Sex & Friendship in Baboons

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FOREWORD

It is difficult to imagine Africa without the ubiquitous baboon. Surviving all but the most ruthless campaigns of extermination, baboons continue to thrive everywhere, from deep forests to the desert edge. The savannah baboon, the subject of this account, ranges in woodland and veldt from the Tibesti Mountains in the north to Cape Town in the south and across Africa from Djibouti to Dakar. Nowhere else on earth are so many wild mammals of this size living in uneasy commensalism with human populations.

Across the centuries humans have assigned many roles to the baboon. Occasionally, as in Pharaonic Egypt, they held a position of honor in the pantheon. Far more often, they are cast as sly, conniving sneak-thieves, determined to destroy the crops of beleaguered African farmers. Tourists most often see them as temperamental cadgers of tidbits tossed from vehicles. But it is in scientific research that the baboon has found its *métier*.

Over the past 25 years, many hundreds of scientists have accumulated tens of thousands of hours of observations on this absorbing primate, for obvious reasons: they are large, diurnal monkeys that are easy to observe when they forage in short grassland; they are flamboyant in appearance and temperament and highly social by inclination. They are, in fact, nature's gift to the behaviorist, and it is fair to say that baboons (together with their close relatives the macaques) have been as important to field biology as *Drosophila* has been to genetics or the white rat to psychology and medicine.

Those who have been privileged to watch baboons long enough to know them as individuals and who have learned to interpret some of their more subtle interactions will attest that the rapid flow of baboon behavior can at times be overwhelming. In fact, some of the most sophisticated and influential observation methods for sampling vertebrate social behavior grew out of baboon studies, invented by scientists who were trying to cope with the intricacies of baboon behavior. Barbara Smuts' eloquent study of baboons reveals a new depth to their behavior and extends the theories needed to account for it.

Indeed, this volume presages primate studies of the 1980s. While adhering to the most scrupulous methodological strictures, the author yet maintains an open research strategy—respecting her subjects by approaching them with the open mind of an ethnographer and immersing herself in the complexities of baboon social life before formulating her research design, allowing her to detect and document a new level of subtlety in their behavior. At the Gilgil site she could stroll and sit within a few feet of her subjects. By maintaining such proximity she was able to watch and listen to intimate exchanges within the troop; she was able, in other words, to shift the baboons well along the continuum from "subject" to "informant." By doing so she has illuminated new networks of special relationships in baboons. This empirical contribution accompanies theoretical insights that not only help to explain many of the inconsistencies of previous studies but also provide the foundation for a whole new dimension in the study of primate behavior: analysis of the dynamics of long-term, intimate relationships and their evolutionary significance. The importance of this achievement is easier to understand when placed against the earlier history of baboon studies.

Systematic field research on baboons falls into a series of broadly overlapping periods. Early descriptive studies, such as my own, were undertaken in the late 1950s and early 1960s, but these were soon supplanted by the establishment of long-term projects at several sites in which detailed observations by successive teams of scientists made it possible to document the behavior of each individual baboon through most of its lifetime. Correlational analyses of large sets of quantitative data were used to test general hypotheses about social organization and life history variables. The most recent period, beginning in the mid-1970s, was structured by the revolution then taking place in evolutionary vertebrate ecology; newly refined hypotheses were formulated and tested against this new paradigm. Research emphases shifted to questions about the "strategies" in baboon life: inclusive fitness, optimal foraging, resource competition, and life history strategies.

In all of these studies, it was necessary to "objectify" the animals and their behavior in order to purge primate studies of the easy anthropomorphism of the turn of the century. Coding and sampling methods were developed to minimize observer bias, and these still form the backbone of all mammalian studies. By wedding such precise methods to the powerful predictive theories of the new behavioral ecology, scientists believed that the major intellectual questions in baboon studies would soon be answered; what remained was the careful doc-

umentation of such principles as kin selection, resource competition, and game theory analyses of aggression. But early returns were puzzling; there were nagging inconsistencies. The most dominant males did not always acquire the most mates. Both males and females exhibited strong mating partner preferences, but the reasons for these preferences were not obvious. Males who were unlikely to have fathered particular infants were nevertheless observed to develop tender, caring relationships with them. And so on. Baboon behavior could not be neatly accommodated by our research methods and theoretical expectations. As this volume so elegantly illustrates, new methods were needed that allowed observers to focus on those behaviors that were most meaningful to the animals themselves, and new theories had to be developed to explain the often surprising findings that emerged.

