stories of her exploits and introduced us to many people who later became close friends. There are numerous other Bagaceños who were kind to us and helped us feel as much at home in Bagaces as in Ann Arbor, and I apologize for not thanking everyone by name.

The Rosales family has helped us in more ways than can be counted, by offering us lodging, food, advice, and companionship over the years. Their hospitality, both to us and to the monkeys that occasionally raid their crops with impunity, is in part responsible for making me love Lomas Barbudal more than any other place on earth. Seidy and Pepin patiently taught us Spanish during my first year in Costa Rica and delighted in teaching us the colorful "dichos" that make them such excellent storytellers. All of the Rosales family -- Pepin, Emilse, Flori, Carlos, Juan, Sandra, Seidy, Adrianita, Seidita, Teresita, Carmen, Chino, Guito, Rebecca, Miguel and Xinia -- were patient with our monkey obsession and understood when we would break off a conversation abruptly to run toward a monkey vocalization. They soon learned to record the time and location of all monkey sightings, so

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as to have an answer to the inevitable question "Ha visto los monos?" The memory that stands out most vividly in my mind is of the wonderful Christmas celebration spent with the Rosales family in 1992.

The other Costa Rican family that has provided us with hospitality over the years is the Cedillos family - the late Don Antonio, Doña Norma, Juanita, Marvin, Jessenia and Esteven. Doña Norma was a second mother to Julie, Laura, Joe and me, feeding us wonderful picadillos, nursing us through illnesses with home remedies, and providing lodging for extended periods of time. Marvin, more than any other person, explained how to be "buena gente" in Tico culture, prevented us from committing some really appalling faux pauxes, improved our Spanish skills, and shared with us the joys of monkey watching. Marvin lived with us during our second year in Costa Rica and became part of our extended family of moneros. Having spent many days in the field with us and listened to monkey gossip every night for over a year, Marvin probably knows more about white-faced monkey politics than any other Tico biologist. We deeply appreciate Marvin's letters, in which he sends us monkey gossip from time to time, and we look forward to many more hiking trips and monkey-watching experiences with him.

Julie Gros-Louis (AKA "La Comandante," "La Muchachona," "auto heroine," "Esa Julia") and Laura Sirot were the perfect field assistants. Although there was plenty to complain about (e.g. 3:30 am wake-ups, the "IWS," weekly wasp stings, the Brow, chiggers, ticks, Vroomers, revolting predawn milkshakes, Festerfest '91, Yogi Perra bites, and certain bichos necios), they never once complained. They learned to identify monkeys and collect data in record time. Not only were they exemplary field assistants and housemates, but they also enriched our lives by introducing us to many Costa Ricans whom we might not have met otherwise, and by forcing us to participate in some cultural experiences (e.g. the discomovil) that we definitely would not have braved on our own.

Of course, my greatest debt is to the monkeys themselves, for allowing me to pry into their private lives for the most enjoyable 26 months of my life. I can't truthfully say

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that they were as hospitable as the local people (who never once slapped me or broke branches over my head), but they certainly were entertaining. Even on the last day of the study, they amazed me by exhibiting new behaviors. Not only do they have one of the biggest brain/body ratios of any primate, but I am certain that they also have the greatest ego/body ratio of any primate: their pugnacious behavior was a constant source of amusement to me, as they daringly slapped bulls' legs, plucked porcupines' quills, and grabbed carnivores' tails. I will not thank each monkey individually, since each one's contribution is apparent in the pages that follow. But I would like to thank Curmudgeon ("Mudge") in particular, because his charismatic nature and complex personality have given me so many insights into capuchin social life, and because he has come to symbolize the essence of capuchindom to Joe, Julie, Laura and I. This dissertation, as well as several silly songs, is dedicated to him.

My greatest debt to a non-monkey is to Joe Manson, my husband and collaborator. He has been involved in every detail of my life of a graduate student, from the day he convinced me (over the phone before I met him) to enter the graduate program at U of M. He has shared an office with me ever since my first semester in graduate school, and has taken time from his own, often hectic, work schedule to listen to the results of every new analysis as soon as it is completed. His constant reassurance that my research is really interesting to someone besides me was critical to maintaining my morale at times. Most of all, I appreciate Joe's willingness to take 2 entire years off from his own research to aid me in collecting the data for my dissertation. Our common knowledge of the intimacies of capuchin and rhesus social life has greatly strengthened our own social bond. I am indeed fortunate to have married Joe, because no one who had not spent as much time with capuchins as Joe has would be able to understand my total obsession with capuchin social life. Anyone else would have divorced me after the 10,000th Curmudgeon anecdote, but Joe enthusiastically listened to every one.

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INTRODUCTION

My interests in the evolution of intelligence led me to study social relationships in capuchin monkeys. Three primary hypotheses have been suggested to account for large encephalization quotients in primates: (1) Milton (1981) suggested that large brains evolved to help primates remember the spatial and temporal patterning of resources, (2) Parker and Gibson (1977) suggested that the primary factor responsible for increased encephalization is the need for fine sensorimotor coordination, necessary for extractive foraging, and (3) several researchers (e.g. Jolly 1966, Humphrey 1976, Byrne and Whiten 1988, Cheney and Seyfarth 1990) have argued that the primary driving force in the evolution of primate intelligence is the need to solve complex social problems, such as assessing and remembering the relationships between third parties, and engaging in "Machiavellian intelligence" (Byrne and Whiten 1988).

The behavioral data used to support the first hypothesis, the ecological hypothesis of primate brain evolution, have come from studies of platyrrhines (New World monkeys) (e.g. Milton 1981), whereas the data used to support the third hypothesis, the social intelligence hypothesis, have come from studies of catarrhines (Old World monkeys and apes) (summarized in Cheney et al. 19[illegible], Cheney and Seyfarth 1990). It was for this reason that I set out to study social relationships in the capuchin monkey (*Cebus*), the New World monkey with the largest encephalization quotient. Comparative examinations of primate sociality commonly portray platyrrhines as less than gifted in the social domain, incapable of the coalition formation and tactical deception observed in many catarrhines (e.g. Dunbar 1991, Whiten and Byrne 1988). This perception may be in part because of the difference in topics traditionally studied by platyrrhine researchers and catarrhine

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researchers. Much of the early work on platyrrhines was performed by biologists such as John Terborgh and his students (e.g. Terborgh 1983; Janson 1985, 1984; McFarland 1986; Terborgh and Goldizen 1985; Mitchell et al. 1991; Wright 1986), and the types of questions they asked about the monkeys dealt with ecology and sexual selection. In contrast, most early students of catarrhine behavior were trained as anthropologists, and they were interested in primates as models of early hominid social relationships and societies (e.g. De Vore 1965). Anthropologists have long been interested in studying primates so as to define the human/nonhuman boundary, particularly with respect to mental abilities. The Japanese school of primatology has also focused largely on catarrhines, and their strong focus on primates as thinking, feeling individuals and on "monkey sociology" has filled the primatological literature with an abundance of anecdotes pertaining to social tactics in catarrhines (e.g. Kawai 1958, Nishida 1966). Therefore, it may be in part due to historical accident that there are more reports of complex social behavior in the catarrhine literature than in the platyrrhine literature.

What I set out to do in this dissertation is to describe the intricacies of white-faced capuchin (*C. capucinus*) social relationships, in a manner that allows comparison with data on catarrhine social relationships. Because this is the first detailed examination of social relationships in this species, the scope is broad, and the content is largely descriptive rather than hypothetico-deductive. I chose to study a single group in depth, rather than collecting small amounts of data on more than one social group, so that I could have a better understanding of the intricacies of group dynamics. The group chosen for study was only slightly larger than the mean group size and had a sex ratio typical of *Cebus capucinus* groups (Chapman et al. 1988). Rather than testing specific hypotheses derived from evolutionary theory on narrowly defined topics, I have attempted to give the reader a complete picture of what social life is like for adult capuchins in my study group. Thus, I have included numerous anecdotes. I hope that this work will provide a solid grounding in the natural history of capuchin social behavior, and that it will highlight theoretically

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interesting aspects of capuchin sociality, thus paving the way for more rigorous hypothesis testing about issues pertaining to capuchin social cognition, social development, and mating systems.

Chapter 1 outlines the methods used in this study and describes some general natural history. This study is based on approximately 1400 hours of focal animal follows, collected during 3700 hours of contact with a single social group of capuchins at Lomas Barbudal Biological Reserve, Costa Rica over a 24-month period.

Chapter 2 describes female-female social relationships. Like macaques and savanna baboons, white-faced capuchin females are philopatric and form strong social bonds with other females. Female-female bonds, as measured by amount of time spent in proximity and amount of time spent grooming, were stronger than male-male or male-female bonds. Females had a stable, linear dominance hierarchy that was reinforced by coalitionary aggression: females supported high-ranking females against low-ranking females. However, females very reliably aided one another in conflicts against adult males, who were dominant to all females.

Chapter 3 describes male-male relationships. Males very rarely associated with one another in an affiliative way, and they spent very little time in proximity. Although they never formed coalitions against females, males supported one another against other males, particularly males of other social groups, and against members of other species. The alpha male manipulated subordinate males' relationships by preventing them from affiliating with one another. Male-male aggression was severe at times, resulting in serious wounding and temporary eviction from the group.

Chapter 4 describes male-female relationships. Females groomed males much more frequently than males groomed females, and the alpha male was the most frequent target of female-male grooming. Sexual behavior was rarely observed and was primarily of a non-procreative nature. Male-female coalitions were common and were directed primarily toward subordinate males and members of other species. Although males consistently won

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dyadic contests with females, females often successfully formed coalitions with other females against males, thus shifting the intersexual power balance.

Chapter 5 describes the causes and consequences of a male rank reversal. The alpha male's popularity with females decreased over time, and the beta female began instigating coalitionary aggression against him. A subordinate male joined the females in seriously wounding and temporarily evicting the alpha male, an event that I refer to as "the coup." This subordinate male then became alpha male and immediately formed affiliative bonds with the adult females. After several attempts, the former alpha male succeeded in rejoining the group as a peripheral member, but he did not retain his former bonds with females. In contrast, the juveniles did not alter their social relationships with males as a consequence of the coup. Capuchin political strategies during the coup are compared with those of chimpanzees during rank reversals.

Chapter 6 describes behavior following conflicts. Using the protocols utilized by catarrhine researchers, I searched for evidence of reconciliation in capuchins and was unable to demonstrate its existence. However, it is possible that reconciliation occurs but is greatly delayed in capuchins, so that standard protocols for demonstrating reconciliation do not detect it. One behavior, the "wheeze dance," appears to be a good candidate for a reconciliatory behavior despite the fact that it occurs long after fights. Because wheeze dances occur in dyads that have tense social relationships, and under conditions likely to put strain on the relationship, it seems likely that wheeze dances serve to reduce tension and negotiate relationships.

Chapter 7 is about inter-group relationships. Encounters with other social groups were invariably hostile. Males typically stayed and aggressed against one another during intergroup encounters, while females and juveniles fled. In the rare instances in which females also participated, only the 2 top-ranking females were involved. Invasion by foreign males has been shown to inflict serious costs on all group members, but on males in particular, in white-faced capuchins studied at another site (Rose and Fedigan 1995).

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The need to cooperate in driving away foreign males during intergroup encounters may be an important force in determining the quality of male-male relationships in an intragroup context. Intergroup aggression is discussed in the context of Wrangham's (1980) and van Schaik's (1989) models of social organization.

The conclusion discusses the relevance of these findings to the debate on the evolution of intelligence. Capuchin social relationships are sufficiently complex that it is not possible to falsify the social intelligence hypothesis. The latter part of the conclusion is devoted to considering future directions in research on capuchin social behavior. The research in this dissertation has laid the groundwork for addressing some interesting questions pertaining to social cognition. Long-term studies of social development may reveal the process by which juveniles acquire the decision rules governing choices of partners and victims in coalitionary aggression. Should genetic paternity data become available, it will be possible to answer many interesting questions about the mating system, as well as patterns of altruistic behaviors (e.g. alloparenting and food-sharing).

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CHAPTER I

NATURAL HISTORY AND METHODS

Duration of Study

A pilot study was conducted in May-August, 1990. Most of our efforts during the pilot study were devoted to censusing, habituating the study group, mapping the area, and cutting trails. Some data were collected in the last 2 months of the pilot study, but these were discarded for most analyses because the monkeys were not yet fully habituated. The main study was conducted between May 1991-May 1993. I spent 6 weeks in the U.S. from early September to mid-October of each year, when the rains were too heavy to allow much data collection. Table 1.1 shows the amount of contact time (time in view of the animals) and the number of hours of focal animal data collected for each month of the study. Contact hours are reported not as person-hours, but as amount of time at least one person was with the group; so if two observers watched the group simultaneously for one hour, there was only one hour of contact time. The total amount of focal data, including the pilot study, was 1418.67 hours of data. The amount of contact time was 3813 hours.

Description of the Study Site

The study group lived along the Río Cabuyo, which forms the northern border of Reserva Biológica Lomas Barbudal. Lomas Barbudal is located in Guanacaste Province, Costa Rica, about 15 km SW of the town of Bagaces and just north of Parque Nacional Palo Verde. In addition to using reserve property, my study group ranged extensively to

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the north of the Río Cabuyo into IDA (Instituto para el Desarollo Agrario) property, and occasionally into privately owned lands at the northeastern end of their range. Most of their core area was composed of an 80-hectare piece of land (also under IDA control) set aside by the community of San Ramón de Bagaces as a watershed and nature reserve. This piece of land was developed by Amigos de Lomas Barbudal and the community of San Ramón de Bagaces for ecotourism. For the sake of convenience, I will hereafter refer to this whole region used by the monkeys as "Lomas."

Lomas is tropical deciduous forest in the Pacific lowland watershed at elevation 10-180 m (Frankie et al. 1988). The area used by the monkeys includes a mixture of habitat types, including dry deciduous forest, riparian and spring forests, savanna, mesic forest, extreme dry deciduous forest, and regenerative forest. The species composition of these habitat types is described in more detail in Frankie et al. (1988). The canopy is fairly low in the drier areas. The leaves fall from most of the trees during the dry season (late November - early May) in all but the riparian and spring forests. These two factors allow for very good visibility of monkeys, compared with rainforests. Lomas receives 1000-2200 mm of rain annually (Frankie et al. 1988), most of which falls in late May-early July and late August-early November. There are strong winds from December through March. In the peak dry season, daytime temperature highs range from 33°-38°C (Frankie et al. 1988).

Figure 1.1 shows a map of the study group's home range. The Río Cabuyo flows from the northeast corner of their range to the southwest corner, and 7 streams flow into it. During the dry season, the monkeys stayed fairly close to permanent water. Therefore, their rainy season range was approximately twice the size of their dry season range. Neighboring groups of monkeys also apparently constricted their ranges to be closer to the Río Cabuyo during the dry season. Therefore, my group's encounter rate with other groups was 30% greater in the dry season than in the rainy season. The extreme northern end of my group's range is composed of savanna, which is used only

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rarely by the monkeys. Because ranging patterns were not a focus of my study, I used very crude methods for measuring home range size. An area was counted as being part of the group's home range if it was used by the group just once a year. Whenever the monkeys went somewhere new, I used flagging tape to mark their route and then went back later to pace off their route with a compass and add it to the map. Some of the areas on the periphery of their range were used extremely rarely, and the rice field marked on the map was used only once.

Lomas is extremely vulnerable to fire in the dry season. Fires are set by poachers, to flush out game, and by farmers and ranchers, to destroy jaragua grass, an African weed species, so that more tender forage can grow in its place. Eighty percent of Lomas Barbudal was burned in 1984/5 (Sheean-Stone, 1990). Since then, with the guidance of Amigos de Lomas Barbudal, a Berkeley-based conservation organization created to protect the area, a fire management program has been created. This program requires the cooperation of the Costa Rican National Park Service and the adjacent farming and ranching communities. Several members of the community formed a volunteer fire-fighting team which is quite successful, provided that someone notifies them of the fire and transports them to it. Although Lomas continues to be plagued by fire, it is much less vulnerable than it was prior to the intervention of Amigos de Lomas Barbudal. In 1991, a fire burning 50% of the reserve extended as far north as the Río Cabuyo, thus destroying a large part of the study group's home range. For many months after the fire, my group did not use the burned area. In 1992 there were some smaller fires on IDA property within the group's home range, but these were quickly brought under control and did not affect the monkeys' ranging patterns. In 1994, a fire burned 95% of the Biological Reserve, but once again, the majority of the group's home range was spared because the fire did not jump to the northern side of the Río Cabuyo.

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Composition of the Study Group

I studied one social group intensively. Table 1.2 shows the composition of this group and summarizes demographic changes that occurred during the study. During the pilot study, May-August of 1990, I could recognize only the adults individually. Because I could not recognize the juveniles individually, I was not sure how many monkeys were in the group during the pilot study, but there were at least 14 and probably 16. One juvenile was found dead within the study group's home range on July 11, 1990. For the purposes of Table 1.2, all monkeys born during the course of the study are termed infants. The juvenile class includes all monkeys who were alive when the study began but had not yet reproduced by the end of the study. Aside from Juege, who was born the week the study began, there were no small infants in the group at the time the pilot study began; however, it is possible that some of the animals I termed juveniles at the start of the study were 2-year-olds. I could not be certain which males were reproducing, so males were classified as still being juveniles if they were no bigger than females who had not yet reproduced by the end of the study. Diablita and Nanny were adolescents at the start of the project. Nanny gave birth midway through the study and hence is termed an adult. Diablita became pregnant toward the end of the study but had not yet given birth by the end; therefore, she is termed a juvenile. I have also included in this table infants born after the study. Some of these data were collected by me during a brief visit to the field site in February-March, 1994. Additional data were collected by Marvin Cedillos Amaya, who was trained to identify individuals during the 1994 field season. The names of individual monkeys in Table 1.2 are sorted by age-sex class.

It is possible that Mani, an infant female during the main study, is not the same monkey whom I named Mani during the pilot study. When I returned to Lomas in May, 1991, after 8 months in the US, there were only two infants remaining in the group, and yet 3 had been born in the 1990 pilot study. One of the remaining two infants was easily recognized as Juege, due to his strong physical resemblance and strong social bond to

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Wiggy, an adult female. The other infant did not have a strong social bond with either Tattle or Abby, the other 2 adult females who had had infants the past year; nor did she have an overwhelming physical resemblance to one or the other. I assumed, since Tattle already had a new baby, that it was Tattle who had lost her baby during our 8-month absence. Otherwise, she would have had an interbirth interval of merely 10.25 months, which is remarkably short for this species, in which the mean IBI is 26.36 months and the shortest published IBI in which the previous infant survived is 13 months (Fedigan et al., in press). Abby gave birth 12.5 months following the birth of Mani (also a short IBI), so it is faintly possible that Mani died and the monkey I now call Mani is really an immigrant. This seems unlikely, since females rarely transfer in this species (Oppenheimer 1968; Fedigan and Rose, pers. comm.), and this was a very young age at which to transfer.

Of course, I can not be sure who are the mothers of monkeys who were not born during the study, and I do not, for the purpose of analysis, assign maternity to any monkey for whose birth I was not present. This dissertation does not include analysis of juveniles' relationships with adult females and other juveniles. But, for the reader's interest, I can make guesses as to the probable mothers of some juveniles, based on physical resemblance to adult females and social ties to females. I am confident that Kola is the son of Wiggy. Kola bears a very strong resemblance to Wiggy, Juege and Yoyo. He frequently grooms, plays, and rests with these three monkeys. I suspect that Hobbes is the son of Abby, due to his strong social bond with her son Rico (for whose birth I was present). Hobbes also rests frequently near Abby and Squint. Quizzler looks a lot like Tattle and frequently grooms with her. Urchin looked almost exactly like Kola and may, therefore, have been a son of Wiggy's. I had not begun collecting behavioral data on juveniles at the time he disappeared. I suspect that Vandal is Squint's daughter. Although she does not have strong bonds with any of the adult females, she is closer to Squint than to any other adult female. I know that Squint was still nursing an infant

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during the 1990 pilot study, and, based on their sizes, only Hobbes, Urchin and Vandal could have been that infant. Of these three, Vandal is the one who most resembles Squint physically.

I have not yet had enough experience in estimating chronological ages of juveniles by their size to accurately assign ages to the juveniles above 3 years of age. However, based on their sizes, I confidently estimate that Hobbes, Vandal and Kola are *at least* a year older than Juege and Mani, and that Diablita and Quizzler are at least a year older than Hobbes, Vandal and Kola.

Five of the females in my group had more than one infant, thus providing me with some data on interbirth intervals, which are summarized in Table 1.3. The average interbirth interval was 18.6 months, if each IBI was counted as a separate data point, or 21.5 months, if IBI's were averaged for each female so that each female contributed only one data point. Excluding the interbirth intervals in which the previous infant died before the next birth, the average interbirth interval was 22.0 months if each IBI is counted as a separate data point, or 23.6 months if each female's average IBI is a separate data point.

History of the Population

The only primate census at Lomas Barbudal was conducted in 1989 by Chapman et al. (1989). They reported a density of 3.7 cebus monkeys per km^2. Capuchins were found in all habitat types within the reserve. There were 11 groups of capuchins in the reserve, averaging 8.1 members per group. The adult sex ratio was 1:2.03, and the ratio of females to immatures was 1:0.64. The average group size at Lomas was smaller than that of Santa Rosa National Park (the site of much previous research on *Cebus capucinus)*, which was 14.2 (Chapman et al. 1989). Capuchin population density at Lomas was low compared to censuses of *C. capucinus* at Santa Rosa, Palo Verde, La Selva, and Panama (Chapman et al. 1989). I suspect that the actual population density at Lomas is somewhat higher than the one reported by Chapman et al. Capuchins are quite

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difficult to census prior to habituation. Of the 5 groups occupying the northern tip of the reserve, all but one (Vampire group: 8 individuals) had group sizes larger than the mean of 8.1 reported by Chapman et al.

There were 4 groups of capuchins with ranges overlapping that of my study group (Figure 1.2). I was not able to census them reliably because they were not habituated. Because I mainly encountered these groups during intergroup encounters, I had more contact with the males than with the other group members (see Chapter 7). Over time, the males became fairly habituated to my presence and I could individually recognize most of them. Rambo II's group was the group with which my study group most frequently interacted. It had at least 12 members, including 4-6 adult males. Rambo I's group had at least 10 members, including 5 adult males and at least 4 adult females. The Vampire's group had at least 8 members, including 3 adult males, 3 adult females, and 2 juveniles. We only saw Abran's group a few times, but it seemed to be a fairly large group, containing at least 5 adult males and 2 adult females.

Habituation

It took several months to habituate the study group. For the first 2 months it was barely possible to keep up with them, and I discarded the first 4 1/2 months of data because I felt that my presence was biasing the monkeys' behavior too much. Habituation continued to improve until about December 1991, by which time the monkeys were habituated enough to play on the ground 6 inches from my feet. By this time, they were so accustomed to my presence that it was difficult to attract their attention, even by yelling or arm-waving. Capuchin monkeys at Lomas seem to be much more afraid of humans than are capuchin monkeys at other national parks I have visited in Costa Rica. This is probably because the Lomas capuchins have a long history of unpleasant interactions with humans. A resident of the area once told me that 30 years ago, he and many other local farmers were hired by a foreigner to hunt capuchins and spider monkeys

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and give him the babies for medical experiments (though my informant suspected that they were sold as pets as well because of the dealer's insistence that the monkeys not have any scars). Babies were caught by killing the mothers and were raised on milk. The dealer paid 35 colones (which was probably about $5 at that time) for each monkey. My informant says that monkeys were much more common then; he sometimes encountered 40 groups in a day. This is most likely an exaggeration, but no doubt the monkey trade did have a big effect on the population. White-faced monkeys are still commonly kept as pets, and this is probably the second biggest problem the population faces now, since pets are generally wild caught. Although white-faced monkeys are not eaten, hunters do use them for target practice. Because they are so small and active, they are challenging to hit. Poaching (primarily of deer and peccaries) is still a big problem in Lomas. I frequently heard shooting in the evening when I was collecting data. The worst threat to the monkeys is fire. Fires are set each year by poachers (to flush out game) and by nearby landowners (to clear fields), and these often burn large areas of forest within the reserve.

Methods

Observation Schedule

In 1990, Joe Manson was my only field assistant, and we generally worked three consecutive days followed by a day off. For the first few weeks, we traveled from our home in Bagaces to the reserve by taxi every day, arriving at the site at about 6:30 am, and staying until 6 PM. We found that the monkeys generally moved during the night, so we started camping in the reserve to get an earlier start. In May-August of 1991, I had three assistants (Joe Manson, Julie Gros-Louis and Laura Sirot), and the four of us worked simultaneously 5 days per week. We tended to work 4 days consecutively followed by a day off. We arrived at the study site around 5:30 am and stayed at least until 6 PM. Often the monkeys moved during the night, especially if it was a full moon.

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From late August 1991-May 1992, Joe Manson was my only research assistant. We worked 5 consecutive days each week, arriving at the site before 5 am each morning and leaving around 6 PM. By arriving at the monkeys' sleeping site before dawn and leaving them after dusk we were able to stay with the group continually, with a few exceptions when there was a full moon and the monkeys traveled during the night. When Julie Gros-Louis returned to help us again in June of 1992, we began a rotating schedule in which two people were in the field and one in Bagaces doing errands each day. From June, 1992 till the end of the study, we were able to follow the monkeys dawn to dusk 25 consecutive days each month, with the exception of some days in which torrential downpours caused us to lose the group briefly.

Choice of Subjects

As originally conceived, the project involved the study of 2 social groups rather than one. I changed plans for several reasons. One reason had to do with the logistics of tracking monkeys in the field. Due to the time expense involved in habituation, and the amount of time (several days, in the early months of the study) required to locate a social group, I would have collected far fewer hours of focal observations had I studied two groups rather than one. Also, the home ranges of the adjacent monkey groups were less navigable than that of my main study group, due to the dense jaragua grass (which replaced the undergrowth burned out in fires), steep cliffs, and Africanized bees. Also, adjacent monkey groups ranged onto private lands or ranged deep into park service lands, which would have meant large park fees. Part-way through the study, the park service decided to start charging $10/person/day for researchers to enter the reserve. Fees this high are not feasible for students doing long-term behavioral research.

The main reason that I decided to study one group, however, was that I was afraid of missing crucial moments in the development of the monkeys' relationships if I continually switched from group to group. The questions I address in this dissertation

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require that I observe the majority of all severe fights, and that I have large amounts of data per focal animal on a regular basis. The cost of studying only one social group is, of course, that I have a very small number of individuals, which limits the types of analyses I can perform. Previous studies of capuchin behavior (see references below) have had larger numbers of social groups (and individuals) with small amounts of data per individual. Prior work on capuchins has addressed issues such as female mate choice (Janson 1984, 1986), feeding competition (Janson, 1985, 1988; Rose 1994; Chapman and Fedigan 1990), and costs and benefits of group living (Robinson, 1988a, 1988b; Rose, 1994; O'Brien, 1991; Rose and Fedigan 1995), and the effects of predation pressure and feeding competition on group structure (Janson 1988, 1990a, 1990b; Robinson 1981, 1982; de Ruiter 1986; van Schaik and van Noordwijk, 1989). For these sorts of questions, large samples of individuals are essential. None of these researchers collected large amounts of data per individual, and therefore none of them have examined the details of social relationships. For these reasons, I decided that I could make a more valuable contribution by studying a single group of monkeys in detail.

Recognition of Monkeys

Adult capuchins are readily identifiable by means of natural markers such as scars, variation in coat markings, and facial contours. The patterning of white and black on the forehead is especially variable in this species. Juveniles are much more difficult to recognize. It took me over a year to identify them quickly and reliably enough to collect focal animal data on juveniles. Infants are especially problematic because, at least in my study group, births are clumped, and allomothering -- including allonursing -- is common; therefore, it is not possible to infer that a baby is the offspring of a particular female just because it is on her back or nursing from her. Infants' facial features change rapidly as they mature. I finally resorted to dying infants with Clairol "Born Blonde" hair dye. I used a 100 cc syringe with the needle removed to squirt infants on their backs

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from a distance of approximately 1-2 meters. The dye produced variable patterns of dark orange on their black coats. Squirting did not distress the infants, though they appeared "puzzled" by it. Some rubbed the dye all over their bodies, which was a problem, as it diluted the effects of the dye and made the dye patterns less clear. Habituation was not set back by the squirting. I was careful to squirt dye only when no monkeys were looking at me. With two exceptions, the monkeys did not seem to suspect that I was the culprit: they generally looked above them to see from where the dye came.

Focal Animal Samples

Most of the behavioral analyses presented in my dissertation are based on 10-minute samples of focal monkeys. I chose the length of 10 minutes because it was the longest amount of time I could follow monkeys during the rainy season without frequently losing them. I followed the focal monkey for 10 minutes, recording continuously all social behaviors in which the focal monkey participated during that time (see ethogram). At 2.5-minute intervals (including the beginning and end of the follow), I recorded the focal animal's activity, and the proximity of all other monkeys in my view. Proximity was measured in units of monkey lengths, with one length equaling the body length, from nose to tail base, of an adult male capuchin. Initially I tried to measure proximity in standard metric units, but interobserver reliability was poor. I found it difficult to gauge distances in the treetops without having some point of reference. The only objects of known length that I always saw near the focal animal were other monkeys (or, at least, the focal animal itself). Because I knew the sizes of all group members relative to the adult males, I could imagine adult male monkey lengths by comparing them to the focal animal and counting out from its body. All adult males were the same body length. Interobserver reliability greatly improved once I adopted this system. Proximity categories used in point samples were (1) contact, (2) within one length of the focal but not in contact, (3) within 1-5 lengths of the focal, (4) within 5-10 lengths of the

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focal, and (5) outside 10 lengths of the focal but in view of the observer. Distances between the focal and the other monkey were measured from between the two closest points of the monkeys' bodies. At the end of each 10-minute sample, the activities of all group members in view were recorded.

Data were recorded onto a microcassette recorder. Unless a conspicuous, unusual event (e.g. a fight or a copulation) was happening elsewhere in the group, both observers helped collect focal data. One person kept his/her eyes on the focal animal and narrated into the recorder. The other person identified the other monkeys in the point samples or monkeys who were approaching the focal animal. Thus, the narrator did not have to risk losing sight of the focal animal while struggling to identify distant monkeys. The person who was not narrating could also run ahead of the focal monkey when it was traveling, to minimize the danger of losing the focal.

I did not use a random method of selecting the focal animals. Capuchins are widely dispersed when foraging, and individuals frequently become separated from the rest of the group. This makes it quite difficult for an observer to find a particular monkey at any given time. Accordingly, I divided the monkeys into 3 classes: adults, juveniles, and infants. I tried to complete follows of each member of each class before starting another round of focal follows on the class. Because of the tendency of individuals to become separated from the group, sometimes for days at a time, I modified this rule such that I had to find all but one member of the class before starting the next round on that class, but that I had to spend a reasonable amount of time looking for the last monkey before starting the next round. I started a follow of the first eligible monkey I saw who had not interacted with the focal animal or been within one length of the focal within the last 2.5 minutes of the previous follow.

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Reconciliation Follows

Following some fights, I used a special protocol to determine whether the monkeys reconciled (see chapter 6 for definition of reconciliation). Criteria for determining whether to use this protocol were as follows: (1) An observer witnessed the start of the fight. (2) The fight involved physical contact and/or was serious enough to cause at least one of the participants to scream. If these criteria were met, I followed the victim of the fight for 30 minutes, using the same procedure as in the normal 10-minute follows. If there were only two participants in the fight, I could use either of them as the focal. But if (as was usually the case) there were several participants, and one monkey was the victim of all the other participants, I followed the victim (i.e. the recipient of the attack, if there was no counterattack, or the loser of the fight; with the exception of some instances in which a large coalition supported the recipient of the original aggressive act, the recipient of the original attack was also the loser). In the case of the 2-participant fights, if I lost the focal animal temporarily, but the focal's opponent was in view at the time the focal was lost, I switched to observing the opponent. As a control sample, I followed the same monkey (or, in the case of 2-participant fights, either of the two participants) for 30 minutes at the same time the next day. Because of the difficulty of finding focal animals, the start time of control periods could be anytime within an hour of the beginning of the fight the previous day. Occasionally I was unable to find the focal animal at the appropriate time the day after the fight, so the second part of the reconciliation protocol was postponed until a later day. I also postponed the second part of the reconciliation protocol if the focal was involved in a fight at the time I wanted to do the control follow, as this might have biased the data.

Interobserver Reliability

Before using data collected by my assistants, I tested them to make sure they could identify the animals correctly and that we were coding all of the behaviors in the

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same way. They had to consistently have 98% concordant records with mine on all relevant behaviors and monkey identifications before I started using their data. The assistants consistently had 100% accuracy on monkey identification and recording of social behaviors, but there was less precision with regard to the recording of distances in proximity for the instantaneous point samples and for the continuous records of approaches and leaves. When I required the observers to be accurate to the nearest monkey length, the percentages of correct responses for the three observers were 90%, 80% and 71% for the three assistants. When I merely required correct assignment to proximity categories (which was all that was necessary during data collection), they all had 100% concordant records with mine. When we collected data, we worked in teams, so the two observers could check each others' work. When there were disagreements that could not be resolved by taking a closer look, the data were discarded. Having two observers work simultaneously reduced the possibility of drift in data collection methods, as we could constantly check one another's methods.

Ad libitum Data

We recorded ad lib data on the following behaviors whenever they occurred (see ethogram for definitions): grooming, aggression, hand-sniffing, dancing, inter-group interactions, sex, coalitional behaviors, fur-rubbing, certain vocalizations (lost calls, wheezes, hysterics, sex grunts, horrible noises, screams), allonursing, urine rubbing, infant-carrying, branch breaking displays, food-sharing or theft, vertebrate predations, and interspecific interactions. We also recorded the group's location regularly so that we could assess their ranging patterns. We did not have an elaborate grid system for determining the group's location; rather, we noted the group's position relative to landmarks that had been noted on the map. These landmarks were placed on the map by pacing off their distances from marked trails and streams, with the aid of a compass.

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Acoustic Data

From December 1991 until the end of the study, I occasionally recorded the monkeys' vocalizations, using a Sony Professional Walkman and a Sennheiser ME88 microphone. Vocalizations were analyzed using the program SIGNAL. I also did some video recording with a Sony camcorder.

Diet

The *C. capucinus* diet in tropical dry forest is composed of roughly 65% plant material (mainly ripe or nearly ripe fruit, and some flowers and seeds), and 35% animals (mainly insects, and some vertebrates) (Chapman and Fedigan, 1990). Capuchins, due to their unusual dexterity, are able to exploit many fruits that are inaccessible to other species. They can overcome the mechanical defenses of trees such as the panamá (*Sterculea apetala*), terciopelo (*Sloanea terniflora*), and guácimo molenillo (*Luehea candida*), so as to obtain fruits just before they ripen and are ready to be released to their "intended" dispersers (birds, in most cases). Their agility, speed and apparent ability to plan escape routes in advance also enables them to consume wasp nests (such as *Polistes instabilis*, one of their staples in the late rainy season) that are inaccessible to most animals due to the fierce defense of the adult wasps. Capuchins are also adept at destroying dead wood, so as to access ants and other insects that hide there. Numerous papers have been published on capuchin feeding ecology (e.g. Terborgh, 1983; Janson, 1985; Freese, 1976; Chapman and Fedigan, 1990; Fedigan, 1990; Rose, 1994; Robinson, 1985, 1986) so no further details are given here.

Interactions with Other Vertebrate Species

Capuchins were aggressive in their interactions with most other vertebrate species. Many, such as coatis (nestlings), small rodents, several small bird species (adult and nestling), squirrels (both adult and nestling), bats, and possibly fish, were eaten by

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the monkeys. Others were treated as potential predators. They responded to various species of large raptors by looking up, calling, and sometimes moving down in the tree or (if the bird was flying low) swinging under the branch. Occasionally adult monkeys charged at perched raptors and chased them from the tree. Juveniles sometimes alarmed at birds that could not have been dangerous, such as vultures and herons. Adult monkeys responded to boa constrictors (*Boa constrictor*) and rattlesnakes (*Crotalus durissus*) by giving alarm calls, moving close to the snake, and shaking or breaking branches over it. Juveniles sometimes alarmed at nondangerous snakes as well. I once saw a juvenile pull the tail of a rat snake. The intensity and length of the monkeys' displays toward dangerous snakes seemed to be much greater when the snake was hidden than when it was out in the open. Generally all or most of the members of the group would participate in aggressive displays against dangerous snakes. The alarm call elicited by snakes was shorter and more intense than the alarm call elicited by raptors. Monkeys responded to bird alarm calls by looking up; they responded to snake-elicited alarm calls by running up into the tree and then looking at the ground or toward the alarmer. The snake-elicited alarm call was also used in response to caiman. The monkeys gave alarm calls in response to several types of terrestrial mammals: coyotes, dogs, jaguarundis, and skunks. The first three are potentially predators. Probably past experience with skunk scent marking has led the monkeys to be fearful of skunks. The monkeys run through the canopy above these terrestrial predators, giving alarm calls and threat vocalizations, and breaking branches. The monkeys occasionally give alarm calls to adult coatis. The monkeys sometimes fight with coatis when they are raiding their nest to capture pups. I have seen adult males bite and pull the tails of adult coatis. Generally the monkeys ignore the presence of adult coatis, however. The monkeys attack tayras and kinkajous, biting them and pulling their tails until they leave the vicinity. These carnivores could conceivably capture baby monkeys, but they do not pose much of a threat to adult or even juvenile monkeys. The only other animal at which the monkeys regularly alarm call is

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humans. The alarm call for humans is of long duration and quite similar to the alarm call used to alert the monkeys to the presence of other groups of capuchins. When an unfamiliar human is spotted, the males alarm call, break branches, bounce, and threaten the human. The females and juveniles usually flee.

White-faced monkeys harass several animals for no apparent reason, as they are too big to be food items and pose no threat to the monkeys. Monkeys regularly harass howling monkeys (*Alouatta palliata*), horses, cows, porcupines, anteaters, pigs, peccaries, and deer. They break branches over the heads of horses, cows, pigs, peccaries, and deer, while chasing them from overhead. Sometimes when the monkeys are on the ground, they walk up to cows and slap them or bounce and threaten them. They slap and pull the tails and legs of anteaters, and they carefully pull on the quills of porcupines. When they find howling monkeys, they often pull their tails, chase them, and push them out of the trees. I have seen them inflict serious bite wounds on baby howlers. At other times, they act as if the howlers were inanimate objects: they step right over them as if they were bumps on a log. It is quite common for howlers to be the victims of redirected aggression following a fight between two capuchins.

On two occasions my study monkeys found dead deer (shot by poachers). Once the whole body remained, bloated and covered with flies. On the other occasion, the deer had been butchered and most of the body removed; all that remained were the legs and some skin. Both times the monkeys reacted quite strongly by giving alarm calls for long periods of time and staring at the carcass. This is quite puzzling, since they do not alarm at live deer. Nor do they alarm at carcasses of other animals. Perhaps the monkeys are making some connection between the dead deer and the poachers.

The only mammal that seems exempt from harassment by the monkeys is the agouti. Only once in hundreds of monkey/agouti associations have I seen a monkey chase or otherwise threaten an agouti. It is possible that the monkeys benefit from associations with agoutis because of additional protection from predators. Being the

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same size as monkeys, agoutis would be subject to many of the same terrestrial predators. White-faced monkeys always react to agouti alarm calls by running up trees, even when the agoutis are only alarming at my presence. The monkeys do not respond this way to the alarm calls of other mammals.

Medicinal Plant Use

The monkeys appeared to be using some plants for medicinal purposes. Eleven plant species were used for fur-rubbing, possibly because these substances have antifungal or insect repellant properties. Table 1.4 lists the species used and the part of the plant used for rubbing. In no case were substances both ingested and used for fur-rubbing. In two cases (*J. pungens* and *E. salamanensis*) a fruit was used for rubbing when it was green and was ingested weeks later when it was ripe. With the exception of the saps, the plant parts were prepared by first chewing them (during which time the monkeys usually had expressions of apparent agony or ecstasy on their faces) and drooling profusely. In some cases (e.g. *Capsicum*) their eyes watered and their noses ran too. The monkeys spit out the plant part and collected the drool and plant material to rub vigorously all over their bodies the way humans shampoo their hair. Fur-rubbing was generally a social activity, with several monkeys rubbing against each other in a squirming ball of monkeys. Rubbing against other monkeys probably helped them coat body parts that were difficult to reach. Aggression and sexual behavior were quite common during fur-rubbing, indicating that the monkeys were highly aroused. When the fur-rubbing substance was easily monopolized, as in the case of *Hymenaea courbaril* or *Pithecellobium saman*, in which the substance was extracted from a hole in the tree, there was intense competition for the rubbing substance.

Some of these plants are known to have secondary compounds toxic to insects. Citrus extracts are commonly used in natural insect repellents. *J. pungens* fruits contain toxins used by local people to produce insecticides and fish poisons; saponin is probably

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the active ingredient. Of the seven genera for which the CRC Handbook of Medicinal Herbs had information, four (*Eugenia*, *Jacquinia*, *Pithecellobium*, and *Citrus*) contained saponins. No single secondary compound seemed to be common to all of the plants used by the monkeys. Extracts prepared from *Hymenaea courbaril* (which was not listed in the CRC Handbook) contain flavenoids, tannins and other complex phenolics effective as insect repellents (Gilmurray, pers. comm.). I tasted most of the fruits used by the monkeys for rubbing, and they tasted truly terrible. I reacted the same way the monkeys did: my eyes watered, and I salivated profusely. After sampling *P. tuberculatum* and *Capsicum*, my mouth burned intensely for about 30 minutes. Of the species I sampled (*P. marginatum, P. tuberculatum, Capsicum, Citrus*, and *J. pungens*), the only one that was strikingly different from the others was *P. marginatum*. The leaves of this plant were sweet and very pleasant-tasting. We experimented with the sap of *Hymenaea courbaril* by coating one leg with it each day and leaving the other leg untreated. We counted the number of insect bites on each leg at the end of each day. For the first week, the treatment seemed fairly effective: On 5 days, the treated leg had fewer bites, and on two days, the number of bites on the two legs was equal (Sign test, p=.07). Either this was merely a coincidence, or the substance lost its potency over time (we did not collect fresh exudate each day). The totals at the end of the experiment were 28 person-days in which the number of insect bites (in this case, usually chigger bites) was fewer on the treated leg than on the control leg, 33 person-days in which the legs had equal numbers of bites, and 21 person-days in which there were more bites on the treated leg than on the control leg (Sign test, p=.39).

Ethogram

Following is a list of the social behaviors that were recorded on a continuous basis during focal animal samples. Where terms are identical to the terms used by other

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researchers, the first person to use the term for this species is cited. Where other terms are used for the same behavior by other researchers, alternative names are noted.

Affiliative Behaviors

1) Hug (Oppenheimer 1973): One monkey embraces another monkey front-to-front; this behavior is usually mutual.

2) Present for grooming (Oppenheimer 1973): One monkey lies down in front of or on top of another, sometimes pushing the other monkey if grooming is not received promptly. If the monkey requesting grooming wants the buttocks region to be groomed, he/she stands in front of the other monkey with the tail arched over the back. One individual, Guapo, had an idiosyncratic method of requesting grooming: he put the other monkey's tail in his mouth and would not relinquish it until grooming began.

3) Tongue out (=tongue tip exposed [Oppenheimer 1973]): The monkey opens its mouth and sticks its tongue out so that it hangs down over the chin. This facial expression was performed mainly by infants.

4) Touch: One monkey gently contacts another, with any body part, but usually with a hand or foot.

5) Gargle (possibly identical to the guttural chatter [Oppenheimer 1973]): This raspy, throaty noise is made mainly by infants, juveniles and adult females and is directed primarily toward adult males, particularly the alpha male. They usually perform it while following the males, but if the male is stationary, they may walk up to him and press their faces against him as they make the noise.

6) Climb on monkey: One monkey climbs on top of a resting monkey and plays on its back or head. This is done mainly by infants toward adults.

7) Fur-rubbing: Monkeys rub their fur with certain plants (see Table 1.4). This is generally a social activity, with one monkey rubbing against another.

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8) Sniff/visual inspect: One monkey approaches another and sniffs it or stares intently at some body part of the other monkey at close range.

9) Grooming (=allogrooming: Oppenheimer 1973): One monkey picks through the hair of another monkey with the hands and/or mouth; the recipient of this behavior is generally in a reclining posture.

10) Hand sniff (Fedigan 1993): One monkey puts its hand over the nose and mouth of another monkey, often with the fingers inserted up the nostrils. The other monkey appears to be inhaling deeply. Sometimes the sniffer initiates the hand sniff by grabbing the partner's hand and inserting the fingers herself. This behavior is performed only by adult females with other adult females.

11) Twitter (possibly inclusive of the purr and the twitter [Oppenheimer 1973]): This vocalization is a series of rapid, high-pitched squeaks (see sonogram), which is usually performed by a monkey who is approaching another monkey with apparent friendly intent (e.g. prior to grooming or hugging). It is often performed in duet by monkeys who are hugging or when one monkey is riding on another's back.

12) Peep: This vocalization is a single-syllable high-pitched noise usually performed as a monkey presents for grooming. It is very similar to a vocalization also performed sometimes in a feeding context.

13) Machine gun noise: This vocalization is a rapid sequence of soft, low-pitched, staccato noises. It is most frequently produced by females and juveniles, and is most often directed toward young infants. Typically the vocalizer's face is within 6 inches of the recipient's body. Sometimes the vocalizer presses his/her face into the recipient's body while producing this vocalization.

Submissive Behaviors

1) Avoid: As one monkey approaches, another monkey leaves or moves from the path of the approaching monkey while watching the approaching monkey.

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2) Flee: One monkey runs away from another monkey, who is typically chasing him/her.

3) Grin (Oppenheimer 1973): The teeth are bared and the lips are drawn back further than in a threat face (see below), with the jaw closed.

4) Head shake (Oppenheimer 1973): The monkey shakes its head rapidly back and forth, usually while doing a wrinkly face and lipsmack; this is typically directed at adult males.

5) Scream: This is a very loud vocalization performed during agonistic interactions. There are several types of screams, but the three that I could distinguish reliably enough to record were the staccato scream, the undulating scream, and the yelp (see sonograms).

6) Cower: One monkey crouches or leans away from a dominant monkey, in response to the dominant's approach or aggressive display.

7) Tail chew/lick: One monkey grabs its own tail and kneads, licks, and/or chews it rapidly. This is performed by monkeys who are the recipients of aggressive behaviors.

8) Lipsmack: The monkey smacks his/her lips together rapidly, often while chattering the teeth. These behaviors are generally performed in conjunction with the head shake and wrinkly face.

9) Wrinkly face: The monkey (usually an adult female, infant or juvenile) contorts the face so that it forms deep wrinkles. It is mainly the lips and nose area that are affected. The monkey continually and rapidly contorts the face.

Sexual/Reconciliation Behaviors

Many behaviors are common to both contexts, presumably because both are tense, ambivalent social interactions. Therefore, I am grouping them together even though sex and reconciliation have different functions. The first eight behaviors are performed in various combinations together as a suite of behaviors which I term the "dance." The main

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items that change from dance to dance are the type of vocalization produced and the presence or absence of piloerection. A dance may be followed by mounting, thrusting and rocking.

1) Duck face (=protruded lips [Oppenheimer 1973]): One monkey stares at another while protruding the lips so that they resemble a duck's bill.

2) Piloerection: The monkey's hair stands on end. This is much more common in males than in females.

3) Grunt: The monkey performs a loud, rhythmic series of low-pitched, forceful grunts.

4) Squeak sequence: The monkey does a quiet, rapid, rhythmic sequence of squeaks that ascend in pitch. This vocalization somewhat resembles the twitter. It is performed while making a duck face (i.e. with mouth closed).

5) Pirouette: The monkey fixes his/her gaze on another monkey, twists his/her head from side to side, spins his/her body around, and looks over the shoulder or under the arms or legs at the monkey to whom the behavior is directed. This is performed with a duck face.

6) Pacing: The monkey runs back and forth, while staring at another monkey. The pacer usually has a duck face. In a dance, both monkeys are pacing.

7) Intense gargle: (see entry for gargle under affiliative behaviors) This vocalization may be performed as a duet between dancing monkeys, usually in the context of reconciliation. It is louder and more rhythmic than the regular gargle.

8) Wheeze: This is a very high-pitched prolonged noise that descends in pitch. It is performed in the context of reconciliation only, and is generally produced in the same dance with the intense gargle duet.

9) Sexual mount: One monkey grasps the hips of another and positions the pair for sex.

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10) Mount and thrust (Oppenheimer 1973): One monkey grasps the hips of the other, clasps the mountee's legs with his/her feet, and repeatedly thrusts his/her pelvis against the genital region of the mountee

11) Mobile mount: The mountee locomotes while the mounter stays mounted and may continue to thrust; the mounter may put his/her feet back on the ground during mobile mounts rather than continuing to grasp the mountee's legs with them.

12) Ejaculation: This behavior is difficult to identify. It is accompanied by a rigid posture.

13) Rocking: When the two monkeys are in mount position, they rock back and forth.

Aggressive and Coalitionary Behaviors

1) Threat (=open mouth, bared teeth [Oppenheimer 1973]): The monkey opens the mouth so that the teeth are visible, lays the ears back, and stares at another monkey.

2) Vocal threat: While threatening, the monkey emits a soft squeak; the tongue generally flickers up and down while the squeaks are being produced, and the monkey may wag the tongue even between squeaks.

3) Intense vocal threat (=chortle [Oppenheimer 1973]?): While threatening, the monkey emits a sequence of loud bursts of sound.

4) Swipe: One monkey attempts to hit another monkey with its hand but does not make physical contact, generally because the victim dodges out of the way.

5) Hit (Oppenheimer 1973): One monkey hits another monkey.

6) Nip (=warning bite [Oppenheimer 1973]): One monkey bites another in a very restrained fashion.

7) Bite (Oppenheimer 1973): One monkey bites another without showing any restraint.

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8) Chase (Oppenheimer 1973): One monkey runs after another monkey without making contact.

9) Display posture (Oppenheimer 1973): The monkey stands stiffly with the limbs bent outward slightly; usually accompanied by piloerection and a threat face.

10) Piloerection (Oppenheimer 1973): The monkey's hair stands on end.

11) Tooth grind (Oppenheimer 1973): The monkey grinds its teeth together audibly.

12) Bounce (Oppenheimer 1973): The monkey bounces up and down, either on a branch or on the ground.

13) Branch shake (Oppenheimer 1973): The monkey grabs a branch and shakes it, usually while staring at an opponent.

14) Branch break (Oppenheimer 1973): The monkey breaks a branch and drops it to the ground while staring at the opponent.

15) Stiff walk (Oppenheimer 1973): The monkey locomotes quadrupedally with a stiff and jerky gait.

16) Pull (Oppenheimer 1973): One monkey grabs some body part (usually a limb) of another monkey and pulls on it.

17) Push (Oppenheimer 1973): One monkey shoves another monkey.

18) Lunge: One monkey moves his/her body toward the opponent in a quick gesture with the arms extended forward but does not make contact.

19) Supplant: One monkey approaches another monkey, taking the second monkey's spot (usually at a coveted resource) as the second monkey moves away.

20) Cough: The monkey produces a low-frequency 1-syllable noise resembling a cough. This is usually produced immediately prior to the monkey running toward an opponent.

21) Urine rub (Oppenheimer 1973): While urinating, the monkey puts his/her hand under the flow of urine and splashes the urine with the hand and one foot. Urine is

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sometimes rubbed on the tail and other limbs as well. This may not be an aggressive behavior, but it is most often performed in conjunction with aggressive behaviors.

22) Wrestle (Oppenheimer 1973): Two monkeys grapple with one another, using quick motions; often accompanied by grunts or screams.

23) Tail branch drag: A monkey (generally a male) grasps a fallen branch in his prehensile tail and runs along the ground, dragging the branch through the leaf litter.

24) Headflag (=glance [Oppenheimer 1973]): One monkey jerks his/her head toward a prospective coalitionary partner and then resumes staring at his/her opponent in an agonistic encounter. The monkey alternates rapidly between looking at the opponent and looking at the prospective partner.

25) Cheek-to-cheek threat: Two monkeys stand in contact with their cheeks together and jointly threaten a third party.

26) Overlord (Oppenheimer and Oppenheimer 1973; =double threat [Fedigan 1993]): One monkey gets on the back of another monkey and clasps his/her hands around the bottom monkey's chest so that their heads are stacked on top of one another. Overlords can be stacked up to 4 monkeys in height. They face toward an opponent monkey. Usually the monkeys are threatening the same opponent while in this position.

27) Embrace (=coordinated display [Oppenheimer 1973]): One monkey puts his/her arm over the shoulders of a coalition partner.

Play Behaviors

These behaviors are essentially the same as their counterparts described in the section on aggressive behaviors. The only difference is that they are often accompanied by a play face, are never accompanied by vocalizations, and are performed in a relaxed manner, often with exaggerated gestures.

1) Play face: The monkey's mouth is open, and the teeth do not show, with the exception of the tips of the canines.

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2) Play bite: One monkey gently mouths another monkey, generally in the context of play wrestling.

3) Play wrestle: Two or more monkeys grapple in slow motion with their arms, legs, and sometimes tail, in silence.

4) Play chase: One monkey gallops in pursuit of another monkey, generally with a bouncy gait, and with no accompanying vocalizations. Play chases are often invited by running away and looking over the shoulder at the other monkey.

5) Play hit: A monkey slaps another monkey with a slow, exaggerated motion, generally in the context of play wrestling.

6) Play lunge: A play lunge is identical to an aggressive lunge, except that it is always performed in silence and in the context of other play behaviors.

Food-related Behaviors

1) Food interest: One monkey approaches a feeding monkey and stares at the food at close range (even contact), often sniffing the food. Oppenheimer (1973) refers to"cheek-to-cheek" food interest, which is a subset of my category of food interest.

2) Food touch: One monkey touches another monkey's food.

3) Tolerated food transfer: The owner of the food allows the begging monkey to bite or take a portion of the food (i.e. the owner does not resist the food transfer).

4) Food-sharing: The owner of the food places some food in front of the beggar or places food in his/her hand or mouth.

5) Food theft: The beggar bites or takes food from the owner, and the owner responds aggressively or fearfully.

Mother/Infant Behaviors

These behaviors are generally performed in mother/infant dyads but can be performed by other age/sex/kin class combinations as well.

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1) Mount: The infant climbs onto the mother's back. This position is not the same as the sexual mount. The infant may ride virtually anywhere on the mother's body, but is typically on the shoulders, perpendicular to the mother's spine, for the first few weeks, and then rides jockey-style (i.e. with the spine parallel to the mother's) thereafter.

2) Dismount: The infant climbs off of the mother's back.

3) Push: The mother attempts to throw the infant off of her back.

4) Nurse: The infant suckles from the female. (Monkeys occasionally place their mouths on the nipples of males or other monkeys who are not lactating, but without making sucking motions with the mouth.)

5) Thwarted nursing attempt: The infant attempts to nurse, by reaching for the nipple with his/her hand or mouth, and the mother responds aggressively.

6) Tantrum: The infant flails its limbs, thrashes its tail (=tail rump waggle [Oppenheimer 1973]), and squirms in a spastic manner. This may be accompanied by screaming.

7) Ventral: The baby moves to the mother's ventrum and clings.

8) Ride invite: The mother approaches the infant and crouches while looking at him/her, so that the infant can get on her back.

Miscellaneous Vocalizations

1) Alarm call (=gyrrah [Oppenheimer 1973]): There are at least 3, probably 4, types of alarm calls, distinguishable from one another by structure and by the context that elicits them. All are raspy, one-syllable bursts of sound. The call used for boa constrictors and rattlesnakes is the shortest in duration and begins with a louder burst of sound than other alarms. Alarm calls for humans and other groups of white-faced monkeys are the longest in duration. Alarm calls for other monkey groups tend to be softer than other alarms. Bird alarms are intermediate in length between snake and human/monkey alarms. Terrestrial predator alarms seem to be a bit shorter than bird

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alarms, but I am not positive that they are acoustically distinct from the other alarm types. The first three types of alarms are sufficiently distinct that my two research assistants and I could reliably predict the type of organism that elicited the call before seeing the organism or direction of visual orientation of the calling monkey.

2) Lost call (=arrawh [Oppenheimer 1973]): This is probably the loudest vocalization, with the possible exception of the intense vocal threat. It consists of 1-3 raspy syllables and is used to establish contact with the group when a monkey is separated from the group and appears lost. Monkeys who are not themselves lost but who are responding to the call of a lost monkey produce the same call, but usually with fewer syllables than monkeys who are lost.

3) Burst-twitter-bray sequence: This is a sequence of vocalizations, beginning with some clear, almost bell-like bursts of sound, followed by a very loud twitter-like noise (ascending in pitch), followed by something resembling a donkey's bray, and ending with an intense gargle. This sequence is produced almost exclusively by the alpha male and seems to function in inducing the group to follow him.

4) Whine bark: This vocalization somewhat resembles an alarm call, but it is louder, and the syllables have much longer duration. It has a peculiar whiny quality to it. This was produced only by the ex-alpha male, following his downfall, and was produced at dawn each morning for a long time after his drop in rank, and also whenever he observed social situations which were apparently distressing to him (e.g. the new alpha male in consort with estrous females, or the new alpha male interacting affiliatively with females who used to be his own close affiliates).

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Table 1.1: Amount of data collected

Month	Contact hours	Focal hours
May 1990	26.92	0
June 1990	26.50	0
July 1990	47.58	11.33
August 1990	8.25	2.17
May 1991	44.28	4.00
June 1991	41.47	13.50
July 1991	153.25	58.67
August 1991	139.70	39.83
September 1991	10.80	2.33
October 1991	20.07	8.17
November 1991	84.67	29.33
December 1991	144.87	56.50
January 1992	151.32	72.83
February 1992	181.37	100.67
March 1992	194.93	87.00
April 1992	170.32	73.67
May 1992	131.40	52.17
June 1992	174.08	49.33
July 1992	199.77	35.33
August 1992	167.97	45.83
September 1992	0	0
October 1992	38.92	6.17
November 1992	201.03	49.67

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December 1992	239.37	86.00
January 1993	281.90	104.83
February 1993	267.63	136.50
March 1993	308.12	146.32
April 1993	294.20	130.33
May 1993	82.30	16.17

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Table 1.2: Composition of the study group.

Name	Sex	Age	Birth Date	Death date	Immigration Date	Mother (1st letter of name)	1st estrus date
Abby	F	adult					
Squint	F	adult					
Nanny	F	adult					
Wiggy	F	adult					
Tattle	F	adult					
Curmudgeon	M	adult					
Paul Bunyon	M	adult					
Guapo	M	adult					
Ichabod	M	adult			11/28/92		
Diablita	F	juvenile					11/92
Vandal	F	juvenile					
Quizzler	M	juvenile					
Kola	M	juvenile					
Hobbes	M	juvenile					
Unnamed	?	juvenile		~7/10/90			
Urchin	M	juvenile		~1/92?			
Mani	F	infant	~6/27/90			A	
Imp	?	infant	~6/27/90	9/90-4/91		T	
Broma	F	infant	5/18/91			S	
Juege	M	infant	~5/6/90			W	
Fester	?	infant	~5/7/91	1/24/92?		T	
Lizano	M	infant	7/8/91			N	
Rico	M	infant	~7/13/91			A	
Yoyo	M	infant	~7/16/91			W	
Eldritch	M	infant	4/8/92			T	
Omni	?	infant	5/5/93	5/7/93		A	
Uva	M	infant	~6/25/93			W	
Fiera	M?	infant	~7/3/92			D	
Loki	M?	infant	~8/1/93			N	
Vino	?	infant	2/28/94			A	
Unnamed	?	infant	~3/15/94			S	
Unnamed	?	infant	~3/15/94			T	

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Table 1.3: Interbirth intervals.

Female	Interbirth interval (months)	Infant death?
Abby	12.5*	no*
Abby	21.8	no
Abby	9.8	yes
Wiggy	14.3	no
Wiggy	23.3	no
Nanny	24.8	no
Squint	34.0	no
Tattle	11.3	yes
Tattle	11.0	yes
Tattle	23.5	no

*this assumes Mani to be Abby's infant; see text.