In retrospect, it is clear that at every stage of research we human observers have underestimated the baboon. These intelligent, curious, emotional, and long-lived creatures are capable of employing strategems and forming relationships that are not easily detected by traditional research methods. In the process of unravelling their complex social relationships, Smuts has revealed that these masters of strategy and aggressive competition are equally capable of patience, tenderness, and concern. Reading this volume, one feels that the real baboon story is now beginning to unfold.

Irven DeVore
Harvard University

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This book reflects the influence of four people who played a central role in my training. Bob Trivers introduced me to evolutionary theory and showed me, by example, the joy of scientific discovery. From Irv DeVore I inherited a fascination with baboons and a conviction that their behavior was complex, multifaceted, and worthy of intensive scrutiny. David Hamburg's wisdom guided me through all phases of my graduate training, and his belief in the evolutionary significance of emotions and enduring social bonds inspired this work. Robert Hinde's insights about how to study relationships helped me to translate my idealistic goals into concrete results.

I watched baboons with several co-workers whose companionship greatly enlivened and enriched my time in the field: Nancy Nicolson, Julie Johnson, Sylvia Howe, and John Watanabe. All four contributed data cited in this book, for which I am very grateful. For helping to make Kenya a home away from home I thank Joab Litzense, Barbie Allen, and the Mehta family of Gilgil, especially Kasim.

Bob Harding and Shirley Strum, codirectors of the Gilgil Baboon Project, made it possible for me to study Eburru Cliffs troop and provided encouragement and support for my research. Dr. Strum introduced me to the baboons and shared her previous knowledge of the troop. During the last phase of this project, Josiah Musau and Francis Milili provided invaluable field assistance under trying circumstances. Robert Sapolsky generously shared information he collected during the capture of the troop's males.

I am grateful to the government and people of Kenya who made this study possible. I thank especially the Office of the President for permission to conduct research and the Gema Cooperative for permission to study baboons on Kekopey Ranch. As it does for all primate researchers in Kenya, the Institute for Primate Research provided me with crucial logistical support. I thank Dr. James G. Else, Director, and the staff of the Institute for their help.

During the long process of writing, Peter Ellison, Paul Harvey, Jim Moore, Shirley Strum, and Richard Wrangham made very useful

comments on various drafts of the manuscript. Dorothy Cheney, Robert Seyfarth, Robert Smuts, and John Watanabe meticulously reviewed the entire book and provided many detailed suggestions for its improvement. Without their help this book would have been very different, and I am deeply grateful to them for sharing their time and thoughts so generously. I also thank Jeff Kurland and Frans de Waal for contributing photographs used to open Chapter 10.

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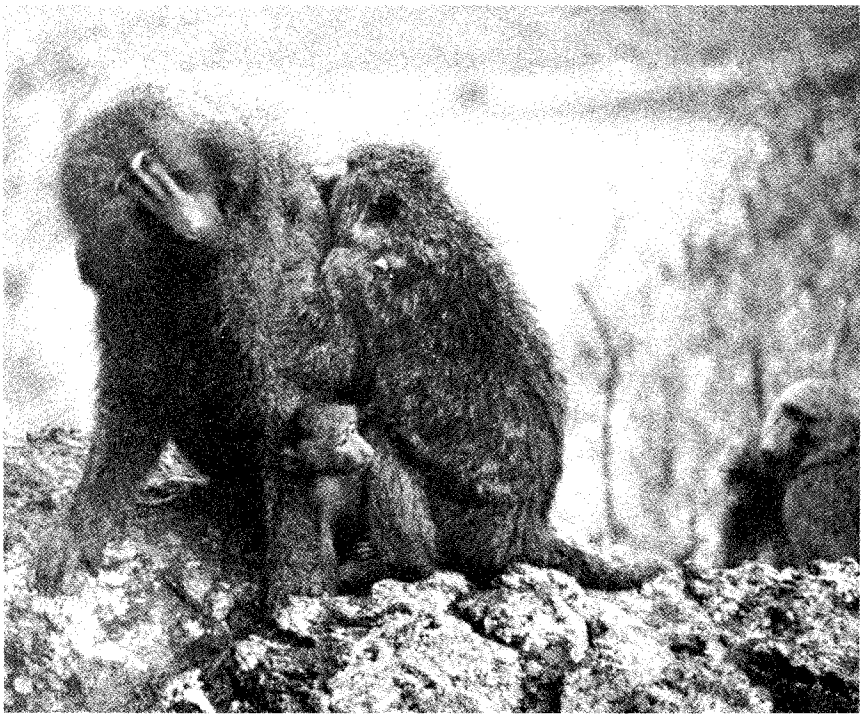
This book is about the role that friendship plays in the lives of baboons, and it is therefore fitting to conclude by acknowledging the critical role that friendships have played in the completion of this book. During every phase of the work, the colleagues who provided critical appraisals were also the friends I looked to when creative energy ebbed and gumption waned. In addition to those already mentioned, I thank Lila Abu-Lughod, Bob Bailey, Vicki Burbank, Tony Collins, Nancy DeVore, Brazy de Zalduondo, Pippi Ellison, Mitzi Goheen, Sarah Hrdy, Lysa Leland, Kathryn Morris, Laura Norman, Nadine Peacock, Elizabeth Ross, Jon Seger, Karen Strier, Tom Struhsaker, and Pat Whitten. Their unfailing generosity of spirit embodies for me the thesis of this book: friendship indeed lies at the heart of social life.