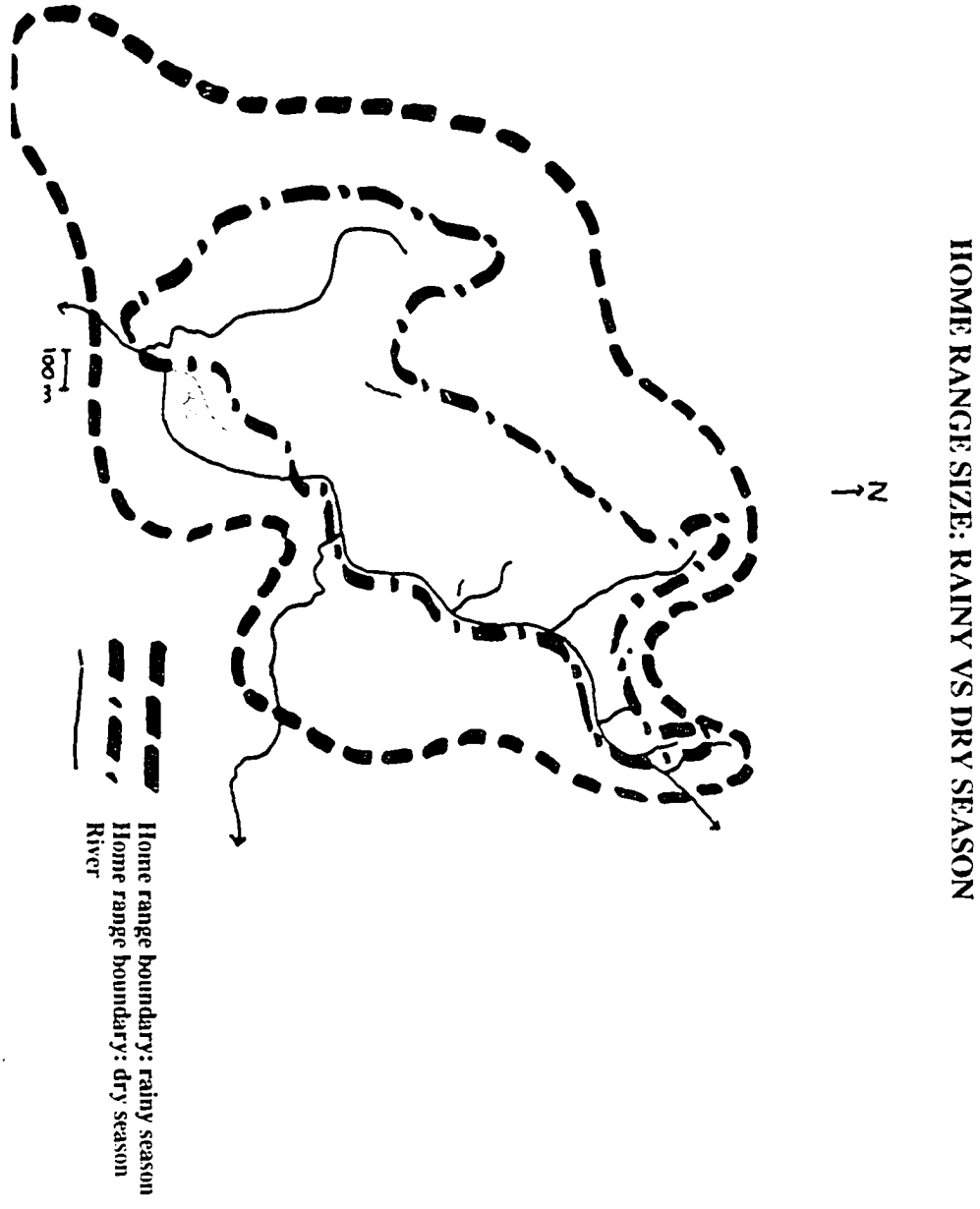
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Table 1.4: Plants used for fur-rubbing.

Family	Species	Common name	Part used
Caesalpiniaceae	*Caesalpinia eriostachys*	saíno	?
Caesalpiniaceae	*Hymenaea courbaril*	guapinol	sap
Melastomaceae	*Miconia argentea*		
Meliaceae	*Trichilia americana*	uruca?	green fruit
Mimosaceae	*Pithecellobium saman*	cenízaro	sap
Myrtaceae	*Eugenia salamanensis*		green fruit
Piperaceae	*Piper marginatum*	candelillos	leaves
Piperaceae	*Piper tuberculatum*	candelillos	immature infructescence
Solanaceae	*Capsicum* sp.	pepper	green fruit
Rutaceae	*Citrus* sp.	limón (lemon)	fruit
		naranjo (orange)	fruit
Theophrastaceae	*Jacquinia pungens*	siemprevivo, siempreverde	green fruit

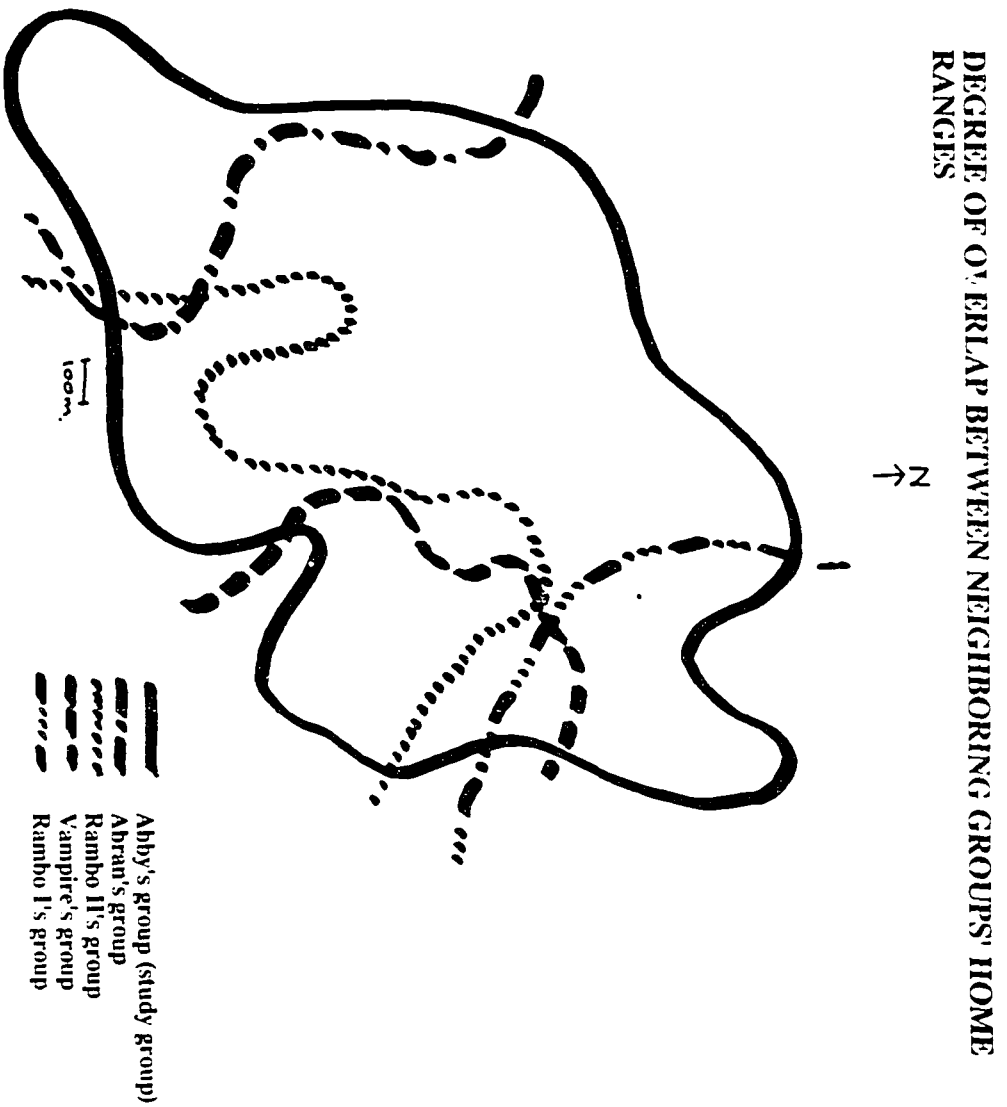
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Figure 1.1: Map of the study group's home range



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Figure 1.2: Home range overlap with other social groups



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CHAPTER II

FEMALE-FEMALE SOCIAL RELATIONSHIPS

Introduction

Female-female relationships (particularly grooming, coalitionary support, rank acquisition, and attraction to others' infants) have been studied extensively in catarrhines, but rarely in platyrrhines. Wrangham (1980) and van Schaik (1989) proposed ecological models of female-female relationships that should apply equally well to platyrrhines and catarrhines. Wrangham coined the term "female-bonded" to refer to primate societies in which females are philopatric and maintain long-term, differentiated, affiliative relationships with other females based on grooming, huddling, dominance interactions and/or coalitionary aid. He suggested that female-bonded societies will evolve when food is limited and is clumped in large, defensible patches, and when sufficient low-quality food exists to provide females with food at times when high-quality food is limited. Under these conditions, females are expected to form cooperative relationships with kin to compete with other groups of females to gain access to feeding sites. Thus, in Wrangham's model, the intensity of intergroup competition was considered to be the most important variable relevant to determination of the quality of female-female relationships. Van Schaik (1989) modified Wrangham's model by focusing more on intragroup competition and by making the important distinction between scramble competition and contest competition: When intragroup competition is mainly of the scramble variety, females are expected to have individualistic and egalitarian ranking systems, with or without female philopatry, whereas when intragroup contest competition is an important factor, female dominance hierarchies

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are expected to be more despotic and nepotistic, with female philopatry. When predation risk is very low, intergroup competition may predominate over intragroup competition, and females may form nepotistic but egalitarian ranking systems with female philopatry.

Most studies of female-female relationships (e.g. rhesus monkeys: Sade 1972; gelada baboons: Bramblett 1970, Kummer 1975; chacma baboons: Seyfarth 1977; stumptail macaques: Rhine 1972; vervets: Seyfarth 1980) have focused on female-bonded primates. Females in these species are philopatric, maintain close relationships with kin, spend large amounts of time grooming, and (in some species) exchange grooming for coalitionary support. Some, but not all, female-bonded species have matrilineal inheritance of rank in which older female kin assist younger females in female-female competition until they are capable of holding their own in one-on-one competition.

Strier (1990) has noted that inclusion of platyrrhines and prosimians in comparative studies of primates provides a way to test the generality of social models of primate behavior that were inductively derived from studies of catarrhines. A phylogenetic analysis using Rosenberger's (1992) phylogeny of the platyrrhines suggests that female philopatry evolved in the Cebus/Saimiri clade independently of its evolution in the cercopithecines, and that the primitive state in platyrrhines is for both sexes to disperse (Figure 2.1). Therefore, comparison of capuchin female-female social relationships with those of female-bonded cercopithecines is particularly interesting, because female philopatry may have evolved independently in the two lineages. Social and ecological models of female-female relationships derived inductively from catarrhine data can be tested on capuchin data without as much fear that common ancestry explains similarities between species.

Female-female grooming patterns in particular have been used as a diagnostic trait of female-bondedness, because grooming is a fairly ubiquitous primate trait; therefore, grooming patterns readily lend themselves to use in comparative analyses. However, there are certainly other means by which primates can service their important social relationships and signal willingness to provide coalitionary support. Some vocalizations are probably

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important for conveying information about social relationships (Seyfarth and Cheney 1993), and there may be species-typical behaviors -- e.g. greetings in baboons (Smuts and Watanabe 1990), hugging in muriqui (Strier 1992), wheeze dancing in white-faced capuchins (chapter 6), and G-G rubbing in bonobos (de Waal 1987) -- that function to negotiate particular aspects of relationships in primates. Although all of these other forms of social interaction are probably just as important conveyors of social information, the fact that they are species-specific makes them difficult to incorporate into comparative models. Therefore, grooming will be an important focus of this paper, as it has been in most other studies of female-female social relationships.

Seyfarth (1977) developed a model of grooming among adult female monkeys with the following features: (1) All females compete for the opportunity to interact with high-ranking females, who are the most valuable coalition partners. Thus, high-rankers receive more grooming than they direct, and grooming rates are disproportionately high among females with adjacent ranks. (2) Females preferentially groom with kin. The relative effects of kinship and rank on grooming decisions vary across groups and species. (3) Young infants are attractive to females; thus, females with new infants receive more grooming than do females without young infants.

Dunbar (1993), like Seyfarth, has suggested that grooming is a means by which females service important social relationships. Indeed, Dunbar argues that grooming is the *primary* regulator of primate social interactions. However, he explicitly states that grooming serves a social function only in catarrhines, and serves only a hygienic function in platyrrhines and prosimians.

In this chapter, I examine patterns of female grooming, coalition formation, alloparenting, proximity and aggression in white-faced capuchins. Results are compared with standard cercopithecine models, as well as with studies of female-female relationships in other capuchin species. I also evaluate Dunbar's conclusion that grooming in platyrrhines serves a purely hygienic function.

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Methods

Data were collected during 10-minute continuous focal animal samples, as described in chapter 1. The subjects of the analyses in this chapter were 6 adult females, one of whom matured to adulthood in October 1992, when she was first observed in estrus. Throughout the data tables in this chapter, females are listed in order of dominance rank, from top to bottom or from left to right. Females are referred to by the first letter of their names in all tables. Table 2.1 summarizes the amount of focal data collected on each female.

Behavioral Definitions

A coalition was defined as joint aggression by two or more individuals toward a third party. Coalitions sometimes consisted of two individuals threatening or chasing a third. Commonly, the coalition partners threatened the victim while in physical contact with one another. They stood cheek-to-cheek, embraced, or did an "overlord." An overlord (Oppenheimer and Oppenheimer 1973) was defined as two or more monkeys stacked on top of one another with their heads aligned, glaring at and/or threatening a third individual. The details of specific aggressive behaviors are defined in the ethogram in chapter 1.

Coalitionary rates were calculated by dividing the number of 10-minute samples in which coalitions by a given dyad toward a specific victim occurred by the total number of samples in which that coalition-victim triad could have interacted (i.e. all focal samples collected during time periods in which all 3 members of the triad were residing in the group). When more than two females formed a coalition, each dyad was scored separately. For example, if Abby, Squint and Nanny formed a coalition against Tattle during a Nanny sample, I scored coalitions of Abby-Nanny and Squint-Nanny against Tattle. If the same three monkeys formed a coalition against Tattle during a Tattle sample, I scored coalitions of Abby-Squint, Abby-Nanny, and Squint-Nanny against Tattle.

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Proximity scores were calculated in the following manner. For each female-female dyad, I tallied the number of times, during the final instantaneous scan of each 10-minute sample in both females' focal follows, that the females were within 0-1 body lengths, 1-5 body lengths, and 5-10 body lengths, of one another. I multiplied these three numbers by weighting factors, such that the closer proximity categories were weighted more heavily. The weighting factors were determined in the following way. Imagine 3 concentric spheres, with the focal animal at the center. The inner sphere has radius 1, the second largest sphere has radius 5, and the outer sphere has radius 10. The weighting value for the number of samples in which the animals of a dyad are within one length of one another is the reciprocal of the volume of a sphere of radius 1. The weighting value for the 1-5 body length category is the reciprocal of the difference between the volume of a sphere of radius 5 and the volume of a sphere of radius 1. The weighting value for the 5-10 category is the reciprocal of the difference between the volumes of spheres of radius 10 and radius 5. Thus, the equation for calculating the proximity score, P, is:

$$P=1{,}000(0.239a + 0.0019b + 0.0003c)$$

where "a" is the proportion of samples in which the dyad is within 1 length of one another, "b" is the proportion of samples in which the two animals are within 1-5 lengths of one another, and "c" is the proportion of samples in which the animals are within 5-10 lengths of one another. The sum of the three weighted values is multiplied by the arbitrary value of 1,000 simply to make the proximity scores more readable; otherwise, they would all be small fractions.

Proximity scores were calculated for two phases of data collection, corresponding to the "reigns" of the two alpha males (see Chapters 3,5). I divided the data into two phases because the male rank reversal had such a dramatic effect on all male-male, male-female and male-immature dyads' relationships, that I thought it was important to look for

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corresponding changes in female-female dyads' relationships. Because no such effect was found for female-female proximity patterns, I did not subdivide the data for the other analyses in this chapter.

On December 30, 1991, the method of recording grooming was changed from merely recording grooming as an event, to recording it as a state, with duration recorded in seconds. The change was made because there was large variation in the length of grooming bouts for many dyads that merely recording the number of bouts of grooming would not accurately represent the inequalities in ratio of grooming directed/grooming received for most dyads. Therefore, the grooming data presented throughout the dissertation are based only on data between December 30, 1991, and May 8, 1993.

Results

Dominance Hierarchy

Table 2.2 summarizes the directions of avoidance and cowering for all adult female dyads based on focal samples. There were very few dyads in which both females were observed to avoid or cower to one another. On the one occasion when Squint cowered to Nanny, Nanny had come up behind Squint and startled her; hence, Squint cowered before she saw who was approaching. On the one occasion when Nanny avoided Wiggy, Paul was following Wiggy, and it is probable that Nanny was really avoiding Paul. The instances in which Nanny and Wiggy cowered to or avoided Diablita may be instances of genuine ambivalence in the relationship, as Diablita was in the process of ascending the female dominance hierarchy. Females could be ranked in a linear hierarchy according to avoidance and cowering. One dyad, Wiggy/Tattle, did not avoid or cower to one another during focal observations, although Tattle was observed to behave submissively to Wiggy during ad lib observations. Appleby's (1983) adaptation of Kendall's (1962) test of linearity revealed that the females' dominance relationships displayed transitivity -- i.e. the

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observed pattern of dominance relationships was consistent with a linear hierarchy to a greater extent than would be expected by chance ($df=30$, $X^2=51$, $p<.05$).

Proximity

Adult females spent much more time with one another than they spent with males (Chapter 3, Table 3.21). Proximity scores for most male-male and male-female dyads changed by an order of magnitude or more following the rank reversal (chapters 3,4,5). However, as Table 2.3 demonstrates, adult females' proximity scores with one another remained fairly stable over time. The only notable change in female-female relationships brought about by the male rank reversal was that Tattle, the lowest-ranking female, became more peripheralized overall following the coup, and hence had lower proximity scores with other females (Table 2.3).

The following description of the data contributing to two data points may provide the reader with a better intuitive sense of what the proximity scores in Table 2.3 mean. Squint and Nanny, during the postcoup period, had a proximity score of 22.206, because they spent 9% of their time within one body length or in contact of one another, 4% of their time within 1-5 body lengths, and 2% of their time within 5-10 lengths of one another. Nanny and Tattle, during the postcoup phase, had a score of 0.501, because they spent 0.2% of their time within a body length, no time within 1-5 lengths, and 0.2% of their time within 5-10 lengths of one another.

Table 2.4 shows each female's proximity scores with other females, averaged across dyads. Most females had roughly equivalent scores, with the exception of Tattle in the postcoup phase, and Squint. If proximity scores are a good indication of social bonds, then Squint, the beta female, has the strongest network of female social partners.

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Grooming

When grooming rates were averaged across dyads for each individual, and then averaged across individual for each sex class, females groomed other females at a rate of 11.53 seconds/hour, which was twice as often as females groomed males, 43-68 times as often as males groomed other males (depending on whether precoup or postcoup data are used), and 144 times as often as males groomed females. Table 2.5 shows the rates of grooming for each female-female dyad between December 30, 1991 and the end of the study. Table 2.6 shows the ratio of grooming directed to grooming received for each dyad. Data from focal follows for both members of each dyad are included in these tables. There was a nonsignificant tendency for females to groom up the dominance hierarchy (Wilcoxon Matched Pairs test, n=15 dyads, T=35, p=.15; mean=14.3 s/hr up hierarchy, SD=11.17; mean=8.75 s/hr down hierarchy, SD=7.22).

Table 2.7 shows rank distances and grooming rates of female dyads sorted, from highest to lowest, according to their rates of grooming (including grooming in both directions). Those dyads who had a smaller rank distance groomed more often overall (Kendall Tau, n=15, tau=-.50, p=.0097). This result was stronger when only down-hierarchy grooming was considered (n=15, tau= -.54, p=.005) than when only up-hierarchy grooming was considered (n=15, tau=-.37, p=.054).

Table 2.8 shows the proportion of females' grooming invitations to females that were ignored. In general, those females who ignored the most grooming invitations were ignored the least. There was very little symmetry within dyads with regard to the proportion of grooming invitations ignored.

Because I did not record durations of grooming prior to December 1991, and 5 of the 6 births occurred during the summer of 1991, it is difficult for me to address the question of whether the presence of a new infant affects grooming rates, as predicted by Seyfarth's model. Examination of grooming data in the 2 months preceding and following the birth of Tattle's infant Eldritch, who was born April 7 1992, indicates that females are

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likely to be groomed more when they have new infants. Tattle was groomed by females at a rate of 2.3 seconds/hour during the 2 months prior to her infant's birth and 22.4 seconds/hour during the 2 months following her infant's birth.

Handsniffing

Handsniffing is a behavior engaged in only by adult female-female dyads. Typically, two females covered each other's noses with one hand or inserted their own fingers in their partner's nostrils, and both females deeply inhaled for a period of up to several minutes. Sometimes the females swayed back and forth while sniffing. Sometimes females sneezed, thus dislodging the partner's fingers from the nostrils, but they then grabbed the partner's hand and reinserted the fingers in their own nostrils. Handsniffing was initiated by either party. Nanny's handsniffing interactions were unusual in that she preferred to sniff her own hand rather than her partner's hand; she sniffed one of her hands while her partner sniffed her other hand. Sometimes Nanny and her partner disagreed about which hand the partner would sniff, and they struggled briefly before settling into handsniffing. Table 2.9 shows the proportion of 10-minute samples in which each dyad engaged in handsniffing. Rates of grooming were correlated with rates of handsniffing (Wilcoxon matched pairs test, n=15 dyads, p=.0007).

Allomothering

Females were often observed to nurse, carry, and groom one another's infants. It seemed that the period of 3-6 months of age -- the period during which infants were first beginning to explore extensively away from their mothers, yet remained dependent on milk for most of their nutritional needs -- was the period during which the most allonursing occurred. During this period, I frequently observed two separate infants nurse in quick succession from the same female, or two infants nursing simultaneously from the same female. Unfortunately, I could not reliably identify infants individually until March, 1992,

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when I marked them with hair dye. Therefore, Eldritch (born in April 1992) was the only infant who was individually recognizable for the entirety of the 3-6 month phase. Fester, who was the first infant of the 1991 birth crop, was independently locomoting before any of the other infants left their mothers' backs and could therefore be positively identified without marking; therefore I was able to collect some allonursing data on him during the summer of 1991. Aside from the data on Fester, all rates are based on adult female focal data collected after March 29, 1992, when all infants but Eldritch were over 10 months of age.

Table 2.10 shows the hourly rates of allonursing of all 6 infants born during 1990-1992 (see Chapter 1, Table 2 for birthdates of infants). All infants, with the exception of Eldritch, were born during May-July 1991. The mean rates of allonursing are calculated both with and without Fester in the sample for the following reason: not all females were known to be lactating on the two occasions when Squint nursed Fester, and therefore not all females were available as potential allonursers. Inclusion of the 1991 data means that Squint, the only available allomother for the only independently locomoting infant during much of the observation time, would have her allomothering rates biased toward a higher value because she had the opportunity to interact with a very young and frequently nursing infant who was not available to be nursed by other females. Ideally, I would control for infant age, but I do not have sufficient data to do so. Excluding data from Fester, higher-ranking females allonursed at lower rates than did lower-ranking females (n=5, tau=.95, p=.02). However, it appears that the rank of the infant's mother, relative to the rank of the allonursing female, is irrelevant. Females frequently nursed infants of lower-ranking females. I compared the rates at which infants nursed from females who were higher-ranking than their mothers to rates at which infants nursed from females lower-ranking than their mothers. This analysis was complicated by the fact that Tattle had two infants during the time that all other females had only one nursing infant. I did this analysis two ways: once counting Fester as Tattle's infant, and once counting Eldritch as Tattle's infant, and

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the results were qualitatively similar. Either way, there was a nonsignificant tendency for infants to nurse from females lower-ranking than their own mothers, but the results reported here count Eldritch, rather than Fester, as Tattle's infant (Wilcoxon: n=10, mean rate of nursing from higher-ranked female=.027, SD=.024, mean rate of nursing from lower-ranked female=.04, SD=.038; T=16, p=.44). Within each adult female dyad, I compared the rate at which the higher-ranking female nursed the lower-ranking female's infant to the rate at which the lower-ranking female nursed the higher-ranking female's infant, to determine whether mothers engaged in reciprocal exchanges of allonursing services. No correlation was found (Kendall: n=10, tau=.133, p=.59). Again, the results were the same, whether I included Fester or Eldritch as Tattle's infant, but the exact figures reported are those including Eldritch.

Table 2.11 shows the proportion of samples in which females were observed to carry infants other than their own. Infants and juveniles up to 3 years of age were carried by adults. Diablita, the nulliparous female, engaged in the most allocarrying. Tattle, who had a young infant of her own for the greatest amount of time due to the early death of her '91 infant, engaged in the least allocarrying. Eldritch and Fester, those infants who were youngest on average during the observation periods, were carried by allomothers the most frequently. Of the four '91 infants who survived until the end of the study, Broma, the only female, was carried by allomothers the most often. It is striking that Abby carried Squint's infant Broma so often, whereas Squint never carried Abby's infant. Although male infants Rico and Lizano were carried at a very low rate by allomothers, they were frequently carried by adult male Guapo.

Aggression

Tables 2.12-2.14 show the rates of female-female aggression for total aggression, mild aggression, and severe aggression, expressed as the proportion of 10-minute samples in which aggression occurred. Severe aggression included physical contact aggression and

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chases; all other forms of aggression were termed mild aggression. The dyad that exhibited the most aggression, both severe and mild, was Diablita/Wiggy. Diablita frequently launched unprovoked attacks on Wiggy, apparently as a way of acquiring and reinforcing her new place in the dominance hierarchy. Aggression was directed primarily down the hierarchy (Wilcoxon matched pairs test: n=15, T=.000000, p=.001; mean up hierarchy = .001, SD=.001; mean down hierarchy = .010, SD=.013). When aggressing against lower-ranking females, females were more aggressive to females with a small rank distance from themselves (Kendall: n=15, tau=-.739, p=.0001). When aggressing against higher-ranking females, there was no tendency for females to be more aggressive to females with a smaller rank distance from themselves (Kendall: n=15, tau=-.235, p=.19). Although low-rankers were more often the victim of attack (Kendall: n=6, tau=.788, p=.03), high-rankers were not necessarily more aggressive than low-rankers (Kendall: n=6, tau=-.358, p=.30).

Food-related Social Interactions

Forced food theft was a very rare occurrence, observed only 4 times during focal observations of females. Twice, a higher-ranking female stole from a lower-ranking female, and twice a lower-ranking female stole from a higher-ranking female. Fruits were stolen on 3 occasions, and the fourth theft was of a coati pup. There were also 3 unsuccessful theft attempts by low-rankers toward high-rankers. Table 2.15 shows female supplants of other females at food and treeholes containing water. All but one of the 43 supplants were by higher-ranking females toward lower-ranking females. Table 2.16 shows the tolerated thefts between females. Tolerated food thefts differed from forced food thefts in that no fear or resistance was displayed by the food owner when the food was taken. Eight of the 12 tolerated food thefts during focal follows involved higher-ranking females taking food from lower-ranking females. There was also one incidence of food sharing, in which Tattle placed a partially-eaten coati carcass in front of Wiggy and

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then walked away. Wiggy sniffed the carcass but did not consume it (see Perry & Rose 1994).

Female-female Coalitions Versus Females

Table 2.17 shows the proportion of samples in which females formed coalitions against other females. In no case did two females form a coalition against a female who was higher-ranking than both of them. In 43 of 45 cases, the victim was lower-ranking than both coalition partners. In the two remaining cases, the victim was intermediate in rank between the two coalition partners. In both of these cases, an adult male also participated in the coalition, and in one case the female being victimized was mating with an adult male. Higher-ranking female-female dyads tended to form coalitions against other females at a higher rate than did lower-ranking dyads (Kendall tau, mean rank of coalition dyad vs. mean rate of coalition formation against other females: n=15, tau=-.555, p=.004).

In 11 instances during focal observations, females solicited coalitionary aid from higher-ranking females by headflagging, and the higher-ranking female ignored the request for aid. In 10 of these cases, the solicitor's victim was lower-ranking than both females. In the remaining case, Squint denied Diablita aid against Abby, who outranked both of them.

Those adult female dyads that groomed more frequently also formed coalitions at a higher rate, both against females (Kendall: n=15, tau=.557, p=.004) and against males (Kendall: n=15, tau=.468, p=.015). Figures 2.2 and 2.3 show coalition rates plotted against grooming rates for female-female coalitions against females and males. When mean rank of the coalition dyad was held constant, there was still a significant correlation between grooming rate and coalition rate against female victims (n=15, tau=.481, p<.02), but not between grooming rate and coalition rate against male victims (n=15, tau=.374, p < .1). The correlation between average rank of the coalition dyad and rate of coalition formation was highly significant for coalitions against both adult male victims (Kendall:

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n=15, tau=-.778, p=.00005) and adult female victims (tau=-.555, p=.004). Chapter 4 provides more details about female-female coalitions against males.

Table 2.18 summarizes the contexts in which female-female coalitions against females occurred. Thirteen of the 36 coalitions were classified as "unprovoked": that is, they occurred when the females in the coalition had not been foraging or socializing with one another. The fact that these unprovoked conflicts occurred disproportionately among adjacently-ranked dyads including young females (i.e. females who had recently acquired their rank) indicates that these conflicts may have served to reinforce dominance relationships. Abby and Squint formed 10 coalitions against Nanny, 8 of which were initiated by Squint. Diablita formed 11 coalitions with various females against Wiggy, 10 of which were initiated by Diablita. Abby, Squint, and/or Nanny were Diablita's partners in coalitions against Wiggy in 10 of the coalitions against Wiggy. Tattle was Diablita's partner in the one remaining coalition against Wiggy, in which they threatened Curmudgeon and Wiggy as they mated.

Adjacently-ranked Dyads

Three of the 5 adjacently-ranked dyads (Abby/Squint, Squint/Nanny, and Diablita/Wiggy) were notable for the strength and/or the ambivalence of their social relationships. These three dyads had the three highest grooming scores of any adult dyad. Diablita/Wiggy had the highest aggression score of any female-female dyad, followed by Squint/Nanny. The only female-female dyads observed to wheeze-dance were adjacently-ranked dyads; wheeze dancing is hypothesized to be a relationship-negotiating behavior, exhibited primarily by dyads with tense relationships (see chapter 6). Abby and Squint had the highest rate of coalition formation, both against males and against females, of any dyad. Squint and Nanny also formed coalitions at a high rate: they had the second-highest rate of coalition formation versus males, and the fourth highest rate of coalition formation versus

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females. Diablita and Wiggy never formed coalitions against females, and had a low rate of coalition formation against males (8th of 15 female-female dyads).

Abby and Squint exhibited low rates of aggression toward one another. The few times that Abby was observed to aggress against Squint were quite striking because of Squint's unusual response. Instead of reciprocating the threat, soliciting aid, or attacking a third party, as Squint normally did when threatened by anyone but Abby, Squint responded by emitting blood-curdling screams while staring into space; these screams were louder than screams uttered by Squint in any other context. Because most of these events were witnessed during ad lib observations, I do not know the exact latency to subsequent social interactions between Abby and Squint, but they were typically seen affiliating or forming coalitions within a few minutes after Abby's attacks. Abby and Squint had the highest rate of wheeze dancing of any female-female dyad (chapter 6), which may indicate a high degree of tension in their relationship. Some of these wheezes occurred when the Squint/Abby alliance was being threatened. Attempts by the alpha male to break up Abby and Squint's alliance produced extreme emotional responses in both females (see chapter 4 for descriptions).

Squint, Abby and Nanny formed the central core of the group, as measured by proximity scores (Table 2.4). Although Squint had even higher proximity scores with Nanny than with Abby (postcoup), as well as higher grooming and hand-sniffing scores with Nanny than with Abby, Squint had much higher coalition rates with Abby than with Nanny (Table 2.17, chapter 4 Table 4.33). Sometimes when Abby, Squint and Nanny were all sitting together, Squint bullied Nanny and recruited Abby's aid, as if to remind Nanny that Squint was higher-ranking than Nanny and an ally of Abby's. The following episode, which took place June 17, 1992, exemplifies this sort of interaction between the Squint-Nanny-Abby triad:

Squint was sitting with Abby while grooming Nanny, who was lying down faced away from Squint. Squint stopped grooming Nanny, sniffed her, and threatened her.

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Squint yanked Nanny's foot, but Nanny ignored her. Abby overlorded over Squint at Nanny, and both Abby and Squint threatened Nanny. Nanny closed her eyes, as if to sleep. Squint pushed Nanny and vocally threatened her; Nanny, with her eyes still closed, clenched the branch with her hands and feet and braced herself so as not to be dislodged from the tree. Abby lay on top of Squint as Squint repeatedly shoved Nanny, while holding Nanny by one foot so that she could not escape. Squint vocally threatened Nanny as she tried to squirm out of Squint's grasp. Squint chewed on Nanny's foot. Juvenile male Hobbes approached and climbed on Abby's back in a triple overlord (Hobbes over Abby over Squint) against Nanny. Squint screamed, and Nanny produced an odd warbling vocalization that I did not recognize. Nanny broke free and fled. Hobbes threatened Nanny. Squint, Abby and Hobbes all vocally threatened Nanny, who chewed her own tail. Hobbes approached Nanny, mounted and thrust on her, and was slapped by Nanny.

Diablita frequently groomed and played with Wiggy, and she also had close relationships with Wiggy's sons, whom she frequently groomed, carried and played with. However, Diablita's play bouts with Wiggy often became aggressive, and Diablita often launched unprovoked attacks on Wiggy. The vocalizations accompanying Diablita's attacks on Wiggy were atypical. Instead of doing the standard vocal threats, Diablita usually screamed at Wiggy (as if Diablita were the victim rather than the attacker) and produced a coo-like vocalization that was produced only rarely by other monkeys, and usually by immature monkeys who were the victims of coalitionary attacks. Wiggy very rarely reciprocated the threats. Sometimes she turned her back on Diablita, as if trying to ignore her screams and threats. Diablita was usually successful in recruiting aid from high-ranking females, who chased Wiggy. Even after Wiggy had been chased away, Diablita persisted in harassing her for several minutes, until all other females had lost interest.

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Discussion

Are White-faced Capuchins Female-bonded?

Several lines of evidence indicate that white-faced capuchins are female-bonded -- i.e. that females maintain long-term, differentiated, affiliative relationships with other females based on grooming, close proximity, dominance interactions, and coalitionary aid (Wrangham 1980). Female-female dyads, relative to female-male or male-male dyads, spent more time in proximity. Females groomed one another approximately 55 times as often as males groomed one another. Females supported one another frequently against males, whereas males never supported one another against females. Female-female relationships were relatively stable throughout the study, whereas male-male and male-female relationships changed dramatically over the course of the study (chapters 3-5). Female relationships were highly differentiated, with some dyads consistently supporting one another against other females. Rank was a good predictor of patterns of coalitionary aid.

White-faced capuchin data provide marginal support for Seyfarth's model of grooming in female-bonded monkeys. There was a nonsignificant tendency for grooming to be directed up the dominance hierarchy. As predicted by the Seyfarth model, those dyads with smaller rank distances groomed more often. I do not know the kinship relationships of the adult females in my study group; therefore I could not assess the affects of kinship on grooming preferences. The limited data available suggest that females with new infants were groomed more than females without new infants.

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Comparisons with Other Capuchin Species

Grooming

Female-female allogrooming has been thoroughly studied in only one other capuchin species: the wedge-capped capuchin, *Cebus olivaceus*. Contrary to what I found, O'Brien (1993) found that female wedge-capped capuchins preferentially directed grooming down the dominance hierarchy. O'Brien interprets his results as signifying that grooming -- at least, in dyads consisting of females with disparate ranks -- serves an appeasement function: low-ranking females solicit grooming from approaching high-ranking females as a way of diverting high-rankers from attacking them. Grooming in O'Brien's (1993) study was not more frequent among adjacently ranked females, despite the fact that adult females of adjacent rank were more consistently nearest neighbors (O'Brien and Robinson 1993).

In other ways, O'Brien's results were consistent both with my findings and with Seyfarth's model. Females with new infants (age 1-2 months) were groomed more often than females without new infants. Female dyads that groomed more often also formed coalitions more often, even after controlling for dominance rank.

The only other published results of rank effects on patterns of female-female grooming in capuchins are Janson's (Janson and Robinson 1987): In a wild group of *Cebus apella*, the alpha female received nearly twice as much grooming as she directed.

Handsniffing

Handsniffing has only been reported at one other capuchin site: Santa Rosa National Park, where Linda Fedigan and her colleagues have studied *C. capucinus* over the past decade (Fedigan, 1993). Interestingly, handsniffing occurs almost exclusively in male-female dyads at Santa Rosa (Fedigan, pers. comm.), whereas it occurs only in female-female dyads at Lomas Barbudal. Fedigan hypothesizes that hand-sniffing is

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related to olfactory communication, as urine is frequently rubbed on the palms of the hands and feet. Whereas it is easy to imagine a reason why males would benefit from gaining access to information about females' hormonal profiles (i.e. to determine when females are fertile), it is more difficult to imagine why females would need such information about one another. Perhaps, if there were a benefit to coordinating the timing of births, females could gain access to information about their female companions' hormonal states via olfactory cues, as has been proposed for other female mammals (McClintock 1978). However, in the absence of data on hormonal mechanisms of female reproduction, such speculations are untestable. Alternatively, bonding could be enhanced via transmission of semiochemicals during handsniffing (Nicholson 1984), or females could be exchanging information about their recent foraging or social activities.

Females at my study site virtually never urine rub, so levels of urinary hormones are not likely to be the type of information transmitted by handsniffing between females at Lomas; nonetheless, it seems likely that some form of chemical communication is occurring. I did not notice any tendency for females to touch particular parts of their bodies prior to handsniffing. Nor did I notice a tendency for females to sniff one another's hands more often during a foraging context or after eating certain foods; thus, it seems unlikely that females are exchanging information about food sources. But these data weren't collected systematically, so further research is needed to examine these hypotheses.

Allomothering

Allomothering has previously been studied only in the wedge-capped capuchin. O'Brien (1988) reported that, in 13 observations of allonursing in 4 adult female/infant dyads, the "infant's rank" (presumably meaning the infant's mother's rank) was always higher than the nursing female's rank. Thus, he interpreted allonursing as being parasitic. Although I found that lower-ranking females engaged in more allonursing than did higher-ranking females, the ranks of infants' mothers were not consistently higher than the

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allonurser's ranks. Therefore, even though low-rankers still bear more of the costs of allonursing than do high-rankers, allonursers were more willing to nurse lower-ranking infants in *C. capucinus* than in *C. olivaceus*. O'Brien's results are consistent with Packer et al.'s (1992) observations that allonursing tends to be parasitic and that milk is generally stolen from allomothers by infants in monotocous species. However, in my study, the females did not typically resist nursing by other females' infants, and they sometimes invited nursing by lifting their arms so as to expose the nipple to the infant.

Because infants are often widely separated from their foraging mothers, even in the first few months of life, it is often difficult for infants to locate their mothers when they need to nurse. Therefore, there could be a great advantage to infants in being able to nurse from the closest lactating female. Even if not all females engaged in allonursing at equal rates, allonursing could be an evolutionarily stable strategy because the cost of giving a small amount of milk to a distantly related infant may be small compared to the benefit of having one's infant receive the same amount of milk from an allomother during a time in which the mother is separated from the group for such a long period of time that the infant could dehydrate or starve without milk. Once, during the pilot study in 1990, Wiggy became separated from the group for 2-5 days, and her 2.5-month-old infant Juege would almost certainly have died, had he not received milk from allomothers. Cheaters could be detected and discriminated against if infants threw noisy tantrums when denied milk by allomothers (which they sometimes do).

Grooming in White-faced Capuchins: Hygienic or Social?

Dunbar (1991, 1993) assumes that platyrrhine grooming serves a primarily hygienic function, because body size explains more inter-specific variance in grooming rates than does group size in platyrrhines, relative to catarrhines. Data from this study, as well as from O'Brien's (1993) study, suggest that grooming serves a social function in capuchins, as in catarrhine primates. The findings that (a) grooming rates correlate with

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rates of coalition formation across dyads, (b) grooming rate varies as a function of the relative rank distance between females, and (c) grooming rates vary as a function of a female's infant's age, are difficult to reconcile with the notion that grooming serves a purely hygienic function. Thus, as argued by Snowdon (1993), Dunbar's (1993) exclusion of platyrrhines from his analysis of the relationships among group size, grooming rate and neocortex size in primates is unjustified, at least for the genus *Cebus*. It remains a possibility that grooming does not serve the same "social glue" function in other platyrrhines (Glezer and Kinzey 1993, Dunbar 1991); if this is the case, then use of grooming to service relationships may be yet another way in which capuchins have converged with female-bonded cercopithecines.

Advantages to Being High-ranking

Costs and benefits of social life were not equally distributed among females in this study, and they tended to vary according to rank. Aggression was 10 times more likely to be directed down the hierarchy as up the hierarchy. Therefore, it is possible that low-ranking females incurred more costs than high-ranking females, due to wounding, stress, and possibly reproductive suppression (though the limited demographic data available from my site do not indicate that low-rankers have longer interbirth intervals than high-rankers). Supplants at feeding sites were directed down the hierarchy 42 times as often as they were directed up the hierarchy, so it is likely that low-rankers had inferior access to preferred food sources. High-ranking females tended to be located in the spatial center of the group, whereas the low-ranking females were more often located on the periphery of the group. Therefore, low-ranking females are probably more vulnerable to predation. Indeed, the lowest-ranking and most peripheral female of the group lost 2 of her 3 infants due to unknown causes, whereas only one of the other females lost an infant, and that infant appeared to have died of an umbilical hernia rather than predation. High-ranking females bore less of the cost of allonursing than did low-rankers, although they appeared to receive

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approximately equal benefits. There was a nonsignificant tendency for females to groom up the hierarchy rather than down, indicating that high-ranking females may receive more of the benefits of grooming than do low-rankers. High-ranking females both gave and received coalitionary aid significantly more often than did low-rankers.

Socioecological Models of Female-female Relationships

White-faced capuchins conform well to van Schaik's predictions about the nature of female-female relationships. Although I did not collect rigorous quantitative data on feeding competition, it seems likely that intragroup feeding competition has a strong contest component to it. The study group relied heavily on fruits such as *Sloanea terniflora*, *Jacquinia pungens*, *Sterculea apetala*, *Chomelia spinosa*, *Ficus*, and *Bromelia pinguin*, which were distributed in defensible patches, and disputes often occurred in the context of feeding on these fruits.

As predicted by van Schaik's model for a species in which intragroup contest competition in strong, female white-faced capuchins have a stable, linear dominance hierarchy. Females frequently formed coalitions, both against males and against females. Female-female coalitions against females almost invariably supported the existing hierarchy. In contrast with Wrangham's (1980) model, but consistent with van Schaik's (1989) model, females rarely participate in intergroup aggression (see chapter 7).

The role of kinship in determining the pattern of female-female interactions has yet to be determined. It is possible that female kin aid immature females in acquiring a place in the dominance hierarchy just below the mother's rank, as in macaques, but further data are needed to confirm this possibility. The tendency for closely ranked females to groom frequently and for certain adjacently-ranked dyads to have strong alliances is consistent with the idea that female capuchin social relationships are nepotistic.

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Table 2.1: Focal data collected on adult females.

Female	Hours
Abby	110.83
Squint	111.00
Nanny	110.50
Diablita	48.00
Wiggy	113.50
Tattle	109.83

Table 2.2: Avoidance and cowering within adult female dyads.

	Recipient					
Actor	A	S	N	D	W	T
A	---	0	0	0	0	0
S	1	---	1	0	0	0
N	4	9	---	1	1	0
D	2	3	4	---	1	0
W	4	3	2	2	---	0
T	1	7	3	1	0	---

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Table 2.3: Proximity scores for adult female dyads, before and after the male rank reversal.

Dyad	Pre-coup	Post-coup
AS	18.306	18.134
AN	6.285	4.528
AD	1.065	7.210
AW	5.258	3.043
AT	1.973	1.020
SN	13.961	22.206
SD	7.382	9.290
SW	6.072	4.013
ST	4.804	1.012
ND	5.309	2.723
NW	5.304	3.984
NT	3.418	.501
DW	6.171	8.276
DT	8.311	1.673
WT	6.606	2.557

Table 2.4: Females' proximity scores with other females, averaged across dyads; females are listed in order of rank, from highest to lowest.

Female	Precoup	Postcoup
Abby	6.577	6.787
Squint	10.105	10.931
Nanny	6.855	6.788
Diablita	5.648	5.834
Wiggy	5.882	4.375
Tattle	5.022	1.353

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Table 2.5: Rates of female-female grooming, seconds/hour, between 12/30/91 and 5/8/93.

	Recipient						
Actor	A	S	N	D	W	T	Mean
A	---	5.8	3.5	2.1	2.3	0.04	2.7
S	41.6	---	28.6	18.1	9.0	7.4	20.9
N	10.3	25.5	---	9.6	9.9	4.3	11.9
D	23.3	9.3	10.5	---	13.4	6.9	12.7
W	21.2	15.2	14.6	25.1	---	10.4	17.3
T	2.5	2.9	3.7	3.6	5.3	---	3.6
Mean	19.8	11.7	12.2	11.7	8.0	5.8	11.5

Table 2.6: Ratio of grooming directed to grooming received for female dyads.

	Partner					
Ego	A	S	N	D	W	T
A	---	.14	.34	.09	.11	.02
S	7.1	---	1.1	1.9	.59	2.6
N	3.0	.89	---	.91	.68	1.2
D	11.3	.52	1.1	---	.54	2.0
W	9.4	1.7	1.5	1.9	---	2.0
T	62.0	.39	.86	.51	.51	---

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Table 2.7: Female-female dyads' dominance rank distances and grooming frequencies (in both directions), ranked according to rates of grooming.

Dyad	Dominance rank distance	Grooming (s/hr)
SN	1	54.1
AS	1	47.4
DW	1	38.5
SD	2	27.4
AD	3	25.4
NW	2	24.5
SW	3	24.2
AW	4	23.5
ND	1	20.1
WT	1	15.7
AN	2	13.8
DT	2	10.5
ST	4	10.3
NT	3	8.0
AT	5	2.5

Table 2.8: Proportion of grooming invitations ignored; total number of invitations for grooming is in parentheses.

	Responder						
Inviter	A	S	N	D	W	T	Mean
A	---	.27	.30	.34	.22	.54	.33
		(107)	(43)	(35)	(64)	(13)	
S	.71	---	.33	.44	.24	.48	.44
	(90)		(158)	(41)	(49)	(25)	
N	.61	.51	---	.66	.42	.54	.55
	(28)	(225)		(32)	(112)	(26)	
D	.75	.40	.33	---	.43	.56	.49
	(32)	(65)	(24)		(101)	(18)	
W	.69	.46	.46	.56	---	.57	.55
	(52)	(56)	(89)	(90)		(44)	
T	.56	.36	.42	.27	.26	---	.37
	(9)	(28)	(19)	(15)	(50)		
Mean	.66	.40	.37	.45	.31	.54	.45

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Table 2.9: Female-female dyads, ranked in order of proportion of samples in which they handsniffed.

Dyad	% of samples with handsniffing
SN	3.01
SW	1.3
SD	.75
NW	.60
ND	.45
AS	.45
DW	.30
ST	.30
WT	.20
AN	0
AD	0
AW	0
AT	0
NT	0
DT	0

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Table 2.10: Hourly rates of allonursing (number of observations in parentheses).

	Allonurser					
Infant	A	S	N	W	T	Mean
R	---	.02 (1)	.03 (2)	.03 (2)	.02 (1)	.025
B	.03 (2)	---	.02 (1)	.10 (6)	.03 (2)	.045
L	0	0	---	0	.03 (2)	.007
Y	0	.02 (1)	.03 (2)	---	.12 (7)	.042
F	0	.14 (2)	0	0	---	.035
E	.02 (1)	.05 (3)	.07 (4)	.05 (3)	---	.047
Mean w/F	.01 (3)	.05 (7)	.03 (9)	.04 (11)	.04 (12)	
Mean w/out F	.01 (3)	.02 (5)	.04 (9)	.04 (11)	.05 (12)	

Table 2.11: Percentage of female focal samples in which allocarrying was observed.

	Female						
Infant	A	S	N	D	W	T	Mean
R	---	0	0.2	1.1	0	0.5	0.4
B	3.0	---	0.9	1.1	1.6	0.2	1.4
L	0.2	1.2	---	0.4	0.2	0.2	0.4
Y	0.5	0.2	0.7	2.5	---	0.2	0.8
F	0	2.5	0	---	3.7	---	1.5
E	0.6	2.3	1.4	5.1	2.0	---	2.3
M	---	0	0.3	0	0	0.3	0.1
J	0	0	0	0.7	---	0.6	0.3
Mean	0.7	0.9	0.5	1.6	1.2	0.2	0.9

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Table 2.12: Proportion of female focal samples containing aggression.

	Recipient						
Actor	A	S	N	D	W	T	Mean
A	---	.003	.008	0	.007	.007	.005
S	.003	---	.015	.011	.006	.007	.008
N	0	.002	---	.011	.006	.008	.005
D	0	.002	.002	---	.055	.008	.013
W	0	0	0	.003	---	.004	.001
T	0	0	.001	.002	.003	---	.001
Mean	.001	.001	.005	.005	.015	.007	.007

Table 2.13: Proportion of female samples containing mild aggression.

	Recipient						
Actor	A	S	N	D	W	T	Mean
A	---	.002	.008	0	.006	.007	.005
S	.002	---	.011	.009	.006	.006	.007
N	0	.0008	---	.011	.006	.006	.005
D	0	.002	0	---	.054	.008	.013
W	0	0	0	.001	---	.004	.001
T	0	0	0	.002	.001	---	.001
Mean	.000	.001	.004	.005	.015	.006	.006

Table 2.14: Proportion of female samples containing severe aggression.

	Recipient						
Actor	A	S	N	D	W	T	Mean
A	---	.002	0	0	.0007	.002	.001
S	0	---	.007	.003	0	.0008	.002
N	0	.0008	---	.002	.0007	.002	.001
D	0	0	.002	---	.01	.002	.003
W	0	0	0	.001	---	.0007	.000
T	0	0	.0008	0	.001	---	.000
Mean	0	.001	.002	.001	.002	.001	.001

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Table 2.15: Supplants at food and water during focal observations.

	Supplantee					
Supplanter	A	S	N	D	W	T
A	---	2	2	1	5	2
S	0	---	10	2	7	1
N	0	0	---	2	3	3
D	1	0	0	---	1	1
W	0	0	0	0	---	0
T	0	0	0	0	0	---

Table 2.16: Tolerated food thefts between females during focal observations.

	Food Owner					
Thief	A	S	N	D	W	T
A	---	1	0	0	0	0
S	1	---	2	0	2	0
N	1	0	---	0	0	1
D	0	0	0	---	1	1
W	0	1	0	0	---	0
T	0	1	0	0	0	---

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Table 2.17: Proportion of focal samples in which female-female coalitions against females occurred (number of coalitions in parentheses).

	Victim						
Coalition	A	S	N	D	W	T	Total
AS	---	---	.0050 (10)	.0029 (3)	.0015 (3)	.0005 (1)	.0099 (17)
AN	---	0	---	0	.0015 (3)	0	.0015 (3)
AD	---	0	0	---	.0038 (4)	0	.0038 (4)
AW	---	0	.0005 (1)	0	---	0	.0005 (1)
AT	---	0	0	0	0	---	0
SN	0	---	---	.0029 (3)	.0005 (1)	.0005 (1)	.0039 (5)
SD	0	---	0	---	.0029 (3)	.0029 (3)	.0058 (6)
SW	0	---	0	0	---	.0005 (1)	.0005 (1)
ST	0	---	0	0	0	---	0
ND	0	0	---	---	.0038 (4)	.0010 (1)	.0048 (5)
NW	0	0	---	0	---	.0010 (2)	.0010 (2)
NT	0	0	---	0	0	---	0
DW	0	0	0	---	---	0	0
DT	0	0	0	---	.0010 (1)	---	.0010 (1)
WT	0	0	0	0	---	---	0

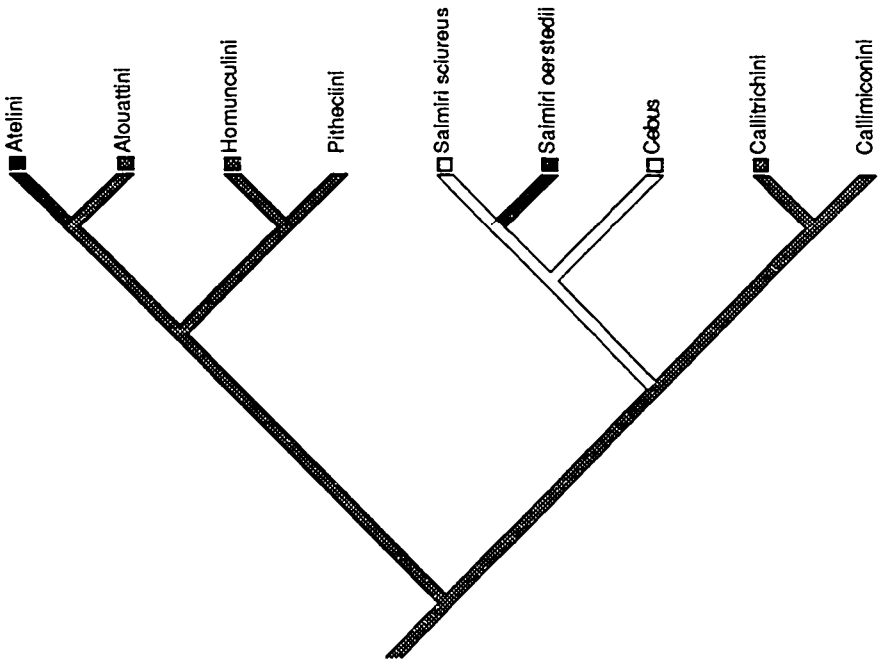
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Table 2.18: Contexts of conflicts in which 2 or more adult females formed a coalition against an adult female.

Unprovoked attack by coalition initiator on victim	13
Feeding competition	9
Coalition initiator breaks up affiliative, coalitionary, or sexual interaction between victim and third party	4
Coalition victim fights with juvenile	4
Coalition initiator redirects aggression toward coalition victim	2
Play bout turns to aggression	1
Conflict preceded by fight between coalition victim and third party	1
Conflict preceded by tantrum by coalition victim's infant toward a member of the coalition	1
Unknown	1

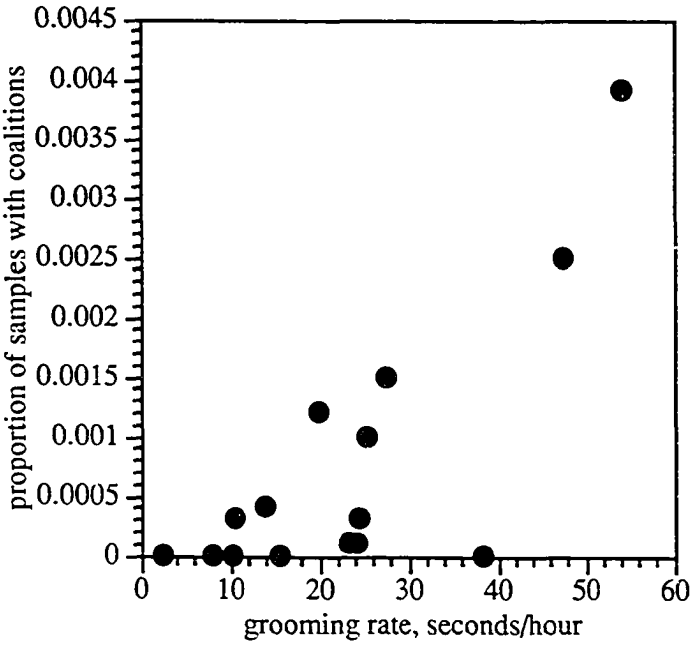
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Figure 2.1: MacClade phylogenetic tree showing modes of dispersal in the platyrrhines; Rosenberger's phylogeny of the platyrrhines is used. Black=male philopatry, white=female philopatry, grey=both sexes disperse



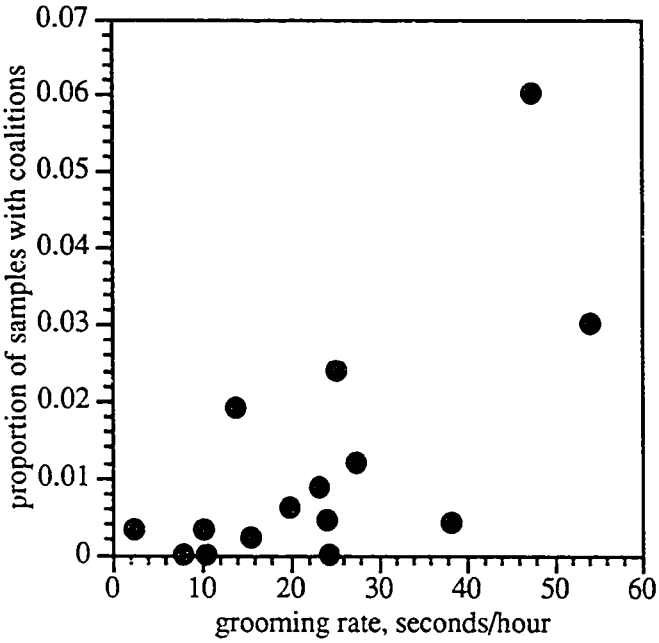
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Figure 2.2: Coalition rates against females, plotted against grooming rates of coalition dyads



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Figure 2.3: Coalition rates against males, plotted against grooming rates of coalition dyads



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CHAPTER III

MALE-MALE SOCIAL RELATIONSHIPS

Introduction

Four of the main adaptive problems faced by group-living male primates are (a) within-group feeding competition, (b) within-group mate competition (for species living in multi-male groups), (c) between-group mate competition, and (d) the need to protect offspring from predators, including infanticidal conspecifics in some species. Strategies that reduce the first two types of competition by reducing the number of males in the group may increase the possibility of incurring the third and fourth types of costs. The relative importance of these 4 problems no doubt varies widely across species and across populations within a species, depending on environmental factors such as socionomic sex ratio, predation rates and the spatial and temporal distribution of resources. Considering within-group feeding and mate competition only, a male will prefer to co-reside with few or no other males. However, a male's success at between-group mate competition and protection of offspring from predators can, in some cases, be enhanced by the presence of male co-residents, if males cooperate in the defense of females and offspring. Males are expected to cooperate in these two tasks only if (a) they are related, and/or (b) mating opportunities are not monopolized by a single male (van Hooff and van Schaik 1992). In situations in which males face severe intragroup competition from unrelated males, yet must rely on the help of other males for the purpose of intergroup defense, it is to be expected that male-male relationships will be tense and ambivalent, as each male strives to exploit his male allies as much as possible in the arena of within-group competition without

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causing the ally to defect in between-group competition (Vehrencamp 1983; van Hooff and van Schaik 1992).

There have been relatively few systematic studies of male-male relationships among primates, and those that have been done have measured variables in ways that make cross-species comparisons difficult. For example, most studies do not distinguish between mild and damaging aggression. However, it is possible to make a few generalizations about male-male relationships with regard to the following variables: time spent in proximity, relaxed affiliative behavior (e.g. grooming, hugging, and resting in contact), coalition formation (for intra-group or inter-group competition), and aggression.

Of the well-studied species that are male-philopatric (chimpanzees, bonobos, muriquis, hamadryas baboons, and Costa Rican squirrel monkeys), the chimpanzee demonstrates the strongest male bonds. Chimpanzee males spend more time together than do females, and they have high rates of grooming relative to females (Nishida and Hiraiwa-Hasegawa 1987; Goodall 1986; de Waal 1982). Male-male coalitions against males are frequent, both for within-group (de Waal 1982, 1984; Nishida 1983) and between-group competition (Goodall et al. 1979; Nishida et al. 1985; Goodall 1986; Manson and Wrangham 1991), and males often inflict severe, even lethal, wounds on one another, mainly in the context of intergroup aggression (Goodall, 1992; Goodall et al. 1979; Nishida et al. 1985; Goodall 1986; Manson and Wrangham 1991). In contrast, bonobo males have fairly weak social bonds, particularly in communities in which most of the males' mothers still reside with them (Ihobe 1992). It appears that males' intense relationships with their mothers prevent them from forming strong bonds with other males. Bonobo males do not associate, groom, or form coalitions frequently in comparison with bonobo male/female dyads or in comparison with chimpanzee male-male dyads (Ihobe 1992; White 1988; Kuroda 1980). However, if there are enough motherless prime males in a community, the relationships of those males begin to more closely resemble chimpanzee male-male relationships. In general, bonobos males appear to be less

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aggressive than chimpanzee males, with regard to both intragroup and intergroup competition (Ihobe 1992).

Muriqui males frequently hug, and have very low rates of intragroup aggression (Strier 1992). Although coalitions for purposes of intragroup aggression are rare or non-existent, males regularly form coalitions against males of other social groups (Strier et al. 1993). Male Costa Rican squirrel monkeys spend more time in proximity than do females. They have low rates of aggression and cooperate in some activities, such as olfactory investigation of females of other groups (with whom they sometimes succeed in mating), challenges to males of other groups (which, at on at least one occasion resulted in a takeover of the group), and antipredator activities (Boinski and Mitchell 1994).