My family has contributed to this book in so many ways that it is impossible to express fully my appreciation for all they have done. I thank my parents for showing me that the pursuit of challenging work is one of life's main rewards and for supporting all of my efforts to put this lesson into practice. To Mal, Marybeth, and Robert, thank you for being there. Finally, thanks to John Watanabe, for his encouragement, inspiration, and humor throughout every stage of this project, and most of all, for going to Kenya to meet Alex, Daphne, and the others and then telling me, "Now I understand why you love baboons."

He who understands the baboon would do more toward metaphysics than Locke.

Charles Darwin

1 INTRODUCTION



Pandora grooms Virgil on the sleeping cliffs at the end of the day. Pyrrha, Pandora's daughter, peeks out at other baboons resting nearby. Friends often groom on the cliffs in the evening before going to sleep.

PROLOGUE

It was late afternoon, and the angled light brought into clear relief the sculptured planes of the baboons' bony muzzles, highlighting the individuality of each face. In this light, I had no trouble recognizing Virgil and Pandora 100 m away, traveling slightly apart from the rest of the troop, wandering slowly toward me. Their steps were leisurely and their movements relaxed as they picked an occasional handful of young grass or dug for a bulb or root. By this time, the baboons had usually satisfied their voracious appetites, and when they sat they tended to lean back slightly as if to offset the weight of their full stomachs, which bulged above their feet, neatly placed close together. Virgil sat just this way, his chin pointed down and resting against his chest so that his expression, when he glanced up without moving his head, looked a little shy. But there was no hint of shyness in his face when he spotted Pandora, shuffling along behind him, apparently intent on finding a tasty bug or two under the small rocks she was turning over, one by one. He hunched his shoulders, pulled his chin in still further, flattened his ears against his skull, and made the skin around his eyes taut, showing the bright white patches of skin above each eyelid. At the same time, he alternately smacked his lips together rhythmically and grunted deeply with the slight wheeze that distinguished Virgil's voice from those of the other adult males. Pandora, 5 m away, looked up and made a similar face back at Virgil and then, abandoning her rocks, headed toward him with the ungainly trot of a baboon anxious to get somewhere fast, but too lazy to run. As she approached, Virgil lip-smacked and grunted with increasing intensity, as if encouraging her to make haste. When she arrived, she plopped herself down on her back next to him and, dangling one foot in the air, presented her flank in an invitation for grooming. Virgil responded promptly, gently parting the sparse hairs on her belly with his hands, every now and then lightly touching her skin with his lips to remove a bit of dead skin or dirt from her fur.

But Virgil, like most male baboons, preferred being groomed to grooming, and after a few minutes he slowly sank to the ground, expelling his breath in a deep sigh. Pandora groomed him intently, working her way up his neck to the area around his eyes, carefully removing the grit that had accumulated there over the course of the day. After a few moments, they were joined by two of Pandora's offspring, Plutarch, a juvenile male, and Pyrrha, an infant female. Pyrrha was in a rambunctious mood, and she used Virgil's stomach as

a trampoline, bouncing up and down with the voiceless chuckles of delight that accompany baboon play. Every now and then Virgil opened his half-shut eyes, peered at Pyrrha, and gently touching her with his index finger he grunted, as if to reassure her that he did not mind the rhythmic impact of her slight body against his full stomach.