Hamadryas baboon males spend most of their time with the females of their one-male units, but they do sometimes groom other males within their clan (Abegglen 1984). Related males in the same clan aid one another in rare but intense inter-band battles (Kummer 1968). Males in a captive colony of mixed hamadryas and anubis baboons also formed coalitions (Colmenares 1991).

In some cases, male mountain gorillas remain in their natal groups rather than dispersing at sexual maturity (Stewart and Harcourt, 1987). Although they do not show particularly high rates of association and grooming and do compete, to some extent, for access to females (Robbins, pers. comm.), they do cooperate in aggression against extragroup males and in herding females during intergroup encounters (Sicotte 1993 and references therein).

In female-philopatric species, adult male co-residents are likely to be unrelated, although in macaques and vervets related males may transfer together or transfer to groups already containing male kin in some cases (Meikle and Vessey, 1981; Cheney and Seyfarth 1983; van Noordwijk and van Schaik 1985). Data on male-male relationships in female philopatric species are available for several macaque species (rhesus, bonnet, crab-eating, and pigtail macaques) as well as from savanna baboons, common squirrel monkeys, and

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capuchins. With the exception of the bonnet macaque (Sugiyama 1971; Rahaman and Parthasarathy 1969), none of these species are characterized by high levels of affiliative behavior or close proximity among males (crab-eating macaques: Poirer and Smith 1974; pig-tailed macaques: Oi 1990; savanna baboons: Smuts and Watanabe 1990; common squirrel monkey: Boinski and Mitchell 1994). Male-male coalitions in an intra-group context have been most frequently reported among savanna baboons (Noë 1992, 1990; Noë et al. 1991; Smuts 1985, Smuts and Watanabe 1990; Bercovitch 1988; Packer 1977; Hall and De Vore 1965), bonnet macaques (Silk 1992a, 1992b, 1993) and pigtailed macaques (Oi 1990).

Very little research has focused explicitly on male-male relationships in capuchins; however, it is possible to glean some information on critical variables from the literature. Much of the information summarized below for the four capuchin species is based on anecdotes or *ad lib* observations. In brown capuchins (*Cebus apella*), the alpha male controls access to food, is almost the exclusive mate of estrous females, and is the social focus of the group (Janson 1984). Subordinate males spend most of their time on the periphery of the group (Janson 1986b; Izawa 1980) and spend very little time in close proximity to one another (Janson 1986a). Subordinate males spend more time in proximity to other subordinate males than to the alpha male (Janson 1986a). Male-male grooming rates are low, compared with male-female and female-female grooming rates (Izawa 1980). Izawa (1980) reports low rates of male-male aggression, but Janson (1986a, 1986b) reports high rates of aggression, particularly by the alpha male toward subordinate males at feeding sites. Although Izawa (1980) and van Schaik and van Noordwijk (1989) report male-male cooperation versus predators, Janson (1986a, 1986b) found that subordinate males typically did not aid the alpha male in defense against predators or against groups of monkeys that sought to supplant the group at feeding trees. Defler (1982) reported that intergroup encounters between *C. apella* groups were fairly peaceful. There is no mention of male-male coalitions for intragroup competition in the literature.

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Male-male relationships in wedge-capped capuchins (*Cebus olivaceus*) are similar to those of *C. apella* in that the alpha male is highly central and appears to monopolize matings, whereas other males are peripheral (Robinson 1988b). No data are available on grooming rates and rates of intragroup aggression. Small groups are vulnerable to takeovers by extragroup males (Robinson 1988b). Unlike *C. apella, C. olivaceus* males cooperate in defense against males of other groups (Robinson 1988b).

White-fronted capuchin (*C. albifrons*) males appear to have more cohesive relationships than are typical of *C. apella* (and, possibly, *C. olivaceus*) males. Several males often aggregate in the center of the group (Janson 1986b), and males spend much more time in proximity than is typical of *C. apella* (Janson 1986a). Janson(1986a) reports strong associations between the alpha male and subordinate male, but Defler (1982) reports the opposite. Although the alpha male sometimes supplants subordinate males (Defler 1982), males often take turns eating, rather than monopolizing a food resource (Janson 1986a, 1986b). In general, rates of male-male aggression are low (Defler 1982; Janson 1986a), though Defler (1982) often observed males with wounds or scars that could potentially have been inflicted by males. The alpha male did not monopolize matings, and females often chose to mate with subordinate males (Janson 1986b). Males cooperated in defense against predators (Janson 1986a, 1986b), in confrontations with other *C. albifrons* groups (Defler 1982), and in evicting *C. apella* groups from feeding trees (Janson 1986a, 1986b). The striking contrast between male relationships in *C. apella* and *C. albifrons* has been attributed to the fact that mating opportunities and access to food are more equitably distributed among males in *C. albifrons* (Janson 1986a, 1986b). Thus, all *C. albifrons* males have a stake in defending feeding trees and in protecting infants from predators.

White-faced capuchin (*C. capucinus*) males spend little time in close proximity (Rose 1994) and groom infrequently (Rose 1994; Mitchell 1989; Oppenheimer 1968; but see Fedigan 1993). Mating data are too scant to determine the extent to which the alpha male monopolizes estrous females, but at least some instances of matings involving low-

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ranking males have been observed (Fedigan 1993; Chapter 4). The level of male-male aggression varies widely from site to site. Oppenheimer (1968) reports very low levels of male-male aggression (based on ad lib data), and at his site (Barro Colorado), even male immigrations were peaceable. At Santa Rosa National Park, male aggression rates appeared to be higher (Fedigan 1993; Rose 1994), and males sometimes wounded one another. Contrary to Oppenheimer's observations, male immigrations were not always peaceful at Santa Rosa. Male takeovers (sometimes by groups of 2-4 males) occasionally resulted in male evictions, infanticide, and death or disappearance of both males and females (Fedigan 1993; Rose 1994; Rose and Fedigan 1995; Fedigan et al. n.d.). Males cooperated in defense against predators and against males of other groups (Fedigan 1993; Rose 1994; Mitchell 1989; Oppenheimer 1968; Rose and Fedigan 1995). No data are available on male-male coalitions in an intragroup context.

None of the previous capuchin studies have focused specifically on male-male relationships, examining all facets of their relationships. I examine the following behaviors for a single set of males: proximity; relaxed affiliative behaviors; aggression; dominance relationships; cooperation in aggression against predators, intragroup conspecifics, and extragroup males; and ritualized behaviors apparently related to relationship negotiation. This chapter examines the nature of *C. capucinus* male-male relationships, as the product of the conflict between 2 factors: (a) the inevitable competition between males within a group for food and mates, and (b) the need to cooperate with other, unrelated, males for the purposes of defense against predators and males of other groups.

Methods and Materials

The analyses in this chapter are based on 364.5 hours of focal data collected on adult males. The protocol for focal follows is described in chapter 1. There were 4 adult males in the group. Three of them, Curmudgeon, Paul, and Guapo, were present at the

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beginning of the study, and the fourth, Ichabod, immigrated into the group November, 1992. Table 3.1 shows the amount of focal data collected on each male.

Proximity scores were calculated in the following manner. For each male-male dyad, I tallied the number of times, during the final instantaneous scan of each 10-minute sample in both males' focal follows, that the males were within 0-1 body lengths, 1-5 body lengths, and 5-10 body lengths, of one another. Body lengths are defined in Chapter 1. Instances in which the monkey was in view of the focal but outside 10 body lengths were scored the same as if the monkey was not in view at all. I multiplied these three numbers by weighting factors, such that the closer proximity categories were weighted more heavily. The weighting factors were determined in the following way. Imagine 3 concentric spheres, with the focal animal at the center. The inner sphere has radius 1, the second largest sphere has radius 5, and the outer sphere has radius 10. The weighting value for the number of samples in which the animals of a dyad are within one length of one another is the reciprocal of the volume of a sphere of radius 1. The weighting value for the 1-5 body length category is the reciprocal of the difference between the volume of a sphere of radius 5 and the volume of a sphere of radius 1. The weighting value for the 5-10 category is the reciprocal of the difference between the volumes of spheres of radius 10 and radius 5. Thus, the equation for calculating the proximity score, P, is:

$$P=1{,}000(0.239a + 0.0019b + 0.0003c)$$

where "a" is the proportion of samples in which the dyad is within 1 length of one another, "b" is the proportion of samples in which the two animals are within 1-5 lengths of one another, and "c" is the proportion of samples in which the animals are within 5-10 lengths of one another. The sum of the three weighted values is multiplied by the arbitrary value of 1,000 simply to make the proximity scores more readable; otherwise, they would all be small fractions.

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The dominance hierarchy was constructed by using the direction of avoids and cowers. I chose to use only these two behaviors because avoids and cowers, unlike other submissive behaviors such as fleeing, tail-chewing, fear-grinning and screaming, are obviously directed at specific individuals, and they are performed primarily in a dyadic context rather then in the context of coalitionary aggression. If submissive behaviors occurring during polyadic aggression were included, I would be confounding a male's fear of another male with his fear of the opponent male's coalition partners.

Results

Dominance Hierarchy

Males spent very little time in proximity, and therefore there were very few submissive behaviors between males. Table 3.2 summarizes the male submissive behaviors during focal observations prior to November of 1992. Both Paul and Guapo directed submissive behaviors toward Curmudgeon, and Curmudgeon did not direct submissive behaviors to either Paul or Guapo. There were insufficient data to determine the relative ranks of Paul and Guapo.

In November, 1992, Curmudgeon was defeated and evicted from the group by a (presumed) coalition of Paul and some of the adult females (Chapter 5). Both males and two females were wounded -- nearly the only wounds I had seen in 20 months of observation. Guapo left the group a few days later without visible wounds, leaving Paul as the only adult male in the group. Curmudgeon made several attempts to rejoin the group and eventually succeeded in returning as beta male, approximately 10 days after his eviction. Two weeks after he left, Guapo returned to the group in the company of Ichabod, a male from a neighboring group who immigrated at that time. I will hereafter refer to

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Curmudgeon's overthrow as the "coup." The details of the coup are described in greater detail in chapter 5.

Table 3.3 summarizes the males' submissive behaviors following the coup. Curmudgeon, Guapo, and Ichabod all directed submissive behaviors toward Paul, and Paul never directed submissive behaviors toward any males. Curmudgeon was clearly dominant over Guapo. Curmudgeon and Ichabod were never observed to direct avoids or cowers at one another. It appears, on the basis of these data and additional ad lib observations, that Ichabod was the lowest-ranking male at the time he joined the group, but that he outranked Guapo by March, 1993.

Due to the low rate at which males perform submissive behaviors, it is difficult to say whether they have a stable, linear hierarchy. My impression was that there was a clear alpha male, and that subordinate males were less clearly ranked. Certainly, subordinate males do not engage in formal dominance displays to reinforce their positions in the hierarchy. If there is a linear hierarchy for males, it is subtle, and, due to the extreme prevalence of coalitions in aggression, a subordinate male's dominance rank with respect to the other subordinates probably has very little impact on access to resources.

Benefits of Being Dominant

The alpha male received 5-22 times fewer attacks from males than did the subordinates. (See below, this chapter, for details.) Before the coup, Curmudgeon was attacked the least by other males, whereas after the coup, Paul received the fewest attacks by males. However, the alpha male may be *more* prone to attack by adult females than are subordinate males (see chapter 4).

Another potential benefit of being alpha male is receiving grooming, although the proximate benefit of being groomed is unclear. The alpha male received far more grooming from adult females than did the subordinate males (see chapter 5).

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The alpha male occupied a more central position in the group than did subordinate males, and this may have afforded him greater protection against predators. I used two methods of ascertaining males' degree of spatial centrality within the group. The first method was to create an index of centrality, which is the average of the focal monkey's proximity scores with all other adult members of the group. Prior to the coup, Curmudgeon's centrality index was 3.67, Paul's was 1.26, and Guapo's was 2.27; thus, Curmudgeon was the most central male. After the coup, Curmudgeon's centrality index was 0.47, Paul's was 3.74, Guapo's was 0.12, and Ichabod's was 0.71; thus, Paul was by far the most central male. Because the centrality index heavily weights the amount of time spent within one body length of other monkeys, it may be a better measure of the strength of social bonds than of actual spatial centrality. That is, hypothetically, monkeys who were peripheral but occasionally engaged in intense social behavior could have had high scores, whereas a dominant monkey who could not easily be forced out of the center of the group, but who had no close friends, could conceivably have had a low score. To check this possibility, I analyzed the proximity data in another way: by simply calculating the amount of time that each male spent out of view of all group members during his own focal follows. Prior to the coup, Curmudgeon, Paul and Guapo spent 5%, 16% and 12%, respectively, of their time out of view of other group members. After the coup, Curmudgeon, Paul, Guapo, and Ichabod spent 16%, 3%, 22%, and 3%, respectively, of their time out of view of other group members. Ichabod's extraordinarily low amount of time spent out of view of the group may have been due to the fact that he was new to the home range, and therefore was more reluctant to lose sight of the group while foraging. With the exception of the tie between Paul and Ichabod for least amount of time out of view of the group, the alpha male spent the least time out of view of the group, both before and after the coup.

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Aggression

Males sometimes imposed costs on one another in the form of aggression. Tables 3.4 and 3.5 summarize the rates of aggression, expressed as bouts/hour, at which males attacked other males, before and after the coup. Two consecutive aggressive behaviors were counted as only one bout if they occurred within the same 10-minute focal follow. Threats (silent and vocal), supplants, lunges, branch shaking and breaking displays, bounces, hits, chases, bites, and overlords are included in this total. Rates of aggression increased following the coup for all male dyads, with the exception that Guapo and Curmudgeon lowered their rates of attack on Paul. Both before and after the coup, the alpha male received less aggression from males than did subordinate males. Overall, rates of aggression tripled following the coup. Figure 1.1 shows the rate at which males directed aggression toward other males, averaged across dyads, pre- and postcoup.

Tables 3.6 and 3.7 summarize the rates of severe aggression during focal follows for male dyads. These tallies include only chases, hits, and bites. Because of the tendency for aggressive behaviors to occur in long sequences, two consecutive aggressive behaviors were counted as only one event if they occurred within the same 10-minute focal follow. Before the coup, the only dyad to engage in severe aggression during 213.83 hours of observation involved Guapo/Paul. Guapo chased Paul 3 times. Although 3 males received wounds during the precoup phase of the study, it is not known whether these were inflicted by males. After the coup, there was considerably more severe aggression. All of the instances of severe aggression observed during focal observations were chases (n=13).

All males, with the exception of Ichabod, received severe wounds during or following the coup (during ad lib observations). During the coup, Curmudgeon received the following wounds (some of which were presumably from Paul because of the depth of the canine slashes-- see Chapter 5): a 4-cm canine slash on the shoulder, a 3 cm canine slash on the sole of his left foot that prevented him from using that foot for several days and caused him to limp for a month, puncture wounds inside his left arm, a puncture

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wound 15 cm above his left foot wound, and a series of puncture wounds inside the right leg. Paul received a canine slash, presumably from Curmudgeon, that extended from above his right eye, to below his chin, slicing through his lip. In a fight with Curmudgeon, during the period in which Curmudgeon was attempting to rejoin the group, Paul received a new foot wound (the nail was torn off of his left big toe), a gash above the right eye, puncture wounds in the left wrist (causing him to limp), and small slashes on each cheek. Following the coup, Paul inflicted a similar wound on Guapo: a canine slash extending from above his left eye to below his chin, resulting in extreme blood loss. This wound never healed properly, and Guapo's left upper canine tooth still protruded through his upper lip 15 months later when I censused the group. All three males received additional wounds from one another during the postcoup period, but I will not describe them all in detail; the wounds described above were the most severe wounds witnessed.

Coalitionary Aggression

I defined a coalition as one monkey joining another monkey in threatening or attacking a common victim. Most coalitions are quite obviously cooperative ventures, rather than coincidental simultaneous attacks on a third party, because the two partners establish body contact while threatening the third party. The typical coalitionary posture is the "overlord" (Oppenheimer and Oppenheimer 1973), in which one monkey gets on the other monkey's back, with their heads stacked like a totem pole, while both threaten in the same direction. One monkey can recruit a partner's aid by either headflagging (i.e. alternately jerking his head toward the prospective partner and threatening the victim), by putting an arm around the prospective partner or jumping on his back in overlord position while threatening the victim, or by backing toward the prospective partner while threatening the victim.

Males formed coalitions with other males to attack males of their own group, males from other social groups, heterospecifics (both predators and nondangerous animals), and

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occasionally to attack juveniles, though such attacks were rarely serious. Adult males were never observed to form coalitions with adult males against adult females. Among the non-capuchin victims of male-male coalitions were human observers, howling monkeys, rattlesnakes, boa constrictors, dogs, birds, stinging insects, and coatis. Sometimes, males formed coalitions against imaginary victims, as when they would jointly threaten bare patches of ground. Attacks on imaginary victims may have served the function of strengthening the males' alliance. In some instances, it was my impression that a subordinate male initiated an attack on an imaginary enemy as the piloerected alpha male came into view, and then recruited the alpha's aid, as a way of diverting the alpha from attacking him.

Male-male coalitions against males of other groups rarely occurred during focal follows, because I concentrated on collecting ad lib data during intergroup encounters so as to keep track of all participants. However, such coalitions were common (see chapter 7). Males very rarely refused to help one another against males from other groups, and I never saw a male refuse aid to another male groupmate after being directly solicited during an intergroup encounter.

During focal observations before the coup, Curmudgeon and Paul formed 6 coalitions against Guapo, and Curmudgeon and Guapo formed 3 coalitions against Paul. Guapo and Paul never formed coalitions against the alpha male, Curmudgeon. During focal observations after the coup, Paul and Curmudgeon formed 8 coalitions against Guapo, and Paul and Guapo formed 3 coalitions against Curmudgeon and 2 against Ichabod. Thus, both before and after the coup, all male-male coalitions involved the alpha male as one of the partners; two subordinate males were never observed to form a coalition against the alpha male. Neither of the alpha males consistently favored certain males as partners and victims.

Tables 3.8-3.16 summarize all coalitions formed by males during focal observations, against all victims, as well as refusals to provide aid when it was solicited.

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Direct requests for aid include headflags, embraces, backing into overlord position, or pouncing on top of a monkey in overlord position; for these behaviors to qualify as requests for aid, the target of the request can not have started aiding yet. An indirect request for aid is when a monkey initiates threatening, and a second monkey spontaneously joins in threatening the same victim (the first one to threaten is considered to have initiated the coalition). As defined, an indirect request can not be refused except by knowing who saw the initial threat and neglected to join; all refusals listed in the table are refusals to aid after direct requests. A successful coalition is merely a request for aid that is granted; nothing is implied about whether the coalition partners accomplish their goals.

Prior to the coup, Paul refused 80% of Curmudgeon's direct requests for aid, whereas Curmudgeon refused only 50% of Paul's direct requests for aid. Curmudgeon only requested aid from Guapo once, and aid was granted. Curmudgeon refused 75% of Guapo's requests for aid; Curmudgeon aided Guapo only when the victim was Paul or a human observer. Guapo and Paul never denied one another aid when it was requested. However, sample sizes are small for this dyad. It appears that willingness to grant aid was not symmetrical for dyads involving the alpha male: Curmudgeon was more willing to help Paul than vice versa, whereas Guapo was more willing to aid Curmudgeon than vice versa.

After the coup, Curmudgeon refused 57% of Paul's requests for aid, only helping when the victim was Guapo or (in one case) a human observer. Paul refused 60% of Curmudgeon's requests. Guapo refused 56% of Paul's requests, and Paul refused 64% of Guapo's requests. Guapo and Curmudgeon refused 67% of each others' requests for aid. Ichabod and Curmudgeon never requested aid from one another. Ichabod requested aid from Guapo only once, against a human, and aid was granted. Ichabod requested aid from Paul twice, unsuccessfully, but Ichabod aided Paul the one time he requested aid. Thus, within dyads of long-term resident males, the proportions of requests refused were similar for both males following the coup. Aid was rarely requested by or from Ichabod, the immigrant male.

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Male Display Behaviors

Four behaviors -- piloerection, urine-rubbing, branch-breaking, and branch-shaking -- were performed primarily by males, and were performed at higher rates by dominant animals. I have not quantitatively analyzed piloerection, because it is difficult to code (there are varying degrees of piloerection; hair isn't just sticking up or lying flat). However, at the time of the coup, I was astonished to see how small Curmudgeon appeared and how large Paul appeared, now that I was seeing Curmudgeon's hair lying completely flat for the first time and Paul completely piloerected for the first time. In general, the alpha male was much more piloerected than any other male. The alpha male was piloerected to some degree at all times, but he became even more piloerected during aggressive encounters or while displaying.

Urine rubbing is when a monkey urinates on his hand, rubbing the urine on the surfaces of the hands, feet, and prehensile tail, and perhaps splashing some urine on the fur of the abdomen and legs. The function of this behavior remains unclear (Robinson 1979; Oppenheimer and Oppenheimer 1973). In this social group, at least, it seems likely that urine marking conveys some important information to other monkeys, because monkeys are very eager to smell other monkeys' urine. When a monkey saw another monkey (particularly an adult male, but often adult females as well) urinate, the observing monkey typically rushed over to collect the urine-soaked leaves and sniff or even lick them. Table 3.17 shows the rate of urine-rubbing, precoup and postcoup for all males. Curmudgeon had the highest rate of urine-rubbing prior to the coup, and his rate fell after the coup. Paul's urine-rubbing rate rose dramatically after the coup, such that Paul had the highest rate of urine-rubbing postcoup. Because there is some seasonal variation in the rate of urine-rubbing, I have broken down the data into 4 quartiles (Table 3.18), corresponding to the rainy and dry seasons: quartile 1 = May 1991-October 1991, quartile 2 = November 1991-April 1992, quartile 3 = May 1992 - October 1992, and quartile 4 = November 1992-May 1993. Quartile 4 corresponds exactly to the postcoup period. Because I did not add

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urine-rubbing to the ethogram until a few months into the study, I have omitted the rates for quartile 1, as they are underestimates. All males urine-rubbed less often during rainy seasons than during dry seasons. This observation could lend some credence to Robinson's thermoregulatory hypothesis of the function of urine-rubbing; however, it seems unlikely that a monkey would use warm urine to cool his body when there is cool spring water nearby. At my study site, particularly in the dry season, monkeys are rarely more than a few meters from running water, which they bathe in frequently. Yet monkeys sometimes urine-rubbed within one meter of a stream. A possible alternative interpretation of the seasonal difference in urine-rubbing is that monkeys are more dispersed during the rainy season than during the dry season and therefore have fewer social interactions during the rainy season; however, I have not yet analyzed the data to test this possibility. Another possibility, which I can not test, is that the composition of the urine changes seasonally.

Table 3.19 summarizes the rates at which males shook and broke branches, precoup and postcoup. (I have lumped the two behaviors together, as they are used in the same contexts and the rates show very similar patterns across individuals.) As was the case with urine-rubbing, Curmudgeon had the highest rate precoup, and his rate fell dramatically after the coup, at which time Paul's rate rose dramatically. The male who showed the highest rate of branch-breaking postcoup, however, was Ichabod, the immigrant male. In Table 3.20, I have broken the data into 4 quartiles, as in the urine-rubbing analysis above, so that it is apparent that the change in rates of branch displays changed abruptly at the time of the coup, rather than occurring gradually over time.

It appears that the presence of the alpha male inhibits other males from urine-rubbing and branch-breaking. The alpha males (both Paul postcoup, and Curmudgeon precoup) were very flamboyant in their urine-rubbing displays: they piloerected, splashed vigorously, and often vocalized (e.g. intense gargles, coughs, or burst-twitter-brays) while urine-rubbing, and they did so in full view of other monkeys, often splashing urine on others. In contrast, subordinate males were very discreet when they urine-rubbed. They

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surreptitiously placed a hand under the trickle of urine, after looking around (apparently to see whether they were being watched), and did not splash or assume the arched-back posture favored by alpha males who were urine-rubbing. Subordinates did not piloerect or vocalize while urine-rubbing. Alpha males, and sometimes adult females, often respond to subordinate males' branch-breaking displays by directing intense vocal threats at them; these threats generally put an end to the display.

During the postcoup period, Paul, the alpha male, was occasionally absent from the group for a few hours, generally while in consort with an estrous female. These instances provided an interesting natural experiment on the effects of the removal of the alpha male on expression of subordinate males' display behaviors. Because I adhered to my normal sampling schedule during these times, the data are scant, but they suggest that subordinate males can quickly adjust their behavior to take advantage of the alpha male's absence. To illustrate this phenomenon, I will describe 3 events that are the clearest examples. These events were chosen because they are the only ones in which (a) the alpha male was away for an extended period of time and (b) I was certain of the location of the alpha male during his absence and thus could confirm that he was sufficiently far from the group to be out of hearing range.

The first absence occurred March 13, 1993. At 8:37 am, Paul left the group with Nanny, who was in estrus, and they rapidly traveled upstream of the group a great distance, with Ichabod and Lizano in pursuit. Guapo followed at a distance and then turned back at 9:03 and returned to the rest of the group, producing vocalizations that I could not identify. Paul returned to the group at 10:02. During Paul's 85-minute absence, I did not do any focal follows of Curmudgeon or Guapo. However, during ad lib observations (which are almost certainly an underestimate of Curmudgeon's actual rates of behavior, as I was collecting data on other monkeys during this time period), I saw 13 urine rubs and 3 branch displays. Thus, Curmudgeon urine rubbed at least 9.15 times/hour and performed branch displays at 2.11 times/hour. Note that the rate of urine

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rubbing is 7.3 times his postcoup baseline rate, whereas the branch display rate is 3.7 times the baseline rate (see Tables 3.17 and 3.19).

Paul's second absence occurred the same day, between 10:22 and 12:38. Once again, Paul left the group in the company of Nanny; this time, Ichabod and Quizzler accompanied them. One focal follow of Curmudgeon was conducted during this time period, during which he urine-rubbed at a rate of 18 times/hour and did branch displays at a rate of 48 times/hour. Additional ad lib observations during this time period yielded rates of 6.19 urine rubs/hour and 8.1 branch displays/hour (again, these rates are highly conservative, since Curmudgeon would not have been in view for much of that time period). Thus, once again, Curmudgeon's rate of display behavior was in gross excess of the post-coup base line. In both of Paul's absences, Curmudgeon was piloerected most of the time and vocalized loudly and incessantly, often while rushing around on the ground, crashing through leaf litter. He also incorporated some unusual elements into his displays, some of which were only seen in this context. Curmudgeon broke the trunks of entire trees by pushing them over, and causing the monkeys foraging in the tree to fall to the ground. He grabbed large branches in his tail and raced through the leaf litter with them, creating a racket. He incorporated me into some of his displays, by leaping out of the tree to land at my feet, and slapping me. Once he heaved a huge chunk of wood, covered with hundreds of squirming daddy-long-leg spiders, into a stream. He also incorporated feral cows into his displays by running along the ground and chasing them, or by herding them from the trees, by slapping them on the heads with branches until they fled.

The third absence of Paul occurred the following day. Paul, Nanny (still in estrus) and Ichabod were gone from noon until 4:00. Although both Curmudgeon and Guapo were highly vocal during this period, and Curmudgeon was piloerected most of the time, the rates of urine rubbing and branch displays were not as high as during absences on the previous day; perhaps the novelty of being "temporary alpha" was beginning to wear off. There was one focal follow each of Curmudgeon and Guapo during Paul's absence, during

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which no urine rubbing or branch displays occurred. In ad lib observations, Curmudgeon urine rubbed at a rate of 0.5 times/hour and performed branch displays at a rate of 1.75 times/hour; again, these ad lib rates are underestimates of actual rates of behavior. Guapo was not observed to urine rub or display at excessive rates during Paul's three absences, though he did appear vocalize more than usual.

Proximity Data

Males spent very little time in proximity to one another, relative to the amount of time males spent with females or the amount of time females spent with females (Table 3.21). Because these data are averaged across dyads, expected values for each category of dyad should be equal under the null hypothesis that time spent in proximity by adult dyads is not affected by sex of the participants. Figure 2.2 shows the proximity scores for male-male dyads before and after the coup. All male-male dyads had much lower scores following the coup. With the exception of Curmudgeon and Ichabod, the scores of the other male dyads were virtually zero, which means that they were never seen within 10 or fewer body lengths of one another during scans. This drop in male proximity is probably because male relationships were still unstable, and because the alpha male punished subordinate males for associating, as I will discuss later in this chapter.

Affiliative Behavior

Males very rarely engaged in affiliative behavior; in fact, rates of aggressive behavior exceeded rates of affiliative behavior for all male dyads, both before and after the coup. Males virtually never groomed other males. I calculated the rates at which males groomed males, compared to the rates of male-female grooming and female-female grooming, averaged across all dyads, for the period between December 30, 1991-May, 1993 (i.e. the portion of the study during which I recorded the precise durations of grooming bouts). Males groomed other males less than one second per hour (0.3 s/hr

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precoup and 0.2 s/hour postcoup). Males groomed females at a rate of 0.1 s/hour, females groomed males at a rate of 6 s/hr, and females groomed females at a rate of 12 s/hr. Tables 3.22 and 3.23 summarize the rates of male grooming, broken down by dyad, before and after the coup. Note that the alpha male never groomed other males.

Other types of male affiliative behaviors besides grooming include play, resting in contact, sexual behavior, and "wheeze dancing." Wheeze dances incorporate several elements of courtship behavior (see Chapter 4), but the vocalizations are different from those used in courtship. The two males pace back and forth, as if they are taking turns chasing one another in slow motion, and they maintain constant eye contact. They are often piloerected, and their lips are generally protruded. They contort their bodies to look at one another over their shoulders or through their legs, and they sometimes stand bipedally and arch their backs as if preparing to do a back flip. Throughout this dance, they do a loud wheezing vocalization that is used by adults only in this context, and sometimes an intense version of the affiliative gargle vocalization. Wheeze dances often culminate in mounting and thrusting, with the males taking turns being on top. Wheeze dances were most common in tense social situations, such as (apparent) reconciliation following major fights (see chapter 6). When the loser of a major fight leaves the group for a period of several hours to a few days and then returns to the group, he sometimes wheeze dances with his opponent upon returning. Although wheeze dances were almost exclusively a male behavior, I did see females wheeze dance after fights on a few occasions during ad lib observations. However, I suspect that the extreme sex difference in wheeze dance frequency may be at least in part an artifact of the timing of my study, since the latter part of the study coincided with a period of social upheaval among the males, whereas female relationships remained relatively stable throughout the study. Before the coup, I saw only one wheeze dance during 213 hours of focal observations of males. After the coup, wheeze dances among males were a commonplace occurrence, occurring at 24 times the rate they occurred before the coup.

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Figure 3.3 summarizes rates of male affiliative behavior, pre- and postcoup, lumping all types of affiliative behaviors. Because of the tendency for affiliative behaviors to be clustered in time, only one affiliative behavior per dyad per 10-minute sample is counted. Therefore, if Paul rested in contact with Guapo and then groomed him 30 seconds later, the two behaviors counted as only one bout of affiliation. Although males spent *less* time in proximity following the coup, they both affiliated *more* frequently and were more aggressive *after* the coup than *before* the coup. These postcoup affiliations appeared tense. Even grooming, which is a relaxed activity under most conditions, was rough and jerky, with the males almost slapping, rather than stroking, one another. I had the impression that the males were trying to establish good relations with one another, but feared an outbreak of violence. And this was with good reason, at least when subordinate (that is, non-alpha) males affiliated with one another. Of 22 postcoup affiliative interactions between subordinate males, 10 were witnessed by Paul, the alpha male. On all 10 occasions, he immediately ran over and broke up the affiliating pair by directing intense vocal threats at them. Soon after Paul started threatening, one of the affiliating males would turn against his partner and threaten him, headflagging to Paul for support. By these means, it appeared that Paul was able to prevent any male dyad from forming an alliance that could be threatening to his position as alpha male. Of the 12 friendly male-male interactions that were performed out of view of Paul, one was broken up by Kola, one was ended in response to intense vocal threats in the distance, and the other 10 ended peacefully, with neither monkey fleeing or aggressing against his partner.

The following two anecdotes illustrate the tension among the males, as Curmudgeon and Guapo apparently attempted to overcome their fear of Paul and form an alliance. They are representative of dozens of similar instances that occurred during ad lib observations, though the first anecdote is slightly unusual in that Paul had to work so hard at breaking up Curmudgeon and Guapo. Generally, one subordinate male began

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threatening the other within a second or two after Paul's threats began, and often the two subordinates began threatening one another simultaneously.

On January 11, 1993, at 10:20, Curmudgeon and Guapo began wheeze dancing. Paul immediately responded by directing intense vocal threats at them. Curmudgeon broke off the dance and threatened Guapo silently, and another monkey in the distance threatened Guapo as well. Curmudgeon ran toward Paul, directed intense vocal threats at Guapo, and headflagged to Paul, who also directed intense vocal threats at Guapo. Juvenile male Juege threatened Guapo vocally, and Guapo began to chew his own tail nervously. Curmudgeon and Juege lunged at Guapo, and he fled and chewed his tail some more. Paul directed intense vocal threats at Guapo. Up the hill, Ichabod, Hobbes and Mani attacked adult female Wiggy, who screamed, and this diverted the males' attention for a second. During this commotion, Curmudgeon approached Guapo to contact, and Paul immediately directed intense vocal threats at them; Guapo fled. Curmudgeon again approached Guapo to contact, and Paul directed intense vocal threats at them, causing Guapo to leave. Guapo crept toward Curmudgeon again, and Paul directed intense vocal threats at him, causing Curmudgeon to silently threaten Guapo. Guapo backed toward Curmudgeon, as if trying to start up another dance with him. Curmudgeon stopped threatening and looked as if he were going to join in the dance, but Paul once again directed intense vocal threats at them. Curmudgeon threatened Guapo silently, and Guapo fled. Curmudgeon continued to watch Guapo intently for awhile, without threatening. Then Wiggy lunged at Guapo and chased him, and Curmudgeon joined in the chase. Seconds later, Curmudgeon ran toward Guapo and initiated a dance. Guapo did not join in the dance, but stood still, watching. When Curmudgeon came to within 5 body lengths of Guapo, Guapo fled a short distance. Curmudgeon began wheezing, but Guapo still did not join in the dance. Wiggy vocally threatened and chased Guapo, and Curmudgeon joined in the threats and chase. However, Curmudgeon's threats were odd-sounding and graded into first a "machine gun noise" (used primarily to greet babies) and then into a twitter. Curmudgeon and Guapo mutually

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approached one another and started wheeze dancing. Paul, Squint and Wiggy directed intense vocal threats at them continually as they danced, and Guapo looked terrified. Curmudgeon kept looking back at Paul. Curmudgeon finally broke off the dance and silently threatened Guapo. Guapo crept toward Curmudgeon, threatened the human observers, and headflagged to Curmudgeon, who aided him in threatening the humans. Paul once again directed intense vocal threats at them. Guapo approached to within one body length of Curmudgeon, and they both threatened the humans again. Paul threatened Guapo silently, but Curmudgeon and Guapo kept threatening the humans. Finally, Curmudgeon left Guapo and joined Paul in threatening him. As Curmudgeon and Paul directed intense vocal threats at Guapo, Guapo clutched his tail and licked it nervously. Guapo crept away from the coalition, and Curmudgeon headflagged to Paul. Then Curmudgeon ran, twittering loudly, toward Guapo, and began dancing. Guapo looked reluctant, but joined in the dance. Paul directed intense vocal threats at them, but they kept dancing, doing both wheezes and gargles. Paul was fully piloerected and threatened loudly and continuously, as the dancing pair continued to wheeze and twitter. As Paul's vocal threats mounted in intensity, Guapo quit dancing and left the vicinity altogether.

The second anecdote illustrates how Paul rapidly alternated between supporting Curmudgeon and supporting Guapo. On December 6, 1992, Paul, who was fully piloerected, threatened Curmudgeon and headflagged to adult female Squint. Squint, rather than threatening Curmudgeon, threatened and bounced at infant Lizano. Paul lunged at Squint, who screamed, and Paul again threatened Curmudgeon. Squint threatened the human observers and headflagged to Paul, who aided her. But then Paul resumed threatening Curmudgeon and backed into Squint to request support. Squint continued to threaten the humans rather than Curmudgeon, and finally left. Paul ran on the ground toward Curmudgeon and directed intense vocal threats at him. Guapo watched this and manipulated his tail nervously. Paul then headflagged to Curmudgeon and threatened Guapo. Paul again headflagged to Curmudgeon and threatened Guapo, and this time

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Curmudgeon joined Paul in vocally threatening Guapo. Guapo licked his tail nervously as the threats continued. Paul once again headflagged to Curmudgeon and silently threatened Guapo, but Curmudgeon walked away. As Curmudgeon left, Paul headflagged to Guapo and threatened Curmudgeon, and Guapo promptly joined Paul in threatening Curmudgeon. Both Paul and Guapo chased Curmudgeon and directed intense vocal threats at him. Curmudgeon dropped his food and fled. Paul again headflagged to Guapo two more times and vocally threatened Curmudgeon.

When Curmudgeon was alpha male, he was much less controlling of subordinate males than was Paul. Of the 19 affiliative interactions between Paul and Guapo that occurred during the precoup period, 5 were observed by Curmudgeon, and he did not break up any of them. However, some ad lib observations, such as the following two anecdotes, suggest that Curmudgeon did, on occasion, go out of his way to break up Paul-Guapo affiliations.

On January 27, 1992, at 10:56, Curmudgeon found a boa constrictor and began to perform alarm calls. The rest of the group joined in the alarms and looked at the snake, and they continued to alarm call for several minutes before calming down. Curmudgeon appeared to lose interest in the snake and rested calmly for a while. When Curmudgeon observed Paul starting to groom Guapo, Curmudgeon leaped to his feet, rushed to within a meter of the snake, alarm called furiously, and shook branches, while glancing repeatedly at Paul and Guapo. Paul and Guapo immediately stopped grooming and rushed to Curmudgeon's aid. All three males alarm called, and then Curmudgeon and Guapo left the site of the snake, while Paul remained with the snake and continued to call.

On August 14, 1992, at 10:15, Curmudgeon, Wiggy and Paul formed a coalition against Guapo. As soon as Curmudgeon broke off his overlord with Paul and began to leave the area, Guapo approached Paul to one body length and threatened the human observers. Paul stopped threatening Guapo and moved to within contact of him, grasping Guapo's tail. Guapo presented for grooming to Paul. Curmudgeon, who was watching

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this, immediately emitted an alarm call, although there was no predator present. Paul and Guapo looked toward Curmudgeon and immediately broke contact with one another. Guapo once again threatened the human observers and left Paul.

Lost Monkeys

Because of the low rate of affiliation and relatively high rate of aggression between males, it is surprising that, when one male became separated from the group for a long period of time, the other males went to considerable effort to find the missing male and bring him back to the group. The alpha male generally instigated searches for subordinate males. Subordinate males were never observed to search for alpha males in the 4 instances in which the alpha male was absent. The following anecdote was the first event of this nature that I observed, but I observed the males behave similarly in at least 8 other instances in which males were lost.

Paul disappeared during the afternoon of August 17, 1991. At dawn on the morning of August 20, while the monkeys were still in their sleeping tree, Curmudgeon began emitting lost calls (defined in ethogram, chapter 1), although he was in the center of the group and was clearly not lost. I did not hear any lost calls in the distance prior to Curmudgeon's calls. Curmudgeon did lost calls continually for five minutes and then left the group. He crossed the river and ran up the hills on the other side, while lost calling at a rate of 150 times/hour, alarm calling at a rate of 378 times/hour, and making occasional gecking sounds as well. Guapo followed Curmudgeon and also did lost calls and alarm calls, but not as often. The rest of the group followed at a greater distance. After 47 minutes of racing through the forest, Curmudgeon and Guapo found Paul, approximately 1/4 km from their starting point. They immediately stopped lost calling. Guapo rushed over to Paul and mounted and thrust on him. Paul and Guapo then embraced. Curmudgeon did not greet Paul, but he stopped to rest near him. When the females finally caught up with the males, they threatened Paul. Paul had a wound on his right shoulder

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and seemed slightly lethargic. Curmudgeon monitored Paul for the rest of the day, seeking him out whenever he lagged behind the group.

Not all of the reunions with lost males involved embracing and sexual interactions. Also, sexual interactions and embracing between males were seen in other contexts besides reunions -- primarily in tense social situations. Reunion behaviors and sexual behaviors are discussed in further detail in Chapter 6.

Discussion

The four capuchin males of my study group had a clearly defined alpha male. This is consistent with results reported by Fedigan (1993), Rose (1994), and Oppenheimer (1968), but contrary to what has been reported at some other sites (Buckley 1983; Mitchell 1989) for this species. The alpha male received submissive gestures from all other males, but did not direct submissive gestures toward others. He directed far more aggression toward males than he received, and what little aggression he did receive was typically a counterthreat in response to a threat he had just given. The alpha male engaged in displays (piloerection, urine rubbing, branch-breaking and branch-shaking) at rates that greatly exceeded those of other males. He was spatially central in the group and had more positive affiliative relationships with females than did other males (see chapters 4 and 5).

The alpha male appears to manipulate subordinate males' relationships and behavior to some extent. When the alpha male is absent from the group, the beta male alters his behavior by greatly increasing the rate at which he performs displays. Males are occasionally punished for exhibiting display behaviors in the presence of the alpha male. Although vigilance toward group members was not systematically recorded in the data, I had the impression that males carefully monitored one another's behavior, particularly after the coup. The alpha male consistently disrupted subordinate males' affiliative interactions with other subordinate males, as described for captive chimpanzees ("separating interventions": de Waal 1978, 1982). I interpret these disruptions as attempts by the alpha

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male to prevent subordinate males from establishing solid social relationships and agonistic alliances that could be threatening to the alpha male's status. The alpha male was not consistent in his choice of which male to support in triadic agonistic interactions involving males (although he never supported the immigrant male against long-term resident males). Both subordinate resident males were willing to support the alpha male against other subordinate males; however, pairs of subordinate males never formed coalitions against the alpha male. It appears that by frequently requesting (and receiving) aid from one male against another, and by often shifting his support from one male to another, the alpha male was able to strengthen his position as the key player in male-male politics.

The alpha male's manipulation of subordinate males may explain why subordinate males do not form strong bonds with one another, but why doesn't the alpha male form strong bonds with subordinate males, as in chimpanzees (de Waal 1982)? Perhaps the difference in male relationships between chimpanzees and white-faced capuchins can be explained by the different patterns of philopatry. In capuchins, unlike chimpanzees, females are philopatric and form the central core of the social network. Female-female coalitions are a major factor in the group's politics, and it is likely that female support is necessary for a male to retain the alpha position (see Chapters 2 and 5). Thus, it may be more important for an alpha male to concentrate on developing alliances with females than with males. Indeed, alpha males spent more time in proximity and in affiliation with high-ranking adult females than with adult males, and they also formed more coalitions with high-ranking females than with males (see chapter 4). Not only are females more valuable as allies in the short term, but they are also less likely to leave the group than males are; therefore, developing a relationship with a female is a good long-term investment.

Although males do not have strong bonds (i.e. they do not frequently associate in a relaxed, affiliative manner), they do reliably cooperate with one another in two contexts: defense against potential predators, and defense against males of other groups (chapter 7). All males engage in at least some mating (although it is not known what percentage of these

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matings are likely to result in conception; see Chapter 4), and therefore it is possible that all or most males have offspring in the group. Thus, cooperation against predators is likely to be mutually beneficial for males.

It seems likely that the main threat to a male's reproductive future is the threat of invasion from extragroup males. I have not witnessed such a takeover, but data from Santa Rosa National Park, where Linda Fedigan and her colleagues have been observing capuchins for the past decade, suggest that male takeovers from groups of 1-4 males occur fairly frequently (Fedigan 1993; Fedigan et al. n.d.; Rose 1994). These invasions by extragroup males can result in eviction of resident males, infanticide, and wounding (even resulting in death) of males (Fedigan et al. n.d; Rose 1994). Rose and Fedigan (1995) suggest that male vigilance is primarily directed toward extragroup males. Males are the primary participants in intergroup encounters, which are invariably hostile (Chapter 7; Fedigan 1993; Rose 1994; Mitchell 1989; but see Oppenheimer 1968). In my study group, males very reliably aided one another in intergroup encounters (chapter 7).

Certain striking affililative behaviors, such as males' active searches for lost males, and wheeze dances, can be explained by the need to balance intense intragroup competition with the need to cooperate against external threats. It is likely that males search for lost males because it is important to have a large number of males to aid in intergroup encounters. Wheeze dances, which are more common between monkeys whose relationships are tense, and between monkeys who have great potential to inflict costs on one another (see chapter 6), may be functioning to negotiate the status of the relationship, much in the way that male savanna baboons' greetings serve to negotiate relationships (Smuts and Watanabe 1990; Colmenares 1991). Wheeze dances are discussed in greater detail in Chapter 6.

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Table 3.1: Focal data collected on each male (hours).

Male	precoup	postcoup	total
C	71.8	39.2	111.0
P	71.0	40.0	111.0
G	71.0	37.2	108.2
I	0	34.3	34.3

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Table 3.2: Submission data, precoup.

	Recipient		
Actor	C	P	G
C	-----	0	0
P	4	-----	2
G	4	1	-----

Table 3.3: Submission data, postcoup

	Recipient			
Actor	P	C	I	G
P	-----	0	0	0
C	3	-----	0	0
I	3	0	-----	1
G	5	2	2	-----

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Table 3.4: Rates of aggression (bouts/hour), precoup.

	Recipient		
Actor	**C**	**P**	**G**
C	-----	0.05	0.08
P	0	-----	0.08
G	0.007	0.06	-----

Table 3.5: Rates of aggression (bouts/hour), postcoup.

	Recipient			
Actor	P	C	G	I
P	-----	0.23	0.42	0.13
C	0.03	-----	0.36	0.07
G	0.03	0.17	-----	0.03
I	0.04	0.07	0.10	-----

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Table 3.6: Rates of severe aggression (bouts/hour), precoup.

	Recipient		
Actor	C	P	G
C	-----	0	0
P	0	-----	0
G	0	0.02	-----

Table 3.7: Rates of severe aggression (bouts/hour), postcoup.

	Recipient			
Actor	P	C	G	I
P	-----	0.04	0.04	0
C	0	-----	0.04	0.01
G	0	0	-----	0.01
I	0	0	0.03	-----

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Table 3.8: Paul-Curmudgeon coalitions, precoup

Victim	# times	# successful	# C direct requests	# P refusals	# P direct requests	# C refusals	# C indirect requests	# P indirect requests
Guapo	6	6	0	0	2	0	2	2
unidentified monkey	1	1	0	0	1	0	0	0
unidentified juvenile	1	0	0	0	1	1	0	0
nonmonkey	25	15	5	4	13	8	6	4

Table 3.9: Curmudgeon-Guapo coalitions, precoup

Victim	# times	# successful	# C direct requests	# G refusals	# G direct requests	# C refusals	# C indirect requests	# G indirect requests	unclear initiation
Paul	5	3	0	0	3	2	0	1	
Kola	1	0	0	0	1	1	0	0	
unidentified juvenile	2	0	0	0	2	2	0	0	
X*	3	2	0	0	1	1	0	2	
nonmonkey	36	20	1	0	13	9	11	9	2

* unidentified monkey; 2 of these were probably imaginary

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Table 3.10: Guapo-Paul coalitions, precoup

Victim	# times	# successful	# G direct requests	# P refusals	# P direct requests	# G refusals	# G indirect requests	# P indirect requests
unidentified juvenile	1	1	1	0	0	0	0	0
nonmonkey	11	5	3	0	1	0	4	3

Table 3.11: Paul-Curmudgeon coalitions, postcoup

Victim	# times	# successful	# P direct requests	# C refusals	# C direct requests	# P refusals	# P indirect requests	# C indirect requests
Guapo	10	8	2	0	4	2	3	1
unidentified monkey	3	1	1	1	1	1	1	0
nonmonkey	8	5	4	3	1	0	2	1

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Table 3.12: Curmudgeon-Guapo coalitions, postcoup

Victim	# times	# success-ful	# C direct requests	# G refusals	# G direct requests	# C refusals	# C indirect requests	# G indirect requests
juveniles	1	1	0	0	0	0	0	1
nonmonkey	10	4	3	2	5	4	1	1

Table 3.13: Paul-Guapo coalitions, postcoup

Victim	# times	# success-ful	# G direct requests	# P refusals	# P direct requests	# G refusals	# G indirect requests	# P indirect requests	unclear initiations
Curmudgeon	7	3	3	1	4	3	0	0	0
Ichabod	3	2	2	0	1	1	0	0	0
Kola	3	2	0	0	2	2	0	1	1
Lizano	2	0	0	0	2	2	0	0	0
unidentified monkey	2	1	1	1	0	0	1	0	0
nonmonkey	42	27	12	8	14	7	6	8	2

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Table 3.14: Ichabod-Paul coalitions, postcoup

Victim	# times	# successful	# I direct requests	# P refusals	# P direct requests	# I refusals	# I indirect requests	# P indirect requests
nonmonkey	5	3	2	2	1	0	2	0

Table 3.15: Ichabod-Curmudgeon coalitions, postcoup

Victim	# times	#successful	# I direct requests	# C refusals	# C direct requests	# I refusals	# I indirect requests	# C indirect requests	unclear initiation
nonmonkey	3	3	0	0	0	0	1	1	1

Table 3.16: Ichabod-Guapo coalitions, postcoup

Victim	# times	# successful	# I direct requests	# G refusals	# G direct requests	# I refusals	# I indirect requests	# G indirect requests	unclear initiation
nonmonkey	3	3	1	0	0	0	0	2	1

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Table 3.17: Hourly rates of urine-rubbing, pre- and postcoup

	Precoup		Postcoup	
Male	N	rate/hour	N	rate/hour
C	110	1.55	49	1.26
P	11	0.16	76	1.91
G	3	0.04	6	0.16
I	-----	-----	4	0.12

Table 3.18: Hourly rates of urine-rubbing, by quartile

Male	quartile 2	quartile3	quartile 4
C	2.22	1.13	1.26
P	0.23	0.07	1.91
G	0.07	0	0.16
I	-----	-----	0.12

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Table 3.19: Hourly rates of branch-shaking and branch-breaking, precoup and postcoup

	Precoup		Postcoup	
Male	N	rate	N	rate
C	64	0.90	22	0.57
P	38	0.54	39	0.98
G	44	0.62	7	0.19
I	-----	-----	81	2.36

Table 3.20: Hourly rate of branch-breaking and branch-shaking, by quartile

Male	Quartile 1	Quartile 2	Quartile 3	Quartile 4
C	0.14	1.11	1.06	0.57
P	0.38	0.69	0.21	0.98
G	0.84	0.51	0.72	0.19
I	-----	-----	-----	2.36

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Table 3.21: Proximity scores for adult monkeys, averaged across dyads for sex classes, pre- and postcoup

Category	Precoup	Postcoup
Male-male	1.51	0.10
Male-female	2.75	1.84
Female-female	7.20	6.01

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Table 3.22: Male-male grooming rates (seconds/hour), precoup

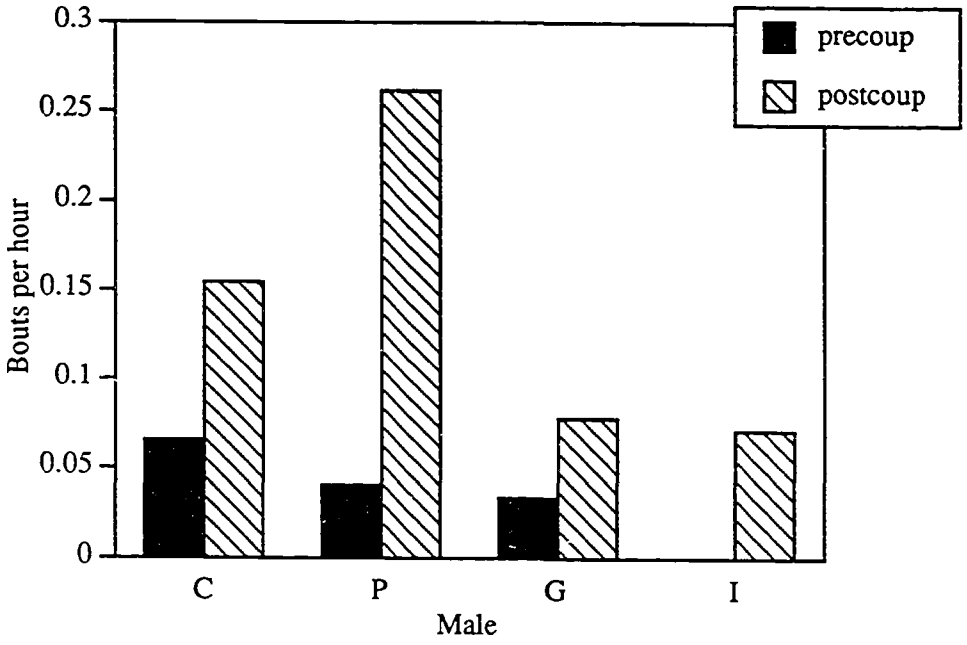
	Recipient		
Actor	C	P	G
C	-----	0	0
P	0	-----	1.63
G	0	0	-----

Table 3.23: Male-male grooming rates (seconds/hour), postcoup

	Recipient			
Actor	P	C	G	I
P	-----	0	0	0
C	.28	-----	0	0
G	0	.46	-----	0
I	0	1.0	.28	-----

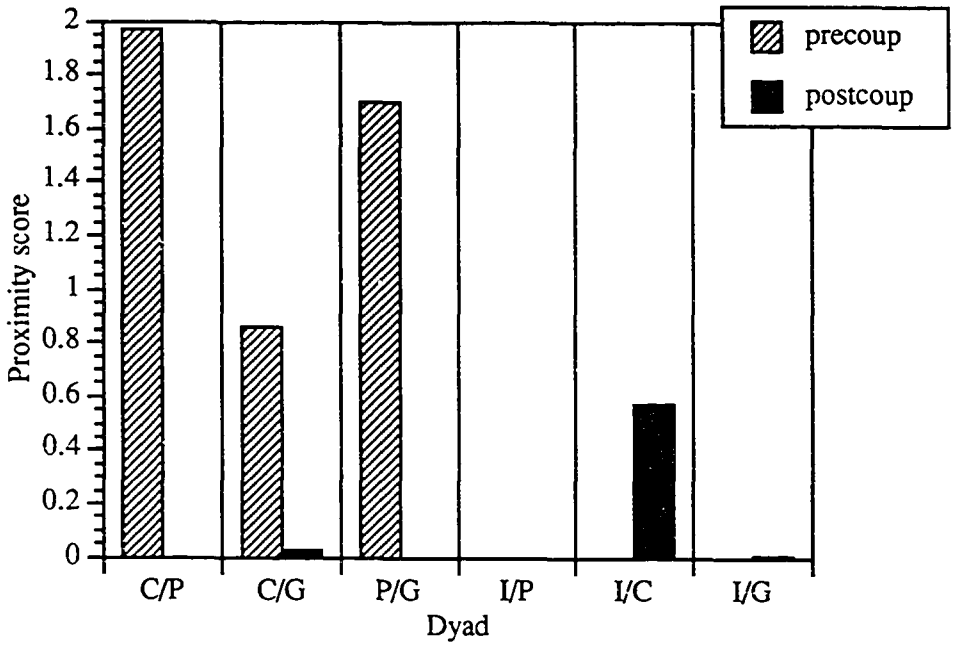
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Figure 3.1: Aggression directed toward other males, averaged across dyads, pre- and postcoup.



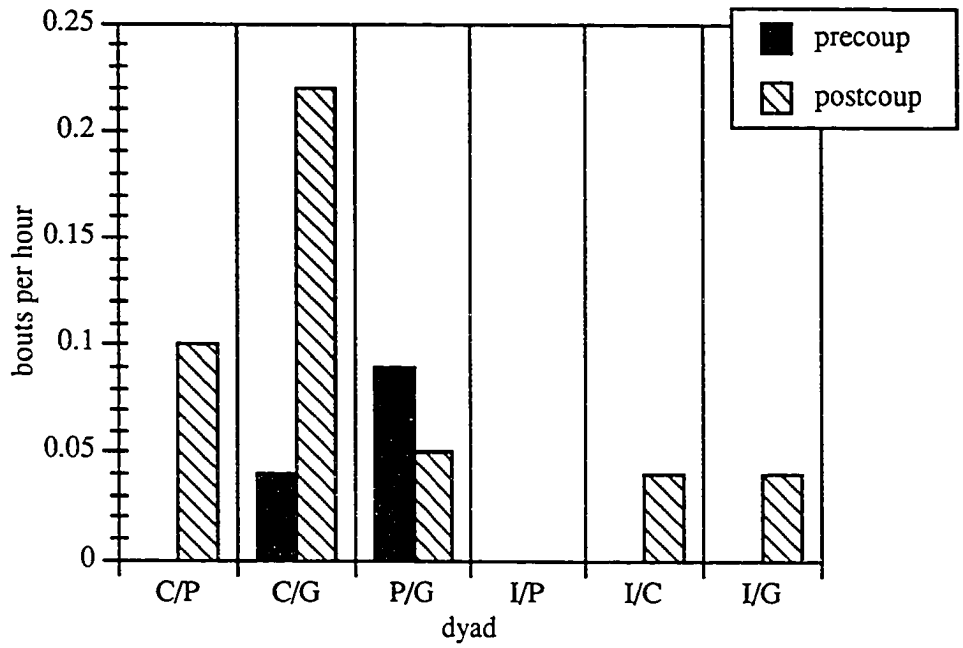
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Figure 3.2: Male dyads' proximity scores, pre- and postcoup



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Figure 3.3: Friendly interactions between males, pre- and postcoup



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CHAPTER IV

MALE-FEMALE SOCIAL RELATIONSHIPS

Introduction

Early studies of male-female relationships in primates focused primarily on sexual behavior (Zuckerman 1932). More recent studies have demonstrated that in some gregarious primates, males often have long-term affiliative relationships with females outside of the mating context (rhesus monkeys: Chapais 1983, Hill 1990; mountain gorillas: Watts 1992; olive baboons: Smuts 1985, Ransom and Ransom 1971; captive chimps: de Waal 1982; Japanese macaques: Takahata 1982, Huffman 1991a,b; ringtailed lemurs and redfronted lemurs: Kappeler 1993b). The fundamentally different reproductive strategies of males and females (Trivers 1972) set the stage for conflicts between the sexes. An extreme, though illustrative, example is infanticide by males unlikely to have sired their victims (Hrdy 1974, 1977), which is interpretable as male-female conflict over the disposition of scarce female parental investment. Less spectacularly, but comparably damaging to female fitness, males may use their superior size to monopolize scarce food and thereby put females at risk of starvation (Dittus 1979). Males and females may also have conflicts over whether to mate, in which males may sexually coerce females (Smuts and Smuts 1993).

In contrast, males may be singularly useful to females. For example, males may take a leading role in detecting and attacking predators (van Schaik and van Noordwijk 1989). In general, male-female relationships in gregarious primates are multi-faceted, including affiliative and aggressive components, and often characterized by behaviors such as grooming and species-specific reconciliation behaviors that apparently function to reduce

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tension (Smuts 1987). The exact nature of benefits exchanged and costs inflicted by one sex on the other varies among species. Few studies have attempted to characterize male-female relationships quantitatively, according to the sexes' relative abilities to confer or withhold benefits and impose costs on one another (Smuts 1985; Rose 1994; O'Brien 1991).

Males are individually dominant to females in most primate species; i.e. males typically win in dyadic disputes over contested resources (Smuts 1987, Kappeler 1993a). However, even in species in which males are individually dominant to females, males can not always win disputes with females when other group members are present (Smuts 1987). Sexual size dimorphism seems to be a factor in determining which sex wins disputes, but even in some species in which males have a size advantage over females, females may have the upper hand in resource acquisition and in determining the outcome of power struggles (Smuts 1987). Females can outcompete males who are individually dominant to them by forming coalitions with other females (Smuts 1987, Smuts and Smuts 1993, Parish 1994) or with some males against others (Smuts 1985, Smuts and Smuts 1993, Chapais 1983). Thus, the power balance between males and females -- i.e. the species-typical outcome of disputes between males and females -- is dependent not only on characteristics of the relationship between the principals, but on each party's ability to recruit aid from third parties.

Although the power balance between the sexes is determined partly by the relative abilities of each sex to impose costs on the other, it is also strongly influenced by their relative abilities to confer benefits that cannot be taken by force (Smuts 1985,1987). Among nonhuman primates, the orangutan is virtually the only species in which forced copulations are common (MacKinnon 1974; Galdikas 1981, 1985; Mitani 1985); in all gregarious species, mating requires some degree of female cooperation. Although, in addition to sexually selected infanticide (Hrdy 1974, 1977; Hausfater and Hrdy 1984), males may use a variety of sexual coercion tactics to acquire matings with reluctant females

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(Smuts and Smuts 1993), they may also increase their chances of mating by investing in females and their offspring, even when those offspring have been fathered by other males (Smuts 1985). Whether coercion or investment is used varies among species as a function of physiological variables (e.g. breeding seasonality: van Hooff and van Schaik 1994), and also intra-specifically as a function of demographic variables (Bercovitch 1991) and even life history stage (Strum 1994). In addition to outright coercion, males may influence females' mating decisions by monopolizing food resources that are critical for female reproduction. In brown capuchins, for example, the alpha male monopolizes food patches and allows his offspring preferential access to food over other group members (Janson 1984). Therefore, females prefer to mate with the alpha male.

In addition to mating access, females may control group membership (patas: Hall 1967; vervets: Cheney and Seyfarth 1990; Japanese macaques: Packer and Pusey 1979) and/or coalitionary support required by males to attain and maintain high dominance rank (rhesus macaques: Chapais 1983; captive chimpanzees: de Waal 1982; vervets: Raleigh and McGuire 1989). If high rank is associated with reproductive success in these species, then female political support is a resource critical to male reproduction.

When females control resources males need, and vice versa, the sexes are in a position to bargain with one another. Although detailed quantitative studies demonstrating reciprocity have not been conducted in many species, it appears that exchanges of benefits are an important component of primate social relationships. Sometimes the benefits exchanged between individuals are in the same type of currency (e.g. exchange of coalitional support for coalitional support: Silk 1992b; Packer 1977), but they needn't always be. For example, grooming could be exchanged for coalitional support (Seyfarth and Cheney 1984). Males and females are often capable of conferring differing types of costs and benefits on one another. Female baboons often choose as mates those males who groom them and protect them and their infants (Smuts, 1985); female brown capuchins mate almost exclusively with alpha males, who offer protection from predators

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and tolerate females and their infants at feeding sites (Janson 1984); and female chimpanzees often consort more with males who groom them and share meat (Tutin 1979).

In this chapter, I characterize male-female relationships in white-faced capuchins by investigating (1) the outcomes of dyadic interactions, (2) the nature and direction of exchange of social favors between the sexes, (3) the types of costs inflicted by one sex on the other, and (4) ways in which the sex that is disadvantaged in one-on-one contests can compensate by recruiting coalitionary aid.

Adult male white-faced capuchins weigh 3.8 kg, on average, which is 1.4 times the average weight of 2.7 kg for adult females (Harvey et al. 1987). Thus, all else being equal, males would be expected to be dominant to females. I examine 4 types of dyadic male-female interactions, to assess females' and males' reactions toward one another in different contexts. In the first analysis, I examine the directions of avoidance and cowering in male-female dyads. In the second analysis, I examine females' reactions to neutral approaches by adult males. In the third analysis, I examine females' reactions to aggressive displays by males. Finally, I examine the frequencies of supplants and food thefts by males toward females and vice versa.

Proximity data are presented at this point, in part because patterns of proximity may reflect, to some extent, mutual social preferences, but also because patterns of proximity affect the probability that a dyad will interact. Thus, a knowledge of the spatial patterning of group members is necessary to interpret some of the data that follow.

The social favors that I investigate are grooming, coalitionary aid, and sexual access. The rates and direction of grooming, as well as the proportion of grooming invitations that are refused, are compared across dyads. The rates at which heterosexual dyads form coalitions are compared across dyads, and examined according to the context in which they are formed. Sexual behavior is described in detail and, to the extent to which it is possible given the cryptic sexual behavior of fertile females, male mating success is examined according to male rank and age.

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I examine costs inflicted by one sex on the other, in the form of aggression, dividing aggression into mild vs. severe aggression. Aggression rates are compared across dyads, with regard to male and female rank.

Finally, I compare males and females with regard to the frequency with which they form same-sex coalitions against members of the opposite sex. I examine coalitions according to context, rank of the members involved, and success of coalitions in defeating their victims. I also discuss male counter-strategies against female-female coalition formation -- i.e. attempts to break up female alliances.

Methods

The analyses in this chapter are based on 953.17 hours of focal data collected on adult males and females (Table 4.1). The protocol for focal follows is described in chapter 1. The top segment of the table shows the adult males, and the bottom half shows the adult females. In subsequent tables throughout this chapter, individuals are referred to by the first letter of their names. In all cases in which female dominance rank is a relevant variable, females are listed in tables according to rank, in descending order. Females were ranked as follows, from top to bottom: Abby, Squint, Nanny, Diablita, Wiggy, Tattle. The procedure for determining female rank is described in chapter 2.

In November, 1992, the alpha male Curmudgeon was overthrown by Paul, a subordinate male. The coup is described in greater detail in chapters 5 and 3. Because of the dramatic effect the male rank reversal had on virtually all male-female dyads' relationships, I divided the dataset into 2 segments -- precoup and postcoup -- for many analyses in this chapter. Two demographic changes coincided with the coup: Ichabod's immigration into the group, and Diablita's first estrous period, which caused her to be moved from the juvenile female category to the adult female category. The change in number of male-female dyads at the time of the coup also necessitated the division of the data set into 2 segments in some analyses.

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Definitions

Proximity scores are calculated according to the methods described in chapter 3. The unit of measurement in all analyses involving proximity is the "body length," which is the length of an adult male capuchin, from nose to tailbase.

My data collection protocol was changed so as to record grooming as a state (with durations measured in seconds) rather than as an event, on December 30, 1991. Hence, all analyses involving grooming rates incorporate data only from December 30, 1991, until the end of the study.

A neutral approach by a male to a female is defined as an approach to within one body length in which the male is not piloerected, threatening, making a non-neutral facial expression, strutting, displaying, or vocalizing, and has not aggressed against anyone within the past 5 minutes.

Analyses of aggression between males and females were divided into two categories: mild and severe. Mild aggression included threats (silent and vocal), overlords, lunges, and bounces. Severe aggression included bites, hits, pushes, grabbing of limbs, wrestling, and chasing. Branch-breaking, branch-shaking, and display postures were not included in analyses of dyadic aggression, as these behaviors were not obviously directed at particular individuals in most cases; however, female responses to male displays are treated separately. Supplants were not included in analyses of aggression, but they are lumped together with food theft in a separate analysis. Because aggressive interactions tended to be clustered together in long sequences, individual aggressive acts were not considered as independent events. For the purpose of calculating rates of attack and rates of providing coalitionary aid, I only counted one aggressive act in each direction per dyad per 10-minute sample.

Conception dates were determined by counting back 160 days from an infant's birth date. Gestation lengths for *Cebus capucinus* are not available, but the gestation length for *C. apella* is 160 days (Harvey et al., 1987). Because the *C. apella* gestation length is likely

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to be slightly different from the *C. capucinus* gestation length, I defined the period during which conception was likely to have occurred rather broadly, as being within 10 days before or after the putative conception date.

Results

Dominance Hierarchy

When the direction of avoids and cowers are used to compute the dominance hierarchy, all females are subordinate to all males. Table 4.2 shows that across all dyads, females directed avoids and cowers to males roughly 100 times more often than vice versa. The few interactions in which males cowered to females occurred during unusual circumstances. Paul cowered to Abby once during a courtship dance. Paul avoided Nanny while she was in estrus and courting him intensely; however, Paul threatened her immediately afterward. Paul's avoidance of Tattle on August 25, 1991 is more difficult to account for, but he was wounded and had recently returned to the group after an absence of 2.5 days.

Female Responses to Neutral Approaches by Males

A female's response to a neutral approach by a male could be a good indicator of the nature of the dyad's relationship, since it shows the female's reaction to the male apart from any unusual social context. Table 4.3 shows the proportion of responses in each category made by females to males who have approached them neutrally in the past minute. The categories of responses are as follows: friendly (grooming, gargling, twittering, presenting for grooming, sex, or cuddling); ignore without leaving; leave before any other social interaction takes place; fear (cower, avoid, flee, scream); attack a third party as the male approaches or immediately after he approaches, with or without explicitly recruiting the approaching male; or attack the approaching male, with or without recruiting aid from

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third parties. Only the first approach by a male was included in this analysis for each 10-minute sample. Only approaches to within one body length were included. In a few instances, more than one category of response was recorded for the same approach (e.g. fear plus aggression, or fear plus redirected aggression); thus, the sum of the proportions of responses in each category may be greater than one for a given female.

Some of the different response profiles can be attributed to quirks of a dyad's relationship, but some differences are apparently due to characteristics of the male, or to personality differences among females, rather than to the unique features of a pair's particular relationship. Table 4.4 shows females' responses, averaged across males. For the most part, the differences between females in their responses conform to my impressions of their personalities. When Abby did not ignore or leave a male who had approached her, her most frequent response was to threaten a third party (often as the male was approaching) and form a coalition with the male. My impression was that she aggressed against third parties, often primatologists, as a way of diverting the male's attention so as to reduce the chances of his attacking her or supplanting her from a feeding site. It appears that this is not a rank-related strategy, as it was also practiced to a great extent by the lowest-ranking female, Tattle, though Tattle differed from Abby in the extent to which she directed fear signals toward males. None of the females seemed genuinely frightened of the observers, or of the other victims of this sort of third party aggression. They often foraged peacefully within a few feet of the observers until a male began to approach, and then suddenly turned and threatened us. Aggression toward third parties was a more common response to the approach of high-ranking males (Curmudgeon and Paul) than to low-ranking males. Wiggy, whom I had considered to be a very calm and friendly female, responded to male approaches most often by directing affiliative behaviors (mainly grooming) toward them. She had very low rates of aggression in response to male approaches. Squint and Nanny ignored or left males most of the time and had low to average rates of response for all other response types. Diablita, the adolescent female, had

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extreme emotional responses to male approaches, exhibiting the highest proportions of affiliative and aggressive responses, as well as a fairly high score for fearful response.

Male characteristics seem to account for much of the variation in female responses to approaches across dyads (Table 4.5). Paul, who was alpha male during 97 of his 165 approaches, received the lowest proportion of affiliation in response to approach, and the highest proportion of third party attacks. Ichabod, the immigrant male, had the most distinctive response profile: females rarely ignored or left him in response to his approaches. They were more likely to respond to Ichabod's approach with fear or aggression than was the case for other males' approaches. Curmudgeon's approaches were more often ignored than were the approaches of other males, and Curmudgeon's approaches elicited fewer fearful responses than was the case for other males. Both Curmudgeon and Guapo had much higher ratios of friendly to fearful responses than did Paul or Ichabod.

The fact that females overall responded to roughly a quarter of males' approaches by showing fear, or threatening either the male or a third party, indicates that even neutral approaches by males often intimidate females.

Female Responses to Male Displays

Table 4.6 shows females' responses to male displays (branch-shaking, branch-breaking, and branch drags). Sometimes females responded in more than one way to the display, and in a few cases, they responded in ways that did not conform to any of the categories (e.g. by inviting sex, gargling, or peeping); therefore, not all of the proportions add up to 1.0. The categories of response are ignore, fear (scream, cower, avoid, flee), aggression toward displaying male, aggression toward a third party, and continued aggression toward third party (in cases in which the female was involved in an aggressive interaction before the male began the display). Unidentified males are noted as "X" or (if they are definitely juveniles) "XJ." The top section of the table shows adult male displays,

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the middle section shows juveniles' displays, and the bottom section shows displays of males who could not be identified during that particular interaction.

Male displays are typically generalized rather than directed at particular individuals. The function of male displays is not entirely clear, but displays probably demonstrate male strength and perhaps signal something about males' emotional states. Females ignored the majority of male displays. This result seems to be in disparity with the result that females responded more emotionally to neutral approaches by males. Two factors are probably responsible for this disparity: the greater distance from the female at which most displays occurred, and the generalized nature of the displays (as opposed to the approaches, which were clearly directed toward particular females).

Table 4.7 shows the females' responses to each adult male's displays, averaged across females. Females never responded fearfully or aggressively to juveniles' displays. They ignored 69% of adult males' displays, on average. Female responses to adult males were fairly similar for the resident males (Curmudgeon, Paul and Guapo), though they responded fearfully more often to Guapo. Females ignored slightly fewer of the immigrant male Ichabod's displays and responded more fearfully to him than to other males. In situations in which I could not identify the displaying male, females tended to respond more aggressively; this is probably because the male was further away, and therefore safer to threaten. In the one instance in which a male from a different social group intruded into the center of the study group and displayed, Squint responded fearfully, by screaming at him.

Table 4.8 shows female responses to adult males, averaged across males. Individual females had different response profiles. Relative to other females, Squint frequently responded aggressively and rarely responded fearfully. Both Nanny and Tattle frequently responded fearfully or attacked third parties. Wiggy and Diablita tended to ignore male displays. Diablita's calm response to male displays is surprising, given her highly emotional response to neutral approaches by males.

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Supplants and Food Theft

Table 4.9 shows the rates at which adult males and females supplanted one another at resources. Repeated supplants occurring within the same minute were scored as a single event for the purpose of this analysis. Males supplanted females 15 times as often as females supplanted males. Aggressive food theft was extremely rare among all group members and was observed only once in adult male-female dyads during focal observations, when Curmudgeon stole a piñuela fruit from Squint. Tolerated theft was much more common, but was observed only once during focal observations among adult male-female dyads, when Guapo took food from Wiggy. Food sharing was never observed in male-female dyads.

Proximity

On average, males associated more with females than they did with other males, whereas females associated more with females than they did with males (see Table 4.10). Tables 4.11 and 4.12 show that there was less variation among females, with regard to the amount of time they spent with members of the opposite sex (SD= .67 precoup and 1.00 postcoup), than there was variation among males with regard to time spent with the opposite sex (SD= 1.78 precoup and 2.53 postcoup). This is because, both before and after the coup (but especially after), the alpha male occupied a central position in the group, near the clique of high-ranking females (Abby, Squint and Nanny -- see chapter 2), whereas subordinate males tended to be more peripherally located. It is possible that subordinate males had low proximity scores with females (particularly high-ranking females) primarily because they were avoiding proximity to the alpha male. Curmudgeon was never observed to approach (to within 1 body length) the 4 top-ranking females after the coup during focal observations. Guapo never approached Squint or Diablita postcoup, and only approached Abby and Nanny once each. The effects of the coup on male-female proximity and affiliation are discussed in greater detail in chapter 5.

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Grooming

Females groomed males 41 times (precoup) to 95 times (postcoup) as often as males groomed females. Tables 4.13 and 4.14 show the rates of male-female grooming before and after the coup; the rates at which males groomed females are in parentheses. Most females groomed the alpha male more than they groomed other males. Because most females spent more time in close proximity to the alpha male than to other males, the alpha male was more available as a grooming partner. Tables 4.15 and 4.16 show the rates at which females groomed males, divided by the proportion of time each male-female dyad spent within 10 body lengths of one another (as calculated from the final point sample of each 10-minute focal sample). When amount of time spent in proximity is controlled, the females' order of preference for male grooming partners is less clear than in tables 4.13 and 4.14. Before the coup, 4 out of 5 females groomed Guapo most, Curmudgeon second most, and Paul least, during the time they spent within 10 lengths of them. After the coup, there was no clear pattern to grooming preferences across dyads, but Paul (the alpha male) was not the top-ranked grooming partner for any female.

As another way of ascertaining male-female dyads' willingness to groom one another, I examined the proportion of grooming invitations that were ignored. Tables 4.17 and 4.18 show the proportion of grooming invitations by males that were ignored by females, precoup and postcoup. Both before and after the coup, the alpha male's grooming invitations were ignored less frequently (10% and 26% less, respectively) than were invitations by subordinate males. Paul was the most frequently ignored male prior to the coup, and the least frequently ignored male following the coup. Curmudgeon was the least frequently ignored male prior to the coup and the most frequently ignored male after he lost alpha status. However, there was considerable variation among dyads, and the mean differences between males during the precoup phase were slight. If males are ranked, for each female, on the basis of proportion of grooming invitations accepted, these preferences differ greatly from preference rankings based on amount of time females groomed males

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per amount of time spent within 10 body lengths. Thus, perhaps neither measure is a good indicator of female social preference for males.

Males ignored about 88% of females' grooming invitations (Tables 4.19 and 4.20). Given the low frequency at which males groomed, it is surprising that females ever bothered to request grooming from them. The male who ignored the lowest proportion of female grooming invitations was Ichabod, the immigrant male. It is possible that Ichabod could not afford to ignore as many grooming invitations, since he was in the process of forming new relationships with females.

Male-female Coalitions

Tables 4.21 and 4.22 summarize coalitions between males and females, before and after the coup. The targets of the vast majority of male-female coalitions were non-monkeys. Some (boa constrictors, dogs, owls, and unfamiliar humans) posed genuine threats to the monkeys, but most (e.g. primatologists, cows, anteaters, dead deer, cow dung, coatis, peccaries, howlers, pigs, and currassows) were harmless and probably served as scapegoats for the purpose of redirected aggression. Coalitions against harmless non-monkeys were frequently initiated by females as they were being approached by males.

Of those coalitions directed at other capuchins, the most frequent targets were adult males. When the distribution of coalitions against adult males and females is compared to the distribution expected if coalitions were directed at adults randomly with respect to sex, males were targeted more often than expected (precoup: sign test, $p=.096$; postcoup: sign test, $p=.003$). In no case during focal observations did a female form a coalition with a subordinate male against the alpha male. Guapo and Paul were both observed to form coalitions with females against one another before the coup. After the coup, Ichabod formed coalitions with females against both Curmudgeon and Guapo, and Curmudgeon formed coalitions with females against Guapo, but never against Ichabod.

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Tables 4.23 and 4.24 show the rates of participation in male-female coalitions, averaged across dyads, for each adult individual, before and after the coup. Males are listed on the top halves of the tables, and females are on the bottom halves; females are listed in descending rank order. The alpha male was the most frequent partner of females in male-female coalitions, both before and after the coup. Curmudgeon's rate of aiding females dropped an order of magnitude following his downfall, and Paul's rate more than doubled. For females, there was no clear association between rank and frequency of participation in male-female coalitions. Prior to the coup, the alpha female (Abby) and the lowest-ranking female (Tattle) had the highest rates of participation, both overall and in coalitions against monkeys only. After the coup, there was a slight tendency for higher-ranking females to form more coalitions with males, due to the fact that Tattle virtually ceased to form coalitions with males.

Aggression

Tables 4.25 and 4.26 show the rates of aggression (including coalitionary aggression) directed by males toward females, and by females toward males. During the precoup phase (Table 4.25), members of the high-ranking clique of females (Abby, Squint and Nanny -- see chapter 2) directed more aggression toward males than they received, whereas low-ranking females (Wiggy and Tattle) received more aggression from males than they directed toward males. The difference in frequency between female attacks on males and male attacks on females was positively correlated with female rank (Kendall's rank order correlation: N=15 dyads; t=.727; p=.0002). The alpha male attacked females more frequently than did subordinate males. There was no significant tendency overall for females to attack males more frequently than males attacked females (Wilcoxon, T=43.5, p=.3).

After the coup (Table 4.26), the pattern was less consistent. Females directed more aggression toward males than they received, overall (Wilcoxon signed rank: n=15, T=54;

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p=.01), but Paul directed more aggression toward Abby, Nanny, Diablita and Wiggy than he received, and Ichabod directed more aggression toward the two lowest-ranking females than he received. The alpha male (both before and after the coup) and the immigrant male (who was present only after the coup) were involved in more aggressive interactions with adult females than were other males. There was still a tendency for higher-ranking females to have a greater difference between rate of attacking males and rate of being attacked by males (Kendall Tau: n=24, t=.247; p=.09). High-ranking females were more often involved in disputes with males, probably because higher-ranking females were more prone to form alliances versus males (see below).

When only those instances of severe aggression (chases and physical contact aggression) are examined (Tables 4.27 and 4.28), the pattern is somewhat different than that seen in Tables 4.25 and 4.26. In the precoup phase, with the exception of 2 dyads (Paul-Abby and Paul-Nanny), males directed more aggression toward females than they received (Wilcoxon signed rank test: n=15; T=3; p=.01). After the coup, there were an approximately equal number of dyads in which the male directed more severe aggression toward the female compared with dyads in which the female directed more severe aggression toward the male (Wilcoxon signed rank test: n.s.). The 2 top-ranking females, Abby and Squint, exhibited higher rates of severe aggression toward males (averaged across dyads) than did the other females. Ichabod, the immigrant male, exhibited the most severe aggression toward females, followed by Paul, the alpha male.

Female-female Coalitions Versus Males

Tables 4.29 and 4.30 show the rates at which each female-female dyad formed a coalition against a male during focal observations of any member of the triad, before and after the coup. When a polyadic coalition was formed against the male, all female dyads within the coalition that involved the focal animal were scored as separate dyadic coalitions for the purpose of this analysis. For example, if Abby, Squint and Nanny formed a

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coalition against Ichabod during a follow of Nanny, the coalition was scored both as a coalition of Abby and Nanny against Ichabod, and as a coalition of Squint and Nanny against Ichabod.

Using the male focal data only, I calculated the rates at which each male received aggression from a coalition of adult females. Ichabod, the immigrant male, was attacked most often (.146 times/hour), then Curmudgeon (.090 times/hour), then Paul (.072 times/hour), and Guapo least often (.018 times/hour). Inspection of Tables 4.29 and 4.30 reveals that both Curmudgeon and Paul were targeted about twice as often when they were alpha males than when they were subordinate males.

The average number of adult females in female-female coalitions varied slightly according to the identity of the male victim. The average number of adult females in coalitions against males (during focal observations of adult males and females) was 2.08, 2.15, 2.16, and 2.47 for Curmudgeon, Paul, Guapo, and Ichabod, respectively. Hence, Ichabod was the victim of larger coalitions of females than were the other males.

When the dominance ranks of the members of female-female coalition dyads are averaged, and plotted against the rate of coalitions formed against males for each female-female dyad (figure 1), it becomes apparent that the dyad's average rank is positively related to frequency of coalition formation against males (Kendall tau test: n=15; tau=-.78; Z= -4.04; p=.00005; rank of 1 = alpha position), i.e. higher-ranking females are more likely than lower-ranking females to form coalitions against males.

Table 4.31 summarizes the contexts in which females formed coalitions against adult males. There were an additional 13 coalitions in which the context could not be determined (because the episode started before the focal sample began), and two coalitions (one in the context of feeding competition, and the other in play) in which the fight appeared to be initiated by the male and the female simultaneously.

Ninety-one percent of adult females' solicitations to other adult females for aid were successful (i.e. the solicited female joined in the attack). Those few solicitations for aid

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that were refused were in one of the following contexts: unprovoked attacks by the female on the male, redirected aggression toward the male, female screams or attacks a male who had just neutrally approached her, or attempts to break up a male's affiliative interaction or coalition with another group member. Females never refused to aid other females against males when the male had actually provoked the female by aggressing against her.

It is difficult to determine the extent to which female-female coalitions were effective in defeating males. Unlike many other primates (e.g. macaques and chimpanzees), who have formal submissive signals that are useful in assigning winners and losers in fights, white-faced capuchins typically continue to threaten one another to the bitter end. Even when a single monkey is confronted by a large coalition of higher-ranking monkeys, it continues to threaten the coalition (after fleeing) until the coalition dissolves and everyone has resumed their normal activities. Two behaviors, fleeing and tail chewing, although they do not appear to be formal indicators of submission, seem at face value to be good indicators of defeat. When a single capuchin is confronted by an unusually hostile coalition of higher-ranking monkeys, it grabs its tail and rapidly chews, licks and/or kneads the prehensile tail tip vigorously while observing and occasionally threatening the attacking coalition. The tail chew appears to indicate extreme anxiety. For those female-female coalitions against males in which one of the parties either fled or engaged in tail-chewing, I assigned winners and losers to the confrontation. Out of the 34 female-female coalitions against males that met these criteria, the females were defeated once, both sides fled or tail-chewed in two instances, and the male was defeated by the female coalition 31 times (though another male aided the female coalition 5 times). Thus, female-female coalitions appear to be effective in defeating males.

Male Attempts to Break up Female-female Coalitions

Unlike male-male alliances (described in detail in chapter 3), female-female alliances are often highly stable across time. The most stable female-female alliance, that of the

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alpha female Abby and the beta female Squint, was a powerful force in the group's politics and may have been a determining factor in Curmudgeon's fall from alpha position (see chapter 5). The third-ranking female, Nanny, frequently joined Abby and Squint in coalitions against males and had a very strong affiliative bond with Squint (see chapter 2). Paul was the only male ever observed to attempt to break up female-female coalitions, and all of his attempts occurred after the coup, when females were forming coalitions against him. His attempts to split the Abby Squint alliance were only partially successful; he sometimes succeeded in separating them briefly and in doing an overlord with one against the other (though the female he sided with would often not look directly at her former ally while threatening), but the females always reunited as soon as they could get away from Paul. These events were always highly emotional and appeared to be very distressing to the females involved. They were virtually the only situations in which females were observed to wheeze dance with one another. The following anecdote typifies Paul's attempts to split the Abby-Squint coalition:

On February 10, 1993 at 1:28, Paul startled Abby, possibly accidentally, and Abby bit Paul. Abby, Squint, and Nanny mobbed Paul, and he lunged at them. Abby and Squint stood a few inches from Paul's face and threatened him. Paul pounced on Squint's back in overlord position facing Abby. Squint screamed, and all three of them looked terrified. Squint, continuing to scream, threatened Nanny, and Paul joined her in threatening Nanny. Nanny fled. Abby vocally threatened Paul. Paul began emitting a vocalization, somewhat like a hybrid between an alarm call and a coo, which Guapo and Curmudgeon also sometimes performed when they were the victims of coalitions. Squint threatened Nanny, and Paul got off of her back. Abby threatened Paul from between her legs. Squint drooled profusely and threatened toward Paul and Nanny. Paul attacked Abby, and Squint turned as if to threaten Abby as well. Paul continued to threaten Abby as Squint and Abby began a wheeze dance, initiated by Squint. Abby did an overlord over Squint at Paul, and both of them threatened Paul vocally. Broma, Squint's yearling

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daughter, threatened Paul too, and the three of them started doing vocal threats that almost graded into "machine gun vocalizations" while facing Paul. Squint broke off the overlord with Abby, and Abby, Squint and Broma threatened Paul as he left. Hobbes and the three females followed Paul, and Paul turned to threaten them. Abby overlorded over Squint at Paul, and Squint drooled. Squint broke off the overlord, and Paul lunged at Squint and backed under her in an attempt to initiate an overlord against Abby. Squint threatened Abby as Paul backed under her, but then Squint ran over to Abby. Paul hit Abby and headflagged to Squint. Abby screamed, and Squint left without turning to look back. Abby, whimpering, followed Squint. Abby screamed at Paul, and Paul lunged at her. Paul gargled loudly, and Abby initiated a dance with Paul, who did not dance, but did the "pirouettes" normally associated with dances. Broma climbed on Squint's back, and Squint carried Broma away from the scene of the fight, as both Squint and Broma gargled and wheezed. Paul and Nanny did duck faces and grunts to one another, and Nanny made wrinkly faces at Paul. Squint gargled and screamed at Paul, and Abby and Squint overlorded at Paul and threatened him and Nanny as Paul and Nanny danced.

Play

Although juveniles play frequently (see chapter 1 for definitions of play behaviors), only 12 bouts of play were observed between adult males and adult females during focal observations, 5 of which occurred before the coup. Curmudgeon, Tattle, and Diablita (as an adult) were never observed to play with adult members of the opposite sex. Paul played 4 times with Squint and twice with Abby. Guapo played twice with Abby, and once each with Nanny and Wiggy. Ichabod played once each with Abby and Nanny. Many of these adult heterosexual play bouts involved exceptionally vigorous wrestling, some sex play, and coalitionary play. Some of the coalitionary play involved odd victim choices: for example, Abby and Paul formed an overlord against Abby's yearling son Rico. In an ad

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lib play observation, Paul formed play overlords with Squint against Abby. Such play may have been part of a strategy on Paul's part, to split the Abby-Squint coalition.

Sexual Behavior

Copulations were preceded by a suite of behaviors that I termed a "dance." In the first stage of courtship, the male and/or the female made "duck faces" (i.e. their lips protruded such that they resembled a duck's bill), stared at the other monkey, and made one of two vocalizations: a grunt, or a sex squeak (i.e. a very soft series of staccato notes ascending in pitch). While keeping his/her gaze fixed on the other monkey, the initiator of the dance began to spin around in a "duck face pirouette," looking at the other monkey between his/her legs, over the shoulder, or under an arm. Males were generally piloerected while doing duck face pirouettes. In the next stage of the dance, the two monkeys chased each other back and forth, in slow motion, while maintaining their duck faces and eye contact, and doing either type of vocalization. These slow motion chases seemed highly ritualized: movements were exaggerated, deliberate, and fairly rhythmic, and the males and females "chased" each other more or less equal distances, usually over the same branch. Sometimes one member of the pair walked backwards during these "chases." Dances could last up to several minutes. Some, but not all, dances culminated in a copulation. Sometimes the female presented her hindquarters, but usually the male gingerly grasped the female's hips to initiate a mount. Both the male and the female seemed highly nervous and ambivalent during dances, and often the female screamed when the male grasped her hips, thus ending the dance, at least temporarily. If the female didn't scream or flee, the male mounted the female by grasping her legs with his feet and thrust several times before dismounting. Sometimes there was only one bout of thrusting, but other times there were multiple mounting and thrusting bouts before the male appeared to ejaculate. It was often difficult to determine whether a male had ejaculated, because there was no conspicuous ejaculatory pause, nor was the ejaculate volume large enough to leave a "plug," as in

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macaques. Sometimes the male remained in mount position after thrusting ceased, and rocked back and forth for several seconds; other times, he remained mounted as the female began walking, and lowered his feet to the branch so that the pair walked on 6 legs. Duck faces were maintained throughout all phases of the dance and copulation.

Matings occurred during all phases of the female's reproductive cycle; in fact, only a 38% of observed matings occurred when females were potentially cycling, and only 1 of 29 matings was when the female could potentially have conceived. Table 4.32 shows the distribution of matings during focal observations across dyads, omitting those matings in which the male was under 3 years old. The first total includes all matings; the second total excludes those matings during which time the female was probably not cycling (i.e. those in which she was pregnant or had given birth less than 2 months previously and was therefore lactating intensively and therefore probably anovulatory). Nine of the 15 matings with adult males and 4 of the 14 matings with juvenile males occurred when females were pregnant; 2 of the matings with adult males and 2 of the matings with juvenile males occurred when the female was intensively lactating. The only copulation that was observed within 10 days of the probable conception date was between Nanny and Hobbes, a small juvenile male. The top half of the table shows adult males, and the bottom half shows juvenile males. The number of copulations (especially the number of potentially conceptive copulations) is too small to permit speculation as to mate choice criteria and determinants of male reproductive success. Because approximately equal amounts of data were collected on all adult monkeys, the approximate frequencies of copulation can be calculated by dividing by 220 hours for all adult male-female dyads, and by 110 hours, for all juvenile male-female dyads. Note that frequencies of mating with juvenile males are therefore more than twice as great as frequencies of mating with adult males. It is remarkable, given the density of observations and the length of the study, that no matings with adult males were observed during times when females could have conceived.

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Several copulations were observed outside of focal observations. I have not yet analyzed the ad lib data from all 26 months of the study, but the data I have analyzed (8 months: May-August 1991, and August-December 1992) conform to the results from the focal data. Twenty-seven copulations were observed during the 8-month period: 17 with pregnant females, 7 with intensively lactating females, and 3 with potentially cycling females (one of which occurred within 10 days of the putative conception date). All of the males were observed to mate during ad lib observations, but all 3 of the matings with potentially cycling females were by juvenile males.

It seems unlikely that juvenile males are responsible for fathering all of the infants. An alternative interpretation is that procreatively important matings (i.e. periovulatory matings with fertile males) are concealed, so as to avoid aggression from other group members. Indeed, in some of the matings I observed between adult males and presumably cycling females, the copulating pair was threatened vocally by other group members (of all age-sex classes). It might be advantageous to females to conceal proceptive behaviors, so that they can exercise greater mate choice. By flamboyantly courting subordinate males, a female could attract the attention of the alpha male, who might then guard her and prevent her from mating with the male of her choice. I sometimes observed what appeared to be intense mate guarding, by males who were not observed to mate with the guarded female, and the female sometimes appeared to be making active escape attempts, as in the following anecdote:

For a period of about 3 days, during which Squint was believed to be in estrus, she followed Curmudgeon continually. For the entire period of time, Paul (who was alpha male) also followed Squint. Neither of the males normally coordinated movements with Squint. Curmudgeon, Squint, and Paul ran, in single file (Paul following Squint, who followed Curmudgeon), at high speed for practically all of their waking hours, barely stopping to eat. It was my impression that Curmudgeon, although he did occasionally make duck faces at Squint, was usually trying to escape from her so that Paul would stop

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following him. Paul monitored Squint incessantly and was almost never observed to eat during that period. Squint and Curmudgeon did not engage in courtship behavior while Paul was watching them.

Because of the prevalence of nonreproductive sex, it is difficult to determine when a female is in estrus. In an attempt to determine whether male or female courtship behavior is a better indicator of whether a female is in estrus (or at least cycling), I compared the patterns of male and female proceptivity with regard to female reproductive state. All of the behaviors described above as being courtship behaviors (dancing, duck faces, grunts, mounts, and squeaky sex vocalizations) are included in this analysis as proceptive behaviors, though they almost certainly serve nonsexual functions as well. Dance behaviors accompanied only by wheezes, rather than the typical precopulatory vocalizations, were excluded from analysis, since wheeze dances between heterosexual pairs have never been observed to culminate in copulation (see chapter 6 for speculation as to the function of wheeze dances).

Table 4.33 shows the proportion of 10-minute focal samples of females in which proceptive behaviors were observed, according to female reproductive state. Females exhibited proceptive behaviors in all reproductive states, but there was considerable variation among individuals as to which state had the most proceptive behavior. Abby and Tattle were most proceptive during pregnancy, Squint was most proceptive while intensively lactating, and Wiggy, Diablita and Nanny were most proceptive when presumably cycling. Only Nanny and Diablita exhibited proceptive behavior during the period in which they actually conceived. With such a small sample of copulations observed, it is difficult to make generalizations; however, it appears that there is a pattern with regard to age. The two youngest females (Nanny, who was primiparous, and Diablita, who was nulliparous) courted males most conspicuously and were particularly aggressive in their courtship during the time in which they conceived. Both Nanny and Diablita were so frenzied in their courtship of Paul, the alpha male, that they physically

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attacked him when he ignored their duck face pirouettes. Once Nanny bit Paul on the tail and pushed him out of a tall tree (holding him suspended, briefly, from her teeth) when he failed to respond to her frenzied courtship. In contrast, Abby (who appears on the basis of physical characteristics to be the oldest female in the group) was so subtle in her courtship of males that I never knew when she was in estrus. All observed matings involving Abby (with the exception of one ad lib observation with a juvenile) were when Abby was pregnant. It is possible that most matings with older females occur at night. Table 4.34 shows the mean scores for old (i.e. multiparous) females (Abby, Squint, Wiggy and Tattle) and young females (Nanny and Diablita), according to reproductive state.

Table 4.35 shows the proportion of 10-minute focal samples in which males courted females, according to female reproductive state. Males courted females the most when females were presumably cycling (particularly during the period surrounding conception), next most during pregnancy, and least when females were lactating (0-6 months postpartum). Thus, it appears that male proceptive behavior is a more reliable indicator of female reproductive state than is female proceptive behavior. Most likely, males rely chiefly on olfactory cues to determine female reproductive state. Males are extremely interested in female urine and frequently stop to sniff locations in which females have been sitting. Males varied with regard to the proportion of samples in which they courted females; those males who spent most time in the center of the group (i.e. had high proximity scores, averaged across dyads) also courted females most often, presumably because they had greater access to females and their urine.

Discussion

Rank-related Effects on the Quality of Male-female Interactions

Both male and female dominance ranks were important determinants of the quality of dyadic interactions and relationships. The alpha male occupied a central position in the

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group and interacted most frequently with the high-ranking females (chapter 5). Subordinate males, particularly after the coup, had few or no interactions with high-ranking females, although they did interact fairly frequently with low-ranking females. The alpha male was groomed much more frequently by females than were the subordinate males, partially due to his more central location in the group, since the preference vanished when proximity was controlled.

Females were more likely to respond to the alpha male's approach by attacking third parties and recruiting the male's aid compared with approaches by subordinate males. It may be in part for this reason that the alpha male was the most frequent male coalition partner of females.

There were several rank-related differences in the distribution of aggressive interactions across dyads. In general, high-ranking males and females were more frequently aggressive than low-ranking members of the same sex. In some cases, high-ranking females were more often aggressive than low-ranking males, despite the fact that all males are individually dominant to all females. High-ranking females were involved in more coalitions against males than were low-ranking females. Part of the reason why high-ranking females are involved in more aggressive interactions versus males than are low-ranking females may be because high-ranking females are recruited more often to take part in attacks.

Comparisons with Other *Cebus* Species

C. capucinus differs from *C. apella* (Janson 1984) and *C. olivaceus* (Robinson 1981) with regard to sexual behavior. Both of the latter species appear to have single breeding males, and courtship, at least by *C. apella* females, is conspicuous and occurs in discrete and regular intervals that presumably correspond to a particular phase of the estrous cycle (Janson 1984; but see Welker et al. 1990). In *C. albifrons*, like *C. capucinus*, mating is distributed more equitably among males (Janson 1986). Genetic

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paternity data are not available for any *Cebus* species, so the relationship between male dominance rank and reproductive success remains an open question. The acquisition of genetic paternity data in *Cebus* is particularly critical, given the prevalence of nonprocreative sex and the furtiveness of adult females around the time of conception in this study.

Izawa reports more reciprocal grooming relationships between male and female *C. apella* than are typical for either *C. capucinus* or *C. olivaceus* (O'Brien 1991), in which females do the vast majority of the grooming. In *C. olivaceus* (O'Brien 1991), as in my study group of *C. capucinus*, the alpha male is the most frequently groomed male. The alpha male is spatially central and therefore the most frequent male partner for social interactions with females in *C. apella* (Janson 1986; Izawa 1980), *C. olivaceus* (O'Brien 1991), and some (but perhaps not all: Fedigan 1993; Mitchell 1989) groups of *C. capucinus* . In C. olivaceus, only high-ranking females have affiliative relationships with the alpha male, due to the efforts of high-ranking females to monopolize access to him (O'Brien 1991).

In *C. olivaceus* (de Ruiter 1986) *C. apella, C. albifrons,* (van Schaik and van Noordjwick 1989), and *C. capucinus* (Rose and Fedigan 1995; Rose 1994), males are more vigilant than females and, at least in the latter 3 species, are better at detecting predators than females are. Thus, females who spend more time in association with males may benefit more in terms of predator detection than females who avoid males. Another benefit that females may receive from males is protection from males of other groups. Males are the primary participants in intergroup encounters in all 4 capuchin species, though only the alpha male typically defends the group in *C. apella* intergroup encounters (Janson 1986; Defler 1982; Fedigan 1993; chapter 7; Rose 1994; Mitchell 1989; Oppenheimer 1968; Robinson 1988b). *C. olivaceus* females spend more time resting, less time traveling, and possibly gain access to more food resources, as a consequence of residence in a group that tends to win intergroup encounters (Robinson 1988b; O'Brien

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1991); it seems unlikely that a feeding advantage is gained by winning intergroup encounters in *C. capucinus* (chapter 7). Observations of infanticide by males in *C. olivaceus* (Valderrama et al.) and *C. capucinus* (Rose 1994; Fedigan et al. m.s.) suggest that foreign males pose a threat to females' reproductive success; hence, male vigilance against foreign males (Rose and Fedigan 1995) and participation in intergroup encounters may incidentally provide benefits to females in the form of reduced threat toward infants.

The benefit in predator detection and defense against males of other groups is counterbalanced at least in part by feeding competition received from males (Rose 1994). Most aggression between males and females occurs in a foraging context (*C. olivaceus*: O'Brien 1991; *C. capucinus*: Rose 1994), and aggression from males appears to be a significant factor in reducing female foraging success (*C. capucinus*: Rose 1994; *C. apella*: Janson 1985, 1990). In *C. apella*, the alpha male monopolizes food and permits preferred juveniles and females to cofeed with him (Janson 1984). The direction of aggression in male-female dyads, as well as the effects of rank on the frequencies of directing and receiving aggression in intersexual disputes, vary not only across populations and across species, but also across time within a single social group. In *C. olivaceus* (O'Brien 1991), high-ranking females were more aggressive to males than were low-ranking females, as in my study group, and subordinate males were involved in a disproportionate number of male-female aggressive episodes, in comparison with the alpha male. In *C. apella*, females threatened males more often than vice versa, but only the alpha female threatened adult males; other females threatened only subadult males (Izawa 1980). Rose (1994) reported approximately equal rates of *C. capucinus* male aggression to females as vice versa, with a slight tendency for males to be more aggressive in one social group.

The Power Balance between the Sexes

Cebus capucinus males are clearly more intimidating to females than vice versa, in the context of dyadic interactions. Within adult male-female dyads, the direction of

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avoidance and cowering was almost exclusively female to male. Females often responded to neutral approaches of males by exhibiting fear, or attacking harmless third parties in what appeared to be an attempt to direct the male's attention away from themselves. Likewise, females were far more likely to respond to male displays by exhibiting fear than by threatening the male. The vast majority of supplants and food thefts were directed by males toward females.

Grooming within male-female dyads was almost exclusively in the direction of females grooming males, as has been reported at other sites (Fedigan 1993; Oppenheimer 1968). Males also ignored a higher proportion of grooming invitations by females than vice versa.

The distribution of periovulatory copulations across dyads is a crucial link to understanding many other facets of male-female relationships. Unfortunately, it appears that most matings by mature estrous females occur at night, when the observers were not present to see them. Despite several attempts to follow estrous females all day long, virtually no copulations were observed. Based on the few data available, both from my site and from other *C. capucinus* sites (Oppenheimer, 1968; Mitchell 1989; Fedigan 1993), it appears that matings are not monopolized by the alpha male. In this respect, *C. capucinus* appears to be more similar to *C. albifrons* than to either *C. olivaceus* or *C. apella* (Janson 1986; Robinson 1981; Fedigan 1993). Examination of the patterns of proceptivity reveals that male proceptive behavior, more than female proceptive behavior, is reliably concentrated during periods in which a female is likely to conceive. The greater degree of proceptive behavior in young as opposed to old females during periods in which conception is likely suggests that older females may have learned to alter their behavior in such a way as to conceal their estrous condition from males who might guard them, thus reducing their power of choice. However, more data on a larger number of females are needed to know whether this trend for older females to be more subtle in their courtship

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tactics is generalizable. The trend for younger females to be more conspicuous in their mating tactics has also been observed in rhesus monkeys (Perry and Manson, 1995).

The prevalence of non-reproductive sex in white-faced capuchins, both at Lomas Barbudal (Table 4.26) and at Barro Colorado (Oppenheimer 1968; Mitchell 1989), remains a mystery. Perhaps, as has been suggested for other large-brained primates who indulge in frequent non-reproductive sex (e.g. bonobos and humans: de Waal 1989), non-reproductive sex serves as a tension-reducing mechanism. Some components of sexual behavior (dancing, duck faces, mounting and thrusting, and mobile mounts) are components of the wheeze dances that are most frequently used by capuchin males during tense periods of their relationships, particularly following major fights or after long absences from the group (see chapter 6). It is possible that play among adults also serves either to reduce tension or to negotiate aspects of the relationship (as when Paul formed play coalitions with Squint against Abby).

Males and females frequently assisted one another in the context of coalitionary aggression. The majority of coalitions formed were against harmless victims; these coalitions may have been "practice" coalitions -- mechanisms for solidifying an alliance and demonstrating willingness to aid in the future, in situations that really "count." Another, not necessarily mutually exclusive, possible explanation for these coalitions against harmless victims, which were primarily initiated by females, is that a female would initiate coalitions against harmless victims in situations in which she feared aggression or supplantation at resources by the male. She would therefore target a harmless victim and recruit the male's aid to distract him from aggressing against her, while simultaneously demonstrating her willingness to be his ally. Males also aided females in mobbing potential predators. Because males are more active in predator defense than are females (unpublished data; Rose and Fedigan 1995; Rose 1994; *C. apella and C. albifrons:* van Schaik and van Noordjwick 1989), it is likely females obtain a greater benefit from males in this context than vice versa.

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Of those male-female coalitions directed against other group members, about 45% were directed at adult males despite the fact that adult males comprised only 19% of the group membership. These coalitions were probably mutually beneficial. Adult males impose costs on females in terms of foraging disruption (Rose 1994). A large proportion of fights between the sexes occur in the context of feeding competition (unpublished data; Rose 1994). In addition to feeding competition, males can impose costs on females in the form of danger to infants. I have never witnessed severe male aggression toward infants, but Rose (1994) has observed infanticide by a male who had recently become alpha male. Infant deaths are often associated with turnovers in adult male membership in the Santa Rosa population (Rose and Fedigan 1995; Fedigan et al, m.s.), suggesting that male aggression can be a significant cost to females. In my study group, within male-female dyads, rates of male aggression toward females were approximately equal, on average, to rates of female aggression toward males prior to the coup, but after the coup, females were more aggressive toward males than vice versa. When only severe aggression was examined, males were more aggressive to females than vice versa, but only prior to the coup.

Although female white-faced capuchins appear to be disadvantaged in competition with males in one-on-one contests, apparently due to their smaller size, they compensate at least in part by forming coalitions with both males and females against males, both at Lomas Barbudal and at Santa Rosa (Rose 1994). In contrast, males never form coalitions with other males against females (chapter 3). The fact that females remain in their natal groups and are presumably related, whereas males transfer, makes it easier for females to form stable alliances than is the case for males. The fact that males are transient members of groups, whereas females are permanent members, means that females, on average know both males and females for longer periods of time than males know males; thus, females have longer amounts of time to establish solid alliances than do males (van Schaik and van Hooff 1994). Because female-female alliances can be influential in determining male rank

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(see chapter 5), and because females are more permanent members of the group, it may be more profitable for males to develop relationships with females than with males; this could explain why males were never observed to support males against females.

Female-female coalitions were formed to defend foraging sites, following attacks by males on females and juveniles, and in response to males scaring females (perhaps inadvertently) by approaching them or by doing displays. Females very reliably aid one another in coalitions versus males; females were never observed to refuse females' direct requests for aid in cases where a male had attacked a female. Paul's attempts to break up female-female coalitions were largely unsuccessful and appeared to be distressing to the females involved. It is sometimes difficult to assign a winner to a confrontation, but in those cases in which a clear winner or loser could be assigned, female coalitions were highly successful in defeating males. However, as Rose (1994) points out, female-female coalitions, although successful in accomplishing immediate goals, may not be capable of driving persistent males out of the group entirely, due to the energetic costs involved in repeatedly chasing and wrestling with males. It appeared that the females in my study group were attempting to prevent Ichabod from joining the group, because they formed daily coalitions against him, many of which culminated in biting, wrestling, and falling out of trees. Females sometimes received wounds from Ichabod. Despite the hostilities he received from females, Ichabod was persistent and succeeded in becoming a central group member in a few weeks' time. Thus, although females' attitude toward males may have some influence over the ease with which males are integrated into the core of the group, females do not have absolute power over male membership; females may require the aid of adult males to evict resident or immigrating males from the group.

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Table 4.1: Hours of focal data collected on each individual, before and after the coup.

Individual	Precoup	Postcoup	Total
Curmudgeon	71.83	39.17	111.00
Paul	71.00	40.00	111.00
Guapo	71.00	37.17	108.17
Ichabod	---	34.33	34.33
Abby	71.50	39.33	110.83
Squint	70.83	40.17	111.00
Nanny	69.67	40.83	110.50
Diablita	---	33.00	33.00
Wiggy	74.17	39.33	113.50
Tattle	71.00	38.83	109.83
	571.00	382.17	953.17

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Table 4.2: Avoids and cowers within adult heterosexual dyads during focal observations.

Dyad	Female to male	Male to female
AC	4	0
AP	9	1
AG	2	0
AI	2	0
SC	3	0
SP	14	0
SG	2	0
SI	0	0
NC	3	0
NP	17	1
NG	2	0
NI	2	0
WC	9	0
WP	16	0
WG	3	0
WI	11	0
TC	9	0
TP	15	1
TG	6	0
TI	9	0
DC	0	0
DP	4	0
DG	0	0
DI	15	0

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Table 4.3: Proportion of female's responses to neutral male approaches in each response category.

Dyad	Response type						sample size
	friendly	ignore	leave	fear	attack third party	attack male	
AC	.15	.26	.15	.03	.41	0	39
AP	.10	.33	.15	.18	.33	0	39
AG	.14	.40	.23	.03	.20	.03	35
AI	.12	.37	.12	.12	.25	0	8
SC	.23	.53	.07	0	.13	.03	30
SP	.14	.35	.33	.09	.14	0	43
SG	.04	.50	.33	.04	.04	.04	24
SI	0	.67	.17	.17	0	0	6
NC	.33	.50	.17	0	0	0	30
NP	.19	.37	.28	.06	.16	0	32
NG	.16	.43	.38	0	.03	0	37
NI	.21	.43	.14	0	.29	0	14
WC	.37	.37	.20	.05	.05	0	40
WP	.23	.27	.35	.12	.08	0	26
WG	.43	.21	.31	.05	0	0	42
WI	.60	0	0	.40	0	0	5
TC	.20	.40	.10	.10	.20	0	10
TP	0	.27	0	.45	.31	.09	11
TG	.11	.44	.11	.22	.11	0	9
TI	--	--	--	--	--	--	--
DC	.43	.14	.71	0	0	.14	7
DP	.43	.14	.36	.07	.07	0	14
DG	1.00	0	0	0	0	0	1
DI	.33	0	0	.50	0	.33	3

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Table 4.4: Proportion of female's responses to neutral male approaches in each response category, averaged across males.

	Response type					
Female	friendly	ignore	leave	fear	attack third party	attack male
A	.13	.34	.16	.09	.30	.01
S	.10	.51	.22	.07	.08	.02
N	.22	.43	.24	.01	.12	0
D	.55	.07	.27	.14	.02	.12
W	.41	.21	.21	.15	.03	0
T	.10	.37	.07	.26	.21	.03
Mean	.25	.32	.19	.12	.13	.03

Table 4.5: Proportion of females' responses to neutral male approaches in each response category, averaged across females.

	Response type					
Male	friendly	ignore	leave	fear	attack third party	attack male
C	.28	.37	.23	.03	.13	.03
P	.18	.29	.24	.16	.18	.01
G	.31	.33	.23	.06	.06	.01
I	.25	.29	.09	.24	.11	.07

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Table 4.6: Female responses to male displays.

Dyad	# displays	Response type				
		ignore	fear	aggression toward displaying male	aggression toward third party	continue aggression toward third party
AC	12	.50	.70	0	.25	.17
AP	15	.60	.13	0	.20	.07
AG	7	.70	.14	0	.14	0
AI	12	.92	0	.08	0	0
SC	21	.57	.05	.19	.19	0
SP	27	.81	.07	.04	.11	0
SG	9	.67	0	.11	.22	0
SI	13	.69	.15	.08	.15	0
NC	12	.67	.25	0	.08	0
NP	14	.50	.07	.07	0	0
NG	3	.33	.67	0	.33	0
NI	19	.42	.37	.11	.11	.05
WC	39	.87	.08	0	.03	.03
WP	14	.93	.07	0	0	0
WG	7	.86	.14	0	0	0
WI	14	.71	.21	0	.07	0
TC	8	.62	.12	0	.12	.12
TP	12	.42	.25	0	.33	0
TG	9	.78	.11	0	.22	0
TI	10	.50	.40	0	.10	.10
DC	5	1.0	0	0	0	0
DP	13	.85	0	.08	.08	0
DG	1	1.0	0	0	0	0
DI	15	.73	.27	.13	0	0
AH	7	.86	0	0	.14	0
SH	4	.25	0	0	.75	0
NH	1	1.0	0	0	0	0
WQ	2	1.0	0	0	0	0
WH	1	1.0	0	0	0	0
TK	1	1.0	0	0	0	0
TH	2	1.0	0	0	0	0
DH	4	1.0	0	0	0	0
AX	5	.60	0	.40	0	0
SX	1	0	1.0	0	0	0
NX	3	.67	0	.33	0	0
WX	4	1.0	0	0	0	0
TX	2	1.0	0	0	0	0
DX	2	1.0	0	0	0	0
TXJ	1	1.0	0	0	0	0

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Table 4.7: Female responses to male displays, averaged across females.

Male	# displays	Response type				
		ignore	fear	aggression toward displaying male	aggression toward third party	continue aggression toward third party
C	97	.71	.11	.03	.08	.03
P	95	.68	.10	.03	.11	.01
G	36	.72	.18	.02	.08	0
I	83	.66	.22	.04	.04	.02

Table 4.8: Females' responses to displays by adult males.

Female	# displays observed	Response type				
		ignore	fear	aggression toward displaying male	aggression toward third party	continue aggression toward third party
A	46	.68	.11	.02	.15	.06
S	70	.68	.07	.10	.17	0
N	48	.48	.34	.04	.13	0
D	34	.89	.07	.05	.02	0
W	74	.84	.12	0	.02	.01
T	39	.58	.22	0	.19	.02

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Table 4.9: Rates (events per hour) of supplants during focal observations (numbers in parentheses are rates of females supplanting males; all other numbers are males supplanting females).

	Female					
Male	A	S	N	D	W	T
C	.018	.0045	.0045	0	.022	.0045
P	.0315	.018 (.009)	.032	.045	.013	.018 (.0045)
G	.014	.005	0	0	.018	.014
I	0	.028	.014	.046 (.015)	.014	.029

Table 4.10: Mean proximity scores (averaged across dyads) for within- and between-sex pairs, precoup and postcoup.

	precoup	postcoup
male-male	1.512	0.099
male-female	2.753	1.939
female-female	7.199	6.011

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Table 4.11: Proximity scores for male-female dyads, precoup.

	Female					
Male	A	S	N	W	T	Mean
C	5.924	4.286	5.682	4.985	1.990	4.573
P	0.864	1.426	0.579	1.107	1.143	1.024
G	3.122	1.731	3.438	3.039	1.979	2.662
Mean	3.303	2.481	3.233	3.043	1.704	

Table 4.12: Proximity scores for male-female dyads, postcoup

	Female						
Male	A	S	N	D	W	T	Mean
C	0.003	0.005	0.504	0.555	2.559	0.017	0.607
P	8.610	8.561	9.449	4.971	1.525	0.524	5.607
G	0.004	0	0.001	0	1.051	0.004	0.177
I	1.702	0.591	1.676	1.242	0.574	0.003	0.965
Mean	2.580	2.289	2.907	1.692	1.427	0.137	

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Table 4.13: Rates of female-male grooming (seconds/hour) during the precoup period; numbers in parentheses are rates at which males groomed females; all other numbers are rates at which females groomed males.

	Female					
Male	A	S	N	W	T	Mean
C	4.1	14.0	17.2	13.2	1.4	1.0 (0)
P	0.5	0	1.3	0	0.4 (0.04)	0.4 (0.01)
G	2.3	6.9	6.8	13.9 (0.6)	6.7 (0.5)	7.3 (0.2)

Table 4.14: Rates of female-male grooming (seconds/hour) during the postcoup period; numbers in parentheses are rates at which males groomed females; all other numbers are rates at which females groomed males.

	Female						
Male	A	S	N	D	W	T	Mean
C	0	1.8	3.8	1.9	21.2	0.7	4.9 (0)
P	1.0	9.7 (0.01)	12.6	31.6 (0.01)	26.8	0	13.6 (0.003)
G	0.6	0	1.7	0	4.3 (0.3)	0	1.1 (0.06)
I	0.4 (0.03)	0.7 (0.01)	1.1	11.7	5.4 (1.4)	0	3.2 (0.2)

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Table 4.15: Rates (seconds/hour) at which females groomed males, divided by % time the dyad spent within 10 body lengths: precoup data.

	Female				
Male	A	S	N	W	T
C	36	130	228	146	34
P	15	0	63	0	14
G	39	164	131	346	237

Table 4.16: Rates (seconds/hour) at which females groomed males, divided by % time the dyad spent within 10 body lengths: postcoup data.

	Female					
Male	A	S	N	D	W	T
C	0	436	367	163	770	31
P	8	65	107	364	751	0
G	266	---	800	---	327	0
I	14	24	29	654	228	0

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Table 4.17: Proportion of male grooming invitations ignored by females, precoup. (Number in parentheses indicates total number of grooming invitations)

	Female						
Male	A	S	N	D	W	T	Mean
C	.82 (17)	.21 (14)	.32 (28)	1.00 (1)	.33 (39)	.86 (7)	.59
P	.33 (3)	1.00 (1)	.29 (7)	--- (0)	1.00 (7)	1.00 (2)	.72
G	.67 (14)	.83 (6)	.71 (17)	1.00 (4)	.39 (41)	.46 (13)	.67
Mean	.60	.68	.44	1.00	.57	.77	

Table 4.18: Proportion of male grooming invitations ignored by females, postcoup. (Number in parentheses indicates total number of grooming invitations)

	Female						
Male	A	S	N	D	W	T	Mean
C	--- (0)	--- (0)	1.00 (1)	1.00 (2)	.38 (21)	1.00 (2)	.84
P	.91 (11)	.25 (8)	.37 (8)	.21 (14)	.08 (12)	--- (0)	.36
G	0 (1)	--- (0)	.71 (7)	--- (0)	.40 (15)	1.00 (1)	.53
I	.29 (7)	0 (2)	.82 (11)	.50 (6)	.37 (8)	1.00 (1)	.50
Mean	.40	.12	.72	.57	.31	1.00	

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Table 4.19: Proportion of female grooming invitations ignored by males, precoup. (Number in parentheses indicates total number of grooming invitations)

	Female						
Male	A	S	N	D	W	T	Mean
C	1.00 (5)	.75 (5)	1.00 (7)	--- (0)	1.00 (4)	1.00 (1)	.95
P	1.00 (2)	--- (0)	.50 (2)	--- (0)	--- (0)	--- (0)	.75
G	.75 (4)	1.00 (2)	1.00 (5)	1.00 (1)	.80 (15)	1.00 (5)	.92
Mean	.92	.87	.83	1.00	.90	1.00	

Table 4.20: Proportion of female grooming invitations ignored by males, postcoup. (Number in parentheses indicates total number of grooming invitations)

	Female						
Male	A	S	N	D	W	T	Mean
C	--- (0)	1.00 (2)	--- (0)	1.00 (1)	1.00 (2)	--- (0)	1.00
P	1.00 (1)	.67 (3)	--- (0)	1.00 (2)	1.00 (10)	--- (0)	.92
G	1.00 (1)	--- (0)	1.00 (1)	--- (0)	1.00 (4)	--- (0)	1.00
I	.50 (2)	--- (0)	1.00 (1)	1.00 (1)	0 (3)	--- (0)	.62
Mean	.83	.83	1.00	1.00	.75	---	

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Table 4.21: Hourly rates of male-female coalition formation.

Coalition dyad	Victim: male	female	immature	non-monkey	unknown	Total	Total vs. monkeys
CA	.042	0	.007	.335	0	.384	.049
CS	.021	0	.014	.196	0	.231	.035
CN	0	.007	.007	.064	.028	.106	.014
CW	0	.007	.014	.123	0	.144	.021
CT	.035	0	.014	.245	0	.294	.049
PA	.007	0	.035	.070	.007	.119	.042
PS	0	.007	.014	.063	.007	.085	.021
PN	0	0	.007	.071	.007	.085	.007
PW	0	0	0	.041	0	.041	0
PT	.021	0	.014	.162	0	.197	.035
GA	.007	.007	.014	.098	.007	.133	.028
GS	.007	.007	.007	.056	0	.078	.021
GN	.014	0	.007	.057	0	.078	.021
GW	.014	0	.014	.041	0	.069	.028
GT	.007	0	.021	.070	.007	.106	.028

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Table 4.22: Hourly rates of male-female coalitions, postcoup.

Coalition dyad	Victim: male	female	immature	non-monkey	unknown	Total	Total vs. monkeys
CA	.013	0	0	0	0	.013	.013
CS	.038	0	0	0	0	.038	.038
CN	0	0	0	0	0	0	0
CD	.014	0	0	.014	0	.028	.014
CW	0	0	0	0	0	0	0
CT	.013	0	0	.013	0	.026	.013
PA	.038	.025	0	.366	.101	.529	.063
PS	.050	.025	.012	.362	.100	.549	.087
PN	.025	0	.012	.136	.012	.186	.037
PD	.055	.014	.014	.110	0	.192	.082
PW	.013	0	.013	.113	0	.139	.025
PT	0	0	.013	.025	0	.038	.013
GA	0	0	0	.052	0	.052	0
GS	0	0	0	.026	0	.026	0
GN	0	0	0	0	0	0	0
GD	0	0	0	0	0	0	0
GW	0	0	.026	0	0	.026	.026
GT	0	0	0	.039	0	.039	0
IA	0	0	.014	.142	.014	.170	.014
IS	.028	0	0	.070	0	.099	.028
IN	.028	0	.055	.111	.014	.208	.083
ID	0	0	.014	.028	0	.042	.014
IW	0	0	.014	.057	0	.071	.014
IT	0	0	0	.016	0	.016	0

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Table 4.23: Individuals' hourly rates of participation in male-female coalitions, averaged across dyads, precoup.