After a while, Pandora stopped grooming, and Virgil moved away, slowly clambering up the cliff face where the troop would spend the night. He glanced back every few steps at Pandora and her family, who followed right behind. Finding a good spot halfway up the cliff, Virgil made himself comfortable. Sitting upright, he leaned backward against the rock face, and, grasping his toes in his hands, let his head sink to his chest—a typical baboon sleeping posture. Pandora sat next to him, leaning her body into his, one hand on his knee, her head against his shoulder. Her offspring squeezed in between Pandora and Virgil, and, in the dimming light, I could not tell where the body of one baboon began and the other left off. This is how they would remain for the rest of the night.

Virgil and Pandora were in late middle-age and had lived in Eburru Cliffs (EC) troop for at least 5 years. For the past year, while I had been spending my days with this troop, and probably for long before that, they had been close associates, feeding near one another during the day and sleeping together at night. Although Virgil and Pandora had probably mated in the past, their bond was not dependent on sexual activity. During my time with EC, at first Pandora was pregnant and later nursing her infant, so she was not sexually receptive during this period.

On the cliffs nearby was another pair, Thalia and Alexander. Thalia was an adolescent female who had not yet experienced her first pregnancy. At the moment, she was in the quiescent phase of her monthly sexual cycle, but in a few days the bare skin on her bottom would begin to swell, and for about 2 weeks she would exhibit the exuberant sexuality characteristic of adolescent female baboons. Alexander, also an adolescent, had a long, lanky body and an unusually relaxed disposition. He had transferred into EC troop just a few months earlier. Thalia, like the other females in the troop, was wary of this interloper and tended to avoid him during daily foraging. But as I watched the two of them sitting on the cliffs about 5 m apart, it was clear that, in Thalia, fear and interest were mixed in an uneasy balance.

Alexander was facing west, his sharp muzzle pointing toward the setting sun, watching the rest of the troop make their way up the cliffs. Thalia was grooming herself in a perfunctory manner, her attention

elsewhere. Every few seconds she glanced out of the corner of her eye at Alexander without turning her head. Her glances became longer and longer and her grooming more and more desultory until she was staring for long moments at Alexander's profile. Then, as Alexander shifted and turned his head toward Thalia, she snapped her head down and peered intently at her own foot. Alexander looked at her, then away. Thalia stole another glance in his direction, but when he again glanced her way, she resumed her involvement with her foot. For the next 15 minutes, this charade continued: Each time Alexander glanced at Thalia, she feigned indifference, but as soon as he looked away, her gaze was drawn back to his face. Then, without looking at her, Alexander began slowly to edge toward Thalia. Their glances at one another became more frequent, the intervals between them shorter, and their interest in other events less convincing. Finally, Alexander succeeded in catching Thalia's eye as she was turning away. He made a "come-hither" face—the same face Virgil had made at Pandora—grunting as he did so (Figure 1.1). Thalia froze, and for a second she looked into Alexander's eyes. Then, as he began to approach her, she stood, presented her rear to him, and, looking back over her shoulder, darted nervous glances at him. Alexander grasped her hips, lip-smacking wildly, and then presented his side for grooming. Thalia, still nervous, began to groom him. Soon she calmed down, and I found them still together on the cliffs the next morning.

This event represented a triumph for Alexander who, as a newcomer, had been trying for several weeks to establish a relationship with Thalia. As far as I knew, this was not only the first time a female had groomed him for more than a few seconds but also the first time he had spent an entire night close to one. From this moment on, he and Thalia spent more and more time together during the day, until they formed a consistent pair within the troop. Looking back on this event months later, I realized that it marked the beginning of Alexander's integration into the troop.

STUDYING SEX AND FRIENDSHIP IN BABOONS

Soon after I began studying wild baboons in 1976, I realized that relationships like that between Virgil and Pandora or Alexander and Thalia were a central feature of baboon society. The idea of studying these long-term, cross-sex "friendships" provoked my interest for several reasons. Traditional studies of male–female relations in nonhuman primates had focused on male–male competition for mates and on brief bonds between males and sexually receptive females. In many of