	Victim						
Individual	male	female	immature	non-monkey	unknown	Total	Total vs. monkeys
C	.020	.003	.011	.193	.006	.232	.034
P	.006	.001	.014	.082	.004	.106	.021
G	.010	.003	.013	.065	.003	.093	.025
A	.019	.002	.019	.168	.005	.212	.040
S	.009	.005	.012	.105	.002	.131	.026
N	.005	.002	.007	.064	.012	.090	.014
W	.005	.002	.009	.069	0	.085	.016
T	.021	0	.016	.159	.002	.199	.037

Table 4.24: Individuals' hourly rates of participation in male-female coalitions, averaged across dyads, postcoup.

	Victim						
Individual	male	female	immature	non-monkey	unknown	Total	Total vs. monkeys
C	.013	0	0	.004	0	.017	.013
P	.030	.011	.011	.185	.036	.272	.051
G	0	0	.004	.020	0	.024	.004
I	.009	0	.016	.071	.005	.101	.026
A	.013	.006	.004	.140	.029	.191	.022
S	.029	.006	.003	.115	.025	.178	.038
N	.013	0	.017	.062	.007	.098	.030
D	.017	.003	.007	.038	0	.065	.028
W	.003	0	.013	.043	0	.059	.016
T	.003	0	.003	.023	0	.030	.006

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Table 4.25 : Hourly rates of aggression between males and females (female aggression against males is in parentheses), precoup.

	Female					
Male	A	S	N	W	T	Mean
C	.098 (.140)	.077 (.182)	.021 (.042)	.055 (.007)	.035 (.007)	.057 (.076)
P	.028 (.098)	.035 (.070)	.035 (.043)	.055 (.014)	.084 (.070)	.047 (.059)
G	.063 (.133)	.035 (.063)	.014 (.021)	.055 (.028)	.049 (.021)	.043 (.053)
Mean	.063 (.123)	.049 (.105)	.023 (.035)	.055 (.016)	.056 (.033)	.049 (.063)

Table 4.26 : Hourly rates of aggression between males and females (female aggression against males is in parentheses), postcoup.

	Female						
Male	A	S	N	D	W	T	Mean
C	0 (.115)	.013 (.126)	0 (.050)	0 (.055)	0 (.038)	.013 (.051)	.004 (.072)
P	.164 (.101)	.125 (.262)	.124 (.074)	.123 (.096)	.038 (0)	.013 (.051)	.098 (.097)
G	0 (.078)	.026 (.129)	.013 (.051)	.043 (.043)	.013 (.118)	0 (.066)	.016 (.081)
I	.099 (.127)	.084 (.155)	.125 (.166)	.077 (.092)	.099 (.014)	.010 (0)	.082 (.092)
Mean	.066 (.105)	.062 (.168)	.065 (.085)	.061 (.071)	.037 (.042)	.009 (.042)	.050 (.085)

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Table 4.27: Rates of severe aggression, precoup. Rates of female aggression against males are in parentheses; other numbers are rates of male aggression against females.

	Female					
Male	A	S	N	W	T	Mean
C	.035 (.007)	.049 (0)	0 (0)	0 (0)	.021 (0)	.021 (.001)
P	0 (.007)	.021 (.007)	.007 (.014)	.007 (.007)	.042 (0)	.015 (.007)
G	.028 (.021)	.014 (.014)	.007 (.007)	.014 (0)	.014 (0)	.015 (.008)
Mean	.021 (.012)	.028 (.007)	.005 (.007)	.007 (.002)	.026 (0)	.017 (.005)

Table 4.28: Rates of severe aggression, postcoup. Rates of female aggression against males are in parentheses; other numbers are rates of male aggression against females.

	Female						
Male	A	S	N	D	W	T	Mean
C	0 (.051)	.013 (.013)	0 (0)	0 (0)	0 (0)	0 (0)	.002 (.011)
P	.038 (0)	.025 (0)	.012 (0)	.014 (.014)	.013 (0)	0 (0)	.017 (.002)
G	0 (.026)	0 (.052)	0 (.013)	0 (0)	0 (.013)	0 (0)	0 (.017)
I	.028 (.042)	.014 (.042)	.028 (.014)	.031 (.015)	.014 (0)	.014 (0)	.021 (.019)
Mean	.016 (.030)	.013 (.027)	.010 (.007)	.011 (.007)	.007 (.003)	.003 (0)	.010 (.012)

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Table 4.29: Precoup rates of female-female coalitions against males during focal observations.

Coalition	vs. C	vs. P	vs. G
AS	.107	.047	.047
AN	.005	.014	.005
AD	0	0	.016
AW	0	0	.005
AT	0	0	.005
SN	.019	.009	.005
SD	.016	0	0
SW	.005	.005	0
ST	.005	0	0
ND	.017	0	0
NW	0	0	0
NT	0	0	0
DW	0	0	0
DT	0	0	0
WT	0	0	0
Average	.012	.005	.005

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Table 4.30: Postcoup rates of female-female coalitions against males during focal observations.

Coalition	vs. C	vs. P	vs. G	vs. I
AS	.017	.084	.026	.065
AN	.008	.025	.008	.046
AD	.036	.027	0	.049
AW	.008	0	0	.028
AT	0	0	0	.009
SN	.008	.016	.017	.083
SD	.018	.035	0	.009
SW	0	0	.009	.009
ST	0	0	0	.009
ND	0	0	0	.019
NW	0	0	0	0
NT	0	0	0	0
DW	.009	0	0	.010
DT	0	0	0	0
WT	0	0	0	.009
Average	.007	.012	.004	.023

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Table 4.31: Contexts of adult female-female coalitions against males.

Context	# coalitions
Female attacks male for no apparent reason.	18
Female attacks male in the context of feeding competition.	12
Male attacks female in the context of feeding competition.	12
Male attacks infant or juvenile, and female intervenes by attacking the male.	11
Male neutrally approaches and/or accidentally startles female, who screams or attacks him.	9
Female attacks male in an attempt to break up his coalition or affiliative interaction with third party.	9
Male attacks female for no apparent reason.	7
Male displays, female responds by screaming or attacking.	5
Female redirects aggression at male.	4
Male redirects aggression at female.	2
As one male approaches her, the female attacks a different male.	2
Male courts female, who then attacks him.	2
Female attacks male while they are fur-rubbing.	2
Female courts male, who then attacks her.	1
Male attacks female while they are fur-rubbing.	1

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Table 4.32: Copulations between adult females and adult or juvenile males during focal observations.

Male	A	S	N	D	W	T	Total	Total: (Female cycling?)
C	2**	0	0	0	2*[2]	0	4	1
P	2**	1[2]	1[1]	0	0	0	4	1
G	2*[1]	0	0	0	2[2,2]	0	4	2
I	1*	0	1*	0	1*	0	3	0
Q	0	1	0	0	1*	4[1,1,2,2]	6	3
K	0	1[2]	1[2]	0	0	2*[2]	4	2
H	0	0	2[2,3]	0	0	1*	3	2
unidenti -fied juvenile	0	0	1*	0	0	0	1	0

*female pregnant

[1]female heavily lactating (i.e. within 2 months postpartum)

[2]female potentially cycling

[3]within 10 days of female's putative conception date

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Table 4.33: Proportion of samples in which females exhibited proceptive behavior, in relation to female reproductive state.

Female	pregnant	0-2 months postpartum	2-6 months postpartum	potentially cycling	within 10 days of conception
A	.047	0	0	.007	0
S	0	.028	0	.004	-----
N	.009	0	0	.033	.148
D	0	-----	-----	.083	.040
W	.016	0	.012	.038	0
T	.034	0	.009	0	0

Table 4.34: Proportion of samples in which old (multiparous) and young (nulliparous and primiparous) females exhibited proceptive behavior, in relation to female reproductive state.

Age class	pregnant	0-2 months postpartum	2-6 months postpartum	potentially cycling	within 10 days of conception
Old	.024	.007	.005	.012	0
Young	.004	0	0	.058	.094
Old + young	.018	.006	.004	.027	.031

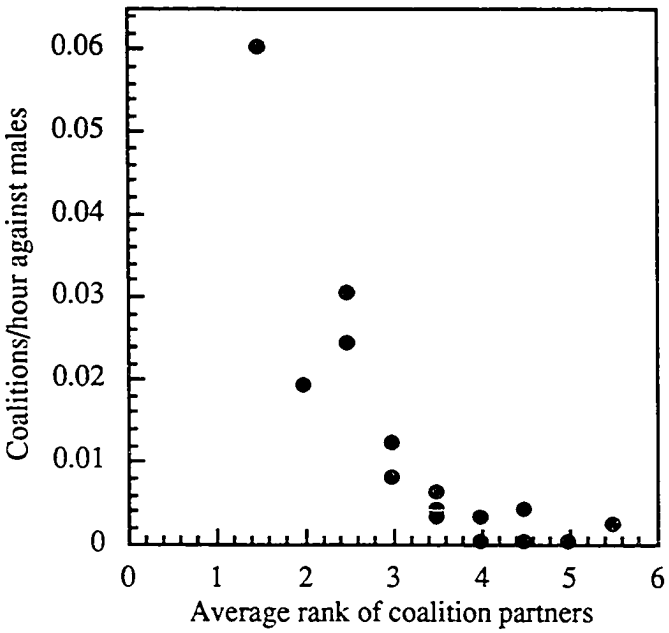
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Table 4.35: Proportion of female focal samples in which females were targets of male proceptive behavior, in relation to female reproductive state.

Female	pregnant	0-2 months postpartum	2-6 months postpartum	potentially cycling	within 10 days of conception
A	.047	0	0	.007	.080
S	0	0	0	.035	-----
N	.028	.018	0	.020	.037
D	0	-----	-----	.007	.040
W	.011	0	.025	.032	0
T	.026	.028	0	.021	0
Mean	.018	.009	.005	.020	.031

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Figure 4.1: Average rank of female-female coalition dyad, plotted against hourly rate of coalitions vs. males



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CHAPTER V

CAUSES AND CONSEQUENCES OF A MALE RANK REVERSAL

Introduction

High dominance rank in gregarious nonhuman primates is sometimes, but not always, associated with centrality in a group's social network. Alpha male vervets are actively supported by adult females, whose support is necessary for maintaining their rank (Keddy and Raleigh 1992, Raleigh and McGuire 1990). In macaques, high-ranking males tend to be more spatially central to the core of adult females and have closer social bonds to females (e.g. Chapais 1983, Samuels et al. 1984, Sade et al. 1988). In contrast, high-ranking savanna baboon males tend to be recent immigrants and generally have fewer female Friends (as defined by proximity and grooming rates) than do lower-ranking males (Smuts 1985). In brown capuchins, *Cebus apella*, the alpha male is preferred by females as a mate and grooming partner and is the most spatially central male in the group (Janson 1984, Izawa 1980). In brown capuchins, the alpha male also has a special relationship with juveniles and infants. The alpha male is more spatially central in *Cebus olivaceus* as well, and appears to father most offspring (Robinson 1981, 1988). However, reports of social relationships in the other two capuchin species (*C. albifrons* and *C. capucinus*) indicate that the alpha male may not always have such a central social position, relative to the other males in the group (Fedigan 1993, Janson 1986).

In this chapter, I assess the extent to which adult males' relationships with adult females and immatures were influenced by a male dominance rank reversal in a group of wild white-faced capuchins, *Cebus capucinus*. I also investigate the means by which the

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rank reversal occurred: particularly, the extent to which females exerted an influence in male-male politics. The political strategies involved in the rank reversal are compared with the strategies employed by chimpanzees during rank reversals, in an attempt to assess the degree of social intelligence employed by *Cebus*.

Methods

The analyses in this chapter are based on focal follows (905.17 hours of 10-minute samples on adult males and females) and ad lib observations. The protocols for data collection are described in chapter 1. Many of the analyses in this chapter divide the dataset into two phases, "precoup" and "postcoup." The "coup" refers to the male rank reversal that occurred in November, 1992.

Hinde's index (Hinde and Atkinson 1970) was used as a measure of proximity maintenance. Hinde's index, for dyad A-B, = (# of approaches of A to B/# approaches of A to B and of B to A) - (# of leaves by A from B/# leaves by A from B and by B from A). Only approaches from outside one body length (as defined in Chapter 1) to within one body length of the focal animal were used in calculations. Likewise, only leaves from within one body length to outside of one body length of the focal animal were scored. Only approaches and leaves during focal observations were used to calculate Hinde's indices. All Hinde's indices were calculated from the female perspective; therefore, a positive index means that the female was primarily responsible for maintaining proximity to the male. A negative Hinde's index means that the male was primarily responsible for maintaining proximity with the female. In some cases, subordinate males did not spend enough time near a female during a 6-month period to generate 10 approaches and leaves during focal observations, so the Hinde's index was not calculated for those dyads during those time blocks; the number "10" was an arbitrarily chosen cut-off selected prior to analysis. For the analysis of female proximity maintenance to Curmudgeon, I was interested in seeing whether the unusually high Hinde's indices during the first 6 months of

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the study represented a short-term peak in female proximity maintenance, or were the tail end of a long-term period in which females maintained proximity to the alpha male. Therefore, I added data from the pilot study in 1990, a year before the main study began. These data are not strictly comparable to the data in the main study because the units used to measure distances were meters rather than body lengths, and although most of the approaches and leaves concerned distances within one meter, some were within the 1-5 meter category; therefore, comparisons of the pilot study data with the other data should be made cautiously.

The method for calculating proximity scores is described in depth in chapter 2. The data used to calculate proximity scores are the distances of all visible monkeys from the focal animal during the final instantaneous sample of each 10-minute focal follow. The higher the proximity score, the more time individuals in a dyad spent in close proximity. Proximity scores are heavily weighted toward the closer proximity categories, such that the main contributing factor to the proximity score is the amount of time the dyad spent within contact or within a body length of one another. Diablita was excluded from analysis of pre- and postcoup comparisons of male-female relationships because she only matured to adulthood (i.e. had her first estrus) at the time of the coup.

Instigations of conflicts between males and females were determined as follows. A female was considered to have instigated a conflict with a male if she threatened or otherwise behaved aggressively toward him, and he had not directed aggression against her, supplanted her, or aggressed against anyone else in the previous 5 minutes. In a few instances, both Squint and Abby simultaneously aggressed against a male, such that it was impossible to assign either of them as the initial aggressor; in these cases, both were given "credit" for instigating the attack. When one female clearly began threatening the male before the other female joined her, only the first female was credited with instigating the attack. A male was considered to have instigated a conflict with a female if he supplanted her from a feeding site immediately prior to being threatened by her, or if he aggressed

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against her when she had not previously aggressed against him within the past 5 minutes. Aggression that consisted solely of supplants, branch-shaking, or branch-breaking was not scored as a conflict.

Data on male-juvenile interactions were not available for the entirety of the study because most juveniles were not identifiable before the end of the dry season, 1992. Therefore, data on juvenile behavior are from the 6-month periods preceding and following the coup (May-October 1992, and November 1992-May 1993). Diablita was eliminated from the sample for precoup/postcoup analyses, because she was considered a juvenile during the precoup phase and an adult during the postcoup phase. Data on male-immature interactions were are all obtained from adult males' focal samples.

Results

The Coup: A Brief Description

When observations were renewed on November 10, 1992, following a 9-day gap, Curmudgeon was found alone and severely wounded. He emitted lost calls (see chapter 1 for definition) when he saw the human observers and then was silent for the rest of the day, aside from peeping softly to himself as he settled into his sleeping tree for the night. He had a 2.5-cm canine slash in the sole of his left foot, a 4-cm canine slash on his left shoulder, and puncture wounds inside his left arm, about 15-cm above the foot wound. There was a series of puncture wounds inside his right leg below the knee. The only limb not injured was his right arm, and he dragged himself up trees primarily by using his arms.

The next day (November 11, 1992), the following event occurred: At dawn, Curmudgeon, who had slept alone far from the group, began giving lost calls and whimpering. His lost calls had a peculiar whiny quality to them that I had never heard before, and the pitch increased at the end of the final syllable as if his voice was cracking. I heard an answering lost call from far away, and Curmudgeon was silent awhile before

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resuming lost calls. Curmudgeon lost called some more, and also peeped. There were more answering lost calls. Curmudgeon began alternating his lost calls with a new vocalization that I had never heard before, the whine bark. The whine barks were more like alarm calls than anything else, but were higher-pitched and less raspy. As the answering lost calls came closer, Curmudgeon's voice began to sound less whiny and more confident; his lost calls no longer "turned up" at the ends of the syllables. Curmudgeon began doing burst-twitter-bray sequences (defined in chapter 1) and broke a branch. Throughout this entire vocal exchange, Curmudgeon had contained his movement to 2 trees and was still hobbling due to his severe foot wound. At 5:42, Paul came into view, and Curmudgeon alarm called twice. I didn't recognize Paul at first because his appearance had changed so much. He was fully piloerected, such that he appeared much larger than I had seen him previously, and he was more agitated than I had ever seen him. Paul had a canine slash that extended from above his right eyebrow, through his right upper lip (so that his canine tooth protruded through it), and into his chin. As soon as they saw one another, Curmudgeon and Paul simultaneously began wheezing. The wheeze is probably the highest-pitched vocalization in the vocal repertoire. It sounds like a cross between a whistle and a twitter: it is as if the pitch and volume of a twitter were increased, and the syllables were run together so that the sound was almost smooth rather than staccato. Curmudgeon and Paul were a few meters apart when they started wheezing. After wheezing for a long time, they began alternating grunts with wheezes; Curmudgeon did more wheezes than grunts, while Paul did more grunts than wheezes. Curmudgeon began spinning around in place (avoiding use of his wounded left foot), while maintaining eye contact with Paul. Paul was completely piloerected and paced back and forth while wheezing at Curmudgeon. Both of them flinched frequently, as if they were nervous of one another. Paul alarm called as the other human observer approached. Paul stopped wheezing and did an intense vocal threat. Paul threatened the observer, headflagged to Curmudgeon, and alarm called a few more times. Paul headflagged to Curmudgeon again

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and threatened the observer, but Curmudgeon neither alarm called nor threatened the observer in support of Paul. As Paul turned to leave, Curmudgeon did a short alarm call (like those elicited by snakes), and Paul did another longer human-elicited alarm call. Paul broke a branch, Curmudgeon emitted a "food call," and Paul once again moved toward Curmudgeon. They simultaneously burst into the wheeze dance again, this time with a larger proportion of grunts interspersed between wheezes. Their grunts and wheezes were rhythmic and gave the impression that they were coordinating their vocalizations with one another. While vocalizing, they flailed their limbs, spun their bodies in circles, and hopped up and down. Curmudgeon yelped as he leaped into the next tree. Observers had the impression that Curmudgeon and Paul were too nervous to approach one another, but didn't want to part either. Both Paul and Curmudgeon emitted alarm calls as Curmudgeon moved closer, and then they moved further apart. Paul looked downhill and threatened that way and headflagged to Curmudgeon, who did not join in threatening. Paul continued to alarm call and headflag to Curmudgeon, who began giving "food calls." Paul left Curmudgeon and went downhill toward the rest of the group, alarming continually. Once he turned back and walked toward Curmudgeon, while doing burst vocalizations and lost calls. The group did not follow Paul, and he returned to the rest of the group, leaving Curmudgeon alone.

When I returned to the group with Paul, I discovered that Paul's role had changed dramatically since the last day of observation. Formerly, Paul spent most of his time on the periphery of the group and rarely initiated social interactions (chapters 3,4). Now, Paul was in the center of the group, was fully piloerected, and engaged in aggressive displays almost continually, in which he broke branches, threatened the observers, and solicited aid from adult females and Guapo. Abby, Squint, Wiggy, and Diablita enthusiastically supported Paul in threatening the observers. Guapo directed mild, silent threats at the observers when solicited by Paul, but he avoided Paul. Squint had a severe tail wound, and her tail was crooked. Wiggy had a deep puncture wound on her right forearm. Mild

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wounds were observed on Abby the following day, but it is not known exactly whether they were acquired during the week of the observers' absence, or on the following day, when Abby was observed fighting with Paul.

Guapo avoided social interactions throughout November 11-13, and he appeared more vigilant and peripheral than usual. On the 13th, he disappeared and was not seen again until November 27th, when he was found foraging solitarily, with some 5-6-day-old minor injuries (nicks on the face and hands). Because Guapo was not seen to be involved in aggression before his departure, it is believed that he left of his own accord rather than being chased away. It is likely that Guapo attempted to join another social group (probably Rambo II's group) during his absence. His injuries indicate that he had been fighting with someone. Also, his return to the group on November 28 coincided with the immigration of Ichabod, a male who had previously been seen in Rambo II's group. Rambo II's group was only 100-200 meters from the study group at the time Guapo and Ichabod joined the study group on November 28. The fact that Guapo and Ichabod were frequently found associating on the periphery of the group during the 2 weeks after they (re)joined the group suggested that they may have known one another prior to November 28th. Also, Guapo did not instigate attacks on Ichabod on the first 3 days after Ichabod's immigration, whereas the other adult males and most adult females did.

Curmudgeon made several attempts to rejoin the group during November 11-28, but he was always driven away by Paul and/or adult females (as described below). He finally succeeded in rejoining the group as beta male on November 28, when Ichabod joined and Guapo returned. The details of his reintegration into the group are discussed later in this chapter. In the discussion, I speculate as to the cause of the coup.

Pre- and Postcoup Comparisons of Male-male, Male-female, and Male-juvenile Relationships

All male-male dyads spent less time in proximity following the coup (chapter 3). Although the amount of time they spent together decreased, their rate of social interaction

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with one another increased. All males directed more aggression toward other males following the coup. Paul received the least aggression postcoup, whereas Curmudgeon received the least aggression precoup. The incidence of wheeze-dancing between males increased 24-fold, and other forms of affiliation increased to a lesser degree following the coup (chapters 3,6). Chapter 3 provides more details on coup-related changes in male-male relationships for each dyad.

Following the coup, Curmudgeon spent less time in proximity to all 5 adult females (figure 5.1) and was never in close proximity to Abby, Squint and Tattle. Paul spent more time with the 4 top-ranking females, and less time with the lowest-ranking and most peripheral female (figure 5.2). Females are arranged according to rank, with the highest-ranking females being at the left. A comparison of figures 5.1 and 5.2 reveals that prior to the coup, Curmudgeon spent more time with adult females than did Paul, whereas following the coup, Paul spent more time with all adult females, except for Wiggy, than did Curmudgeon. Although Guapo did not appear to suffer a loss of dominance rank as a consequence of the coup, he was more peripheral following the coup as well. Figure 5.3 shows the changes in Guapo's proximity with adult females. Guapo spent much less time with all adult females following the coup.

To what extent were the changes in proximity between adult males and adult females a result of the sudden rank reversal, rather than of other social changes? To assess the timing of the changes, I broke the precoup period into 6-month blocks, to see whether changes in proximity patterns occurred gradually over time, or suddenly at the time of the coup. Figures 5.4-5.6 show the changes in proximity patterns for male-female dyads over time. It is important to remember, when interpreting these changes, that monkeys may tend to forage further apart and have lower rates of some types of social interactions during the rainy season (i.e. the first and third 6-month blocks) when wasps and caterpillars are staples of their diet than during the dry season. Also, three times as many data were collected in the dry season as in the rainy season; hence there may be some degree of

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sampling bias in the first and third blocks, in which scores are based on only 81-88 samples per monkey. Curmudgeon's proximity scores with adult females dropped dramatically between the rainy season of 1991 and the following dry season, and decreased once again following the coup (Figure 5.4). Paul's proximity scores with high-ranking females increased markedly at the time of the coup, and his proximity score with Squint increased during the 6 months preceding the coup (Figure 5.5). Guapo's proximity scores declined gradually over time and did not show particularly marked changes at the time of the coup as opposed to other times (Figure 5.6).

Following the coup, Curmudgeon was groomed less frequently by 4 out of 5 adult females (figure 5.7). Paul was groomed more often by 4 out of 5 females following the coup (figure 5.8). Note that, prior to the coup, all females groomed Curmudgeon more than they groomed Paul; whereas after the coup, all but the lowest-ranking female groomed Paul more than they groomed Curmudgeon. All females groomed Guapo less following the coup (figure 5.9). Males virtually never groomed females, either before or after the coup (chapter 4).

The patterning of production of one vocalization, the gargle, changed dramatically following the coup. The gargle is a low, raspy-sounding, atonal vocalization that sounds a little like a cercopithecine threat; however, capuchins produce it in an affiliative context, as when approaching, following, or grooming the alpha male (see ethogram in chapter 1 for more details). Tables 5.1 and 5.2 show the rates of gargling by adult females. Preceding the coup, adult females gargled only to Curmudgeon. Following the coup, adult females gargled only to Paul. Thus, it appears that the gargle is used by adult females as a formal acknowledgment of alpha male status.

The patterning of gargling was less consistent for immature monkeys. Tables 5.3 and 4 represent data on immatures' gargling rates toward males for the 6 months preceding and the 6 months following the coup. Infants gargled to all adult males, and even occasionally to adult females. Juveniles gargled more consistently toward high-ranking

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males. Prior to the coup, virtually all juveniles gargled at higher rates to the alpha male than to other males. Figures 5.10 and 5.11 show the change in immatures' gargling rates toward Curmudgeon and Paul following the coup. In these and subsequent figures, juveniles are arranged by age, with the oldest monkeys being at the left; females are asterisked. During the 6 months preceding the coup, juveniles gargled significantly more often to Curmudgeon than to Paul (Wilcoxon Matched Pairs test: n=11; T=2; z=2.028; p=.043). During the 6 months following the coup, there was no significant difference in the rates at which juveniles gargled to Curmudgeon and Paul (Wilcoxon Matched Pairs test: p=.2). Postcoup, 6 juveniles gargled more to Paul than to Curmudgeon, and 4 juveniles gargled more to Curmudgeon than to Paul. All juveniles gargled to males at higher rates after the coup than before the coup, and many of them gargled to all 4 adult males, including the new immigrant male. In fact, 3 juveniles gargled more often to the new immigrant male than to either Curmudgeon or Paul.

Juveniles' patterns of proximity to males did not shift in a predictable way following the coup. Tables 5.5 and 5.6 and figures 5.12-5.15 show the changes in male-juvenile proximity between the precoup and postcoup phases. Prior to the coup, all but one of the juveniles spent more time with Curmudgeon than with Paul. Following the coup, only 3 juveniles spent more time with Paul than with Curmudgeon. Although Paul increased the amount of time spent with some juveniles following the coup, Curmudgeon did not decrease the amount of time spent with juveniles after the coup. Seven juveniles increased their time with Curmudgeon following the coup, and 5 decreased their time with him. Nine juveniles increased their time with Paul following the coup, and 3 decreased their time with him.

Responsibility for Changes in Social Dynamics Preceding the Coup

Figures 5.16-5.18 show changes in female proximity maintenance to males over time. The data are broken into 6-month blocks of time. All of Guapo's Hinde's indices

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were negative -- that is, females avoided being in proximity with him. Most of Paul's indices were also negative. There were no consistent changes in females' Hinde's indices with Paul or Guapo over time. Many of Curmudgeon's Hinde's indices with females were positive -- that is, the females were largely responsible for maintaining proximity to Curmudgeon. However, female proximity maintenance to Curmudgeon declined throughout the period preceding the coup. In order to better assess the length of time during which females maintained proximity to Curmudgeon, I also incorporated data from the pilot study in 1990 into figure 5.16. It was not possible to incorporate pilot study data for Guapo and Paul, because the number of approaches and leaves with females was too few.

Figure 5.19 shows the rates at which females instigated conflicts with Curmudgeon prior to the coup. Four of the 5 adult females instigated conflicts at a fairly constant rate during the 17 months preceding the coup. However, Squint's rate of conflict instigation more than tripled during the 6 months preceding the coup. In 75% of her unprovoked attacks on Curmudgeon, Squint succeeded in recruiting other females' aid against Curmudgeon.

Figure 5.20 shows the rates at which Curmudgeon initiated aggression against each female. His rates of conflict instigation did not increase over time, and they decreased for some dyads. Curmudgeon's lowest rate of conflict instigation with females was during the 6 months immediately preceding the coup. The rate at which Curmudgeon instigated conflicts with Squint dropped steadily, and he did not instigate any conflicts with her during the final 6 months during focal observations.

Several months prior to the coup, Squint and Abby began doing rather striking aggressive displays against Curmudgeon. At first, they threatened him silently from behind his back while he was asleep. They gradually escalated their aggression toward him by doing overlords and vocal threats toward him, so that he could not help but notice them. His typical response to their threats was to ignore them and turn his back or walk away.

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Their aggression toward Curmudgeon became more intense over time throughout the precoup period, until it reached its peak on the last day of observation before the coup (October 28, 1992). At 2:58 PM, I heard exceedingly loud undulating screams from more than one monkey and ran toward the commotion, where I saw Curmudgeon biting either Abby or Squint. Abby and Squint chased Curmudgeon, who then turned and lunged at them and bit them both. The three of them lunged back and forth several times, and Curmudgeon bit Squint again. He chased one of them out of the tree and stood between them, while piloerected and producing intense gargles. The screams and threats were louder than any I had heard previously, and the biting was also more severe than any I had witnessed previously. Curmudgeon attacked Squint and tried to drive her out of the *Eugenia* tree. She screamed and ran around Curmudgeon so that she was reunited with Abby. Curmudgeon left the tree, but Abby and Squint continued to vocally threaten him. They increased the intensity of their threats as Curmudgeon moved further away. Curmudgeon gargled, and Abby ran after him. Squint did not follow Abby. Abby vocally threatened Curmudgeon, and he gargled again, while Abby squeaked and wheezed. Abby ran toward Curmudgeon, gargling and wheezing, while Curmudgeon gargled. Curmudgeon and Abby circled around one another and danced while wheezing and gargling. Squint resumed vocally threatening Curmudgeon as Abby and Curmudgeon wheeze danced. Abby followed Curmudgeon as he piloerected and urine rubbed. Curmudgeon looked over his shoulder at her and continued gargling. Abby threatened him, and he left. The entire fight and wheeze dance took place within a space of 6 minutes. Although several monkeys observed the fight, no one else participated. Fifteen minutes after the wheeze dance, some monkeys found a rattlesnake, and most group members including Abby ran over to stare at it and do alarm calls. Although Curmudgeon was near enough to see the snake, he did not participate. His lack of participation was significant, because he typically is very involved in snake mobbings. He only alarm called at the snake after the rest of the group had departed. Curmudgeon did not interact with Abby or Squint

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for the rest of the day. As I left the group just after nightfall, I heard another severe fight break out, with extremely loud and prolonged undulating screams and vocal threats.

The data and descriptions above suggest that Squint was the instigator of Curmudgeon's fall in rank. Because Squint increased the amount of time spent with Paul during the 6 months preceding the coup, I examined the complete record of her interactions with Paul during focal observations in the 6 months preceding the coup to see whether there were indications that she was cultivating a relationship with him. There were no noteworthy affiliative interactions between them that indicated a change in their relationship. The following is a summary of all of their social interactions during focal observations in the 6 months preceding the coup: They did not groom at all during that period; nor did they play, though Squint did invite play from Paul once in August and was ignored. Squint and Paul formed one coalition each against Quizzler and Kola, and Squint formed two coalitions with Paul against the observers. Abby, Squint and Paul formed a coalition, consisting of a long series of threats and overlords, against an insect-covered pile of monkey feces. Squint formed coalitions with females against Paul twice. Thus, the rates of Squint's coalition formation with and against Paul were not unusually high.

There were no noteworthy changes observed in Curmudgeon and Paul's relationship with one another during the precoup period. Their relationship was characterized by low levels of proximity and extremely low rates of affiliation throughout the precoup period (chapter 3). Paul never aggressed against Curmudgeon during focal observations prior to the coup, though he did join the females in threatening Curmudgeon once during ad lib observations when Curmudgeon was mating with Wiggy on March 23, 1992.

Observers did note some subtle changes in personality in Paul and Curmudgeon during the week preceding the coup. On October 27, observers remarked in the field notes that "Curmudgeon has been really nervous and twitchy all day; he can't relax." His tension may have been due, in part, to the fact that Wiggy was in estrus and followed him for much

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of the day; Paul followed Wiggy and Curmudgeon. Once, on October 28, Curmudgeon chased Paul and Wiggy after Paul solicited sex from Wiggy and she followed him. Several times during the three days preceding the coup, observers noted that Paul seemed unusually furtive and vigilant. His behavior seemed so out of character that there were several times when one of the observers remained with Paul to collect ad lib data on his behavior, while the other observer conducted focal observations. Paul engaged in an unusual display of bravado toward a human observer (Julie) on October 27, which seemed to be an attempt to impress Squint: Paul sneaked up behind Julie until he could practically touch her. He threatened her and headflagged to Squint, but Squint ignored him. He shook branches at Julie and threatened her, and headflagged to Squint several more times until she finally joined in threatening Julie. Paul went down to the ground, stood practically within arm's length of Julie, and threatened her again. Then Paul dislodged an enormous rock more than half his body size and pushed it toward Julie. He moved back toward Squint and embraced her, and both Paul and Squint threatened Julie. During the month following the coup, Paul often incorporated humans in aggressive displays (e.g. by slapping them or grabbing their feet), but he typically ignored humans during the precoup period, aside from the display described above.

Who Was Responsible for Curmudgeon's Postcoup Peripheralization?

The number of approaches to one body length between Curmudgeon and most females during the postcoup period was too low to permit the calculation of Hinde's indices. In fact, Curmudgeon was *never* observed to approach the 3 top-ranking females during focal observations in the postcoup period, and the number of approaches by females to Curmudgeon varied from 0 (Abby) to 5 (Wiggy) approaches during the entire postcoup period. Therefore, it was difficult to be certain on the basis of close-range approach/leave interactions whether Curmudgeon was choosing to stay on the periphery of the group (perhaps to avoid Paul, who tended to be near the high-ranking females), or whether the

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adult females were actively avoiding being near Curmudgeon and/or excluding him from the center of the group. To increase my sample size of interactions, I examined approaches to within 10 body lengths for Curmudgeon/female dyads during focal observations during November, 1992. Also, I extracted every Curmudgeon/female interaction from the ad lib and focal data for the month of November, after the coup occurred.

Even when larger distance categories were incorporated in the focal follows, there were insufficient approaches to calculate Hinde's indices. Curmudgeon approached to within 10 body lengths of Diablita and Wiggy once each during focal observations in November. He was approached to within one length once by Squint, and to within 10 lengths twice each by Nanny, Diablita, and Wiggy. Tattle approached Curmudgeon to within 10 lengths once, but she immediately threatened him. Curmudgeon was responsible for 5 of the 7 observed leaves to outside 10 body lengths of females. Thus, the picture is still unclear, but it appears that Curmudgeon may have been less motivated to be near females than vice versa.

Curmudgeon's first contact with females following the coup occurred on November 16, at 7:20 am, when Nanny approached him to within 5 lengths and threatened the observers. Nanny then stood bipedally, scanned her surroundings, and left. A few minutes later, Abby spotted Curmudgeon and threatened him. Abby and Hobbes directed an overlord at Curmudgeon, and several monkeys joined in threatening Curmudgeon vocally. They chased him from the tree he was in. Several minutes later, when Curmudgeon was socializing with juveniles, Paul threatened Curmudgeon, and Abby and Squint joined Paul in chasing and vocally threatening Curmudgeon. The next time Curmudgeon came into Abby's view, she again threatened him vocally.

Curmudgeon's next social interaction with females was the following day, when Wiggy, who was in estrus, accompanied him on an overnight consortship away from the group. She actively followed him and made duck faces at him throughout the day.

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Although Paul lost called within her hearing range numerous times, Wiggy made no attempt to leave Curmudgeon and return to the main body of the group.

November 18, at 7:43: Abby and Squint screamed at Curmudgeon when he returned to the group. Again at 11:40, Abby directed intense vocal threats and a gyrrah (alarm call) at Curmudgeon when he came into her view. At 12:30, when Nanny first came into Curmudgeon's view, he fled from her. In contrast to his interactions with females, Curmudgeon's interactions with immatures were more relaxed. Curmudgeon and the immatures actively initiated affiliative interactions (gargling, feeding in proximity, grooming, and other forms of nonaggressive physical contact) with one another throughout the day.

November 19: Abby, Squint, Nanny, Diablita, Quizzler and Lizano chased and vocally threatened Curmudgeon when he came into their view at 5:55 am; Curmudgeon may have wheeze danced with Paul right before this incident. Much later in the day, at 4:00 PM, Curmudgeon once again spotted an adult female (Abby or Squint) in the distance and began fidgeting nervously.

November 20, at noon: Curmudgeon vocally threatened someone in the distance. Quizzler danced and overlorded with Curmudgeon against the distant monkey. Abby headflagged to Curmudgeon, and he approached her to 10 lengths. Abby, Curmudgeon and Quizzler all threatened in the same direction -- possibly toward Paul, but the monkey was too far away to be positively identified. Approximately an hour after this incident, Paul, Abby and a third monkey chased and bit Curmudgeon, and Squint and Wiggy chased Curmudgeon even further.

November 21, at 5:30 am: Curmudgeon was seen within 5 lengths of Tattle, but he soon left her outside of 10 lengths; no direct social interactions were observed, though some may have occurred before I located them. At 9 am, Paul threatened Curmudgeon within view of Abby and Squint, who observed but did not join in the threats. At 10 am,

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Curmudgeon did burst-twitter-bray sequences, as if trying to lead the group, and both Abby and Paul followed him.

November 22, at 9:45: Curmudgeon was alone, doing alarm calls and scanning vigilantly. Abby did a vocal threat in the distance, apparently in response to Curmudgeon's alarm calls, and approached to 30 lengths of Curmudgeon. He urine rubbed and alarm called again. Abby moved further away, but 2 minutes later, both Abby and Tattle vocally threatened Curmudgeon while he continued to alarm call. Later, at 11:30, Tattle entered the *Jacquinia pungens* tree in which Curmudgeon was foraging. She threatened the observer and headflagged to Curmudgeon. He did not resist her entry of the tree, but he did not help her threaten the observer. Tattle again threatened the observer, broke a stick, and headflagged to Curmudgeon, who moved away from her. Curmudgeon crept quietly out of the tree as he heard other monkeys approaching and disappeared into the undergrowth, walking on the ground. Throughout most of the day, he was very attentive to the sounds of approaching monkeys and consistently moved away from them. At 4:10 PM, Curmudgeon appeared to be leading the group. Tattle threatened and lunged at Curmudgeon, who fled and threatened the observer. Tattle screamed at Curmudgeon and headflagged to an unidentified monkey. Curmudgeon again threatened the observer, and Tattle threatened Curmudgeon, who avoided her.

November 23, at 8:15: Curmudgeon looked vigilantly toward the main body of the group as Squint and Paul approached in the distance. Curmudgeon alarm called and looked at Paul, who threatened the observers. Curmudgeon may have subtly threatened the observers as well, but it was hard to see his face. Paul headflagged to Curmudgeon, who emitted an alarm call similar to a snake-elicited alarm call. Curmudgeon threatened and bounced at the observers. At 12:17, both Abby and Squint were in view of Curmudgeon, but neither of them threatened him. Curmudgeon seemed to be leading the group. Paul and Curmudgeon walked in opposite directions, and the group followed Curmudgeon. At 2:40 PM, Paul and Curmudgeon did a wheeze dance with gargles, and Abby joined in the

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dance. Paul left, and Curmudgeon threatened silently in the direction of Paul. Abby also threatened toward Paul and followed him. Diablita threatened Curmudgeon, and Kola threatened Paul. Diablita danced with Curmudgeon, groomed him, and left. Everyone followed Paul.

The monkeys were not observed on November 24-26. On the 27th, Curmudgeon was not with the group. On the 28th, Curmudgeon and Guapo rejoined the group, and Ichabod immigrated at dawn. The details of the males' interactions are described later in this chapter. At 6 am, Abby and Curmudgeon made nonaggressive physical contact for the first time since the coup approximately 3 weeks earlier, in the following context: Curmudgeon and Ichabod were wheeze dancing, and Quizzler and Abby threatened Ichabod. Abby headflagged to Curmudgeon. As Ichabod approached closer to Quizzler and Abby, Curmudgeon backed to within one length of Abby, and they both threatened Ichabod. Hobbes backed into Curmudgeon, and Abby, Curmudgeon and Hobbes did a triple-decker overlord toward Ichabod, with all three of them threatening him vocally. Ichabod left the area. At 9:36, Abby and Curmudgeon once again cooperated: Curmudgeon and Paul vocally threatened and chased Guapo, and Abby joined them in vocally threatening Guapo, who fled and chewed his tail. Paul and Curmudgeon both headflagged to Abby, who continued to aid in threatening Guapo for the next 12 minutes. Eventually, Curmudgeon ran, gargling, toward Guapo, and Paul and Abby threatened Curmudgeon. Curmudgeon and Guapo wheeze danced while Paul and Abby threatened them vocally. At 10:30, Curmudgeon was observed for the first time since the coup foraging in the vicinity of several adult females and juveniles. At 12:50, Squint and Hobbes approached Curmudgeon, gargled at him, and groomed him for several minutes. At 12:55, Squint paused in the middle of the grooming bout to silently threaten Curmudgeon behind his back before resuming grooming. At 1:05, Paul vocalized, and this apparently startled Squint, who stopped grooming Curmudgeon and bit him. Squint, Hobbes and Lizano then threatened Curmudgeon silently, and Paul vocally threatened

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Curmudgeon from a distance. Curmudgeon ran away from Squint and threatened Paul. Curmudgeon urine rubbed, did a burst-twitter-bray sequence, and gargled. Squint followed Curmudgeon. At 1:50, Broma threatened Curmudgeon and solicited Abby's aid. Broma and Abby stood cheek-to-cheek as Broma threatened Curmudgeon, but Abby did not actively threaten him. At 3:39, Nanny, Abby and a third monkey began grooming Curmudgeon. Four minutes later, Paul directed intense vocal threats at Curmudgeon, who broke off the grooming bout and crept away from the group.

November 29, at 7:04: Vandal groomed Curmudgeon and threatened Ichabod. Both Vandal and Curmudgeon threatened an unidentified monkey. At 7:12, Vandal ran over to Nanny and threatened Curmudgeon. Vandal headflagged to Nanny, but Nanny did not join her in threatening Curmudgeon. Instead, Nanny groomed Vandal. At 8:30, two monkeys vocally threatened Paul, who redirected threats at Curmudgeon. Everyone joined Paul in threatening and chasing Curmudgeon, who fled. Hobbes and Abby chased Curmudgeon the farthest, and one of them was bitten. At 11:17, Curmudgeon "food called" and then ran past Squint while making duck faces at her. Squint watched Curmudgeon intently but did not respond.

November 30, at 9:01 am: Curmudgeon began doing "whine barks." Whine barks are a vocalization produced only by Curmudgeon, and only after the coup. They were similar to alarm calls, but the calls were of longer duration, and were exceptionally hoarse and whiny-sounding. Curmudgeon whine-barked repeatedly and rapidly, occasionally interjecting an alarm call (i.e. one that sounded identical to a snake-elicited alarm call) between whine-barks. Paul, Squint and Abby vocally threatened Curmudgeon as he whine-barked. Hobbes approached them, threatened Curmudgeon, and overlorded over Paul at Curmudgeon. Curmudgeon continued to alternately whine bark and alarm call; when he did whine barks, he stared into space or looked at his antagonists, but when he alarm called, he looked at the ground. No snake was present. Abby, Squint, Paul and Hobbes all vocally threatened Curmudgeon as he continued vocalizing. Squint and Abby

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occasionally stopped threatening to groom one another. Paul backed toward Squint and Abby. Squint left the area, and then Paul and Curmudgeon broke into a chorus of gargle-like vocalizations. Following this outburst, Curmudgeon began flailing and doing anguished-sounding screams. Abby and Hobbes renewed their threats against Curmudgeon. Curmudgeon continued to vocalize (whine bark, alarm, and scream) constantly over the next several minutes, while Paul, Abby and Hobbes directed various forms of aggression against him. Nanny and Squint also joined in threatening Curmudgeon. The entire episode lasted about 15 minutes, and Curmudgeon continued vocalizing after his aggressors had departed. Soon afterwards, at 10:05, Diablita, Abby and Squint vocally threatened Paul. Abby and Squint overlorded at Paul, and Nanny threatened Paul. Nanny threatened Curmudgeon and headflagged to Paul, and Squint joined Nanny in threatening Curmudgeon. At 2:07, Tattle yelped at Curmudgeon, but there was no further aggression. At 2:55, Diablita and Curmudgeon foraged near one another and exchanged food calls.

Male-male Interactions in the Month Following the Coup

Curmudgeon's first observed meeting with Paul after the coup has already been described above. Following are all subsequent male-male interactions in the 17 days following the coup. The other observers and I made a concerted effort to keep adult males in view at all times throughout this period, so it is unlikely that many interactions were missed.

November 11 at 4:30: Paul and Guapo began lost calling. They ran through the forest ahead of the group, lost calling continually, until 5:25 PM, when Paul stopped lost calling and did an alarm call. It was too dark to identify monkeys by this time, but I heard what sounded like Curmudgeon's voice doing intense vocal threats, followed by vocal threats by several other monkeys. One monkey fled, and two males chased him, while doing vocal threats.

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November 12: Curmudgeon was found near the group at dawn, and the monkeys were dispersed and lost-calling. One observer followed Paul while the other followed Curmudgeon. Both of them were alarm calling, and they were far from the rest of the group. Paul ran quickly through the forest and gave the impression that he was looking for someone. Curmudgeon kept alarm calling softly and was not using his feet; he pulled himself up trees using only his hands. He spent most of the morning in the same tree, foraging on vine fruits and licking his wounds. At 11:00, Curmudgeon heard the rest of the group approaching and stared vigilantly toward their branch-breaking and vocalizations, without producing any noise himself, aside from a single, soft whine that I had never heard before. At 12:10, Paul discovered Curmudgeon and ran toward him, doing intense vocal threats. Curmudgeon responded with more vocal threats, and either Paul or Curmudgeon gargled. Paul ran toward Curmudgeon, vocalizing, and Curmudgeon sat still. Quizzler, who was piloerected, also ran toward Curmudgeon. Paul and Quizzler chased Curmudgeon far from the rest of the group. The observers, Paul and Quizzler lost Curmudgeon in the undergrowth. Paul and Quizzler searched the undergrowth for awhile and eventually returned to the rest of the group.

November 13th, at 3:45: Paul began lost calling and looking up a cliff. Guapo had disappeared earlier in the day, and Curmudgeon had not been seen since he was chased the day before. Paul continued lost calling and led the group up the cliff. At 4:40, he stopped lost calling and I heard the sounds of a serious fight, followed by alarm calls. I had not yet reached the top of the cliff and could not see what was happening, but a few minutes later, Curmudgeon emerged from the direction of the fight, running as fast as he could and still limping. The rest of the group followed Curmudgeon at a distance. Curmudgeon slept alone that night, but within hearing distance of the group.

Curmudgeon was not seen all day on Nov. 14th or 15th, though Paul may have interacted with Curmudgeon twice -- at least, vocally -- on the 15th: At 5:55 am, Paul ran at top speed through the forest, lost calling and alarm calling continually, until 7:08. The

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alarm calls were fairly soft and of long duration, like the ones used when another social group of monkeys has been spotted. The rest of the group followed him at a distance. Soon after Paul stopped calling, I heard a serious fight down in a ravine, but the vegetation was too dense to see the participants. Later, at 1 PM, I heard vocalizations that sounded like Curmudgeon's voice, in the distance, and Paul ran toward the voice, doing vocal threats and alarm calls. I heard Paul and the other monkey doing intense gargles in the distance.

November 16 at 6:30 am: Curmudgeon lost called, and someone from the group answered with intense vocal threats. Paul ran toward Curmudgeon, followed by Abby, Wiggy and Diablita. Curmudgeon returned to the group at 7:23. Paul directed intense vocal threats to Curmudgeon when Curmudgeon emitted "food calls." At 7:58, Paul chased Curmudgeon away from the group, with the aid of Abby, Squint, and some juveniles. Curmudgeon remained near the group for the rest of the day.

November 17, at approximately 1 PM: Wiggy left the group to consort with Curmudgeon (see chapter 6). They spent the night together, far from the rest of the group. Paul began to lost call at 1:20 on the 17th, and he continued to lost call periodically for the rest of the day. At dawn on the morning of the 18th, Paul and several other group members lost called until Wiggy returned to the group at 6:10 am. Curmudgeon returned with Wiggy, but he hid in the undergrowth and avoided interaction with other group members. Curmudgeon emitted several soft alarm calls as he returned, hobbling on the ground. Paul observed Curmudgeon's return but did not interact with him. At 7:48, Curmudgeon emitted some "food calls," and Paul directed intense vocal threats at him. Hobbes, Yoyo and some other juveniles followed Curmudgeon and gargled at him. Curmudgeon wheezed and did whine barks in response, after which Paul charged toward Curmudgeon and directed intense vocal threats at him. Curmudgeon and Paul threatened one another. Curmudgeon alarmed and headflagged to Quizzler, who ran away from Curmudgeon and turned to threaten him. Curmudgeon continued to threaten Paul, pausing

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occasionally to scan the area, over the next 10 minutes. Curmudgeon alarm called and moved toward the group. When he approached to 20 lengths of Quizzler, Quizzler threatened him. Curmudgeon continued to monitor Paul's behavior for the next half hour. At 1:23, Paul and Abby directed intense vocal threats at Curmudgeon, and Paul continued to watch Curmudgeon for the next 10 minutes.

November 19, at 5:40 am: It appeared that Curmudgeon was leading the group and vocalizing loudly. Paul ran toward him, doing intense vocal threats. I heard a wheeze dance, which was probably between Curmudgeon and Paul. Soon afterwards, Paul vocally threatened Curmudgeon, and several monkeys helped Paul chase Curmudgeon (see previous section for more details). At 4:22, in the same tree where Paul had confronted Curmudgeon on November 12, Curmudgeon threatened the observers and headflagged to Paul, who ignored him. Curmudgeon threatened the observers vocally and headflagged to Paul. Curmudgeon threatened and headflagged several more times, to no avail. Curmudgeon began alarm calling intermittently while threatening the observers and headflagging to Paul. Curmudgeon gargled intensely, and Paul also gargled, at 4:25. Curmudgeon resumed threatening the observers, emitted human-elicited alarm calls, and headflagged furiously to Paul, but Paul still refused to threaten the observers. Paul and Curmudgeon exchanged vocalizations (probably intense gargles) again at 4:36. Hobbes approached and overlorded with Paul against Curmudgeon. Curmudgeon alarm called while looking at the observers and then headflagged to Paul and Hobbes. Curmudgeon lay on his side and alarm called. Paul left the area. Hobbes urine rubbed and then followed Paul.

November 20 at 5:35 am: The observers found Curmudgeon doing alarm calls and whine barks; he appeared to be alone, far from the rest of tne group. Twice he stopped vocalizing briefly to threaten the observer. At 5:50, the observers noticed Paul about 20 meters from Curmudgeon. Curmudgeon headflagged to Paul and threatened off in the distance. The rest of the group was in the next valley. Paul threatened the observer once.

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Paul and Curmudgeon responded to a lost call from the main group. Curmudgeon continued to alarm call and whine bark, and Paul did some lower-pitched, longer-duration alarm calls in conversation with Curmudgeon. They continued to exchange vocalizations for the next 10 minutes as Curmudgeon moved away from Paul. At 12:02, Curmudgeon cooperated with Abby and Quizzler in threatening toward where Paul had last been seen (see above section for details). At 12:45, Curmudgeon was leading the group, piloerecting, and urine rubbing. Curmudgeon, along with Wiggy, Abby and 2 juveniles, threatened Paul. Paul rushed back to the group, doing intense vocal threats, and everyone turned on Curmudgeon, biting him and chasing him away (see above for more details). Paul was wounded in the skirmish with Curmudgeon.

November 21, at 6:35 am: Curmudgeon alarm called twice while looking at me and headflagged to Paul. Someone in the distance lost called, and both Paul and Curmudgeon answered. Both Paul and Curmudgeon alarm called several times, and Curmudgeon threatened the observer continuously. At 6:53, Paul threatened Curmudgeon, who continued doing alarm calls and threatened toward an empty field. Curmudgeon resumed threatening the observer. Curmudgeon answered another lost call. Alarm calling continually, Curmudgeon moved rapidly toward the rest of the group. Paul climbed to the ground and alarm called, while running. Curmudgeon threatened the observer and headflagged to Paul. Paul ran away from Curmudgeon and looked over his shoulder at him as he ran, while doing alarm calls and burst-twitter-bray vocalizations. Later, at 8:54, several females threatened Paul vocally. Paul ran away on the ground, vocalizing loudly, and threatened Curmudgeon, who was sitting in the middle of the road in the distance. Paul ran, screaming, toward Curmudgeon, who stood bipedally to observe the situation. Abby and Squint did not join Paul in threatening Curmudgeon. Ten minutes later, Curmudgeon did burst-twitter-bray sequences, and Paul followed him. At 9:54, Paul and Curmudgeon both did burst-twitter-bray sequences, and Paul and Abby followed Curmudgeon. Both Paul and Curmudgeon continued to do bursts and burst-twitter-bray

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sequences in duet for the next 40 minutes. At 10:45, they began gargling at one another. The group continued to follow Curmudgeon. At 3:07, Paul and Curmudgeon exchanged some strange vocalizations that I could not identify.

On November 22, at 8:34, I heard intense vocal threats. When I arrived at the location of the threatening, Curmudgeon and Paul were doing a wheeze dance, with gargles and other vocalizations interspersed between wheezes. Curmudgeon ran away, still wheezing, and they resumed dancing at a greater distance. At 8:40 they stopped vocalizing abruptly. Paul threatened the observer and headflagged to Curmudgeon, who also threatened the observer. Both Paul and Curmudgeon began alarm calling and left the area, with Curmudgeon following Paul at a distance.

On November 23, at 8:21, Curmudgeon was sitting alone at the edge of the group, vocalizing continually and occasionally glancing toward the group. As Squint and Paul approached in the distance, Curmudgeon alarm called and looked at Paul. Paul threatened the observer, and Curmudgeon threatened as well. Paul headflagged to Curmudgeon, and Curmudgeon alarm called, threatened the observer, and bounced. Again at 1:00, Curmudgeon was "food calling" at the edge of the group, when Abby and Paul approached to within 15 lengths. Curmudgeon started to leave, and Paul threatened the observer and headflagged to Curmudgeon twice. Curmudgeon briefly threatened the observer. At 2:15, I heard a wheeze dance, but arrived too late to identify the participants. Squint, Curmudgeon, and Paul were the monkeys in the vicinity, so it is likely that the dancers were Curmudgeon and Paul. Curmudgeon threatened the observers. Quizzler approached and began grooming Curmudgeon. Paul threatened Quizzler and Curmudgeon, and Quizzler stopped grooming to threaten Curmudgeon. Curmudgeon threatened first Quizzler, then the observer, and headflagged to Paul. Paul did not aid in threatening. At 2:40, Paul and Curmudgeon wheeze danced, and Abby joined Curmudgeon in threatening Paul (see previous section for further detail).

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Curmudgeon was gone when observations were renewed on the 27th. November 28th was the day when Ichabod immigrated and Curmudgeon and Guapo returned to the group. Suddenly, Paul was confronted with the task of socially manipulating 3 males, one of whom was unknown to him. This was no doubt the most challenging political task with which he had been confronted since becoming alpha male. Up until now, he had been the sole adult male for much of the time. Even when Curmudgeon had been present, he had been crippled, and the adult females had been quite willing to cooperate in driving him away from the center of the group when solicited. Although the adult females were willing to support Paul against Curmudgeon, they had not been supportive of Paul in other contexts; in fact, they had had several serious fights with Paul since he rise to alpha status, and they had even wounded him. Therefore, Paul may have had reason to worry about retaining alpha status in the presence of 3 male rivals.

When I arrived at the group's sleeping site at dawn on the 28th, the group was widely dispersed, and I could hear at least 2 monkeys doing alarm calls. I heard a wheeze dance up the hill from the main body of the group and headed toward the wheeze dance, in the company of one of the alarm calling males. The wheeze dance resumed, and the two males involved were Paul and Curmudgeon. At the end of the dance, Paul fear grinned, headflagged to Curmudgeon, and threatened toward Ichabod, the male whom I had followed up the hill. Curmudgeon and Paul's demeanor was a striking reversal of their patterns of interaction during the previous 2 weeks: Paul was fear grinning spasmodically toward Curmudgeon, jerking his head continually while scanning the area, and twitching as if he were under mob attack, whereas Curmudgeon appeared completely calm and unflustered by the arrival of the new male. Curmudgeon did not aid Paul in threatening Ichabod. Paul began alarm calling at a high rate, doing the types of alarm calls normally elicited by humans and other monkey groups. A few minutes later, Paul moved toward Curmudgeon, and Curmudgeon appeared slightly more nervous. Curmudgeon scratched himself, alarm called quietly, glanced at Paul, and began threatening downhill toward

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Ichabod. Curmudgeon headflagged toward Paul, gargled, and whine barked. He looked back toward Paul and grunted before resuming whine barks. Paul disappeared, but Curmudgeon kept glancing toward where Paul had last been seen, and whine barking. Then Curmudgeon wheezed and gargled toward Ichabod, and they wheeze danced. Ichabod did human-elicited alarm calls, and either Curmudgeon or Ichabod broke a branch. They resumed the wheeze dance, and Quizzler vocally threatened the dancers. Abby threatened Ichabod and solicited Curmudgeon's aid against Ichabod (see above section for details). After aiding Abby in driving away Ichabod, Curmudgeon followed Ichabod and did two more wheeze dances with him at 6:08. Several monkeys whom I could not identify chased Ichabod away, but he returned to do another wheeze dance with Curmudgeon. Paul was nowhere to be seen. At 6:16, I heard another wheeze dance but could not identify the participants. Ichabod followed the study group; meanwhile, Rambo II's group (which is presumed to be Ichabod's former group) departed across the river, after having been approximately 100 meters from the study group.

As he hobbled up the hill, Curmudgeon vocalized incessantly, doing burst-twitter-bray sequences, gargles, and twitters. Juvenile males followed Curmudgeon. At 6:38, Curmudgeon encountered Guapo for the first time since the coup, at the same spot where Curmudgeon and Paul had wheeze danced at dawn. Curmudgeon and Guapo began a particularly energetic wheeze dance at very close range (1-2 lengths apart), while Squint and an infant watched in silence. When the dance had been going on for 12 minutes, Curmudgeon established contact with Guapo, and Guapo backed away, still dancing. Guapo paused briefly to headflag to Curmudgeon and to threaten someone in the distance. The dance continued, but Guapo occasionally cowered to Curmudgeon. At 6:54, Guapo threatened the observer and headflagged to Curmudgeon, and they both stopped wheezing. Guapo followed Curmudgeon, and they resumed the dance for another minute. Guapo threatened the observers, headflagged to Curmudgeon, and approached him to contact. Curmudgeon resumed the wheeze dance. Guapo cowered, threatened the observer, and

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moved away. Curmudgeon approached, presented for grooming, and was groomed by Guapo for 12 seconds. They both wheezed, and Guapo mounted Curmudgeon. They both made duck faces and then wheezed. Guapo thrust for several seconds, dismounted, and resumed the dance. They stopped wheezing, and Curmudgeon left. Guapo ran after Curmudgeon and they danced briefly again. Curmudgeon gargled, and Guapo peeped in response.

For the next 50 minutes, I did not witness any interactions between adult males, but the group was widely dispersed, and I heard several wheezes, gargles and vocal threats that may have involved males. Curmudgeon piloerected, stayed near the center of the group, and vocalized loudly and incessantly. At 7:53, Paul came toward Curmudgeon and directed several intense vocal threats toward him. Paul was also piloerected, and he snarled at Curmudgeon. Curmudgeon continued to vocalize loudly, mainly doing "food calls," and ignored Paul's threats. Paul continued threatening and scanned the area, as if looking for prospective allies, but he did not move closer to Curmudgeon. Paul moved close to Nanny and then resumed threatening Curmudgeon. Curmudgeon started a long-distance wheeze dance with a monkey I could not identify, and Paul burst into intense vocal threats and ran toward the dancers. Paul chased Curmudgeon, and Guapo threatened Curmudgeon silently. Paul threatened Guapo, and Curmudgeon overlorded with Paul against Guapo. Paul then overlorded over a juvenile at Guapo, and they both vocally threatened him. They ran toward Guapo, and Paul lunged at Guapo. Curmudgeon vigorously directed vocal threats at Guapo. Quizzler threatened Curmudgeon, who then lunged at him. Paul threatened Curmudgeon, and Quizzler headflagged to Paul. Paul ran away, and Curmudgeon ran after him. At 8:19, Curmudgeon gargled; Paul piloerected and directed intense vocal threats toward him. Curmudgeon loudly produced food calls, and Paul ran toward him, vocally threatening him. Paul, hair standing on end, continued to vocally threaten Curmudgeon, who observed him calmly. Curmudgeon spun around and threatened someone in the distance (probably Guapo) and looked back at Paul. Paul

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threatened the same monkey and headflagged to Curmudgeon repeatedly. Paul produced "burst" vocalizations. Curmudgeon calmly foraged for insects while Paul scanned the area vigilantly. At 9:02, Abby, Squint, Broma and Nanny fought with Paul, but no other males became involved.

At 9:35, Curmudgeon vocally threatened Guapo, who fled. Paul also ran toward Guapo and vocally threatened him. Curmudgeon chased Guapo. Abby approached Paul, and they threatened Guapo cheek-to-cheek as he fled even further and chewed his tail. Guapo threatened the observers and headflagged to his three opponents, but they continued to threaten him. Guapo threatened an imaginary victim and again headflagged to Curmudgeon, Paul and Abby, to no avail. Guapo kept running further away and chewing his tail as the vocal threats continued. Finally, at 9:49, Curmudgeon ran toward Guapo and initiated a brief wheeze dance. They foraged briefly, and then Curmudgeon and a juvenile threatened Guapo, who fled. Paul chased and vocally threatened Guapo, who threatened a bare patch of ground and moved slightly toward Paul. Guapo threatened the observer, and Paul joined in threatening and breaking branches at the observer. At 10:36, Paul silently threatened Guapo, who ignored him. At 10:53, Guapo threatened toward Paul and Ichabod, and Paul again threatened Guapo. Ichabod alarm called, and Guapo threatened the observers. Paul continued threatening Guapo, who turned and threatened a juvenile. Paul continued threatening Guapo for a few more minutes, while Guapo attempted to redirect aggression at the observer or distant monkeys. Paul alarm called while looking at Guapo and then fear grinned. Paul directed an intense vocal threat at Guapo. A minute later, he lipsmacked at Guapo and then resumed threatening him. Guapo threatened a monkey in the distance. Paul coughed and continued to threaten Guapo. Squint approached to contact of Paul and also threatened Guapo. At 11:05, Paul headflagged to Guapo and threatened a monkey I couldn't identify, but he soon resumed threatening Guapo and continued to do so for the next half hour. At 11:37, Paul headflagged to Guapo and switched to threatening someone in the distance. Guapo aided Paul in threatening that

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monkey. Ten minutes later, Paul vocally threatened Guapo. At 11:57, Curmudgeon headflagged to Paul and threatened in the same direction in which Paul had most recently been threatening.

At 12:02, Curmudgeon emitted "food calls" extremely loudly, and Paul directed intense vocal threats toward Curmudgeon. At 12:06, Curmudgeon produced intense vocal threats, Paul did intense vocal threats in return, and Paul ran toward Curmudgeon. Both were piloerected. They stood near one another, and both stared in the same direction. Four minutes later, Curmudgeon slinked away from the group, on the ground, and was very vigilant, as if searching for someone. He produced raspy-sounding grunts as he walked.

At 1:01, after Squint bit Curmudgeon (see above section for details), Paul vocally threatened Curmudgeon from a distance, and Curmudgeon silently threatened Paul. After Curmudgeon left the area, Ichabod threatened someone, and Curmudgeon did burst-twitter-bray sequences as several monkeys followed him. Guapo and Curmudgeon wheeze danced within 5 lengths of one another and then went uphill (away from the group), where they encountered Ichabod. I heard a wheeze dance and vocal threats from them, but I didn't arrive in time to see which monkeys were responsible for which vocalizations. Ichabod fled when I arrived, and Guapo sniffed where Ichabod had been sitting. At 1:09, Curmudgeon, Guapo and Ichabod did a 3-way wheeze dance far from the rest of the group. Ichabod did a human-elicited alarm call while looking at me. Guapo and Ichabod did another wheeze dance, and Paul vocally threatened them from a distance. Curmudgeon threatened Ichabod, and then both Curmudgeon and Guapo chased Ichabod. Ichabod vocally threatened the observers and alarm called. Ichabod also alarm called at two parrots. At 1:14, after Ichabod left the vicinity, Curmudgeon headflagged to Guapo and attacked an adult coati, grabbing it by the tail. Guapo threatened the observer but did not aid Curmudgeon against the coati. Two minutes later, Guapo shook branches while staring at an imaginary enemy on the ground; there was clearly nothing in the place he was

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threatening. He headflagged to Curmudgeon, threatened the ground, and headflagged again. Paul could be heard vocally threatening someone down the hill. Ichabod began "food calling" nearby. Curmudgeon gargled, and Paul once again did a vocal threat in the distance. Curmudgeon and Guapo "food called" while the vocal threats continued. At 1:26, Paul came up the hill, still threatening Curmudgeon and Guapo. Guapo cringed when he saw Paul, but Curmudgeon continued to "food call." Paul continued to threaten them for the next 14 minutes, and then Curmudgeon and Guapo wheeze danced. I could not see Paul's reaction through the heavy rain. Curmudgeon and Guapo continued to wheeze, and Curmudgeon and a juvenile gargled. Someone alarm called. Curmudgeon and Guapo remained in close proximity, "food calling." Curmudgeon gargled, and someone did a vocal threat. Curmudgeon threatened three times in the direction of Ichabod and the rest of the group, and he headflagged to Guapo twice. Guapo did not assist Curmudgeon. Abby and Squint joined Curmudgeon in his foraging tree, and Guapo left. Curmudgeon threatened Guapo three times and headflagged to Paul. At 1:51, Paul threatened someone (possibly Curmudgeon). An unidentified monkey chased Ichabod, and Paul ran toward the chase. Ichabod ran past Curmudgeon and then turned to start a dance with him. They both danced, and several monkeys threatened Ichabod until he left. Curmudgeon also threatened Ichabod. Rico overlorded over Curmudgeon at Ichabod. Curmudgeon and Rico returned to the rest of the group, and Ichabod followed them.

At 2:25, both Curmudgeon and Paul did burst-twitter-bray sequences from opposite sides of the group; Paul piloerected and moved rapidly toward Curmudgeon. At 2:39, Curmudgeon emitted exceptionally loud "food calls," and Paul ran toward him on the ground, doing intense vocal threats and piloerecting. He stood bipedally to monitor Curmudgeon's behavior. Curmudgeon vigorously threatened Paul. Abby, Squint and Diablita vocally threatened Paul and continued to harass him with overlords and threats for several minutes, after which time they chased Paul. At 2:52, Paul did a burst-twitter-bray sequence, and Curmudgeon threatened him silently.

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At 3:22, Paul directed intense vocal threats toward someone in the distance, and Curmudgeon threatened in the same direction. At 3:43, Paul encountered Curmudgeon being groomed by 3 females, and he directed intense vocal threats at him until he crept away from the females. At 4:25, Paul heard a gargle and possibly a wheeze in the distance, and he directed intense vocal threats in that direction while running that way. He threatened Guapo, who fled and chewed his tail. At 5:08, Curmudgeon was involved in affiliative social interaction (gargling and grooming) with a monkey who could not be identified, and Paul ran toward them doing vocal threats.

In the interest of being concise, I will not describe the male-male interactions on subsequent days. For many days, there was continual social chaos, especially with regard to male-male social interactions. As on November 28, males constantly monitored one another's behavior, and Paul consistently disrupted subordinate males' dances and affiliative behaviors. Paul alternated between recruiting Curmudgeon's aid against Guapo and recruiting Guapo's aid against Curmudgeon. He never formed coalitions with Ichabod against other males. Paul seemed to ignore Ichabod as much as possible; even when Ichabod attacked females in Paul's vicinity, Paul typically did not aid the females in the first month after Ichabod's immigration. Whereas both Guapo and Curmudgeon danced with Ichabod immediately upon meeting him, Paul's first wheeze dance with Ichabod occurred on December 9, 11 days after he joined the group. Both Curmudgeon and Guapo, but particularly Guapo, danced frequently with Ichabod on the edge of the group during the first two weeks after his immigration. Paul followed them at a distance and protested dances vocally, but he seemed reluctant to interact with Ichabod at close range.

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Discussion

Female Choices and Female Power

To what extent were females responsible for the coup? Data on male-male relationships provided no clues that a male rank reversal was about to occur. The most noteworthy change in adult relationships during the precoup phase was the females' steady decline in proximity maintenance to Curmudgeon. If any one monkey was responsible for Curmudgeon's fall from alpha rank , it was Squint. She was the one monkey who actively antagonized Curmudgeon with increasing intensity in the months before the coup. Other females participated in coalitions versus Curmudgeon, but it was almost always Squint who initiated these attacks, which were often unprovoked. Although I did not witness the critical fight during which Curmudgeon was decisively deposed, it seems obvious from the patterns of wounding that females were actively involved. Both Squint and Wiggy had wounds that appeared to have been inflicted by male canines, and Abby may have been wounded in that fight as well. Also, the distribution of wounds on Curmudgeon, including damage to his shoulder and three limbs, almost certainly indicates a gang attack. One-on-one fights between males typically result in damage to the face and hands, but not to the rear limbs. It seems likely that the females held and bit Curmudgeon while Paul inflicted the more damaging wounds. Given the frequency and intensity of the females' attacks on Curmudgeon in the week preceding the coup, the most likely scenario is that the females attacked Curmudgeon first, and Paul took advantage of the situation to defeat his rival and become alpha male.

Although Squint appeared to have initiated the coup, it seems improbable that she and the other females could have brought about Curmudgeon's downfall without Paul's help. Females are capable of wounding monkeys, but their canines can not inflict nearly as much damage as can males' canines, and the few wounds that I saw inflicted by females all healed rapidly. The females' subsequent confrontations with Paul and Ichabod were

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enlightening in terms of demonstrating the limits of female power. Large coalitions of females -- typically composed of the 4 top-ranking females, but sometimes including additional females and juveniles -- attacked both Paul and Ichabod on a regular basis following the coup. Their attacks on Ichabod were a daily occurrence for long after the coup, and were notable for their intensity. These fights involved biting and wrestling, and often ended with all participants falling out of the trees in a screaming ball of monkeys. It seemed quite clear that the females did not want Ichabod in the group, but his persistence eventually wore them down. Paul was notable for his lack of aid to females during the females' confrontations against Ichabod. In no case during focal observations did he offer more than vocal assistance, even when females were biting Ichabod, and he sometimes denied them even vocal aid when they headflagged for assistance.

Thus, females have the power to support a favored alpha male, or -- with the assistance of an adult male -- to bring about the downfall of a disfavored alpha male. But they can not determine the male membership of the group without the assistance of other males.

Why did the females want to depose Curmudgeon? My initial suspicion was that Curmudgeon had become too greedy or too hostile to the females. But an analysis of rates of conflicts provoked over time (in which food theft, supplants, and aggression count as conflict provocation) shows that, if anything, Curmudgeon provoked increasingly fewer conflicts with females during observations preceding the coup. It is possible that Curmudgeon's levels of feeding competition with females increased at a more subtle level than could be detected merely by recording supplants and thefts, but I have no way of assessing that with my dataset. If alpha males largely control mating access to fertile females, as in *C. olivaceus* and *C. apella* (Robinson 1981, 1988; Janson 1984), then the females might have wanted to depose Curmudgeon so that they could mate with a different male. However, the available evidence contradicts this hypothesis. Squint, the apparent instigator of Curmudgeon's downfall, actively avoided Paul and pursued Curmudgeon

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when she came into estrus in January, 1993, and she was seen to mate with Curmudgeon but not Paul. Wiggy went on consortships with Curmudgeon on two occasions after the coup, one of which was immediately after the coup when Curmudgeon was still crippled. It is unlikely that Curmudgeon succeeded in mating with her on this first occasion, because his back limbs were too severely injured, but Wiggy courted him nonetheless. Another possibility, which can not be adequately tested, is that the females are selected to evict or depose breeding males when their daughters mature, so as to prevent inbreeding. Indeed, the two youngest females, Diablita and Nanny, actively courted Paul but not Curmudgeon during the postcoup period. The coup coincided with Diablita's first estrus.

Ichabod's Immigration and Its Effects on Intragroup Relationships

It is likely that Ichabod succeeded in immigrating and rapidly integrating himself into the group only because of the social chaos at the time of his migration. Because he arrived at a time when the alpha male's ties to other males were extremely weak, and when the two subordinate males had not seen each other for at least 17 days, the resident males were unable to present a united front against Ichabod. In fact, Guapo and/or Curmudgeon might even have viewed Ichabod as a possible ally against Paul. Curmudgeon danced with Ichabod almost immediately upon encountering him. Guapo also danced with Ichabod on his first day in the group, and it is likely that Guapo met Ichabod prior to his immigration. In contrast, Paul did not dance with Ichabod until many days later. In 2 prior attempts by extragroup males to immigrate, the resident males had not danced with the foreign males; rather, they had joined in threatening and chasing the intruders.

As discussed elsewhere (chapters 3,7), it seems likely that the threat of invasion by foreign males plays a role in shaping resident males' social relationships with each other. The events surrounding the coup provide a case study for investigating this possibility. If foreign males posed a threat to the group, Paul should have been nervous about being the only male in the group during the week following the coup. Also, Paul's attitude toward

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his male rivals should have changed on the day of Ichabod's immigration if he perceived them as allies against Ichabod. Because male immigrations have been associated with infanticides and death or disappearances of females at Santa Rosa (Fedigan et al. n.d.), the females might also be expected to change their attitude toward Curmudgeon when faced with the threat of a male immigration.

Paul actively searched for Curmudgeon and/or Guapo by lost calling on all but one of the 8 days that Curmudgeon was absent from the group during the 3 weeks following the coup. If his goal were to evict Curmudgeon from the group completely, it seems unlikely that he would have sought out his company and advertised the location of the group. Paul's dramatic wheeze dances with Curmudgeon also seemed indicative of a desire to repair the relationship rather than to sever ties with Curmudgeon completely (see chapter 6 for a discussion of the function of wheeze dances). On the other hand, Paul was careful not to allow Curmudgeon to assume the alpha male role again. He responded hostilely on several occasions to Curmudgeon's attempts to lead the group by doing burst-twitter-bray sequences, and he also responded aggressively to Curmudgeon's attempts to interact affiliatively with other group members. In short, it seemed that he was attempting to mold Curmudgeon into assuming Paul's old role: that of a peripheral group member who rarely interacts with other group members, but provides coalitionary aid against predators, other subordinate males, and foreign males. Paul seemed unusually anxious on the morning of Ichabod's arrival, and he wheeze danced with Curmudgeon as Ichabod approached them. Paul vigorously solicited Curmudgeon's aid against Ichabod; this was the first instance in which Paul solicited Curmudgeon's aid against a monkey after the coup. Paul also solicited Curmudgeon's aid against Guapo later in the day. However, Paul's apparent need for Curmudgeon's aid against males did not prevent Paul from threatening Curmudgeon when he attempted to affiliate with other group members. Nonetheless, whether it was due to greater tolerance by Paul or to Paul's preoccupation

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with other matters, Curmudgeon succeeded in affiliating with other group members on this day more than on any other day since the coup.

For the first 10 days following the coup, the females responded to the sight of Curmudgeon by threatening him away before he could get anywhere near them. Wiggy was not aggressive toward him when they were in consort, but she was aggressive in the group context. Between November 20 and 28, the females were still not behaving in an affiliative manner toward Curmudgeon, but Abby twice cooperated with Curmudgeon in threatening Paul from a great distance. Also, the females seemed reluctant to follow Paul during this time period. Paul's burst-twitter-bray sequences, the vocalizations used to signal group movement, were peculiar-sounding at first; I had never heard him perform these vocalizations prior to the coup, and he seemed to require practice at them. Perhaps in part for this reason, the females tended to follow Curmudgeon as often as they followed Paul during the week of November 20-28. Often they followed neither of them, and there seemed to be no consensus about group movement. During this week, it seemed possible that Curmudgeon would once again attain alpha status, once his wounds healed. Curmudgeon's first physical contact with females occurred on November 28, when Ichabod immigrated. On that day, he aided Abby in coalitions against both Ichabod and Guapo. Curmudgeon was groomed by several females later in the day and succeeded in foraging near females without being chased away. It seems likely that the females were less aggressive toward Curmudgeon on the 28th because of his aid against Ichabod, but because they had been increasingly more tolerant of Curmudgeon during the previous week, it is hard to assess the impact of that one change.

Juveniles' Reactions to the Coup

The juveniles responded to the coup in a very different manner from the adult females. The adult females suddenly switched from gargling exclusively to Curmudgeon to gargling exclusively to Paul, indicating that the gargle may be a formal indication of

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status. The juveniles gargled significantly more often to Curmudgeon than to other males before the coup, but they gargled some to Paul as well. Eldritch, the youngest group member, gargled to all males. Following the coup, the juveniles did not gargle significantly more often to Paul than to Curmudgeon. They increased their rate of gargling overall, and all males received gargling, especially from the younger juveniles. Either the juveniles did not immediately comprehend the social implications of this rank reversal, or they thought it best to "pay respects" to all males during this period of social upheaval.

For the most part, those immatures who had spent a great deal of time in proximity to Curmudgeon and Guapo prior to the coup continued to do so after the coup, despite the males' peripheralization. Although 9 of 11 immatures increased the rates at which they gargled to Paul postcoup, only 3 immatures noticeably increased the amount of time they spent near Paul when he became alpha male. Perhaps juveniles and infants who had formed special relationships with Curmudgeon and Guapo (and perhaps even been sired by them) continued to associate with them so as to receive their protection and/or tolerance at feeding sites. I rarely observed adult males protect infants in disputes with adults or intervene in quarrels between immatures. But males were very tolerant of immatures observing their foraging techniques and sometimes permitted them to share feeding sites. Also, adult males were quick to defend immatures against external threats such as potential predators.

Comparisons with Other Capuchin Studies

Although the details of alpha male takeovers have not yet been published for other *Cebus capucinus* groups, takeovers have been observed both at La Selva and at Santa Rosa. Aimee Campbell (personal communication) observed a rank reversal in a group of white-faced capuchins at La Selva, in which the alpha male was evicted and the former beta male became alpha male. The old alpha male died of his wounds a week later.

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At Santa Rosa, most takeovers are by extragroup males, who often arrive in groups of 2 or more (Fedigan et al. n.d., Mackinnon pers. comm.). Male takeovers have resulted in deaths to infants (Rose 1994) and evicted males (Fedigan et al. n.d.), and in disappearances of adult females (Fedigan et al. n.d.) at Santa Rosa. Because such great costs have been documented in association with male membership changes, I was amazed to see how calmly adult females interacted with recently immigrated adult males during a visit to Santa Rosa in 1993. Katie Mackinnon was studying the capuchins at that time and explained to me that all of the males in her two study groups had immigrated in the past 2 months, and the former males had been evicted and/or died. The immigrants in at least one of the groups had come from more than one source and therefore were unlikely to have known one another. Because of the extreme social tension following the coup in my own study group, which lasted for several months, I expected even greater tension in a group that was developing ties with an entirely new set of males. But the females acted as if they had known these new males for years; indeed, watching them reminded me of the calm state of my study group early in Curmudgeon's "reign" as alpha male. On the day of my visit, there were no wheeze dances and very few instances of aggression, all of which were very minor, aside from two brief chases in which the alpha male broke up matings. Mackinnon confirmed that the observations on this day were typical of the state of the group's social relationships. Perhaps it is easier for females and males to "start from scratch" by forming relationships with new males than it is to make drastic alterations in existing relationships, as is necessary when males rise or fall in rank.

Published anecdotal reports of rank reversals in *C. apella* and *C. olivaceus* groups do not provide information on the process by which the rank reversal occurred, but they do provide some information on changes in male-female relationships following the rank reversal. In at least one case, a *C. apella* female has shown a strong mating preference for the alpha male immediately after his rise to the alpha position, after previously ignoring him (Janson 1984). An anecdotal account of a male rank reversal in *C. olivaceus* indicates that

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females began grooming a previously ignored male immediately after he assumed the alpha position (O'Brien 1991).

Until more data have been collected on the social dynamics of male rank reversals and immigrations at other sites, it will be difficult to know whether these types of social changes have the profound impact on social relationships that are suggested by the results of this study. Also, the types of social tactics used by males in negotiating rank changes may prove to vary widely across individuals and across populations.

Comparisons with Chimpanzees

Although rank reversals have been observed in numerous primate species, I will focus the discussion on comparison with chimpanzees for the following reasons. First, the most detailed account of the politics involved in male rank reversals come from de Waal's study of the Arnhem Zoo chimpanzee colony. Second, chimpanzees are generally used as the "yardstick" by which other nonhuman primates' cognitive abilities are measured. Comparisons of chimpanzee and capuchin tool use ability have already yielded some interesting differences (e.g. Visalberghi and Limongelli 1994, Westergaard and Suomi 1994), but there have been no attempts to compare capuchins' social strategies with those of other primates. Therefore, a comparison of political strategies between chimpanzees and capuchins in a similar social context may illuminate further differences in the two species' social cognitive abilities. Because of the exceptionally large brain size of capuchins (Stephan et al. 1988, Bauchot 1982), such questions are relevant to the debate concerning the evolution of primate intelligence (e.g. Cheney and Seyfarth 1990, Milton 1988, Gibson 1986, Byrne and Whiten 1988).

Although chimpanzees and capuchins have opposite patterns of philopatry in the wild, the Arnhem chimpanzees differ from wild chimpanzees in that females are always in close proximity to males and therefore have more opportunity to interfere in male politics. Because females were less opportunistic and more loyal in their choice of allies and friends

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than were males (de Waal 1982), the Arnhem chimp females, in a sense, formed the stable core of the group in the same way that capuchin females of my study group did. In both species, female support was necessary for the alpha male to maintain his position, in spite of the fact that males were dominant to females. A striking similarity between chimpanzee and capuchin alpha male tactics was the pattern of "separating interventions" (de Waal 1978, 1982), in which the alpha male disrupted the affiliative and coalitionary interactions of subordinate males, so as to prevent them from forming alliances that could threaten his status.

In de Waal's study, "pant grunts" were a sign of respect used to acknowledge dominance, and it was only when the former alpha male began pant grunting to the new alpha male than the social tension and instability due to the rank reversal could be reduced. The pant grunt was a sign of formal dominance: even though recipients of pant grunts could lose fights to coalitions of animals who pant grunted to them, the hierarchy as indicated by the direction of pant grunts was rigid and stable over long periods of time. Although not strictly analagous to the pant grunt, the gargle appears to function in a somewhat similar way, in that it seems to indicate respect (sensu de Waal) and is rank-dependent, at least when used by adults. Gargling occurs in 3 different social contexts. The most frequent context is unidirectional low-intensity gargling, in which a lower-ranking monkey approaches or follows a high-ranking monkey (almost always an adult male, though immatures have been observed on occasion to gargle to adult females) and gargles. The gargler sometimes squirms, grovels, or head-shakes (see ethogram in chapter 1) while gargling and may be piloerected or have a genital erection. The gargler often grooms or touches the male after gargling. The recipient of the gargle usually ignores the gargler. This context is the one that most resembles that of the chimpanzee pant grunt, though one striking difference is that unidirectional gargles are never directed by one adult male toward another adult male. The other contexts are even more intriguing, and warrant further investigation. Adult males do intense gargles, a slight modification of the gargle

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(see ethogram), in tense social situations, such as when under coalitionary attack by females. Sometimes a male begins intense gargling immediately after supplanting a female but before she retaliates. Adult males sometimes gargle intensely when surrounded by gargling infants. In these types of situations, it appears that the function of the intense gargle is to appease the females who have been offended, or to reassure the infants. The last context is the gargle duet, which involves intense gargles, exchanged in a highly rhythmic conversation. Gargle duets occur in the context of dancing, often in combination with wheezing. Abby and Squint also did gargle duets while overlording against males during particularly intense fights. In the latter two contexts, gargling appears to promote solidarity between the garglers.

A possible similarity between Curmudgeon's and the alpha male chimp Yeroen's responses to loss of status and coalitionary support is tantrum-throwing. When confronted by the ascending alpha male Luit's displays, Yeroen screamed, flailed and thrashed uncontrollably in a similar fashion to an infant having a weaning tantrum, and beseeched the adult females for aid. De Waal (1982) interpreted Yeroen's tantrums as a strategy for obtaining aid, by evoking the sympathy of the adult females. Curmudgeon's "fits" were not very similar to infant weaning tantrums, but rather consisted primarily of vocal displays. He howled, whine-barked, and alarm called piteously at the top of his lungs for long periods of time -- sometimes 30 minutes or more -- when waking up in the morning, and also when observing Paul socializing with adult females or consorting with an estrous female. Although Curmudgeon's outbursts aroused considerable sympathy from the human observers, they did not appear to have the same effect on the monkeys. The other capuchins appeared to be irritated and distressed by Curmudgeon's vocalizations, and they often responded by threatening him. In contrast to the chimpanzees' response to Yeroen's early tantrums, capuchins never consoled Curmudgeon with embraces or grooming. It is impossible to know whether Curmudgeon's outbursts were deliberate strategies, or

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uncontrollable expressions of mental disturbance due to the stress he was experiencing; regardless of the reason, he did not appear to improve his social position by doing them.

A major difference between the patterns of coalitionary aggression in chimpanzees and capuchins is that two simple decision rules appear to explain the vast majority of support decisions in capuchins, whereas chimpanzees seem to be more flexible in their support decisions. The two decision rules used by capuchins are (1) support females over males, and (2) when deciding which of two same-sexed opponents to support, support high-rankers over low-rankers (chapters 2-4). There are some exceptions to these rules, and more careful analysis may reveal more complex strategies in those cases. For example, the effects of friendship, loyalty and revenge on coalitionary decisions have not yet been investigated. The one social situation in which it was impossible to predict whom would be supported was when the alpha male supported one subordinate male against another. De Waal writes that alpha male Luit chose to support Yeroen over Nikkie because he feared a coalition between Yeroen and Nikkie otherwise. But both alpha male capuchins (i.e. Curmudgeon and later Paul) seemed to adopt a strategy of alternating which subordinate male they supported against the other, and of separating the males whenever they affiliated so that an alliance of subordinates could not form (chapter 3).

In contrast with capuchins, chimpanzees frequently form coalitions against apes higher-ranking than any of the coalition partners, and even the alpha male can be the victim of coalitionary attack without losing his formal rank. Aside from the month of the coup in the capuchin group, the alpha male was never attacked by a coalition of males, and the alpha and beta females were never attacked by a coalition of males or by a coalition of females. Thus, the political landscape for capuchins is much more predictable than that for chimpanzees, and it could be argued that less social intelligence is needed to cope with the social situations that arise on a day-to-day basis. On the other hand, there are fewer windows of opportunity for status-enhancement in capuchin society, due to the inevitability of third-party involvement in serious fights combined with the relative inflexibility of

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coalitionary decision rules, and therefore it may be even more challenging to negotiate a rise in rank than is the case for a chimpanzee.

A striking aspect of chimpanzee politics that implies an advanced degree of social intelligence perhaps lacking in capuchins is third-party reconciliation and conflict mediation. de Waal (1982) reports that previously uninvolved third parties often encourage reconciliation between two opponents by bringing them together and involving them in some sort of positive social interaction. Adult females also mediate conflicts in a nonaggressive way by removing weapons from the hands of displaying males, thus perhaps preventing the conflict from escalating. Reconciliation has not yet been conclusively demonstrated for white-faced capuchins (chapter 6), and the one strong candidate for reconciliatory behavior, the wheeze dance, is more often protested than encouraged by third parties. However, dances are protested by individuals who could suffer a cost if the dancers formed an alliance, so protests of these dances may be an indication of social perceptiveness rather than lack thereof. The only possible indicator of third-party reconciliation that I have observed in capuchins is a few observations of infants gargling towards and climbing on the backs of adult males who have just fought with their mothers. Such behavior seems risky for the infants, since the males have just shown themselves to be in an aggressive frame of mind, but the infants in these observations were not injured by the males. Unfortunately, the number of observations of this nature is too few to permit analysis.

Although capuchin politics appear to be less Machiavellian than chimpanzee politics in some respects, the complexity of capuchin social relationships is still remarkable in comparison to anything that has been reported for other platyrrhine primates. The prevalence of coalitionary aggression and the alpha male's strategy of disrupting rivals' affiliative interactions indicate advanced cognitive ability in the social domain.

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Table 5.1: Precoup hourly rates at which adult females gargled to males.

	Female				
Male	A	S	N	W	T
C	0.16	0.14	0.10	0.05	0.41
P	0	0	0	0	0
G	0	0	0	0	0

Table 5.2: Postcoup hourly rates at which adult females gargled to males.

	Female				
Male	A	S	N	W	T
C	0	0	0	0	0
P	0.06	0.04	0.26	0.01	0.27
G	0	0	0	0	0
I	0	0	0	0	0

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Table 5.3: Hourly rate at which immatures (ranked in order of age from oldest to youngest, left to right) gargled to adult males during the 6 months preceding the coup.

	Immature										
Male	Q	K	H	V	J	M	B	L	R	Y	E
C	.14	0	0	.07	0	.07	.35	0	.28	.07	.85
P	0	0	0	0	0	.07	.07	.07	.14	0	.35
G	0	0	0	0	0	0	0	0	0	0	.29

Table 5.4: Hourly rate at which immatures (ranked in order of age from oldest to youngest, left to right) gargled to adult males during the postcoup phase.

	Immature										
Male	Q	K	H	V	J	M	B	L	R	Y	E
C	.03	0	.05	.03	.03	.13	.05	.33	.44	.23	.88
P	0	0	.02	.65	.28	.33	.75	.38	.50	.18	.48
G	0	0	0	0	.05	.21	0	.03	.11	.05	.21
I	0	.03	.06	0	0	.12	.06	1.40	.20	0	.12

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Table 5.5: Adult males' proximity scores with immatures in the 6 months preceding the coup.

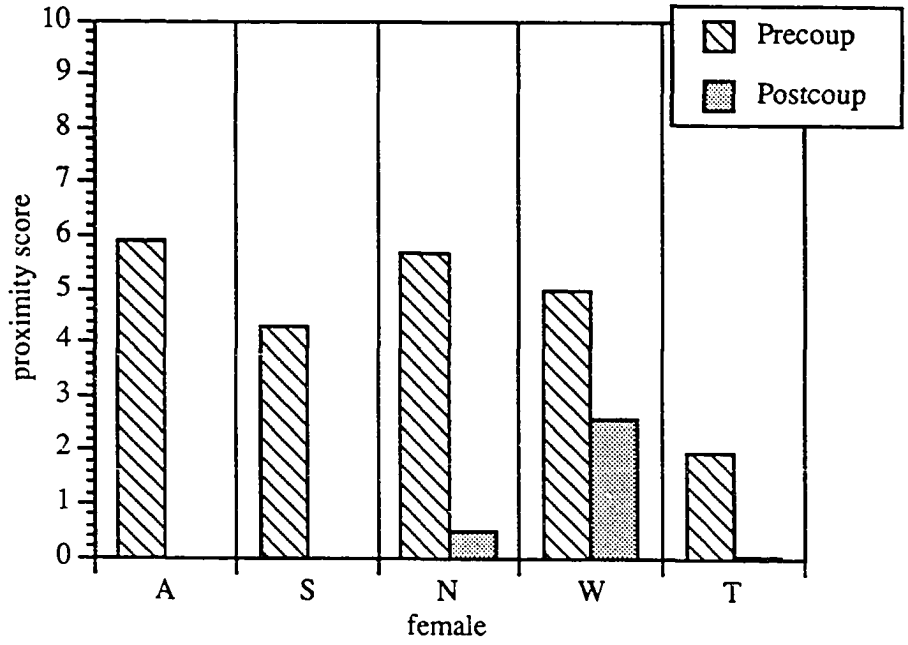
	Immature										
Male	Q	K	H	V	J	M	B	L	R	Y	E
C	2.915	5.646	2.879	2.812	2.819	2.812	2.822	0.021	0.119	0.011	2.812
P	0.011	0.026	0	0.026	0.004	0	0.011	2.838	0.033	0.004	0
G	2.902	0.034	2.883	0	0.069	0	0.023	2.906	5.789	0.004	0

Table 5.6: Adult males' proximity scores with immatures, postcoup.

	Immature										
Male	Q	K	H	V	J	M	B	L	R	Y	E
C	5.162	1.054	5.139	5.138	1.046	1.052	0.009	1.061	2.077	2.064	2.091
P	1.003	0.010	0.055	0.017	0.003	0.015	0.036	4.069	1.069	0.009	0.001
G	9.652	4.317	3.222	0	0.021	0	0.009	1.072	1.082	0.018	0.003
I	2.335	1.174	0.012	0.036	1.171	0.023	0.017	0.023	0.023	0.001	0.012

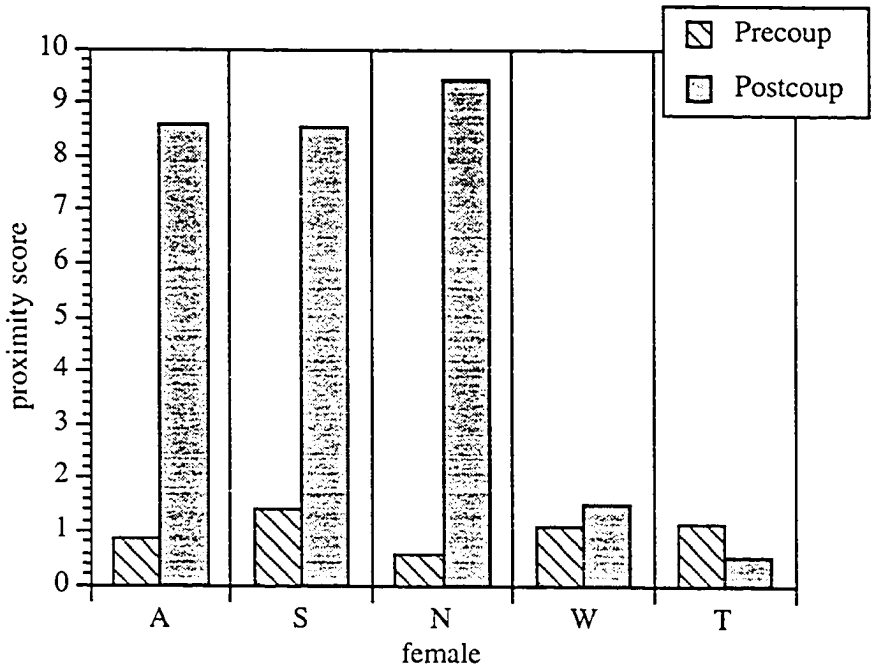
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Figure 5.1: Curmudgeon's proximity scores with adult females



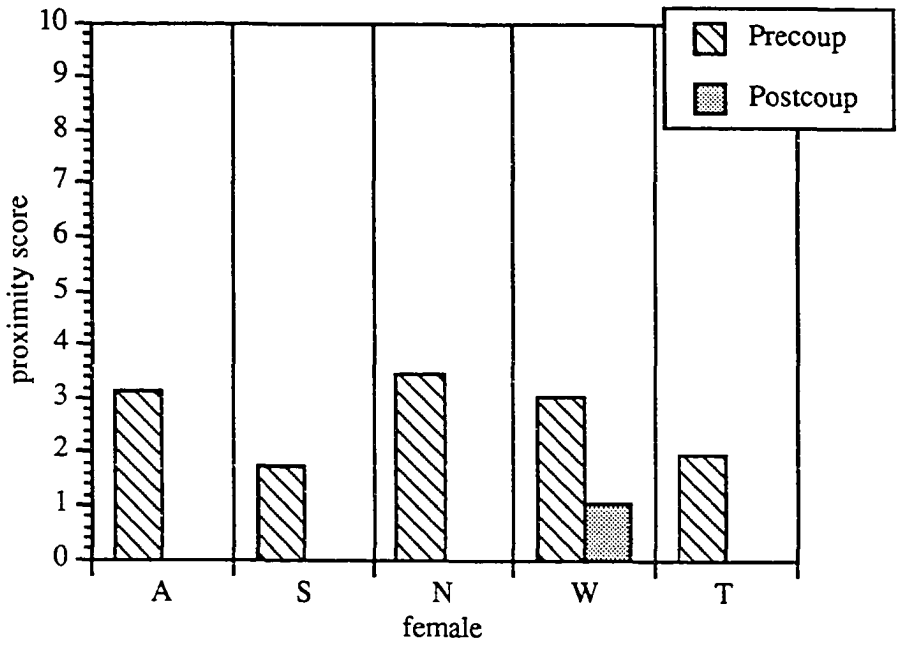
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Figure 5.2: Paul's proximity scores with adult females



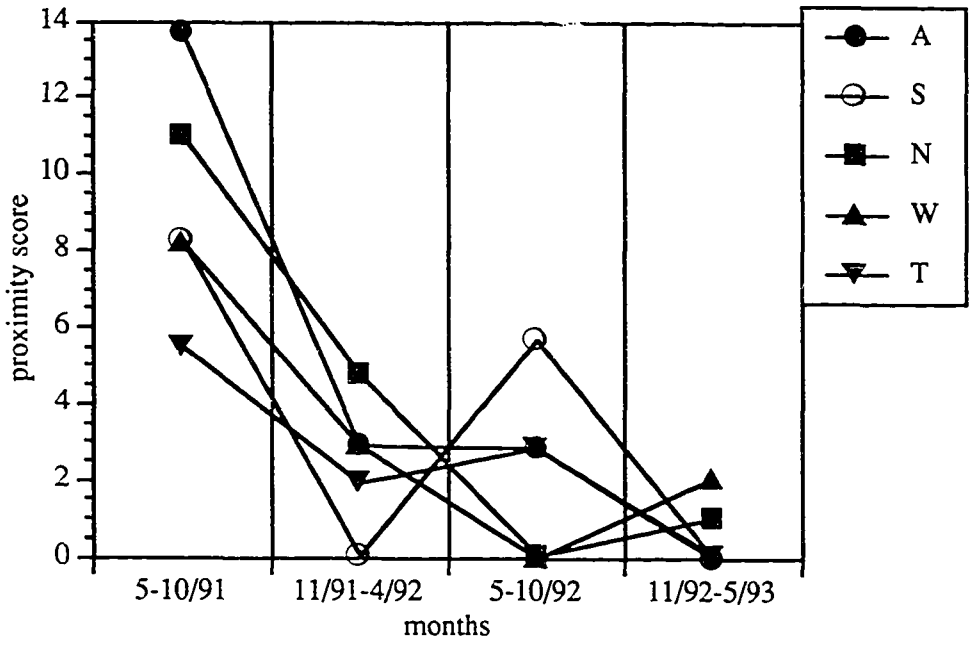
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Figure 5.3: Guapo's proximity scores with adult females



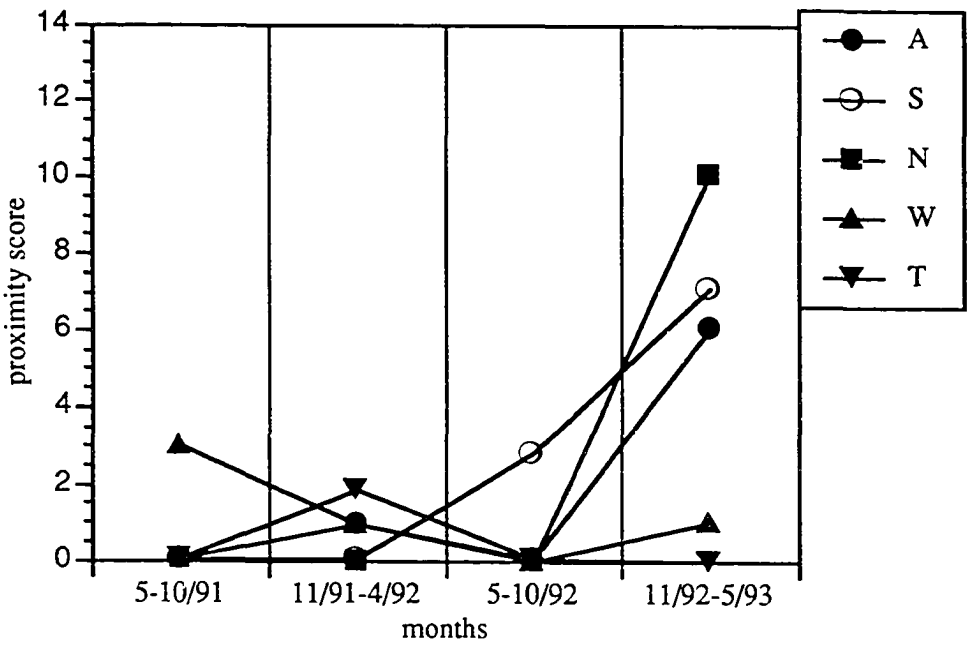
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Figure 5.4: Changes in Curmudgeon-female proximity patterns over time



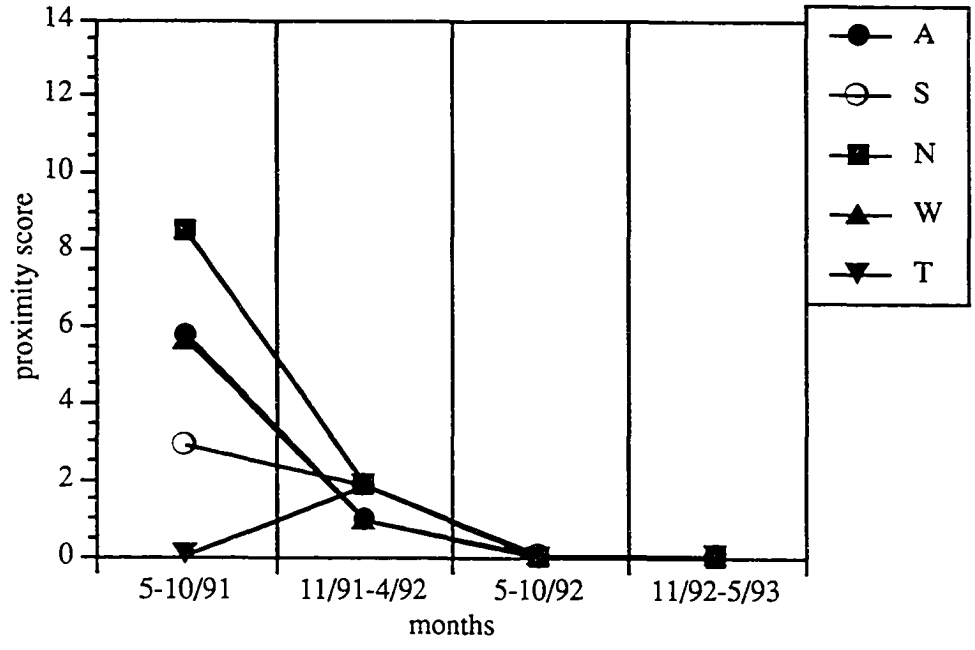
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Figure 5.5: Changes in Paul-female proximity patterns over time



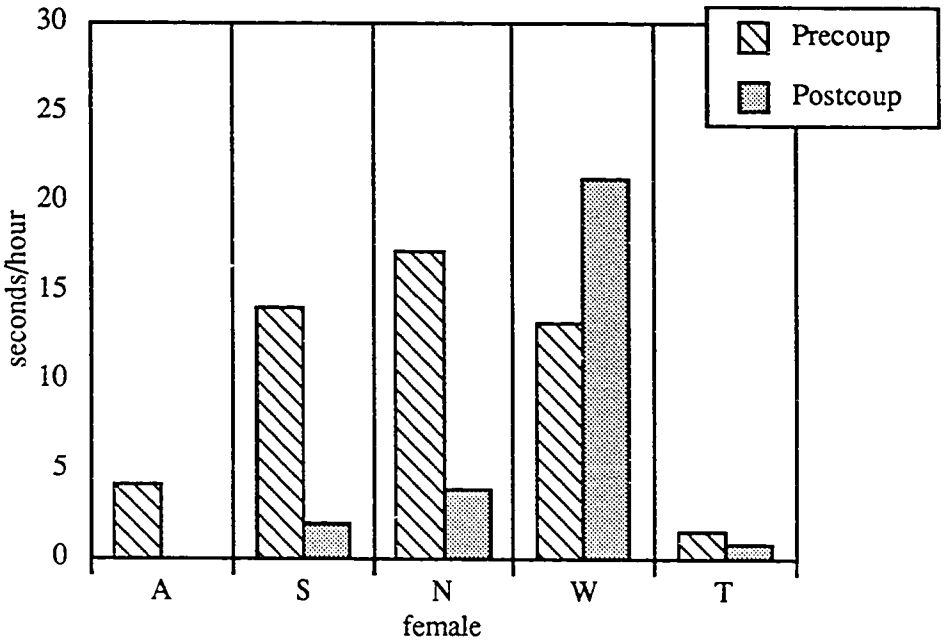
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Figure 5.6: Changes in Guapo-female proximity patterns over time



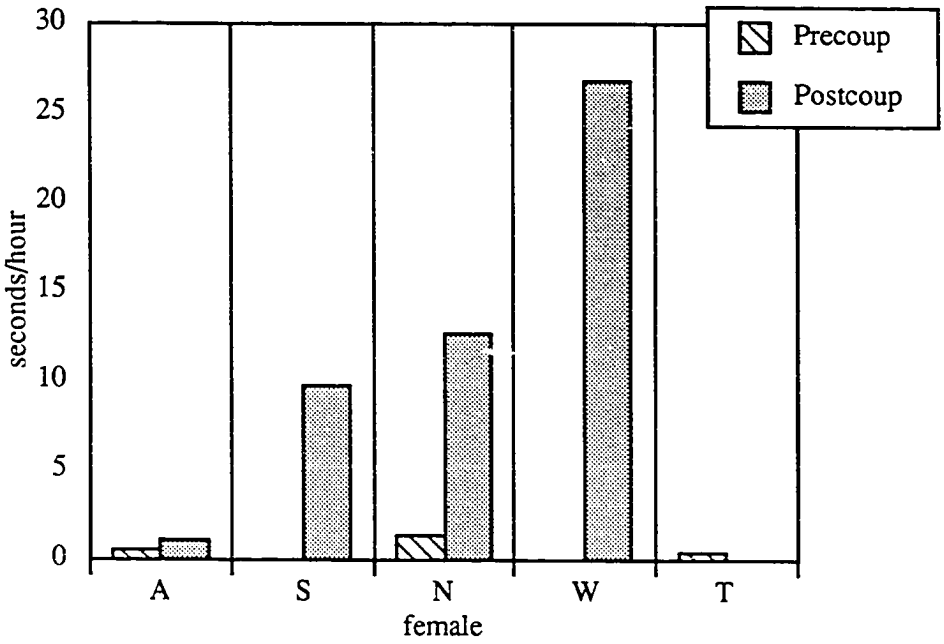
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Figure 5.7: Rate at which adult females groomed Curmudgeon



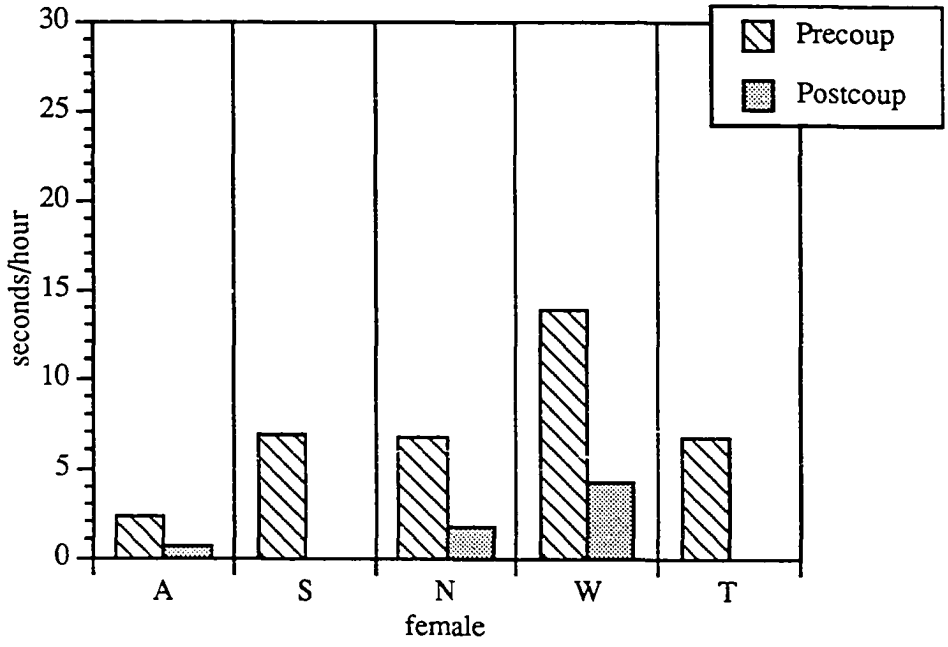
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Figure 5.8: Rate at which adult females groomed Paul



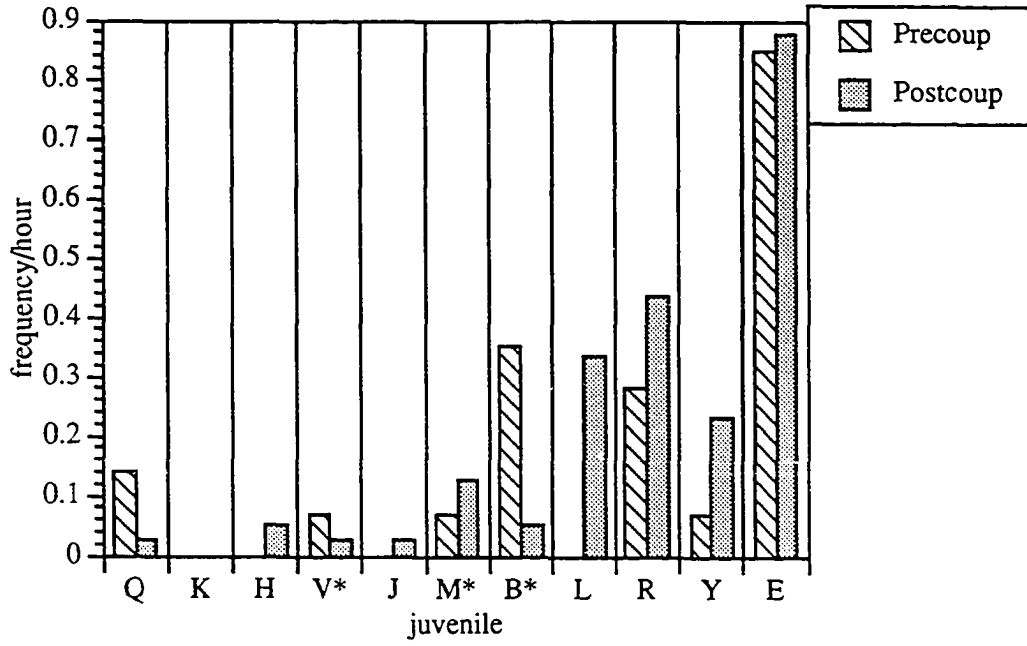
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Figure 5.9: Rate at which adult females groomed Guapo



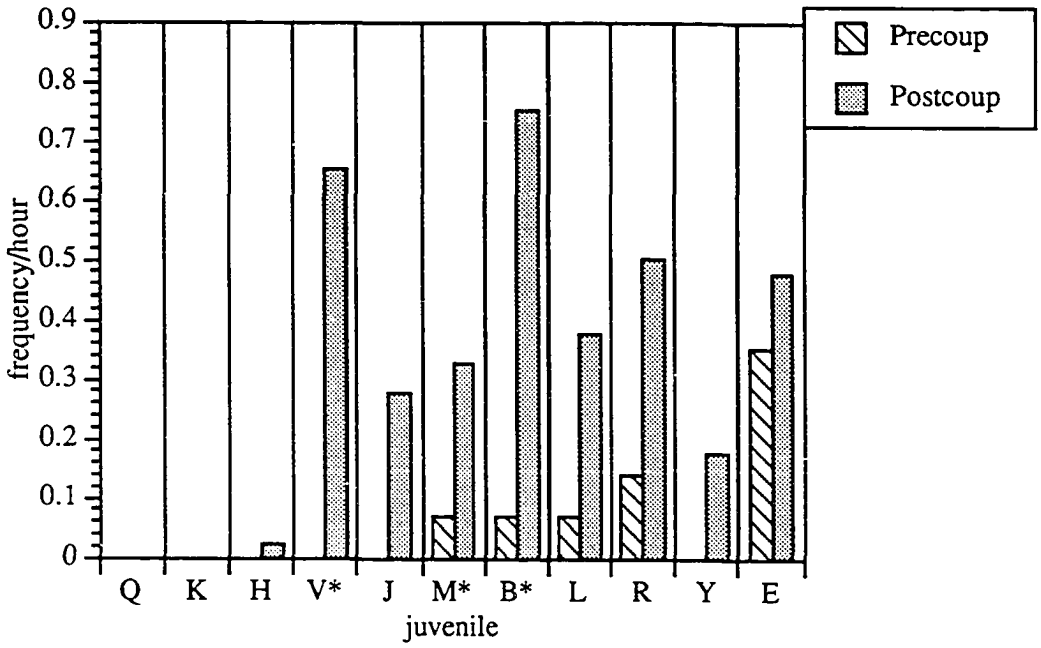
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Figure 5.10: Rates at which juveniles gargled at Curmudgeon



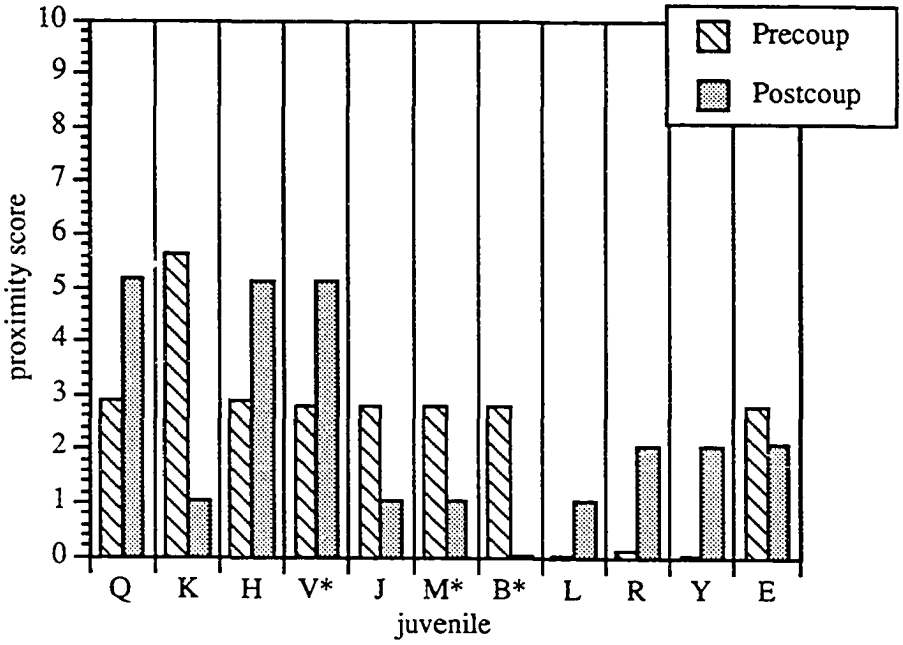
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Figure 5.11: Rates at which juveniles gargled at Paul



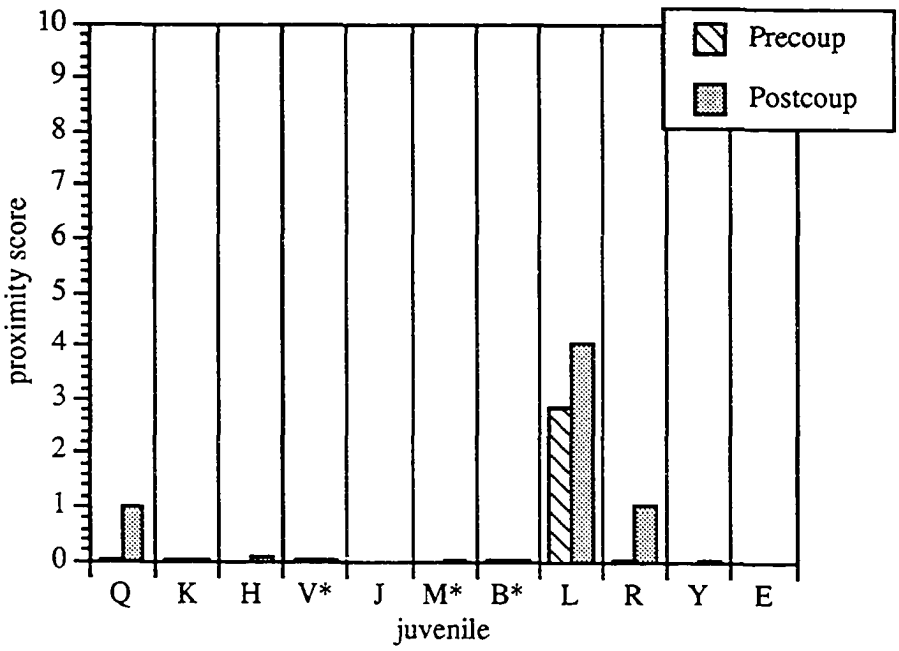
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Figure 5.12: Curmudgeon's proximity scores with juveniles



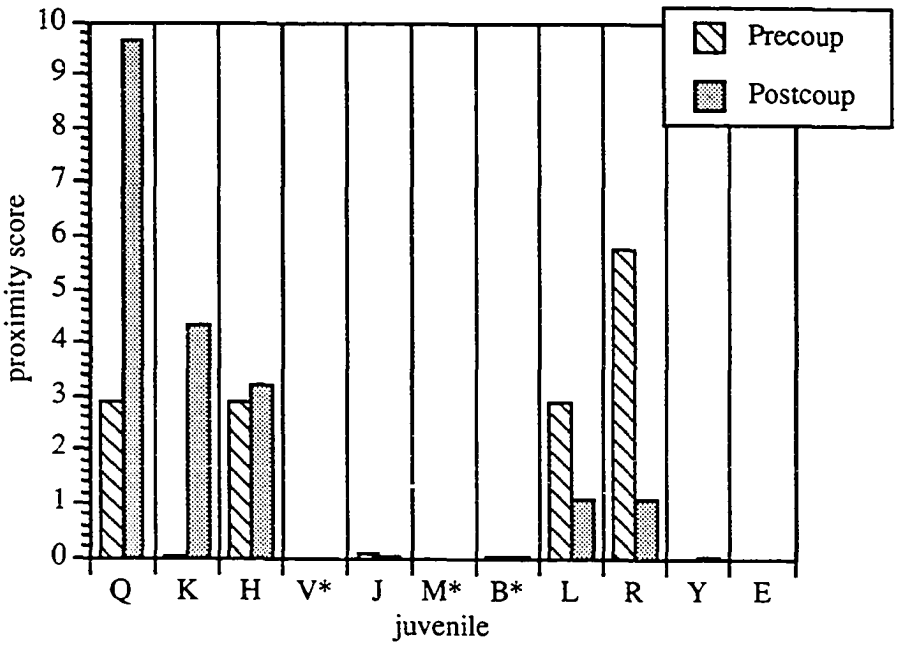
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Figure 5.13: Paul's proximity scores with juveniles



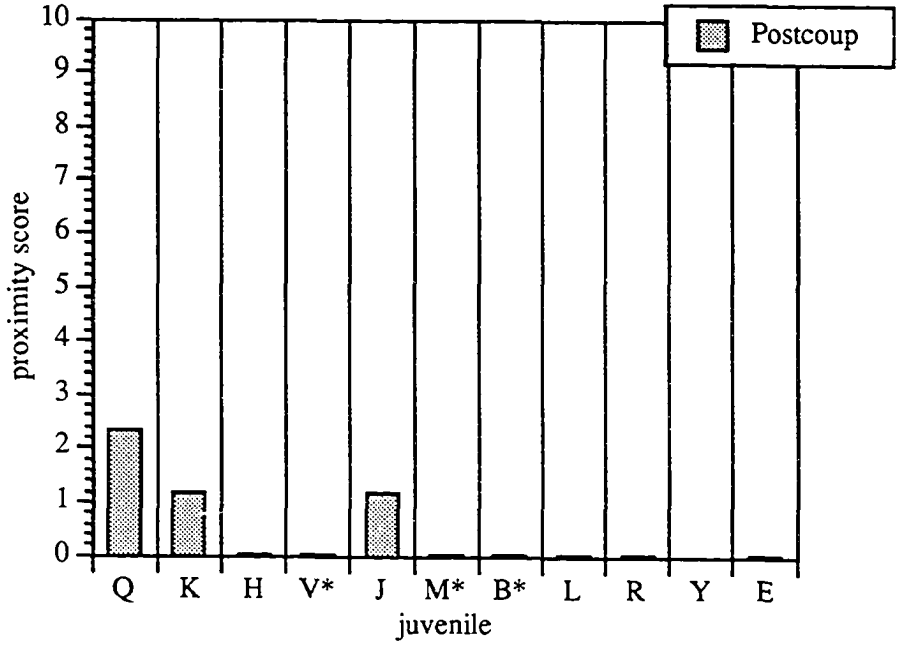
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Figure 5.14: Guapo's proximity scores with juveniles



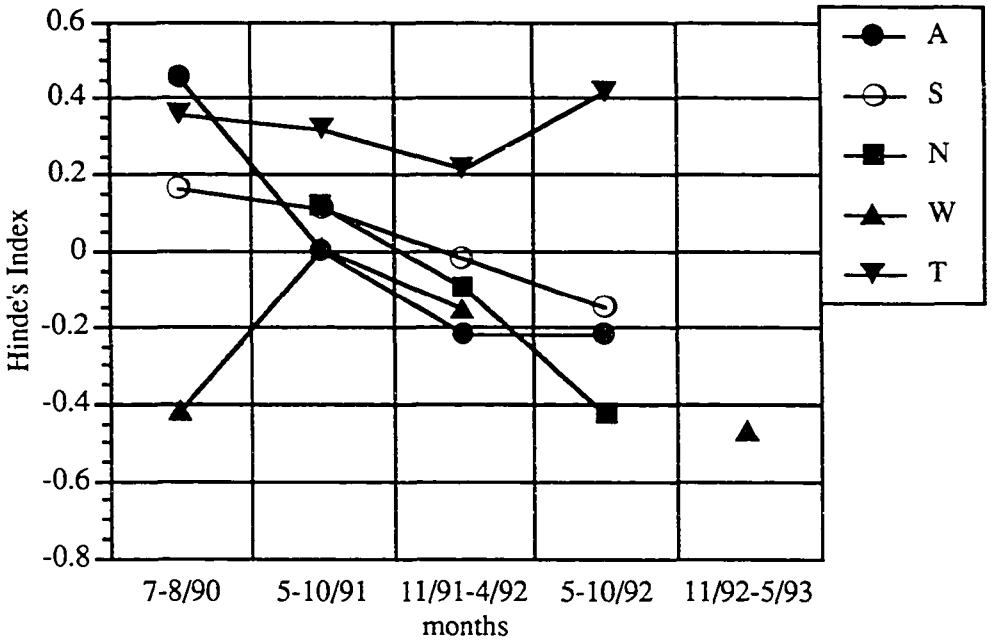
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Figure 5.15: Ichabod's proximity score with juveniles



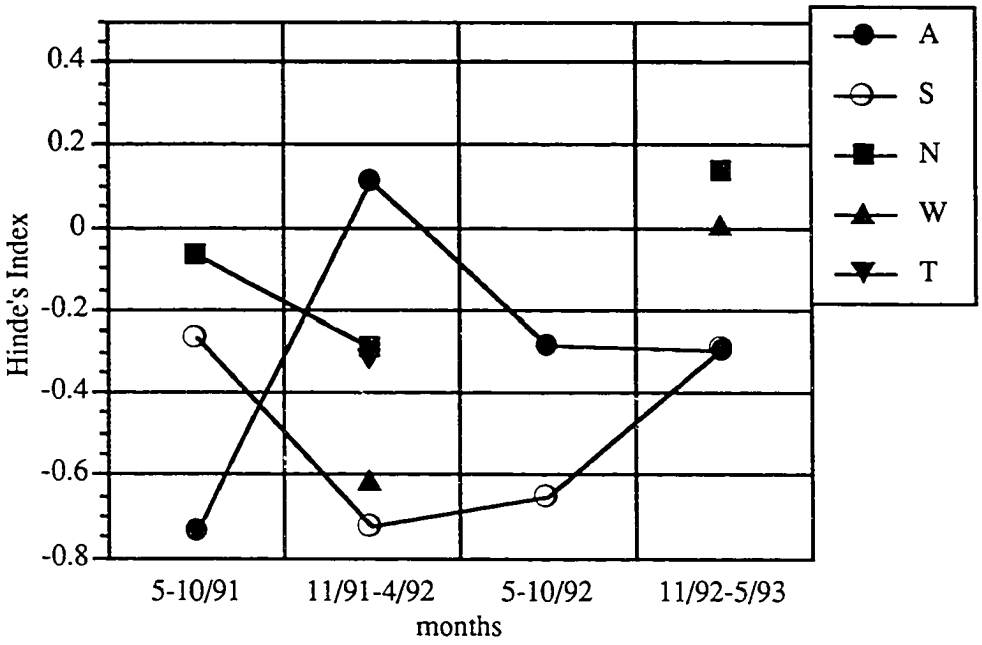
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Figure 5.16: Changes in adult females' proximity maintenance to Curmudgeon over time



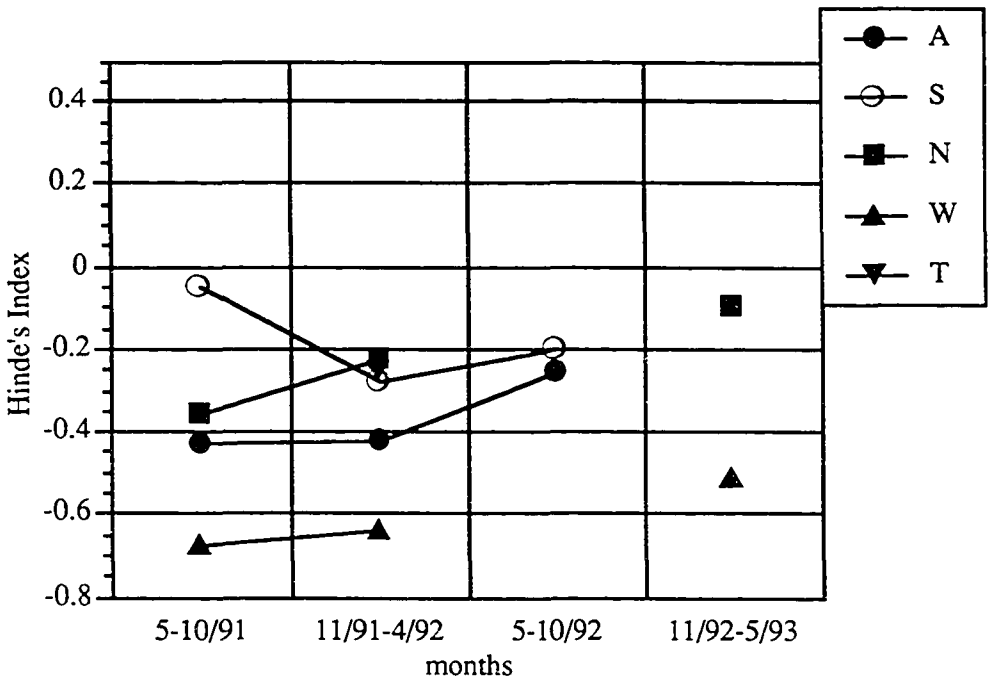
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Figure 5.17: Changes in adult females' proximity maintenance to Paul over time



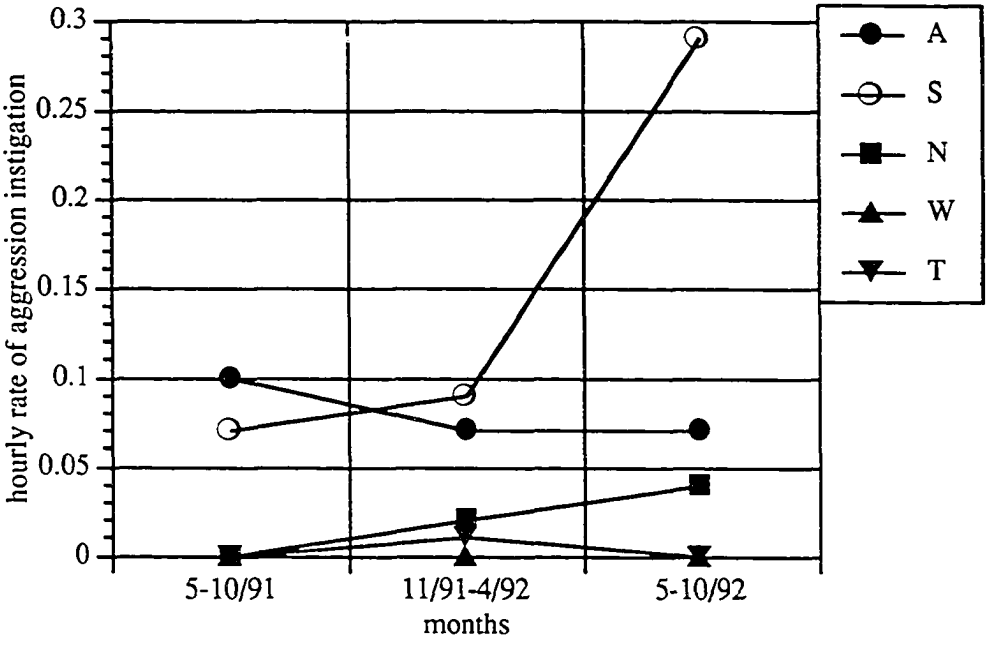
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Figure 5.18: Changes in adult females' proximity maintenance to Guapo over time



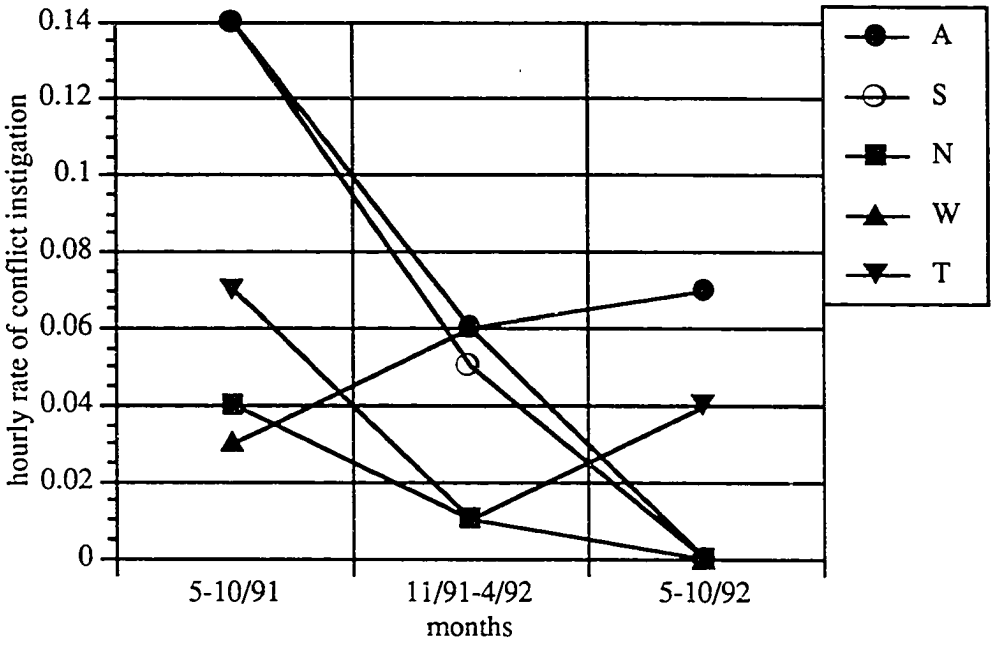
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Figure 5.19: Changes in rates at which adult females instigated conflicts with Curmudgeon over time prior to the coup



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Figure 5.20: Changes in rates at which Curmudgeon initiated aggression against each female during the precoup period



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CHAPTER VI

POSTCONFLICT BEHAVIOR AND RELATIONSHIP NEGOTIATION

Introduction

Numerous studies of postconflict behavior in nonhuman primates have reported increased frequencies of affiliative behaviors between the opponents following fights. Such behaviors have been termed "reconciliation" because of their presumed function in restoring relationships damaged by conflict (de Waal 1989). Reconciliation has been reported in rhesus macaques (de Waal and Yoshihara 1983, de Waal and Ren 1988), stumptail macaques (de Waal and Ren 1988), long-tailed macaques (Aureli et al. 1989; Cords 1988, 1992, Cords and Thurnheer 1993; Aureli and van Schaik 1991a,b; Cords and Aureli 1993; Cords 1993; Aureli 1992), pig-tailed macaques (Judge 1991), Barbary macaques (Aureli et al. 1994), Japanese macaques (Aureli et al. 1993), patas monkeys (York and Rowell 1988), vervets (Cheney and Seyfarth 1989), redfronted lemurs (Kappeler 1992), golden monkeys (Ren et al. 1991), mountain gorillas (for male-female dyads only: Watts 1995a) and chimpanzees (de Waal and Roosmalen 1979; de Waal 1986, 1987). The one primate study that has failed to find reconciliation is Kappeler's (1992) study of ring-tailed lemurs. In all of the above studies, reconciliation typically occurs within a few minutes after the conflict.

Redirected aggression -- i.e. a case in which the victim of an attack responds by attacking a previously uninvolved third party -- is another commonly reported response to conflict among primates (Walters and Seyfarth 1987; Aureli and van Schaik 1991; Cheney and Seyfarth 1989; Judge 1991; Aureli et al. 1992; Watts 1995b). Redirected aggression by the victim is often directed at kin of the original aggressor. Because such aggression

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potentially reduces the original aggressor's inclusive fitness, it has been hypothesized to provide an incentive to reduce the future probability of repeated attack by the original aggressor (Kappeler and van Schaik 1992; Aureli et al. 1992; Clutton-Brock and Parker 1995). Alternatively, in societies such as white-faced capuchins, hyenas (Zabel et al. 1992), and Japanese macaques (Machida 1990) in which large coalitions typically support the higher-ranking of two opponents, redirected aggression could merely serve to distract the hostilities of other group members toward a lower-ranking scapegoat.

In this chapter, I investigate some mechanisms by which capuchins may negotiate the status of their relationships and/or reduce tension following fights and other stressful circumstances. Because of their complex, long-term social relationships and strong dependence on coalitionary support (chapters 2-5), it seems likely that capuchins would reconcile following fights. The first portion of the results is devoted to testing whether white-faced capuchins reconcile or redirect aggression immediately following fights, using the standard post-conflict/matched control methodology used by most other reconciliation researchers (de Waal and Yoshihara 1983; Kappeler and van Schaik 1992; Veenema et al. 1994).

Some dramatic and stereotyped primate behaviors, such as olive baboon "diddling" (Smuts and Watanabe 1990), stumptail macaque "hold-bottom rituals" (de Waal and Ren 1988) and bonobo "G-G rubbing," (de Waal 1987) do not fall neatly into the category of relaxed affiliative behavior because of the high degree of tension apparent in the interactants; nor do they qualify as aggression. Rather, they appear to serve to reduce tension and/or negotiate the status of the social relationship. The second portion of the results is devoted to examination of a single behavior, the wheeze dance, that appears at face value to be a likely candidate for a relationship-negotiation or tension-reducing behavior, due to its ritualized appearance and the contexts in which it usually occurs. The wheeze dance (described below) may serve a reconciliatory function, although it tends to occur long after the dyad's previous interaction rather than immediately following fights. It

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is virtually impossible to demonstrate that two behaviors separated by large amounts of time are related to one another, particularly in an observational study such as mine; therefore I am unable to rigorously test whether wheeze dances are a way of reconciling after fights. However, some testable predictions can be derived from the more general hypothesis that wheeze dances serve to reduce tension and negotiate relationships:

(1) Those dyads that can inflict the highest costs on one another and/or confer the greatest benefits on one another will be most concerned with maintaining good relationships with one another and will therefore exhibit the highest rates of wheeze dancing.

(2) The rate of wheeze dancing in the group overall will be greatest during periods of high social tension, such as the disruption caused by rank reversals, immigrations, or presence of estrous females.

(3) Of those monkeys who have spent several hours or more separated from the group, wheeze dances will be more common in reunions of dyads whose last social interaction prior to separation was a fight than in dyads whose most recently observed social interaction was non-agonistic.

(4) If alliance formation is beneficial to the members of the alliance in terms of priority of access to resources, the formation of a new alliance almost certainly results in increased costs to some other group members who are not members of the new alliance. Therefore, if wheeze dances serve to negotiate relationships and reduce tension, it is to be expected that certain group members will disrupt the wheeze dances of those dyads that could inflict costs on the disrupter by forming alliances.

Methods

The data for the analyses pertinent to reconciliation and redirected aggression derive from 30-minute postconflict and matched control focal follows. The postconflict/matched control protocol for studying reconciliation was first introduced by de Waal and Yoshihara

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(1983) and has been used by most reconciliation researchers (see Kappeler and van Schaik 1992 for a review). Following fights that were severe enough to elicit a scream from the victim, I followed one of the opponents (usually the victim) for 30 minutes and recorded all of its social interactions. At 2.5-minute intervals, I also recorded its activity and proximity to all other group members in view. On the next observation day, I did a 30-minute matched control follow of the same individual at the same time of day, plus or minus one hour. The follow was postponed a day if the opponents had been involved in a fight during the previous hour. The matched control follow was discarded and redone on the following day if the opponents were not in view of one another for at least part of the matched control follow. The data set consists of 70 postconflict and matched control paired samples, from 53 different dyads. Commonly, when there was a fight, other monkeys joined in the attack. In these instances, I assigned one monkey as the primary opponent for the purpose of analysis. The primary opponent was the monkey most aggressively attacking the victim; in cases where the level of aggression appeared similar for more than one attacker, the first monkey to initiate the attack was designated as the primary opponent. Generally the initial attacker was also the most aggressive attacker. The following behaviors were classified as affiliative behaviors: approaches to within one body length, hugging, two affiliative vocalizations (the twitter and the gargle), grooming, playing, coalitionary behaviors, and dancing.

White-faced capuchin monkeys often disperse widely while foraging. Therefore, the rates of social interaction were probably lower than they would be in captivity, where most reconciliation studies have been performed. I was limited in my options for statistical tests because of the large number of postconflict/matched control pairs in which no affiliative interaction occurred between the opponents, in either the postconflict or control 30-minute sample. Thirty-six of the 70 postconflict/control pairs engaged in no affiliative interactions in either sample, and only 7 of the 70 pairs had affiliative interaction in both of the two samples. Because most observation intervals were censored with respect to the

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event of interest (that is, they ended before the first affiliative interaction), the Wilcoxon and Kolmogorov-Smirnov tests used by most reconciliation researchers to determine whether reconciliation had occurred were inappropriate to my sample. Instead, I used survival analysis (Allison 1984) to compare the curves of proportion of pairs reconciled for postconflict vs. control situations. Survival analysis incorporates data from censored intervals to produce and compare survivorship functions. A Cox's F test was used to compare the postconflict and matched control survivorship curves.

The same methods used to investigate reconciliation were used to examine redirected aggression. The sample size was reduced to 47 postconflict/matched control pairs because some of the follows for the reconciliation analysis, in which only interactions between the two opponents were relevant, were of the attacker rather than of the victim. To determine whether redirected aggression occurred, I needed both the postconflict and the control follows to be of the victim. Of the postconflict samples, 43% were uncensored, and 30% of control samples were uncensored. Only 7 pairs had aggressive interactions by the victim in both the postconflict and the control follows.

Analyses pertinent to the social function of wheeze dances were based on a different data set. Because wheeze dances are rare behaviors (only 28 occurred during 968 hours of focal observations of adults), I combined observations from 10-minute focal samples, 30-minute postconflict/matched control follows, and ad lib data. I could not identify the participants for all dances occurring during ad lib observations; nor could I be certain that I observed all relevant social interactions preceding and following dances in the ad lib data. The analysis of wheeze dance rate over time includes all wheeze dances, including those for which I could not identify participants. Other analyses were restricted to those dances for which both participants were known. Analyses of reunion behavior following a participant's absence from the group included those absences during which (a) an observer was with the absent monkey and could radio to the other observer to confirm that it was

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alone and not with the group, and/or (b) a monkey was not observed during data collection for more than half a day (7 hours).

Behavioral Definitions

The wheeze dance incorporates many behavioral elements used in courtship (see chapter 4 for descriptions of precopulatory behavior), but the vocalizations are different from those used in courtship. Wheeze dances last from approximately 3 seconds to 20 minutes. During a dance, the two participants pace toward and away from one another with deliberate, somewhat exaggerated motions, maintaining eye contact. When they change directions while pacing, the two monkeys pause to twist and contort their bodies, sometimes flailing their limbs and virtually doing back flips. The two monkeys give the impression that they are both attracted and repelled by one another as they alternately approach and leave one another. In contrast to the courtship dance, the duck face is typically not exhibited during the wheeze dance, possibly because monkeys can not wheeze while making duck faces.

Four vocalizations are produced, in varying combinations, during dances in an intragroup context: the wheeze, the intense gargle, the grunt, and the sex squeak. The wheeze is probably the highest-pitched vocalization in the vocal repertoire. It sounds like a cross between a whistle and a twitter: it is as if the pitch and volume of a twitter were increased, and the syllables were run together so that the sound was almost smooth rather than staccato. The wheeze dance, by definition, is always accompanied by a wheeze, but it often includes intense gargles or grunts as well. Grunts and/or sex squeaks are the types of vocalizations produced in precopulatory dances, but they are also produced in some dances that do not end in copulation. Sex squeaks and wheezes are never produced in the same dance. Intense gargles can be produced as the only vocalization during a dance, or in combination with wheezes or grunts. Intense gargles are typically exchanged in rapid,

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rhythmic succession. Wheezes are sometimes produced by infants who are riding on the backs of adult males, particularly if the males are running and leaping.

A dance generally ends in one of three ways: (1) Some dances end abruptly with both monkeys leaving the vicinity. (2) Others end in a sexual interaction. The two monkeys involved (usually males) may take turns mounting and thrusting on one another in the same positions used by heterosexual mating pairs. The "mating" pair usually makes duck faces. Sometimes the one who just mounted will present to be mounted, but in other cases, the one who was just mounted will squirm out from under its partner and "insist" on a turn at mounting by grasping the hips of the former mounter and forcing him into position. The partners can change roles several times. (3) Most wheeze dances are interrupted by third parties before the dancing dyad has a chance to finish. Because the wheeze is one of the loudest vocalizations in the repertoire, wheeze dances can not escape the notice of other group members even when the dancing pair is a few hundred meters from the group. Typically one or more monkeys runs over to the dancing pair, doing intense vocal threats, and then one of the dancers threatens the other dancer.

A consortship, for the purposes of this chapter, was defined as a disappearance from the group of a female in the company of one or more males. It is difficult to be certain that a female is in estrus (see chapter 4); however, it is highly likely that these missing pairs were in consort because (a) the females were seen exhibiting proceptive behaviors at other times during that week, and (b) females typically spend so little time with adult males on the periphery of the group that it is highly unlikely that an adult male and an adult female would coincidentally become lost at the same time. In those cases in which the consort pair was located away from the group, observers were able to confirm that the female was behaving proceptively toward the male.

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Results

Do White-faced Capuchins Reconcile?

Figure 6.1 shows the Kaplan-Meier estimate of the survivorship function for the postconflict and matched control curves, based on 41 affiliative interactions observed in 70 pairs. Note that the curve was steepest during the first 2 minutes of the sample. Although the first affiliative event tends to occur earlier in the postconflict sample than in the control sample, the difference is not significant (p=.085). Thus, reconciliation could be occurring, but at low rates.

Next, I examined the data to see whether these few early affiliative interactions could be functioning as reconciliations. To do this, I looked at the events following the first affiliative interaction. Of the 23 cases in which there was an affiliative interaction during the postconflict follow, 13 cases were followed by renewed attacks by the aggressor within the following 2 minutes. Obviously, these affiliative interactions did not succeed in reconciling the opponents. In the other 10 cases, no further aggressive interaction was observed between the opponents; nor were the victims observed to engage in displacement behaviors such as tail chewing which indicate anxiety. I grouped the 23 cases of post-conflict affiliation into two groups: successful and unsuccessful. Successful affiliative interactions could potentially have accomplished reconciliation (i.e. they were not followed by renewed aggression), whereas unsuccessful affiliative interactions definitely did not accomplish reconciliation (i.e. they were followed by renewed aggression). The unsuccessful behaviors occurred on average 2.6 minutes following a conflict (SE=.79 min.), whereas the successful behaviors occurred on average 10.1 minutes after the conflict (SE= 2.6 minutes). The difference in timing of successful versus unsuccessful affiliative behaviors was significant (Mann-Whitney U test: U=19.5, p=.004).

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Redirected Aggression

Figure 6.2 shows the Kaplan-Meier estimate of the survivorship function for the postconflict and matched control curves, with "death" corresponding to the first aggressive behavior directed by the victim toward an individual other than the original opponent. As in the reconciliation analysis, the curve was steepest during the first 2 minutes of the sample. There was a tendency for the victim to direct aggression earlier in the postconflict than in the matched control samples, but the difference was not significant (p=.08). The objects of redirected aggression in this sample were human observers, monkeys subordinate to the victim of the original conflict, a recent immigrant male, and a large garrobo lizard. Although the immigrant male was higher-ranking than most group members, all group members with the exception of the alpha male regularly participated in attacks on this male (chapters 3,4). In observations not included in this analysis, monkeys frequently redirected aggression at other species of animals, and when there was no obvious target available, the victim would sometimes redirect aggression at an imaginary target and recruit the opponent's aid in threatening a bare patch of ground.

Not all attempts to redirect aggression were successful; that is, the victim was not always able to divert its attackers' attention from itself to a new victim. Eleven of the 19 attempts to redirect aggression were followed by renewed attacks on the original victim by either the opponent or another group member. With 2 exceptions, these attacks occurred within 2 minutes of the attempt to redirect aggression . In 7 of 19 cases, the original victim succeeded in obtaining some coalitionary support against the redirect victim, but this support was not always from the original opponent. In one of the 7 cases, the original opponent helped the original victim threaten a third party, but soon after resumed aggression against the original victim.

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Dominance Rank and Wheeze Dance Rate

When dominance rank is used as an estimate of an individuals' ability to confer benefits and impose costs on other individuals, the first prediction (i.e. that those dyads that can inflict the highest costs on one another and/or confer the greatest benefits on one another will be most concerned with maintaining good relationships with one another and will therefore exhibit the highest rates of wheeze dancing) is upheld (n=45 dyads, Kendall tau=-.62; $p<<.0001$). Table 6.1 shows the number of wheeze dances (n=152, including some triple dances) observed for each adult dyad. Individuals are listed from left to right in order of postcoup dominance rank, with the highest-ranking monkeys at the left. Figure 6.3 plots the number of wheeze dances for each dyad, according to the dyad's mean dominance rank. The relative dominance ranks of Guapo and Ichabod were ambiguous; however, switching their ranks did not affect the results.

Wheeze Dance Rate over Time, as a Function of Social Tension

As predicted, wheeze dances were more frequent during periods of social tension. Figure 6.4 shows the hourly rate of wheeze dances (i.e. number of wheeze dances heard in a day, divided by number of observation hours that day) plotted over time for the latter portion of the study, October 1992-May 1993. The data from May 1991 until October 1992 are not presented graphically because values for all but 3 observation days were zero; the remaining 3 days, 11/26/91, 3/1/92, and 3/23/92, had one wheeze dance each. The two events that appear to have had the greatest impact on wheeze dance rate are: (a) the male rank-reversal that occurred during the first week of November (see chapters 3,5), and (b) the immigration of Ichabod, a young adult male, on November 28. Because these two events occurred within 3 weeks of one another, it is difficult to assess the relative impacts of the two events. The presence of estrous females was much more common following the coup, since the coup (perhaps not coincidentally) coincided with the return to cycling of many females, four of whom conceived in the 4 months following the coup. Only one

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conception occurred during the study before the coup, in October 1991. At least one female exhibited some type of proceptive behavior on most days during the period from October 27, 1992 - February 23, 1993, whereas virtually no female proceptive behavior was observed prior to October 27, 1992. Following is a time line outlining major fights, demographic changes, and putative conception days. The events in this time line, when superimposed on figure 6.4, appear to explain most of the increases in wheeze dance rate.

October 27, 1992: Wiggy comes into estrus and courts Curmudgeon intensively; Curmudgeon and Guapo wheeze dance.

October 28, 1992: Diablita, Abby and Wiggy are all seen to exhibit proceptive behaviors. Abby and Squint launch a vicious attack on Curmudgeon; this fight is more severe than any observed up to this date.

November 10, 1992: Curmudgeon is discovered alone and wounded; therefore the coup occurred sometime during the previous 12 days. Paul and Curmudgeon were severely wounded during the coup, and Squint, Abby and Wiggy received more minor wounds (chapter 5).

November 11,1992: Paul seeks out Curmudgeon for a wheeze dance.

November 12, 1992: Curmudgeon attempts to rejoin the group and is chased away.

November 13, 1992: Guapo leaves the group.

November 14-16, 1992: Curmudgeon makes brief visits to the group, but Paul is essentially the only adult male member of the group.

November 17-18, 1992: Curmudgeon and Wiggy are away on a consortship.

November 19-20, 1992: Curmudgeon is a peripheral member of the group but is missing when observations are renewed on November 27 following a 3-day gap in observations.

November 27, 1992: Abby's putative conception date.

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November 28, 1992: Curmudgeon and Guapo return to the group, and Ichabod immigrates. All adult male dyads with the exception of Paul and Ichabod wheeze dance, most of them several times.

December 3-5, 1992: Guapo is severely wounded by one or more males and returns to the group 2 days later.

December 24, 1992: Squint and Paul are in consort all day, and Curmudgeon follows them.

January 11, 1993: Squint is in estrus, and Abby appears to be having a postconception estrus period.

January 18, 1993: Wiggy's putative conception date.

January 23, 1993: Guapo is severely wounded by Paul and returns to the group the following day.

January 25, 1993: Diablita's putative conception date.

February 23, 1993: Nanny's putative conception date; she vigorously courted Paul on both this and the previous day.

March 13-14, 1993: Paul and Nanny spent most of both days in consort away from the group; Ichabod and Quizzler accompanied them much of the time. Curmudgeon assumed the role of alpha male during this time (chapter 3). There were dramatic reunions whenever the 2 subgroups reunited.

During the study, the wheeze dance rate never dropped back down to the baseline rate of virtually zero that was observed prior to the coup. During a census trip in February-March, 1994, the rate of wheezing had fallen to .08 wheezes/hour, which was slightly above the baseline rate for 1991, but way below the rate observed during the 6 months following the coup (figure 6.4).

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Reunions as a Function of the Conditions of Separation

I examined 23 instances in which one or more adult monkey was separated from the group for a long period of time, either singly or as part of a consort pair, to see how the circumstances of the separation affected the behaviors of the monkeys upon being reunited. If wheeze dances serve to reduce tension, it might be expected that males would wheeze dance more often following separations preceded by fights than after separations in which the monkey simply became lost while foraging for insects. Also, members of the main group might be expected to wheeze dance more with returning consort pairs than with single monkeys, due to sexual rivalry between males. Males were separated from the main group 35 times, and females 11 times. Nine of the eleven cases in which females were separated from the group were consortships with an adult male; in three of these instances, an additional adult male and/or a juvenile male accompanied the estrous female as well. Fights did not precede any of the females' separations from the group. Of the 35 male separations observed, 9 were preceded by fights, 12 were consortships, one was preceded by a wheeze dance, and 13 disappearances were due to unknown circumstances: 11 of these cases appeared to be instances in which the monkey became accidentally separated from the group while foraging, whereas in the other 2 instances, the monkey disappeared on a day when no observers were present.

Separations following Fights

Of the 9 separations preceded by fights, 3 involved Curmudgeon and 6 involved Guapo. Curmudgeon's 3 separations all occurred during the first week of observations following the coup. One separation was followed by a wheeze dance with Paul, and another was not accompanied by any striking reunion behaviors. In the third case, juveniles and infants were gargling and touching Curmudgeon, and Paul, with the aid of Abby and Squint and 3 immatures, chased Curmudgeon out of the group.

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In four cases, Guapo was involved in mild aggression (mainly threats and/or chases by coalitions) at the time he was last seen with the group. In one case, he returned during an intergroup encounter; although I did not see any dramatic reunion behaviors with the males in his own group, I could have overlooked something in the chaos of the intergroup aggression. In the other three cases, Guapo was involved in wheeze dances upon his return. The first time, in the separation immediately following the coup, Curmudgeon and Guapo wheeze danced, and Paul threatened Guapo. The second time, following a fight between Diablita and Guapo in which Paul supported Diablita, Paul and Guapo wheeze danced upon Guapo's return. Juvenile male Hobbes cuddled with Guapo and did an overlord with Guapo against the observers, and Curmudgeon threatened Guapo vocally. The details of the third reunion were difficult to discern, since it occurred at dawn when the light was dim. However, there were numerous wheeze dances and threats. Guapo was confirmed to wheeze dance with Curmudgeon, and he danced and gargled with juvenile male Kola as well. Paul and Tattle threatened Guapo.

On December 3, 1992, Guapo received a severe tail wound during a fight involving Quizzler, Curmudgeon, and Paul; it is not certain which of the males inflicted the wound. Guapo suffered severe blood loss and disappeared for two days. His last interaction with a group member before leaving was to dance and gargle with Ichabod. Upon returning to the group, Guapo was threatened by a coalition of Curmudgeon and Paul, and then Curmudgeon wheeze danced with Paul. Paul initiated a coalition with Guapo against the observers soon afterwards. On January 23, 1993 at 10:44, Paul, with the aid of Abby, Squint and Diablita, severely wounded Guapo, who fled from the group. Paul also received wounds from Guapo. Guapo returned the following day just before sundown. Immediately, Ichabod and Guapo rushed toward one another, gargling, and began to wheeze dance. Paul rushed toward the dancing pair as Guapo attempted to mount Ichabod. Ichabod squealed and then mounted Guapo; both of them gargled throughout the sexual interaction. When they broke contact, Ichabod threatened Guapo and left the area. Some

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juveniles followed Guapo. Paul threatened Guapo, as yearling male Lizano rode on Guapo's back, and Guapo fled. Curmudgeon aided Paul in threatening Guapo, and Curmudgeon headflagged to Paul. Lizano jumped off of Guapo's back and also threatened Guapo. Curmudgeon attempted to mount Guapo, who screamed and leaped away. Curmudgeon and several juveniles threatened Guapo, and Quizzler did an overlord over Paul against Guapo. Quizzler mounted and thrust on Guapo, while a juvenile threatened them. Then Curmudgeon mounted and thrust on Guapo, and they did a mobile mount accompanied by sex squeaks. Meanwhile, the rest of the group left the area. Curmudgeon headflagged to Guapo, and they both threatened toward a fight in the distance.

Thus, in 6 of 9 reunions following separations preceded by fights, the returning male wheeze danced with at least one monkey. The primary aggressor in the fights could not always be determined, but in at least 3 cases, the dance partner was not the same individual with whom he fought previously.

Separations Due to Unknown Circumstances

In 15 cases, no fights were observed prior to the monkey's disappearance, and the monkey is assumed to have become separated from the group while foraging for insects. However, it is possible that some fights were not observed. In two cases, the missing adult was a female. In these cases, no wheeze dances occurred upon the missing monkey's return, but the female immediately formed coalitions with high-ranking adult females upon her return. When Tattle was found by Abby, their first interaction was to jointly threaten the observer. When Diablita rejoined the group, she threatened and/or lunged at Ichabod, an infant, and an unidentified monkey. Then she overlorded with Squint against Paul, who had just ignored Diablita's headflag as she threatened the unidentified monkey.

Paul was absent from the group on three occasions during the precoup period. Twice, the other males actively searched for him (see chapter 3 for a description of a

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search), and once Guapo mounted and thrust on Paul upon being reunited with him, but wheeze dances were not observed in any of the 3 cases.

Curmudgeon became separated from the group once while he was alpha male, and the other males did not appear to search for him. Upon his return, he formed overlords with Abby and a juvenile against the observer, and Curmudgeon and Paul may have jointly threatened Guapo. Curmudgeon became separated from the group under unknown circumstances three times during the 17 days following the coup . In one case, Paul actively searched for Curmudgeon and emitted alarm calls but did not dance with him. In the second case, Paul responded aggressively to Curmudgeon's return: visibility was poor, but Paul appeared to vocally threaten and chase Curmudgeon away from the group. In the third case, which was the day when both Curmudgeon and Guapo returned to the group and Ichabod immigrated, Paul wheeze danced with Curmudgeon. Paul had actively searched for Curmudgeon and/or Guapo the preceding evening. The one other instance in which Curmudgeon became separated from the group under unknown circumstances was January 31, 1993, and Paul wheeze danced with Curmudgeon upon his return. In both of these latter 2 instances, there were no observers in the field on the day of the separation, so a fight could have been missed.

Guapo disappeared twice during the precoup phase. Once Curmudgeon actively searched for Guapo, but there was no striking reunion behavior when he was found. The second time Guapo returned after an absence, he was not greeted by adults, but Lizano approached him and rode on his back. Guapo disappeared under unknown circumstances 3 times following the coup . After the first return, Paul chased Guapo, Curmudgeon vocally threatened Guapo, and Curmudgeon and Paul formed an overlord against Guapo. Ichabod mounted and thrust on Guapo, until Paul ran over and broke up their sexual interaction, and Ichabod immediately threatened Guapo when Paul ran toward them. Both Paul and Ichabod chased Guapo. Yearling male Rico then groomed and gargled at Guapo. Rico mounted and thrust on Guapo. It is possible that Guapo returned to the group before

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I saw him and wheeze danced with a monkey, because I heard a wheeze dance a few minutes before Guapo was spotted by Paul and chased away. After Guapo's second postcoup disappearance, Paul, Abby and a juvenile chased Guapo away upon his return. Guapo's third postcoup disappearance occurred under unusual circumstances: just before sundown, the group began crossing the river to go to the place where they ultimately spent the night. Guapo watched them depart and began wheezing, alone. This is the only time I saw a monkey wheeze alone. Squint and Wiggy were the only ones in view, and they ignored Guapo. Guapo took a few steps toward the departing group and then stopped and remained alone on the other side of the river. Following Guapo's return 2 days later, it is possible that he wheeze danced with a monkey before I spotted him. I heard a wheeze dance shortly before I first saw Guapo, but I could not identify the dancers before other group members broke up the dance.

Thus, the limited data available suggest that, when monkeys become separated from the group while foraging for insects rather than under aggressive circumstances, they tend not to wheeze dance upon their return. However, because it is difficult to pinpoint the exact timing and circumstances of separation from the group in an ad lib data set, this result should be treated cautiously. In 2 of 15 cases, wheeze dances were observed, but the circumstances of the separation were highly dubious in both cases, as observers were not present at the time of the separation. In two additional cases, it is possible that the missing monkey returned before he was seen by the observer, and he may have been involved in a wheeze dance with a peripheral monkey. In the remaining 11 cases, returning monkeys definitely did not wheeze dance. Therefore, *at most* 27% of returns to the group following separations due to unknown circumstances (or 31% of *males'* returns under those circumstances) resulted in wheeze dances, whereas 67% of returns to the group following separations due to fights resulted in wheeze dances, though not necessarily with the separated monkey's opponents.

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Separations Due to Consortships

There were 9 instances in which a female left the group in the company of an adult male. In 5 of the 9 cases, observers were able to locate the pair while it was away from the group and confirm that the female was exhibiting proceptive behavior toward the male.

With one exception, females did not wheeze dance upon returning to the group. The one exception was when Nanny returned from a consortship with Paul and carried yearling female Broma on her back while they both wheezed.

Twice prior to the coup, Paul and a female were absent from the group; in neither case could it definitely be confirmed that the female was in estrus. There were no wheeze dances in either case when Paul and the female returned to the group. In one case, Curmudgeon actively searched for Paul and/or Tattle. He found Tattle first, but continued to search for Paul. Curmudgeon did not interact with either Paul or Tattle when he found them.

In three cases following the coup, Paul left the group in consort with Nanny. In all three cases, Nanny and Paul were confirmed to be actively courting one another. In the first consortship, Ichabod and Nanny's yearling son Lizano accompanied the consort pair while they were away from the rest of the group. When the consort group returned to the main group, Paul formed overlords with Squint and Abby against the observer, and Nanny formed an overlord with Squint against Hobbes and Lizano. Paul wheezed and did intense gargles with Squint. Paul also wheezed and grunted with Kola. Curmudgeon, who had been engaging in frequent displays in Paul's absence (see chapter 3), avoided Paul. Later the same day, Paul and Nanny left the group again, this time in the company of Ichabod and juvenile male Quizzler. When they returned, Paul wheeze danced with a monkey out of my view. Then Paul and Curmudgeon wheeze danced, gargled and grunted at one another. Squint and Abby, while wheezing and rhythmically exchanging intense gargles, did an overlord against Paul as he danced with Nanny. Abby and Squint danced with one another until Guapo joined them; Squint stopped dancing when Guapo started.

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Curmudgeon and Guapo danced and gargled, and Paul directed intense vocal threats at them.

The following day, Paul and Nanny again left the group, in the company of Ichabod. When they returned in the evening, chaos ensued. First, Diablita greeted Paul with gargles. Paul, Diablita, Abby, Squint, and Curmudgeon all produced intense vocal threats, but it was not clear who was threatening whom. Paul and Guapo wheeze danced 3 times, and Curmudgeon directed intense vocal threats at Paul and Guapo until Guapo fled and Paul threatened Guapo. Tattle lipsmacked at Paul. Nanny carried Broma, who wheezed. Guapo ran to Ichabod and mounted him. Paul and Curmudgeon threatened Guapo and Ichabod as Guapo gargled and thrusted on Ichabod, who made duck faces. Squint and Nanny danced. Paul ran toward Ichabod and Guapo on the ground, dragging a branch in his tail, and they broke off their sexual interaction. Ichabod threatened Guapo, and Guapo chewed his own tail. Paul threatened the observers and then ran over to break up an overlord between Squint and Nanny. Paul began gargling intensely, and Squint did an overlord over Paul. Squint and Paul rhythmically exchanged intense gargles, and one of them wheezed. Squint and Paul jointly threatened the observers. Squint once again danced with Nanny. Nanny mounted and thrust on juvenile male Hobbes; then Hobbes carried Nanny dorsally while Hobbes twittered and Nanny thrust on him. Hobbes and Nanny danced and did duck faces, while Paul threatened them. Nanny and Hobbes play wrestled. Paul gargled, wheezed, and mounted and thrust on juvenile male Kola, who also wheezed. Hobbes mounted Paul, and then they did an overlord. Paul gargled, and Rico lipsmacked at him. Rico mounted and thrust on Nanny, while alternately lipsmacking and making duck faces at her; Nanny also made duck faces. Broma once again rode Nanny, and they twittered and wheezed. This burst of intense social behavior was way outside the normal range of behavior.

Curmudgeon left the group on 3 consortships following the coup. The first, which occurred the week after the coup and was confirmed as a sexual consortship, was with

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Wiggy. Paul searched for them in the evening, unsuccessfully, and the entire group lost called the next morning until Wiggy rejoined the group. Paul kept searching until he found Curmudgeon, who was hobbling on the ground nearby, due to an earlier injury, emitting soft alarm calls as he neared the group. There were no dramatic interactions between the returning monkeys and the other members of the group. Paul's next interaction with Curmudgeon was over an hour later, when Paul directed intense vocal threats at Curmudgeon, who was surrounded by gargling juveniles.

The second time Curmudgeon disappeared in an apparent consortship with Squint, which lasted 3 days. I was unable to locate the pair to confirm that they were behaving proceptively toward one another. Squint returned first, and Ichabod initiated a courtship dance with her. Squint attacked several monkeys by threatening, chasing, and/or biting them, and formed some coalitions; she was wounded in a fight with Ichabod. Squint did a courtship dance with Paul. The only monkey with whom she interacted in an affiliative way was Tattle's infant son Eldritch, whom she nursed. Squint and Eldritch exchanged grunts. Curmudgeon was probably involved in a wheeze dance with Paul immediately upon his return, though I could not be positive of the identities of the dancers. Curmudgeon mounted and thrust on Ichabod while Quizzler threatened them vocally. Ichabod groomed Curmudgeon. Curmudgeon headflagged to an unidentified monkey and threatened Ichabod, and two juveniles aided Curmudgeon in threatening Ichabod, who reciprocated the threat. Curmudgeon did a gargle duet with an unidentified monkey, and shortly afterwards I heard a wheeze dance. Curmudgeon and Guapo danced, while Curmudgeon did sex squeaks and Paul threatened them. Guapo mounted Curmudgeon, and Paul continued to threaten them vocally. Guapo broke off the sexual interaction, threatened Curmudgeon, and headflagged to Paul, who increased the intensity of his vocal threats. Curmudgeon fled.

Curmudgeon's third consortship was an overnight absence with Wiggy. Wiggy was not greeted upon her return. Shortly before Curmudgeon was first spotted, I heard a

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wheeze dance and intense vocal threats. At the time Curmudgeon was first spotted, Paul was wheeze dancing with Guapo. Curmudgeon threatened Guapo, and then did an overlord over Paul, with Curmudgeon threatening Guapo as Paul threatened the observers. Then the three males did a three-way dance with gargles. Curmudgeon overlorded over Guapo, and they both threatened in the same direction. Guapo gargled. After Curmudgeon and Guapo ended their overlord and split up, Guapo ran toward Curmudgeon and Paul while doing wheezes, squeaks and twitters. Paul and Curmudgeon did an overlord, and then Paul chased both Guapo and Curmudgeon. Ichabod and Curmudgeon did an overlord against Guapo. Guapo presented his hindquarters to Ichabod, who mounted him and they both did sex squeaks as they walked in mount position. Then Curmudgeon did a mobile mount over Guapo, and Paul directed intense vocal threats at them. Paul wheezed, and then Curmudgeon and Guapo broke into a wheeze dance. Paul did an alarm call and intense vocal threats and then headflagged to Curmudgeon and Guapo, who were in mount position. Curmudgeon broke off the mount and presented his hindquarters to Guapo, who mounted him. Curmudgeon broke off the mount and mounted Guapo. They made duck faces and did sex squeaks throughout. Guapo broke off the mount, and they wheeze danced again. Guapo backed away from Curmudgeon, who ran toward Guapo. They wheezed, squeaked and twittered at one another. Curmudgeon presented his hindquarters to Guapo, who approached and held Curmudgeon's tail for a few seconds before cautiously mounting him. They made duck faces and did sex squeaks while walking in mount position and thrusting. Guapo dismounted and remounted for another mobile mount. Guapo dismounted and backed away; the two separated without further interaction. Meanwhile, the rest of the group had departed.

Guapo only had one potential overnight consortship, with Nanny, and it could not be confirmed that there was sexual interaction between them while they were away. Five minutes before Guapo was first seen back in the group, I heard a fight and a wheeze dance. Curmudgeon broke a branch, gargled intensely, and did a burst-twitter-bray sequence.

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Paul also gargled and did a burst-twitter-bray sequence before leaving the area. Guapo and Curmudgeon danced, and Curmudgeon mounted and thrust on Guapo. Guapo threatened in the direction in which Paul had last been seen, and Curmudgeon also threatened that way. An infant rode Guapo.

In summary, the return of male-female pairs to the group typically caused social disruption, particularly when the female was confirmed by the observers to have engaged in courtship behaviors with the male while they were away. Females, with one exception, were not involved in wheeze dances upon their return. In 6 of 9 reunions, the return of a male appeared to incite other males to wheeze dance, either with the returning male or with others. In four cases, the return of a consorting male was immediately followed by sexual interactions between the returning male and another male or males.

Disruption of Wheeze Dances

Of the 152 wheeze dances between adults in which both participants were identified, 31% were protested by third parties; that is, the third monkey threatened one or both dancers, usually by doing intense vocal threats, and sometimes charged toward the dancing pair. Thirty-five percent of protests resulted in an abrupt end to the wheeze dance. Nineteen percent of protests resulted in not only an end to the dance, but also in one dancer immediately threatening the other. In contrast, only 4% of nonprotested dances ended in one partner threatening the other. Sixty-seven percent of successful dance protests (i.e. those that resulted in an end to the dance) were by monkeys higher-ranking that both dance partners, whereas 48% of ignored protests were by monkeys higher-ranking than both dance partners.

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Discussion

Do White-faced Capuchins Reconcile?

The equivocal results obtained in this study do not enable me to answer this question definitively. It is probable that, with a larger sample size of postconflict/matched control pairs, the result that affiliation occurs earlier in the postconflict than in the matched control sample would have attained statistical significance. However, even if the p-value had been smaller, I would be skeptical of using this test to make the claim that reconciliation occurs, for the following reason. My finding that early postconflict attempts at affiliation are followed by renewed attack casts doubt on the relevance of early affiliative events as a demonstration of reconciliation. If postconflict affiliative events that were immediately followed by aggression (and therefore clearly did not reconcile the opponents) were excluded from analysis, the trend toward earlier affiliation in the postconflict sample than in the matched control sample would disappear entirely.

I can not conclude that white-faced capuchins *never* reconcile either, for the following reason. The analysis of the latency to successful versus unsuccessful postconflict affiliative behaviors indicates that these monkeys need a longer time (relative to other species) to "simmer down" after a fight before reconciliation is possible. I suspect that some reconciliations occurred after the 30-minute observation period ended. Because the distance in time between the conflict and the reconciliation is apparently greater in capuchins than in most other primate species, it is more difficult to demonstrate that reconciliation has occurred, using the common criterion that the first affiliative interaction must occur earlier in the postconflict than in the matched control. This is because the probability of an affiliative interaction occurring earlier in the matched control than in the postconflict is higher when the time to reconciliation is longer. Wheeze dances appear to be likely candidates for reconciliatory behaviors occurring long after fights. Unfortunately, it is difficult if not impossible to demonstrate that a potentially reconciliatory behavior is

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causally linked to a fight that occurred hours or even days before. If white-faced capuchins could be followed all day, such that it could be demonstrated that wheeze dances were the first interaction between opponents following a fight, and that they did not occur or occurred at much lower frequencies than under circumstances in which the dyad had not fought, then perhaps wheeze dancing could be confirmed to be a reconciliation behavior. However, the currently available evidence is insufficient to conclude that white-faced capuchins reconcile.

Do Capuchins Redirect Aggression Following Fights?

As in the case of reconciliation, results are equivocal, but in the predicted direction, regarding the tendency for aggression toward third parties to occur earlier in the postoconflict than the matched control samples. It is likely that a larger sample size would increase this difference to statistical significance. In all cases in which the victim of a fight directed aggression at a third party immediately after being attacked, such aggression was directed either at a harmless non-monkey, a lower-ranking monkey, or the recent immigrant male. All victims were animals against whom the attacker would normally have no difficulty in recruiting aid. Thus, although redirected aggression may not be a common response to receiving attack, the limited redirected aggression that does occur appears to serve as a means of distracting other group members' attention from the original victim to the secondary victim. Not only did the monkeys occasionally redirect aggression and solicit the aid of the monkeys who just attacked them, but they also sometimes threatened non-monkeys or low-rankers and solicited the aid of peacefully approaching high-rankers, apparently to forestall aggression by the high-ranker (chapter 4). Because the victim of the original attack almost always solicited the aid of the original attacker when engaging in redirected aggression, cooperating with the aggressor in an attack on a third party may be more important than the act of aggression itself. Thus, the act of cooperative redirected

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aggression could be a way of reconciling the original opponents. This data set, unfortunately, is not big enough to address this possibility.

Which Dyads Are Most Likely to Wheeze Dance?

It is difficult to objectively quantify which group members are in the best position to confer large benefits and impose large costs on one another. In this paper, I used rank as an approximation of individuals' ability to impose costs and confer benefits on one another. A more fine-grained analysis would take into account: individual's physical abilities to inflict wounds on one another, and individuals' abilities to wield political power (i.e. the ability to influence other monkeys' behavior to one's own advantage). Ideally, each dyad's relationship would be scored with regard to its frequency of severe aggression (i.e. wounding) and its coalitionary loyalty, whereas each individual would be scored with regard to its ability to give and receive successful coalitionary support. Dyads with high scores of severe aggression would be considered capable of inflicting large costs on one another, whereas dyads that mutually provide valuable coalitionary aid would be considered capable of conferring large benefits. Of course, there are other forms of costs and benefits outside the realm of aggression: for example, female capuchins may provide sexual favors to males and grooming to either males or females. However, it seems likely that the threat of aggression, whether in the context of mate competition, feeding competition, or status disputes, is the source of more tension in relationships than is the withholding of benefits such as grooming.

Males are indisputably better equipped anatomically to inflict wounds than females are, due to the greater canine length of males (Harvey et al. 1987). In this study, virtually all of the wounds in which observers saw the wound inflicted were inflicted by males (see chapters 2-4). However, there are other, more subtle ways in which females can exert influence. Female capuchins form the social core of the group, remain in their natal groups, have larger coalition networks, and tend to have more solid alliances than do males

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(chapters 2-4). Thus, they may exert more political influence in the group than do males, despite their disadvantage in one-on-one interactions with males (chapters 4-5). Not all females are equally capable of exerting influence, however. In this study group, the alpha and beta females had the tightest alliance of any female dyad. The 3 top-ranking females were much more likely to attack males than were the 3 lower-ranking females (chapters 2,4), and the 2 top-ranking females appear to have exerted considerable influence in the male rank reversal that occurred in November 1992 (see chapter 5). Coalitions of females versus other females almost always support the existing dominance hierarchy (chapter 2).

The adaptive problems faced by males and females are different, and therefore require differing social strategies. Males are primarily concerned with acquiring and maintaining access to females. To do this, their primary goals are (a) to exclude extragroup males from the group, and (b) to avoid being wounded by males within their group. Despite the inevitable tension caused by intragroup male-male mate competition, males must maintain good enough relationships with the other males of their own group so that they can cooperate in defense of females against extragroup males or males of other social groups (chapters 3,7). Females, with the occasional exception of the alpha and beta females, do not cooperate with males in driving away foreign males during intergroup encounters.

Male white-faced capuchins are far more likely than females to inflict wounds (pers. obs.) and to inflict certain types of feeding competition on females (Rose 1994); therefore, males are probably more capable of inflicting damage and more likely to inflict costs on females than are females. However, males are arguably less valuable as social partners to females than are other females. Females form coalitions mainly for the purposes of attacking males, and their most frequent and most reliable partners in these endeavors are other females (chapters 2,4). In general, it appears that there are fewer conflicts of interest between females in a group than between males in the same group. Females, being the philopatric sex, are presumably more closely related to other female group members than

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males are to other male group members. In only one instance did I observe 2 females to simultaneously court the same male; hence, it seems unlikely that within-sex mating competition is as severe for females as it is for males. For all of these reasons, it is plausible that the most tension will exist in male-male dyads (which are also the highest-ranking dyads, since males are individually dominant to females). Second to male-male dyads, the next most tension is likely to exist between males and high-ranking females, who wield considerable political clout due to their stable coalitionary networks, and frequently attack males. It is interesting to note that two dyads of high-ranking females also had wheeze dance scores roughly equivalent to those of male-high-ranking female dyads. Half of these female-female wheeze dances occurred during a context that was exceedingly rare for male-male wheeze dances: namely, when both wheezers were fighting a male, or when a male had forced one female to threaten the other (for example, by pouncing on her in overlord position and threatening her partner: see chapter 4 for description). Abby and Squint, the tightest female-female coalition, sometimes wheezed and exchanged rhythmic gargles while overlording against a male with whom they had just fought, particularly when the male attempted to separate them during the fight. It was my impression that wheezing enhanced female solidarity during these highly stressful interactions with males.

What Types of Social Change Affect Wheeze Rate?

The dramatic increase in wheeze dance frequency from virtually zero in May 1991-October 1992, to several dances daily between November 1992 until the end of the study in May 1993 coincided with 3 changes that undoubtedly introduced additional social tension, particularly in male-male relationships. One of these changes was the return to estrus of numerous females. All of the group's adult females had given birth during the first 4 months of the study; hence, with the exception of Tattle, who lost her infant during the first year, they had all been pregnant or lactating for the vast majority of the time preceding the

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coup in November, 1992. The first time a mating was observed between a male and a potentially ovulating female was March 23, 1992, when Curmudgeon mated with Wiggy in the presence of Paul. While observing the courtship dance between Curmudgeon and Wiggy, Paul threatened Curmudgeon, for the first and last time prior to the coup, and continually produced odd alarm-like vocalizations that were somewhat similar to Curmudgeon's postcoup whine barks. Curmudgeon initiated a wheeze dance with Paul, which was protested by several adult females and juveniles. Only after wheeze dancing with Paul did Curmudgeon mate with Wiggy. I never observed males physically attack one another in the immediate context of mate competition, but observations such as the one just mentioned, the mate-guarding described in chapter 4, and the response of males to returning consort pairs suggest that the sexual rivalry induced by the presence of estrous females may be a source of tension in males' relationships. Wheeze dancing may be a way of reducing that tension, and/or of expressing commitment to continued cooperation in an intergroup context.

Coincident with the return of several females to estrus was the rank reversal between Curmudgeon and Paul. During the coup and its aftermath, the three males received severe wounds, and the high-ranking females received more minor wounds; hence, all of these individuals had good reason to fear one another during this time period. The nature of the males' relationships, both with one another and with all other members of the group, changed dramatically as a result of the rank reversal (chapters 3-5). The uncertainty involved in these changing social dynamics was probably an additional source of stress to the monkeys, and wheeze dancing may have been useful in reducing stress and in negotiating the future quality of the relationships. The rate of wheeze dancing increased immediately following the coup, but because Paul was the only consistent male member of the group for much of the month of November, the wheeze dance rate did not rise dramatically until November 28, when all male group members returned to the group to stay, except for some brief absences described above.

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Another major contributing factor to the increase in wheeze dance rate was the immigration of Ichabod, who arrived with Guapo and Curmudgeon on November 28, when wheeze dancing reached its peak. It is likely that Ichabod succeeded in immigrating only because the resident males' relationships were in such a state of flux that they could not cooperate to evict him. Paul had not even seen Guapo for over 2 weeks, and his rare encounters with Curmudgeon had been largely hostile and tense at best. Of the 26 wheeze dances observed on the day of Ichabod's immigration, there were 16 in which both participants could be identified: all involved adult males, and 8 dances were between Ichabod and either Curmudgeon or Guapo. The details of Ichabod's immigration are described in greater detail in chapter 5. The high frequency with which males, particularly Curmudgeon and Guapo, wheeze danced with Ichabod during his first few days in the group may indicate that wheeze dances are an important aspect of relationship negotiation.

Responses to Reunion after Separation

Separation, even under normal circumstances such as accidental separation from the group while foraging, could induce additional stress in a relationship, particularly if the relationship was stressed prior to the separation. When two individuals have been separated for some time, they can not monitor one another's behavior, and hence any tension and uncertainty about a social partner's behavior that was present *before* the time of the separation could be enhanced by lack of information over a long period of time. The separated monkey could have missed social events such as fights that are critical to its understanding of new social developments. Likewise, when males leave their group, either alone or in the company of a female, members of the main group may miss out on important information critical to their relationship with the missing male: for example, a single missing male may have had interactions with males of other social groups (as was apparently the case when Guapo disappeared after the coup), or a missing male-female pair may have mated.

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The results of reunions after separations must be treated with caution, since information regarding the exact circumstances and timing of separations and reunions may be inaccurate in some cases, because they are from ad lib observations. However, the results are consistent with the idea that males' relationships are more tense than those of females, and that sexual rivalry is a source of tension in male relationships. Females, whether they were returning from a lone separation or from a consortship with a male, virtually never were involved in dramatic reunions with other group members, but rather resumed their normal activities as if they had not been gone. In contrast, the return of males usually sparked dramatic social interactions such as wheeze dances and male-male sexual interactions, particularly if the male had been in the company of a female or if the male's last observed social interaction prior to departure had been a fight. In some cases the returning male was one of the participants in these interactions, but in other cases the wheeze dancing dyad was a pair of males that had remained in the group. Hence, it is possible that concern over the missing male's activities triggers a need for the remaining males to reinforce their bonds with one another.

These results may shed some light on some interesting observations by Matheson et al. (1994), who experimentally removed various combinations of brown capuchins (*C. apella*) from their groups and videotaped the social interactions that took place during their return to the group. As was the case in my study, females typically did not engage in any particularly noteworthy behavior during reunions. However, the pair of adult males typically hugged and vocalized loudly immediately upon being reunited after a separation. The vocalizations produced by the hugging males bore some resemblance to the *C. capucinus* wheeze vocalization. During 3 of the 13 days in which males were reunited and responded in this way, an estrous female was present. Matheson et al. interpret their results as demonstrating that their capuchin group is "male-bonded" in the sense that the males have a non-competitive, cooperative relationship. Unfortunately, the investigators do not provide data on the baseline social interactions of the males: only behavior during

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reunions are used to arrive at these conclusions. An alternative explanation of their results, suggested by the behavior of wild *C. capucinus*, is that their males also have a tense competitive relationship, and that it is the tension produced by one male leaving one's group while the male rival remains with the females that causes the reunited males to engage in this dramatic social behavior. As Matheson et al. note, the captive *C. apella* males, unlike the wild *C. apella* in Janson's (1984,1986) study, cooperate in threatening males of other groups. Thus, there may be some advantages to maintaining positive relationships, and the combination of the need to cooperate with the inevitable tension due to sexual rivalry could be responsible for the strikingly ambivalent and dramatic nature of both captive *C. apella* and wild *C. capucinus* reunions.

Protests of Wheeze Dances

Roughly a third of all wheeze dances were protested by other monkeys, and a third of all protests resulted in an abrupt end to the wheeze dance. Often one of the dancers threatened his partner immediately following a protested wheeze dance. Thus, if wheeze dances are indeed a means by which monkeys can repair or solidify their relationships, it would be beneficial to a monkey to protest wheeze dances of dyads who could be a threat to the protester if the dancers succeeded in forming a strong alliance. The vast majority of protests were by the alpha male in response to wheeze dances of subordinate males. However, there were a few instances in which high-ranking females or subordinate males protested other males' wheeze dances, and one instance in which the beta female (Squint) protested a wheeze dance of the alpha female (Abby) with the alpha male during a fight in which both females had initially attacked the alpha male. Thus, the pattern of protester/wheeze dancer combinations does seem to suggest that individuals protest wheeze dances of those monkeys whose alliances could be threatening to them. Protests against wheeze dances and other affiliative interactions between subordinate males by the alpha

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male is reminiscent of separating interventions in chimpanzees, first reported by de Waal (1978).

If noisy wheezing attracts the attention of monkeys who break up the dance and cause dancers to aggress against one another, why would monkeys use such a conspicous behavior as a means of negotiating their relationships, rather than a quiet, inconspicuous behavior such as grooming or silent sexual interaction? Perhaps the noise and attraction of protesters is essential to the communicative function of the interaction. A quiet interaction such as grooming, performed out of view of other group members, has no cost to the interactants and therefore is not an effective way of expressing commitment (Smuts and Watanabe 1990; Grafen 1990; Zahavi 1977). In contrast, if two monkeys can maintain their poise and continue dancing without betraying one another while other group members are threatening them, they are expressing a commitment to cooperating with one another. The strategy used by the alpha male to break up affiliative interactions between subordinate males is to threaten one male and solicit the aid of the other; if the first male refuses to aid, then he threatens him and solicits aid from the second male (chapter 3). Therefore, a male who refuses to aid the alpha male in attacking his dance partner risks being attacked by both the alpha male and his partner. Unless the dancers have complete confidence in one another, the optimal strategy is to attack one's partner as soon as a high-ranking protester threatens the pair. Thus, wheeze dances may be somewhat similar to a self-imposed prisoner's dilemma game, or -- if the reward is greater than the temptation -- the "staghunt" (Poundstone 1992). Unfortunately, it is difficult to estimate the costs of being betrayed (i.e. the sucker's payoff in Table 6.2).And it may be impossible to estimate the benefits of mutual cooperation (the "reward") in wheeze dances. Table 6.2 provides a more detailed explanation of the proposed pay-off matrix for the wheeze dance game.

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Directions for Further Research

It seems clear that no immediate benefits are gained by wheeze dancing, since dancers typically leave one another, play, engage in homosexual interactions, or -- if the dance is protested -- attack one another after wheeze dancing. Because there is often a cost to wheezing in the form of attack by the dance partner and/or a dance protester, I infer that wheezing and the accompanying dance and/or sexual interactions serve a function in solidifying the wheezers' social bond. Although this inference makes theoretical sense, it is important to note that reconciliation was not demonstrated to have a long-term effect on the quality of social relationships in one study that has looked for such effects (baboons: Silk et al n.d.). It will be particularly difficult to investigate whether there is a long-term positive effect of wheeze dancing on white-faced capuchin social relationships, due to the tendency of other monkeys to protest wheeze dances. It may even be the case that a disrupted wheeze dance damages a relationship more than a completed wheeze dance solidifies a relationship. Because wheeze dances are such rare events, it is impractical to design an entire field project to study them. To fully understand the social implications of wheeze dancing, it would be necessary to have a complete record of the social interactions of dancers for long periods preceding and following the dance. Focal follows of that length are virtually impossible in rapidly-moving, forest-dwelling primates. However, it might be possible to investigate wheeze dances more systematically in captivity, where conflicts could be provoked and conditions for cooperation established, as Cords has done for long-tailed macaques (Cords 1993, Cords and Thurnheer 1993).

I have focused on the wheeze dance in this chapter, because it is the most striking and obvious candidate for a tension-reducing and relationship-negotiating behavior in the study species. However, there are other behaviors that may also play a role in relationship negotiation. Nonreproductive sex is prevalent in capuchins (chapter 4), and may serve to reduce tension, as is the case in bonobos (de Waal 1987). The manner in which males take turns in mounting one another is intriguing; with a larger sample size, it might be possible

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to investigate how the quality of the relationship varies with the degree of symmetry in assumption of the active role, as has been done for olive baboon male greetings (Smuts and Watanabe 1990). Intense gargles, like wheezes, are commonly associated with tense social contexts such as dances, reunions, postconflict interactions, and coalitions. During dances or overlords, intense gargles are often exchanged in a strikingly rhythmic way that highlights the coordination of the two partners. It seems probable that careful analysis of the initiation, coordination, symmetry, and termination of videotaped dances and nonreproductive sexual interactions would yield a goldmine of information on the mechanisms of relationship negotiation.

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Table 6.1: Number of wheeze dances observed; monkeys ranked from highest to lowest, from left to right.

	Individual									
	P	C	G	I	A	S	N	D	W	T
P	-----	30	20	4	7	10	8	2	0	0
C		-----	35	12	2	2	0	0	0	0
G			-----	6	3	3	1	0	0	0
I				-----	4	0	0	0	0	0
A					-----	9	0	0	0	0
S						-----	5	0	0	0
N							-----	1	0	0
D								-----	0	0
W									-----	0
T										-----

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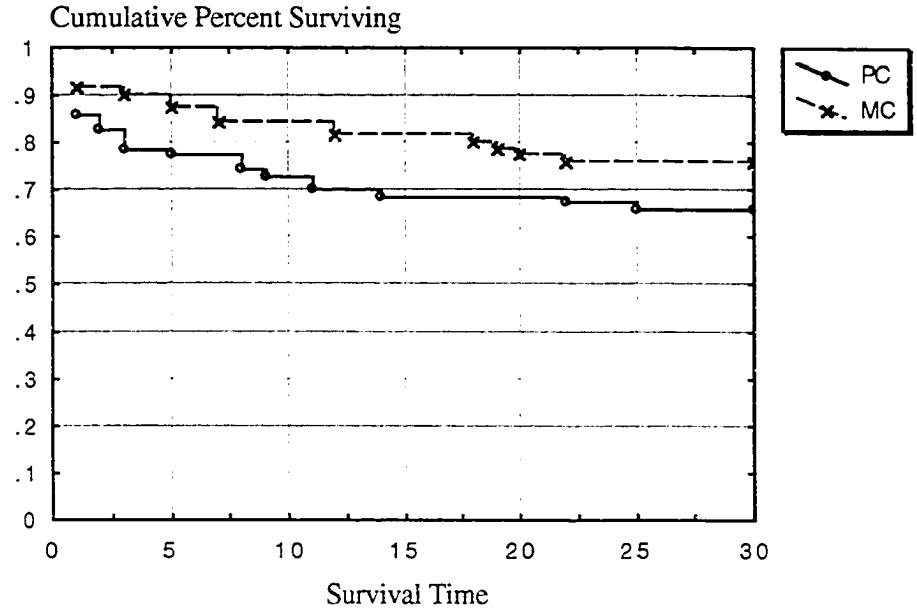
Table 6.2: Payoff matrix for the wheeze dance game: A and B are the wheeze dancers (A=Ego); P is the protester.

	B defects	**B cooperates**
A defects	Punishment: Both A and B are attacked; A's and B's costs in any one game are unequal, but neither consistently bears the greater cost.	Temptation: A and P attack B; the A-P alliance may be strengthened slightly, or the chances of future punishment of A by P may be reduced
A cooperates	Sucker's Payoff: B and P attack A; the B-P alliance may be strengthened slightly, to the possible detriment of A.	Reward: Neither A nor B attacks one another; putative long-term benefit to both A and B due to A-B alliance

Assumptions: (1) P attacks more intensely when one dancer is willing to defect but the other wants to cooperate. This is because the cost of continued protest is too great if the A-B alliance is very strong, and the benefit of intense attack is low if the A-B alliance is very weak. (2) P does not support A over B consistently or vice versa. (3) It is possible for A and B to form a stable alliance versus P.

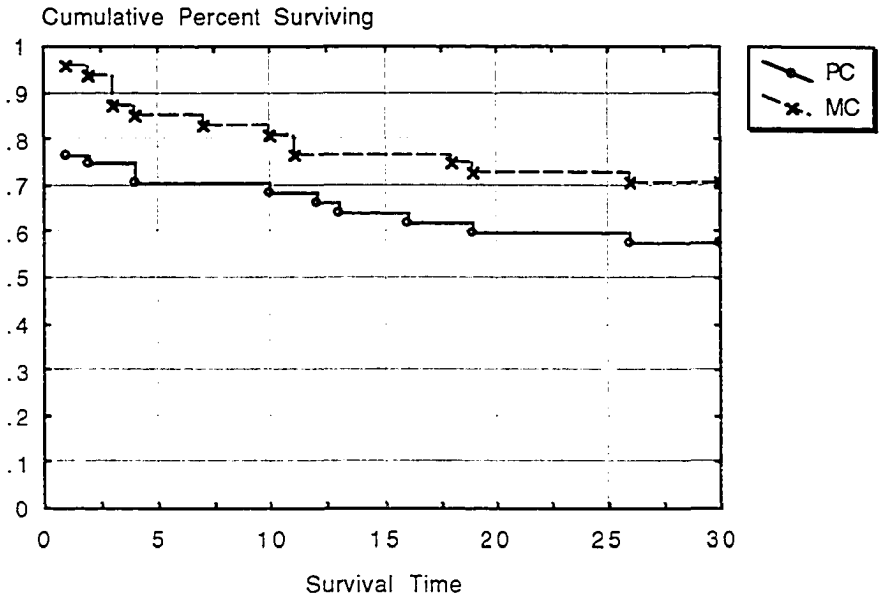
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Figure 6.1: The difference between the Kaplan-Meier estimates of the survivorship functions of time to first affiliation in the postconflict and matched control samples



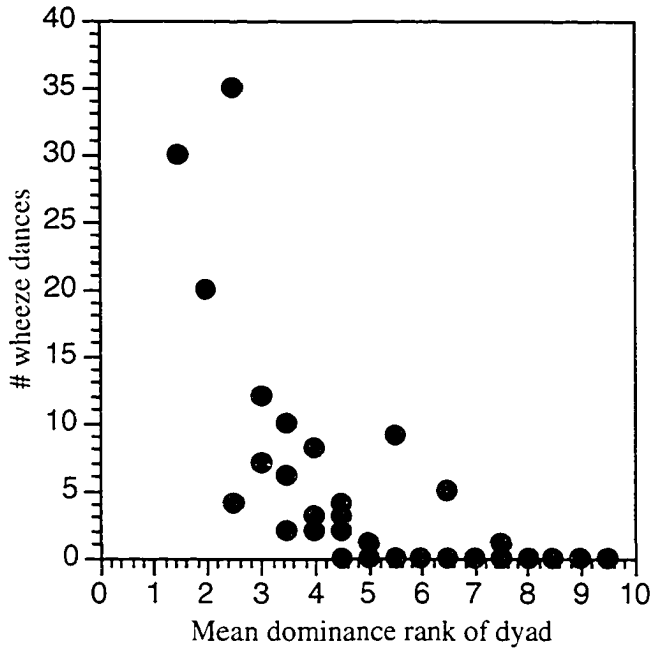
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Figure 6.2: The difference between the Kaplan-Meier estimates of the survivorship functions of time to first aggression to a third party in the postconflict and matched control samples



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Figure 6.3: Number of wheeze dances plotted against the dyad's mean dominance rank



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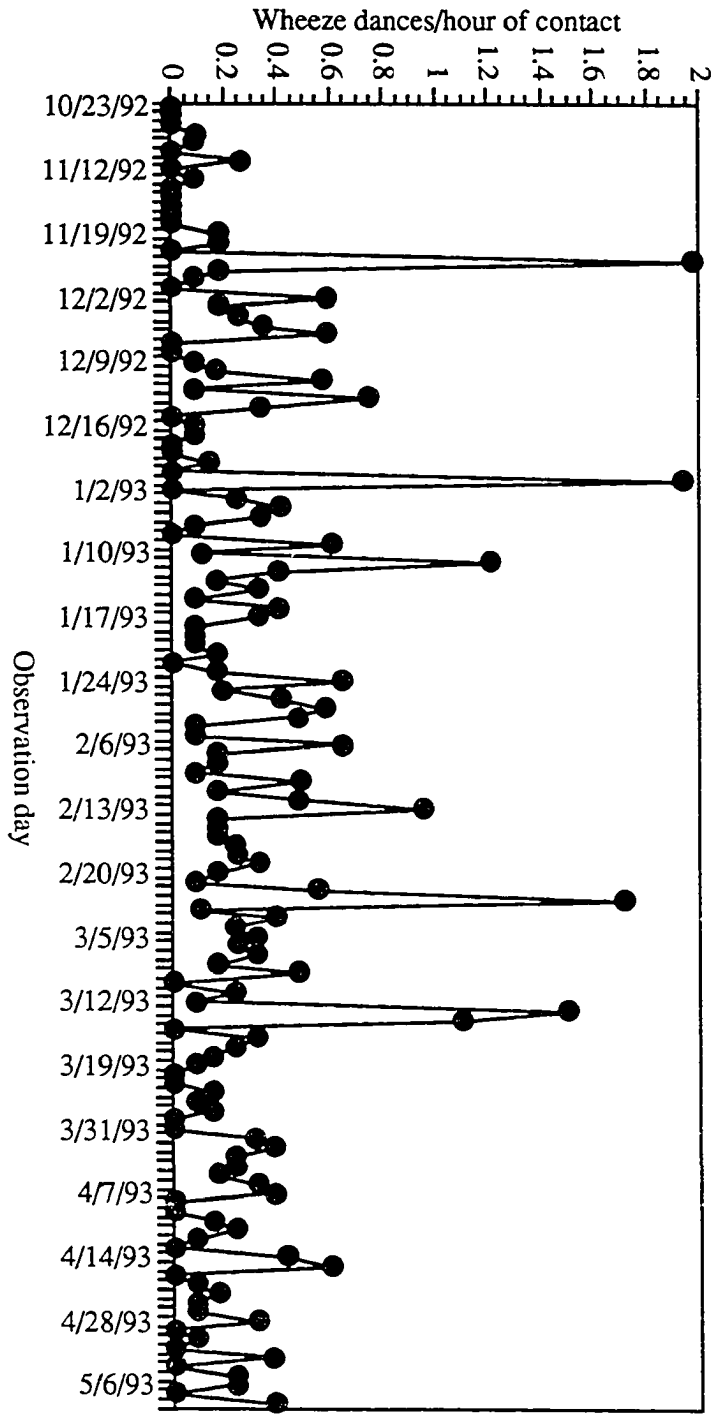


Figure 6.4: Hourly wheeze dance rate in the group overall, plotted over time for the period between October 1992 and May 1993

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CHAPTER VII

INTERGROUP ENCOUNTERS

Introduction

Although hypothesized to be crucial to understanding primate social relationships and social organization (Wrangham 1980), intergroup encounters in wild primates are rarely described in detail in the literature, due mainly to the rarity of these events. Also, the often chaotic nature of intergroup encounters makes it difficult for observers to identify all participants and observe all of their relevant social interactions. In this chapter, I describe the nature of intergroup encounters in a group of wild *Cebus capucinus* and discuss (a) the significance of intergroup encounters in determining the nature of intragroup male-male and male-female relationships in *Cebus capucinus*, and (b) whether the pattern of intergroup encounters in this species conforms to theoretical predictions (Wrangham 1980, van Schaik 1989, Isbell 19[illegible]).

Female Participation in Intergroup Encounters

Wrangham (1980) proposed that primate societies are female-bonded (i.e. females are philopatric, with strong affiliative bonds and differentiated social relationships) or non-female-bonded, according to the degree of inter-group feeding competition. Because access to food is thought to limit female reproductive success to a greater extent than male reproductive success, effects of feeding ecology on social relationships will be mediated primarily through female strategic decisions. In species whose "growth diet" consists mainly of resources that are distributed in high-quality patches, rather than being evenly distributed, females are hypothesized to form coalitions in order to defend patches from

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other groups. The high-quality patches are supplemented by widely distributed low-quality foods, on which low-rankers can feed when there are insufficient feeding sites in a high-quality patch for all females, or when high-quality foods are rare. All else being equal, kin tend to cooperate with one another so that the benefits of cooperation will accrue to kin, and so that the costs of being the victim of a coalition will be inflicted on nonkin. In Wrangham's model, the advantages of cooperative resource defense outweigh the costs of intragroup competition. Females, in a sense, manipulate group size by attracting males to aid them in intergroup competition. Thus, intergroup feeding competition is proposed to be the driving force in determining the nature of female relationships and primate social organizations in general. Wrangham's female-bonded model has been criticized by many researchers (van Schaik 1983; Terborgh and Janson 1986; Dunbar 1988) for neglecting the importance of predation and for underestimating the role of intragroup competition relative to intergroup competition in determining social organization. Consistent with Wrangham's emphasis on the importance of female intergroup competition in determining social structure is Isbell's (1991) expectation that females will participate in intergroup aggression whenever food is limited, regardless of the distribution of resources and the type of intragroup competition.

Van Schaik (1989), in an extension of the female-bonded model, proposed that it is not intergroup competition, but rather the nature of intragroup competition, that is the most critical factor in determining the nature of female social relationships. If intragroup competition is of the scramble variety, females may or may not be philopatric, and dominance relationships will be egalitarian and individualistic in nature because high rank is not beneficial in obtaining food. If intragroup competition is largely by contest, females will be philopatric, and dominance hierarchies will be nepotistic and despotic because the best food resources are monopolizable. Hence, kin benefit by helping one another attain high rank. According to van Schaik's model (see type B in Table 2, p. 201 in van Schaik 1989), females of a primate society having strong affiliative bonds, despotic and nepotistic

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ranking, and female philopatry, would not necessarily be expected to have a high degree of participation in aggressive intergroup encounters. Because females in that type of society feed primarily in clumps too small to contain all group members (van Schaik 1989), low-ranking females would be excluded from feeding sites and would therefore experience little or no benefit from participation in defense of these sites. Thus, to the extent that females do participate in intergroup aggression in societies characterized by high degrees of intragroup contest competition, high-ranking females are expected to participate more often than low-ranking females (van Schaik 1989, Cheney 1987). Van Hooff and van Schaik (1992) expect that intergroup competition will be a strong determining factor in female relationships only when intragroup contest competition is low, due to (a) wide dispersal during foraging, or (b) patch sizes large enough to accommodate the entire group for long periods of time.

Male Participation in Intergroup Encounters

Male reproductive success, in contrast to female reproductive success, tends to be limited by access to fertile mates (Trivers 1972). Thus, males are predicted to be more active than females in intergroup aggression when the purpose of the contest is to defend mating access to females, rather than access to resources (van Schaik et al. 1992). In some cases, males may gain access to females by defending resources critical to female reproduction; in such cases, both males and females might be expected to participate in intergroup aggression, depending on the ecological circumstances.

According to the mate defense hypothesis, males in multi-male groups are expected to cooperate in intergroup aggression only if males are closely related or if mating access is shared among males. Mating access does not necessarily have to be divided equally for cooperation among non-kin to be effective (Nöe et al. 1991; Nöe 1992). However, it is expected that those males who have the greatest mating access will also be the most active participants in intergroup aggression (Cheney 1987).

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Characteristics of *Cebus capucinus*

Cebus capucinus in tropical dry forest spend about 17-44% of their time foraging for insects, and 53-81% of their time foraging for fruit (Chapman and Fedigan 1990). Although some of the fruiting trees used by capuchins are large enough to accommodate an entire group, the trees most frequently used are small (0-20 cm DBH in rain forest: [Phillips 1994]), holding only a few monkeys. Monkeys are typically widely dispersed when foraging for insects, whereas they often forage on fruit while in close proximity. Foraging-related aggression is common (Rose 1994; pers. obs.). Predation rates on capuchins are not well documented, but capuchins are certainly vulnerable to some predators (see chapter 1).

Female-female relationships are stable and differentiated and are characterized by a linear, despotic, dominance hierarchy (see chapter 2). It is not known whether females aid their female offspring in acquiring a place in the dominance hierarchy. At Santa Rosa (Fedigan et al. m.s.) and BCI (Oppenheimer 1968), female migrations were rare, and new groups formed by fissioning.

The data necessary to place this and other species precisely within the contexts of Wrangham's, van Schaik's, and Isbell's models -- precise data on spatial and temporal distribution of food resources, variation in food quality, and relative effects of intragroup versus intergroup feeding competition -- are not available for this or any other species. However, a qualitative examination of the available data suggests that *C. capucinus* conforms to Wrangham's ecological criteria for female-bonded species and conforms to the type characterized by "strong within-group contest only" in van Schaik's model (1989). According to van Schaik's model, *C. capucinus* females would not necessarily be expected to participate in intergroup aggression, whereas according to Wrangham's (1980; see also Manson & Wrangham 1991) model, females would be expected to participate in intergroup aggression as much as or more than males.

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Methods

At the first sign of an intergroup encounter (social interaction between two social groups), I switched from collecting focal animal data (after finishing the sample) to collecting ad lib data. Intergroup encounters were chaotic, and individuals tended to spread out over an unusually large area during these encounters; thus, it would have been impossible to determine the identities of all participants in aggression had I continued doing focal follows. Generally the groups segregated by sex during intergroup encounters such that the males of the two groups moved toward one another, and the females of the two groups moved away from one another (see results). One observer followed the males of the study group, while the second observer followed the females. Observers communicated via two-way radios when long-distance vocalizations were produced, so that both the identity of the vocalizer and the response of the receivers on the other side of the group could be noted. Also, when an observer noted that a male was leaving the site of the encounter to rejoin the females, one observer could notify the other observer to be on the lookout for reunion behaviors. Use of radios to communicate between the two subgroups made it possible for the observers to locate all group members at least once during intergroup encounters. However, even with two observers, it is likely that some interactions were missed.

A monkey was scored as participating in an intergroup encounter if he/she remained in visual contact with members of the other group after the initial flight of the females and immatures, and engaged in some type of social interaction (either affiliative or agonistic, and including facial expressions, vocalizations, and gestures) with a member of the other group.

It was often difficult to determine which group, if either, had won the aggressive encounter. I scored a group as winning an encounter if the monkeys on the front line of the attack gained more ground than the other group, between the time of initial contact between the two groups and the time at which the groups finally parted. In addition to gaining

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ground, a party of capuchins had to part from the other group in a sedate manner, rather than fleeing, to qualify as having won the encounter. There were numerous encounters in which (a) neither party gained much ground, (b) the parties took turns chasing each other, and/or (c) the encounter culminated in a long stare-off between the males of the two groups, after which both parties of males slowly drifted back to their own groups. In these cases, I did not declare either group the winner.

Four capuchin groups had home ranges overlapping that of the study group (see Chapter One, Figure 7.2). At the start of the study, none of these groups were habituated to human observers, and they uttered alarm calls during intergroup encounters, apparently elicited by the presence of the observers. (The members of our own study group did not call in this context.) I was unable to recognize the members of the other groups at the start of the study. By the end of the study, I was able to identify most of the males in the adjacent social groups and could therefore keep record of which groups were most frequently encountered by the study group. By the end of the study, the males of the other groups emitted alarm calls toward us at much lower rates than was previously the case, and they no longer visually oriented toward the human observers during intergroup encounters.

Results

Description of Intergroup Encounters

The presence of another group was in the vicinity of the study group was signalled in one of three ways. Sometimes a monkey on the front edge of the study group emitted a quiet alarm call of long duration, acoustically quite similar to the alarm call elicited by the presence of unfamiliar humans. At other times, the first sign of an impending intergroup encounter was an intense vocal threat, from either of the two groups. This vocalization was generally produced by males, at least at the start of an intergroup encounter, but females occasionally produced it as well. Often there was no vocal warning before an

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intergroup encounter began, and the first sign that something unusual was happening was that group members became silent and ran at top speed, wide-eyed, in the direction from which they had just come. Before fleeing, females ran to retrieve their own and others' babies. (Active baby retrieval by mothers is exceedingly rare and is typically seen only in one other context: the presence of large birds of prey.) Almost without exception, adult females, juveniles and infants fled as soon as another group was spotted. Adult males sometimes fled as well, but they usually ran toward the other group, emitting intense vocal threats. Males of the two opposing groups rarely had any physical contact in these encounters. Unlike *C. albifrons* males, who maintain close proximity with one another during intergroup aggression (C. Janson, pers. comm.), *C. capucinus* males often spread out over a great distance even while simultaneously directing threats at the other group's males. Occasionally two monkeys of the same group joined in an overlord, but more often participants on the same side stood far apart, vocally threatened the other group, broke branches, urine-rubbed, bounced, piloerected, and headflagged to the males of their own group. Occasionally the males of one group chased the males of the other group; these chases usually took place on the ground. Chases were often reciprocated. Sometimes, in place of chasing, the males stood still, glaring at and threatening one another. During especially heated encounters, the males of both sides took breaks from hostilities to bathe in the river, while observing one another, before renewing their attacks.

Rarely, the males interacted in what seemed to be an affiliative way. They made duck faces, piloerected, spun around, looked under their arms at one another, made squeaky vocalizations (used only in this context), and ran back and forth while staring intently at one another. These behaviors, aside from the vocalizations, occurred frequently in an intragroup context during sexual solicitations, following major fights, and at other tense moments in specific dyadic relationships (most often in dyads that had ambivalent relationships: see Chapters 3 and 6). Following the encounter, the monkeys who had participated in the hostilities either fled back to their own groups, or wandered slowly back,

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pausing occasionally to glare or threaten toward the other group. Because the females and immatures sometimes fled a great distance, the males often had difficulty in relocating their own groups afterwards and produced lost calls.

I observed 44 intergroup encounters, during 3703 hours of observation. Thus, encounters occurred at a rate of approximately one per week. Intergroup encounters typically lasted 15-60 minutes. Table 7.1 shows the distribution of intergroup encounters across seasons. There was a slight tendency for intergroup encounters to occur more frequently in the dry season (0.013 encounters/hour) than in the rainy season (0.010 encounters/hour). Intergroup encounters almost always occurred close to rivers and streams, probably because all social groups tend to focus their ranging patterns disproportionately in such areas. Because monkeys spend much more time near running water during the dry season than during the rainy season, it is no surprise that groups tend to encounter one another more often in the dry season.

Male Participation

Adult males were the primary participants in intergroup encounters. Males were the sole participants in 39 out of 44 intergroup encounters, and they were the primary participants in all 44 encounters. Juvenile males accompanied the adult males in some intergroup encounters. In all but one case in which at least one male participated aggressively in an intergroup encounter, he was aided by at least one other male from his group. Table 7.2 shows the proportion of intergroup encounters in which each male participated. In some instances, the observers could not positively identify a male as he ran past during an intergroup encounter, but could narrow the identity down to two possibilities. Thus, some cells in the table are ranges, rather than precise values.

The alpha male was the most frequent participant in intergroup encounters. Curmudgeon's rate of participation dropped when he fell from alpha to beta male, whereas

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Paul's rate of participation increased when he became alpha male. Juveniles participated at lower rates than did adults.

Female Participation

Females participated in only 5 intergroup encounters. Three of these involved the alpha female, and four involved the beta female. Low-ranking females were never seen to participate. Abby, the alpha female, never got very close to the males of the other group. Most of her participation was vocal, though she aided Paul in chasing a male once, and she once did an overlord with Ichabod against a male from another group.

The most severe aggression ever observed in an intergroup encounter (either by males or by females) was when Squint (the beta female) wrestled with a member of another group (which was almost certainly a female). That particular intergroup encounter was unusual in that it was the only time the females of both groups did not flee immediately: rather, members of both groups (both male and female) intermingled, and most group members were fully piloerected (which is virtually unheard of for females), vocalizing loudly, and running on the ground.

Squint was once chased by a foreign male, in the only case of male aggression against females observed in an intergroup encounter. Squint differed from all other females in that she sometimes followed the males great distances in pursuit of males from other groups. Squint's participation in these excursions was generally confined to observation and vocal threats; she usually did not get close enough to chase the other group's males. It is worth noting that Abby and Squint did not begin participating in intergroup encounters until their infants were at least 20 months old.

Outcomes of Intergroup Encounters

The outcomes of intergroup encounters are summarized in Table 7.3. The monkeys in the unknown category include some of the 4 neighboring groups listed in the top part of

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the table, as well as some roving males that were apparently in the process of migrating. The results are broken down by year, to demonstrate the (dis)continuity over time with regard to outcomes of intergroup encounters. An examination of the outcomes when all groups are lumped together (in the bottom row of the table) reveals that the ratio of wins to losses did not change much from one year to the next; therefore, the presence of observers during the first year of the study, when males of other social groups were less habituated, probably did not greatly affect the outcomes of these encounters. There was no stable inter-group dominance hierarchy.

Affiliation with Members of Other Groups

Although all males who participated in intergroup encounters were hostile to the males of the other group, some males occasionally engaged in affiliative interactions, in addition to aggressive interactions, with extragroup males. There was no apparent pattern to which males directed affiliative behavior toward foreign males. Curmudgeon only did this once (as beta male), Paul 5 times (3 times as alpha male, and twice as beta male), Ichabod twice, and Kola and Guapo once each. Males of other groups were observed to direct affiliative behaviors toward the males of the study group during 9 encounters (sometimes more than one male per encounter). Following are three descriptive accounts of intergroup affiliation.

Incident #1: On April 1, 1993, Curmudgeon ran into the middle of Rambo II's group. Amidst the ensuing chaos, I could see Curmudgeon lunging and doing intense vocal threats; it also appeared that he was engaged in some physical fighting. Meanwhile, Paul and Guapo fled. Ichabod helped Curmudgeon threaten the other group. After Ichabod left and everyone had stopped threatening, Curmudgeon, glaring, strutted on the ground toward Rambo II's group. Then he broke into a run, still following them, and squeaked at them. Curmudgeon made a duck face at one of the males and danced with him. Both did whiny squeaks and duck face pirouettes. Curmudgeon kept spinning

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around vigorously, looking at the other male from under his arm or between his legs, while doing quiet squeaks and whines that I had never heard before. Another male from Rambo II's group approached and began to do branch-shaking displays at me; this startled Curmudgeon, who stopped dancing. Curmudgeon shook a branch at the male, who retreated. Then both Curmudgeon and the other male did branch displays at me. The other males returned to their group, which was drifting away, and Curmudgeon returned to his own group.

Incident #2: On April 7, 1993, approximately 30 minutes into a particularly aggressive encounter with Rambo II's group, two foreign males pursued Curmudgeon and Paul and made duck faces at them. Paul peeped at the foreign males. Both Paul and Curmudgeon bathed, while threatening the males. Curmudgeon did an overlord over Paul at the males, and Paul and Curmudgeon both threatened them vocally. One of the foreign males did a duck face and whimpers at Paul, and then produced some odd vocalizations (which sounded more like coati screams than monkey vocalizations) before fleeing. Paul and Curmudgeon directed intense vocal threats toward him as he fled. Paul and Curmudgeon ran in the opposite direction of the male, and then stopped and stood side by side. The same foreign male returned and resumed the odd coati-like vocalizations. Two more foreign males came to join him, and they all made the same odd vocalizations. One of them did duck face pirouettes at Curmudgeon and Paul, both of whom stared at him. Paul retreated slightly, but Curmudgeon did not move. One male, who was still doing coati noises, advanced somewhat, and Curmudgeon retreated slightly. Curmudgeon did an overlord over Paul and threatened the three foreign males. Paul broke off the overlord. A second male joined in the coati noises. Ichabod and Hobbes joined Curmudgeon and Paul, and the four of them threatened the 3 foreign males and directed overlords at them for awhile. . . . .Later, after the 3 males chased Paul and Curmudgeon, Paul initiated a sex dance with one of the males and squeaked at him. The three males began to leave, and Paul began producing odd vocalizations while running back and forth. Curmudgeon and

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Ichabod charged the enemy, and Paul directed intense vocal threats toward them. The fight resumed and ended inconclusively, with the study group gaining slightly more ground.

Incident #3: January 24, 1993, following a brief intergroup encounter, Kola (a juvenile male) twittered at the other group and followed them. A juvenile male of the other group began to dance, fear grin, and scream (machine gun scream) as Kola approached. Kola ran toward the juvenile, who kept making strange squeaking noises and running. The foreign juvenile finally left.

All instances of affiliation between males of different social groups could be characterized as highly tense and emotional. There was no physical contact in the context of affiliation. The most unusual feature of intergroup affiliation was the array of vocalizations, which were not heard in any other context.

Intragroup Male-male Affiliation, Cooperation and Defection During Intergroup Encounters

If, as I suggested in Chapter 3, males need one another's aid during intergroup encounters, males should monitor and encourage one another's participation. Males sometimes wheeze danced (see chapter 6) and gargled with other males of their own groups during intergroup encounters, possibly as a way of demonstrating their commitment to cooperation during intergroup encounters, or as a way to solicit participation. Although males frequently headflagged to one another, did overlords against foreign males, and simultaneously chased foreign males, the males of a single social group often spread out over a great distance while threatening the other group. Under these conditions, it was difficult for males to coordinate their behavior, and it was even difficult to know who was still participating in the attack. Often, particularly when the other group appeared to be winning, one or more of the males in the study group would quietly leave the fight and rejoin the females. The following incident was particularly intriguing:

Incident #4: On June 29, 1992, all of the adult males of the study group were involved in a particularly aggressive intergroup encounter with Rambo II's group, which

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occurred on top of a hill overlooking the river. One observer (Julie) was on top of the hill watching the fight, and I was at the bottom of the hill, between the males and the females. The juvenile males left the fight early on, and passed me as they returned to the females. Julie reported that the fighting was continuing on top of the hill, and that some of the study group males were retreating. She saw a foreign male chase Paul along the ground; meanwhile, I saw Curmudgeon slink down the hill. Curmudgeon stopped to rest near where I was, and I could hear the fighting continuing. Soon afterwards, I saw Paul, who had apparently retreated from the fight via a different route. As soon as Paul and Curmudgeon saw one another, Paul grimaced at Curmudgeon, and screamed. Paul and Curmudgeon both grimaced and screamed back and forth, while running toward one another. Then they charged back up the hill together and resumed chasing the other group. It was my impression that both males were in the process of returning to the females, apparently leaving Guapo to fight the other group single-handedly, and that they would not have returned to fight, had they not "caught" one another in the process of defecting.

Incident #5: Probably the single most striking event to occur during an intergroup encounter was when Ichabod, 3.5 months after joining the study group, switched sides during an intergroup encounter. The fight was with Rambo II's group, and I am fairly confident that Ichabod was a member of Rambo II's group before he transferred to my study group because I had seen him with them previously. Paul had just fled, and Curmudgeon was threatening the other group's males, when Ichabod began to threaten Curmudgeon. Ichabod did an overlord over a foreign male toward the males of my study group, and then he switched places such that the foreign male was doing an overlord over Ichabod. Paul returned and helped Curmudgeon charge at the foreign males and Ichabod, and the foreign males fled. A long series of chases and counterchases ensued, and at the end of the encounter, when my study group had won, I found Ichabod with Curmudgeon and Paul, watching Rambo II's group retreat. Ichabod grimaced at Paul. Unfortunately, because of the extreme chaos that occurred between the time of Ichabod's "treachery" and

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the end of the encounter, I was not able to determine whether the males of my study group retaliated against Ichabod for siding with the foreign males.

Range Use as a Function of Number of Males in the Group

If male-male cooperation is vital for defense against incursions of extragroup males, as is suggested by Robinson's (1988b) finding that number of males in the group is a decisive factor in the outcomes of intergroup encounters in *C. olivaceus* (see discussion section), then it might be expected that groups with smaller numbers of males would actively avoid areas in which they were likely to encounter other groups. The hidden assumption here is that the group members responsible for determining the direction of group movement are the same members who bear the brunt of the costs of intergroup encounters, and I do not know whether that is the case.

In order to test whether Paul, in the brief period (Nov 11- Nov 28, 1992) following the coup during which he was the only consistent male member of the group, avoided encounters with other groups, I compared the data on ranging patterns for the month of November in 1991 and 1992. First, I plotted the locations of the 44 intergroup encounters I had observed, and I noted that with one exception, they all occurred within 100 meters of rivers and streams, or to the south of the Río Cabuyo. The one riverine area in which the study group never encountered other groups was in the northern half of Quebrada Congo. Thus, I designated all areas within 100 meters of running water (aside from the upper half of Q. Congo) and all areas to the south of the Río Cabuyo as "danger zones." Then I counted the number of days in November of both years in which the group entered a danger zone. In 1991, the group entered danger zones on 9 out of 12 observation days (75%), whereas in 1992, the group entered danger zones on 8 out of 14 observation days (57%). Although the trend is in the right direction to suggest that the study group avoided danger zones more when it had fewer males, the difference between the two years is not great enough to be convincing. There were no intergroup encounters during the period in

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which Paul was essentially the only male in the group. However, there were no intergroup encounters during the comparable period in the previous year's data either.

Males' Reunions with Females Following Intergroup Encounters

If males, by driving away foreign males, are able to (a) preserve the group's access to good foraging areas, and/or (b) prevent a male takeover, thus reducing the risk of infanticide and stress to females, it might be expected that females would encourage or reward males for successful participation in intergroup encounters. When males returned to the rest of the group following intergroup encounters, the females' responses to them were quite varied: most of the time, males were ignored or even threatened when they returned to the group (in fact, females sometimes ignored even the males' lost calls as they searched for the group), but at other times, males were greeted enthusiastically upon their return. It was impossible to analyze reunions in a very systematic way, since all data were from ad lib observations. Thus, I do not have complete records for each male of his participation in the intergroup encounter and the interactions that occurred immediately upon his return to the group. However, use of two-way radios enabled me to coordinate observations with the other observer such that it was sometimes possible to monitor an individual's behavior both during the fight and as the male returned to the group.

The following anecdotes typify the reunions observed:

Incident #6: April 28, 1992, after all of the adult males, plus Quizzler and Kola had chased away another group's males, Curmudgeon, Kola and Guapo simultaneously returned to the rest of the group. Kola made duck faces toward the group as he approached. Curmudgeon did a burst-twitter-bray sequence, and everyone ran toward Curmudgeon. Curmudgeon and Guapo hopped across the river toward the center of the group, and Curmudgeon urine rubbed. Squint and Abby gargled at Curmudgeon, and Squint groomed him. Then Squint did an overlord over Abby at Curmudgeon, and they both threatened him, but he ignored this. Squint and Abby resumed gargling while looking

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at Curmudgeon. Curmudgeon walked away, and the group followed him, still gargling at him. The females and juveniles did not react at all to the return of the other 4 males.

Incident #7: On March 7, 1992, after the 3 adult males won an intergroup encounter, the males began lost calling. The females looked toward the males' calls but did not respond. Finally, Curmudgeon located the females and ran up the hill toward them while twittering loudly. The females did high-pitched vocalizations at him as he approached, and then Curmudgeon and Squint did an intense gargle duet. Hobbes joined in the gargling, and various group members twittered. Squint pressed her face into Curmudgeon's back and did machine gun noises (typically used to greet small infants) to Curmudgeon while he continued to do intense gargles.

On two occasions, females were observed to copulate with males following intergroup encounters. Because matings were exceedingly infrequent, it is unlikely that the timing of these matings was coincidental. On both occasions (which occurred when Paul was alpha male), the females were pregnant, and the matings were with subordinate males. To my knowledge, Paul did not witness either of these matings. One mating was between Curmudgeon and Wiggy. The other, between Abby and Guapo, occurred after hostilities between males had ceased, but while an extragroup male was still observing the mating pair.

It appears that there are some predictable patterns to the females' responses when males return to the group, but these results should be treated with caution due to the lack of systematic rigor with which the data were collected. I did not always witness males' returns to the group, and thus there may be exceptions to the patterns stated here. Females enthusiastically greeted males during reunions only in those instances in which I had scored the encounter as a win or a tie for the study group. Of the 44 encounters, I scored 20 wins (10 when Curmudgeon was alpha, and 10 when Paul was alpha), 11 ties, and 13 losses for the study group. In most cases, the alpha male was the focus of reunions. Curmudgeon was greeted enthusiastically by females and juveniles in at least 7 reunions when he was

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alpha male, whereas Paul was never greeted with such enthusiasm. The most positive response to Paul ever noted following an intergroup encounter was when Squint quietly groomed Paul.

To know whether females actively reward males for successful participation in intergroups, two difficult questions remain to be resolved: (1) What criteria do females use to decide how to respond to returning males? and (2) What is the motivation behind their responses? Because females typically can not see what the males are doing during intergroup encounters, it seems likely that females judge the outcome of the encounter on the basis of vocal and postural cues from the returning males. It was my impression that males returning from successful intergroup encounters tended to be more piloerected, walked with a swaggering gait, and (in the case of Curmudgeon particularly) sometimes produced intense gargle vocalizations, whereas males returning from an unsuccessful intergroup encounter were often still fleeing as they returned, had their hair lying flat, did not vocalize, and tended to look nervously over their shoulders as they approached their own groups.

Perhaps females groomed and gargled to Curmudgeon upon his return from successful intergroup encounters because his body language and vocalizations indicated that he had been successful, thus implying to the females that he had just conferred some benefit on them. However, it is possible that Curmudgeon's behavior following successful intergroup encounters merely implied to the females that Curmudgeon was still in an aggressive frame of mind and should be appeased (via grooming and gargling) so as to prevent him from redirecting aggression toward them. Indeed, the behaviors typically exhibited by Curmudgeon during his returns to the group were most often shown, in other contexts, when males were engaging in intragroup aggression. The second interpretation was suggested to me by the following incident (as well as incident #6):

Incident #8: On Aug. 2, 1992, Curmudgeon returned from routing the other group's males, and urine rubbed as he entered the group. As a group of juveniles and

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infants ran toward Curmudgeon, he gargled and did a burst-twitter-bray sequence. The infants and juveniles gargled at Curmudgeon as he urine rubbed some more. Squint and Curmudgeon did a gargle duet. Abby and Squint followed Curmudgeon, and all three of them gargled, screamed, and did other loud vocalizations. However, moments after Curmudgeon returned, he lay down to rest and closed his eyes. Broma, Squint and Abby, who were still in the vicinity after greeting him, began silently threatening Curmudgeon as soon as he began to nap.

Discussion

Comparisons with Other Capuchin Populations

My observations of capuchin intergroup behavior are consistent with observations of the same species at other sites. At BCI, Oppenheimer (1968) reported that males were the primary participants in intergroup aggression, which consisted mainly of displays and chasing. However, there did not appear to be much (if any) cooperation between males of the same group during intergroup encounters (except that a male spider monkey who had joined a capuchin group sometimes accompanied the alpha male into the other group). Oppenheimer reported that, when intergroup encounters occurred within the study group's territory, those adult females who did not have young offspring remained with the alpha male rather than fleeing (just as Squint did, toward the end of my study). Following a group fission, but before the smaller fission-product contained an adult male, females of both groups participated in intergroup encounters by vocalizing in an apparently aggressive manner. Mitchell (1989), who also studied the capuchins of BCI, reported that, although all group members participated in intergroup encounters to some extent, males were the primary participants. Because intergroup aggression did not tend to start at large food patches, and neither group remained in the vicinity after an encounter was over, Mitchell

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concluded, as I did, that intergroup aggression was not related to the defense of a resource that was immediately present.

Fedigan (1993) found that among the white-faced capuchins of Santa Rosa, males, but not females, actively participated in group defense against extragroup males and against males of other bisexual groups. Rose (1994) found only a slight tendency for males to participate more often than females, and when females did participate, they were more aggressive than were the males. For the most part, aggression occurred within sexes rather than between sexes. All of the 6 intergroup encounters observed by Rose were between "LV" and "Sendero" groups, and females participated in 3 of these encounters. The unusual degree of participation by females in these 3 encounters may be due to one of 2 reasons (Rose, pers. comm.): (1) Sendero group was led by an unusually assertive female during part of the study, when the group contained no males, and (2) during the latter portion of the study, an LV male migrated to Sendero group, where he was the sole male; perhaps because of his former alliance with LV males, the LV males were less aggressive to him than would otherwise be the case. The females of LV group targeted the alpha female of Sendero group during these aggressive encounters, perhaps because she was the acting leader of the group (Rose, pers. comm.). Rose's (1994, pers. comm.) and Oppenheimer's (1968) observations seem to suggest that, when males do *not* behave aggressively in intergroup encounters (e.g. because there are no males in one of the groups), females who normally do not participate in intergroup aggression take up the slack by aggressing against one another. The lack of female participation in the typical intergroup situation, in which there are males in both groups, may be due to one of 2 non-mutually exclusive reasons: (1) Females are afraid to participate in fights involving unfamiliar males because of the high potential cost of wounding or infanticide, and (2) there is no need for females to participate in intergroup encounters if the males are willing to play the role of "hired gun" by chasing away the other group.

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Rose and Fedigan (1995) suggest that the main object of male vigilance is foreign males, rather than predators or members of one's own social group. At Santa Rosa, male takeovers appear to be a potential threat to all group members (Rose 1994). One to several males can invade a group and sometimes succeed in evicting resident males. Infanticides, severe wounding of males, and deaths and disappearances of both males and females, are associated with male takeovers (Rose, 1994; Fedigan et al. m.s.).

Observations of intergroup encounters in *C. olivaceus* (Robinson 1988b) are similar to those of *C. capucinus* in several ways. As in *C. capucinus, C. olivaceus* males (both adult and subadult) are the primary participants in intergroup aggression, and high-ranking adult females participate occasionally. The number and identity of males seemed to be the most important factor determining a group's success in displacing other groups during intergroup encounters. Contrary to what happened at my site (see Table 7.3), there was a fairly stable intergroup dominance hierarchy at Robinson's site.

C. albifrons males are noted for their conspicuous male-male cooperation during intergroup encounters (Janson 1986). In contrast to *C. capucinus* males, who often remain widely dispersed while confronting another group, *C. albifrons* males form a tight unit during intergroup encounters (Janson, per. comm.). In *C. apella*, the alpha male is the only participant in intergroup encounters. Janson (1986) explained the difference in male cooperation between *C. apella* and *C. albifrons* in terms of feeding competition and mate competition. In *C. apella*, the alpha male monopolizes access to food, and females mate almost exclusively with the alpha male. Therefore, subordinate males have little to gain by aiding the alpha male in resource defense and vigilance against predators. In *C. albifrons*, there is less contest competition over food, due to the fact that this species tends to feed in larger fruiting trees than those used by *C. apella*. Females often choose to mate with subordinate males; thus, it is conceivable that all adult males have offspring in the group. Because food and matings are more equitably distributed among *C. albifrons* males than among *C. apella* males, it is more profitable for *C. albifrons* males to cooperate in resource

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defense and anti-predator behaviors (Janson 1986). Defler (1982) reported that intergroup encounters between *C. albifrons* are far more aggressive than those between *C. apella*.

Implications of Intergroup Encounters for Capuchin Social Relationships and Social Organization

C. capucinus' patterns of intergroup encounters conform to the predictions of van Schaik's (1989) model, but not Wrangham's (1980) model. Contrary to the predictions of Wrangham's model, it is males, rather than females, who are the primary participants in intergroup aggression. Males are the targets of other males' aggression during these encounters. Another line of evidence suggesting that intergroup aggression in this species is mainly about mate defense rather than resource defense is that neither group gains access to food resources as an immediate result of the encounter. It is possible that winning intergroup encounters has the effect of increasing home range size over the long-term. Because neither proportion of intergroup encounters won (Table 7.3), nor home range size, appeared to change dramatically over the course of the study, I have no way of assessing that possibility.

As predicted, those group members (high-ranking males and females) who presumably obtain the greatest share of resources (food and/or matings), and thus have the greatest interest in maintaining the status quo by keeping group membership constant, participate most extensively in intergroup aggression.

Because of the large potential costs associated with incursions of foreign males (Rose 1994), there is great value to males in cooperating with the males of their group in defense against foreign males. The costs of sharing food and matings with other males within the social group are presumably offset by the benefits of cooperative defense of females. The need to cooperate with males in intergroup aggression may help explain anomalous instances of altruistic behavior (e.g. searching for lost males) and the highly ritualized sexual behavior (i.e. wheeze dances) that punctuate males' otherwise competitive relationships (see Chapter 3).

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Although intergroup encounters are invariably hostile in nature, males do occasionally engage in non-aggressive interactions with males of other groups. These apparently affiliative interactions are similar in nature to the wheeze dances, which are hypothesized to function in negotiating the future quality of relationships in an intragroup context (see Chapter 6). It seems likely that males are using intergroup encounters as an opportunity to become acquainted with males in other groups, as a way of assessing their options for transfer in the future. Although males sometimes migrate in groups of 2-4, in which case they generally evict the resident males of the group they invade (Fedigan 1993; Rose and Mackinnon pers. comm.), they may also migrate singly and join the resident males of the new group (Oppenheimer 1968; pers. obs.). A male considering taking the latter option should be particularly interested in knowing more about the personalities of males who might become future collaborators and rivals.

If males are doing females a service by repelling foreign males, it might be expected that females would reward males for successful participation in intergroup encounters. One way in which females could reward males for participation in intergroup encounters would be simply by tolerating their presence in the group and by occasionally mating with them. Females, by virtue of the fact that they rarely participate in intergroup encounters themselves, have incomplete information with regard to the extent of male participation in intergroup encounters (although they do know when males flee with them, rather than remaining in the vicinity of the other group). Nonetheless, they often greet males (particularly the alpha male) enthusiastically upon their return from intergroup encounters that were scored as wins or ties (but not from encounters scored as losses). It is impossible, using the current data set, to eliminate the possibility that females are greeting returning males as a means of appeasing them so as to avoid becoming targets of redirected aggression, rather than greeting them because they have successfully routed the other group's males.

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Table 7.1: Rates of intergroup encounters.

Season	Dates	# encounters	observation hours	rate/hour
rainy	5/91-10/91	2	390	.005
dry	11/91-4/92	10	927	.011
rainy	5/91-10/92	8	712	.011
dry	11/92-4/93	22	1592	.014
rainy	5/93	2	82	.024

Table 7.2: Percentage of intergroup encounters in which each member participated*

Male	Age-sex class	overall	as alpha male	as beta male
C	adult male	68-73%	85-95%	54-62%
P	adult male	82-86%	87-96%	75-85%
G	adult male	59-61%		
I	adult male	58%		
K	juvenile male	11-14%		
Q	juvenile male	14%		
H	juvenile male	7%		
A	adult female	7%		
S	adult female	9%		

* members not included in the table never participated

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Table 7.3: Outcomes of intergroup encounters.

Opponent	Year*	Win	Loss	Tie
Rambo II	1st	1	3	1
	2nd	5	3	6
	Total	6	6	7
Vampire	1st	2	0	0
	2nd	0	1	0
	Total	2	1	0
Rambo I	1st	0	0	0
	2nd	0	0	1
	Total	0	0	1
Abran	1st	0	0	0
	2nd	0	0	2
	Total	0	0	2
Unknown	1st	3	2	0
	2nd	9	4	1
	Total	12	6	1
All Groups	1st	6 = 50%	5 = 42%	1 = 8%
	2nd	14 = 44%	8 = 25%	10 = 31%
	Total	20 = 45%	13 = 30%	11 = 25%

* 1st year = May 1991 - April 1992; 2nd year = May 1992 - May 1993

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CONCLUSION

The results of this study of capuchin social relationships indicate that capuchin society is more intricate than previous reports (Buckley 1983, Mitchell 1989, Oppenheimer 1968) have suggested. Several lines of evidence indicate that capuchins have a complex social life in comparison to what is known about smaller-brained platyrrhines such as howling monkeys (Glander pers. comm.), sakis, marmosets (Digby pers. comm.) and muriquis (Strier 1992). Capuchins' social relationships are highly differentiated, and triadic interactions are frequent. Coalitionary aggression is common, and the monkeys show consistency with regard to the partners and victims chosen during conflicts. The two primary decision rules used by both males and females to determine which opponent to support in a conflict are: (1) support females over males, and (2) if the opponents are of the same sex, side with the higher-ranking monkey. There are a few exceptions to these rules, especially when younger females are working their way into the dominance hierarchy. Friendship, as measured by grooming frequency, is another factor that influences the willingness of females to provide coalitionary aid. I have not yet examined the data to determine whether factors such as loyalty or revenge (see Silk 1992b) influence monkeys' willingness to become involved in disputes. Because these have been shown to be important in the coalitionary decisions of some catarrhines (Silk 1992b, de Waal 1982), these analyses promise to be very illuminating regarding capuchin social intelligence.

Because chimpanzees are generally accepted as the yardstick by which other nonhuman primates' social intelligence is measured, it is useful to compare the types of social strategies employed by capuchins and chimpanzees. There are some striking similarities between alpha males of the two species with regard to "separating

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interventions," in which the alpha male breaks up the affiliative interactions of individuals who could pose a menace if they formed an alliance (de Waal 1978). The most striking difference between capuchin and chimpanzee coalition formation is the greater degree of flexibility in chimpanzee patterns of coalition formation. Unlike chimpanzee (de Waal 1978, 1982) or savanna baboon (Nöe 1990, 1992; Smuts 1985) males, capuchin males virtually never form coalitions against individuals higher-ranking than both members of the coalition. Thus, it could be argued that the political landscape for capuchins is more predictable than that of chimpanzees, and therefore requires less social intelligence on a day-to-day basis. On the other hand, the virtual inevitability of third-party involvement, in combination with the relative inflexibility of coalitionary decision rules, provides fewer opportunities -- and therefore greater challenges -- for ambitious capuchins seeking to enhance their status than is the case for chimpanzees.

One aspect of chimpanzee politics that appears to be lacking in capuchins is third-party reconciliation and conflict mediation. In de Waal's (1982) study, adult females often encouraged reconciliations between males or removed weapons from their hands. It was to the advantage of the female chimpanzees to reconcile males, because tension between the males would often result in the males redirecting aggression toward females and immatures. Reconciliation could not be conclusively demonstrated in this study of white-faced capuchins, and the wheeze dances (the best candidates for potentially reconciliatory behaviors) were more often protested than encouraged by third parties. Although capuchins were never seen to encourage the development of affiliative relationships in third parties, or to aid in the repair of other dyads' relationships, capuchins were observed on numerous occasions to disrupt other dyads' attempts at affiliation and relationship negotiation in cases in which alliance formation by the affiliating dyad could have been a menace to the disrupter. Therefore, third party conflict instigation in capuchins may show the same type of cognitive abilities that are implied by conflict mediation and third-party reconciliation in chimpanzees.

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It seems obvious that there is sufficient complexity in capuchin social relationships, particularly in comparison to smaller-brained platyrrhines, that it is not possible to falsify the social intelligence hypothesis for primate brain expansion. "Social complexity" is not a concept that is easily operationalized. Hopefully, with the increase in interest in "Machiavellian intelligence" over the past few years (Byrne and Whiten 1988, Cheney and Seyfarth 1990), researchers across a wider range of taxa will collect systematic data on the sorts of variables that are necessary in order to construct a comparative index of social complexity (Whiten 1994).

Directions for future research

As is the case with most behavioral research, the work described here has raised more questions than it has answered. My next research goal is to address directly questions about social cognition, so that I can make more detailed comparisons of capuchin and catarrhine cognitive abilities. Coalitionary aggression is likely to be a particularly productive area to investigate because of the triadic nature of the interactions and the obvious costs and benefits to the actors. To make an intelligent decision about whom to support in a conflict, an animal must make rapid assessments of its own relationships with both opponents, as well as their relationship with one another. Examination of the exceptions to sex- and rank-based decision rules may reveal that the monkeys base recruitment and support decisions on criteria such as friendship, loyalty, revenge, or past history of sexual interactions. I would also like to examine whether capuchins, when selecting the victims for redirected aggression (i.e. victimization of a previously uninvolved third party immediately after being attacked) take into account the relationship between the redirect victim and the original aggressor. Ultimately, I will synthesize all these analyses to create a nested hierarchy of decision rules used by capuchins in choosing their victims and allies, which will serve as the foundation for an "expert system" of *C. capucinus* coalitionary decisions.

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Once the cognitive rules used in adult coalitionary decision-making are understood, I would like to proceed to examine the development of social cognition in juveniles. Infants and young juveniles make coalitionary decisions that would be completely inappropriate for adults (unpublished data), but young infants' aggression is ignored by adults. As they mature, infants and juveniles begin to be "punished" by adults for behaving inappropriately. I have not yet analyzed these data, but I expect that studying the process by which juveniles acquire the decision rules used in coalitionary aggression will be enlightening.

A more rigorous examination of capuchin vocalizations may yield interesting information about social cognition and the mechanisms by which the monkeys negotiate aspects of their social relationships. Particularly interesting are those vocalizations that are loud enough to incorporate into playback experiments and that are associated with tense social situations. There are several scream types that may, upon careful analysis, prove to convey information about social attributes of the opponent and the intensity of the conflict, as is the case for rhesus monkeys (Gouzoules et al. 1984). Individuals' responses to lost calls may vary depending on the nature of both the long-term relationship between the caller and the listener and the nature of their recent social interactions. It appears that subtle differences in alarm calls correspond to different types of menaces, as is the case in vervets (Seyfarth et al. 1980). More interesting still, there is good anecdotal evidence that white-faced capuchins use alarm calls deceptively, e.g. to distract their antagonists when they are victims of coalitionary attack. Some monkeys' alarm calls are attended to more carefully than others, suggesting that some monkeys have greater credibility than others. Carefully designed playback experiments using alarm calls might be able to determine which monkeys are most credible, and under what circumstances monkeys lose credibility. Wheezes and intense gargles might also provide good material for playback experiments, because they are associated with tense social situations and seem to be instrumental in negotiating relationships. Some individuals are particularly prone to breaking up wheeze

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dances of certain dyads, so by playing back wheezes and intense gargles of certain dyads to certain other individuals, I might be able to determine why some individuals but not others are interested in breaking up wheeze dances.

Playback experiments might also help me better understand the dynamics of intergroup relationships and male-male relationships. Because I was often unaware of the proximity of a neighboring group until the intergroup encounter was underway, and could not immediately locate all of the males, I missed crucial social interactions that might have helped me determine how males decided whether to fight or flee. The issue of intragroup male-male cooperation for the purpose of intergroup male-male competition is critical to an understanding of many other aspects of capuchin social life, as discussed in this thesis. By recording vocalizations (e.g. intense vocal threats, intense gargles, wheezes, lost calls and screams) from males of neighboring groups and playing them back to males in my study group, I might be able to gain insight into the factors that determine whether they initiate an attack on the neighboring group, sneak over to investigate, or flee. Factors that might influence these decisions include proximity of other males at the time the call is played back (e.g. if a male of his own group is watching, the focal male might be more prone to threaten toward the speaker than to flee), degree of despotism by the alpha male (e.g. if the alpha male consistently prevents a subordinate male from affiliating with anyone, the subordinate may be less likely to aid the alpha male in chasing away foreign males), and strength of bonds with immatures (i.e. if a male has fathered offspring in the group and/or has close social relationships with immatures, he may be more prone to defend the group from intrusion by extragroup males).

Obviously, a better understanding of the mating system is critical to understanding many factors about capuchin social life, such as the remarkable strength of some subordinate male/immature relationships, the prevalence of nonprocreative sex, the differential treatment of alpha versus subordinate males by adult females, and the willingness of all males to participate in intergroup aggression. Because of the cryptic

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nature of sexual behavior in fertile females, it will be necessary to obtain genetic data to assess paternity. Determining the relative roles of female choice and male-male competition in determining mating relationships will require daily hormone assays, to pinpoint the timing of estrus, and nocturnal observation with night vision scopes.

A better knowledge of the genetic relationships between group members and the role of female reproductive state in influencing social interactions may also illuminate some intriguing aspects of female capuchin social behavior. It will be interesting to know how females acquire their rank, and whether they are assisted by kin. Another interesting issue is the degree of reproductive competition and cooperation between females. It appears that births are clumped, to some extent, and comparison with data from Santa Rosa (Fedigan et al. n.d.), which is ecologically similar to Lomas Barbudal, reveals that the birth peak is not correlated with any particular season across social groups. Thus, the reason for the synchrony is probably a social one, rather than an external ecological one. One possible benefit to coordinating births is that there are more allonursers available for infants when their mothers are foraging far away. Also, certain locations in the home range might be preferable for mothers of young infants for various reasons (e.g. predator avoidance, avoidance of other social groups, access to certain foods), and having more females with similar interests might give those females more "votes" in determining the direction of group movement. Are the benefits to birth synchrony equal for all females, or do high-ranking females receive disproportionately more of the benefits? The allonursing data in this thesis, though preliminary, imply that high-rankers incur fewer costs at least in that domain. How do females coordinate their reproductive schedules? One possibility is that hand-sniffing plays a role in communicating olfactory information about reproductive state. There are various ways in which females could conceivably control other females' reproductive timing, including pheromonal influences, reproductive suppression via aggression (Wasser and Barash 1983, Wasser and Starling 1988), and interference with mating.

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In some ways, male-male relationships are even more intriguing than female-female relationships. The Santa Rosa data indicate that pairs or groups of males transfer together (Fedigan et al. n.d.). It is not yet known whether the males of these apparent long-term coalitions are related. Perhaps one of the reasons why males have such extended juvenile periods and sometimes remain so long in their natal groups before transferring is that they are assembling a cohort of male relatives before transferring. Or perhaps one of the reasons why adult males, even immigrant males, form close relationships with juvenile and infant males, is that they are forming bonds with males who may have lifelong alliances with them. Only long-term behavioral data at sites where several groups are habituated will be able to answer these intriguing questions.

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