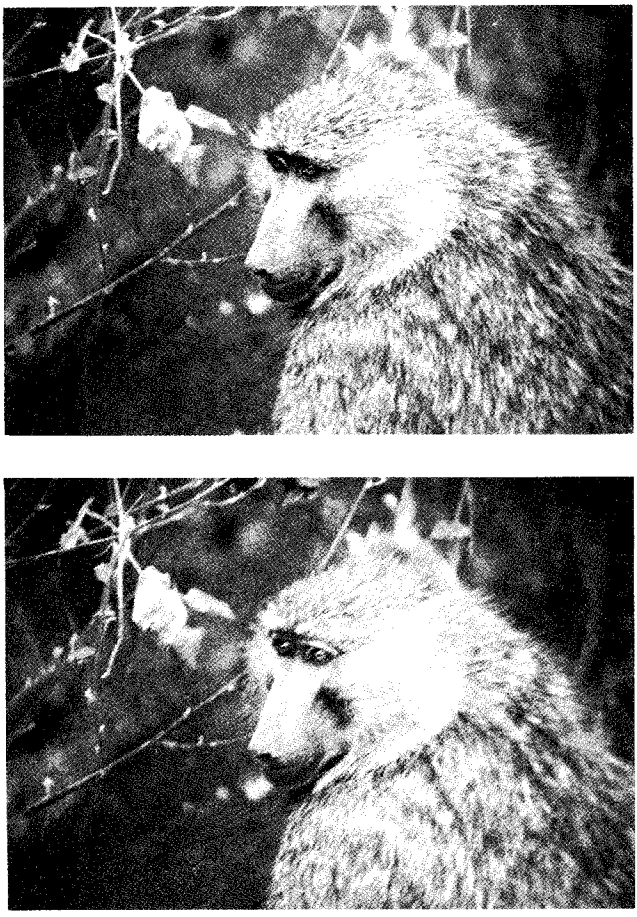


Figure 1.1. (*Top*) Adult female with normal facial expression. (*Bottom*) Same female making the "come-hither" face.

these studies, females were treated as relatively passive objects of competition who were of little interest once they conceived and were no longer sexually active.

Because female monkeys are normally either pregnant or lactating, however, periods of sexual activity constitute a very small proportion of their adult lives, and so the vast majority of interactions between males and females from the same troop are not explicitly sexual. Surely these "nonsexual" interactions—whatever they involve—must be crucial to understanding what goes on in the sexual arena. In particular,

I suspected that a detailed knowledge of cross-sex relationships might provide important insights into the role females played in mate selection. Female choice of mates is considered an important force by evolutionary biologists (e.g., Darwin, 1871; Fisher, 1930; Bateman, 1948; Trivers, 1972), but, until recently, primatologists have paid it little attention.

Furthermore, a perspective that included female choice as well as male–male competition might help to explain several puzzling findings. If, as many primatologists had assumed, successful competition against other males was the primary determinant of male access to mates, then high-ranking males consistently should breed more often than lower-ranking ones. This, it turned out, was not always the case; numerous studies reported higher than expected frequencies of mating by lower-ranking, often older, males (DeVore, 1965; Saayman, 1971a; Hausfater, 1975; Packer, 1979b; Manzolillo, 1982; Strum, 1982). Another puzzling finding was the high degree of association between some adult males and particular infants, first documented by Ransom and Ransom (1971). What were these large, ruthless fighters doing in the "female domain," looking slightly out of place as they cuddled and carried tiny infants? Models that focused on aggressive competition among males did not predict the existence of prolonged, affiliative relationships between either males and females or males and infants, yet such relationships clearly existed. I thought that a detailed study of cross-sex friendship might help to explain these findings and also contribute to a more complete understanding of baboon society.

This investigation of baboon friendship involved two major problems: one related to theory and the other to observation. My curiosity about issues like female choice and male–male competition reflects my interest in evolutionary theory, an interest shared by many of the scientists who spend their time watching animals. As intellectual descendants of Darwin, we are all concerned with the problem of ultimate or evolutionary causes of behavior. Has natural selection favored friendships among baboons? Specifically, does having a friend of the opposite sex help an individual to maximize his or her genetic contribution to future generations? These questions assume that male–female friendships are not simply historical accidents or idiosyncratic expressions of baboon psychology, but rather that they are products of evolution analogous to phenomena with more obvious adaptive value, such as maternal care or predator avoidance. This assumption, in turn, allows one to take full advantage of a series of powerful theories for explaining behavior developed by evolutionary biologists over the last 100 years.

This evolutionary perspective played a large role both in formulating my goals at the start of the study and in interpreting results during data analysis. The research itself, however, often took on a very different character due to the powerful influence of my subjects—the baboons. Many primate field workers compare their jobs to watching soap operas, except that the characters are real and they do not speak. This is an apt comparison because what captured my interest and motivated me to return to observe my subjects again and again was the daily drama of baboon life. As a result, all of the larger questions we begin with—for example, how do friendships contribute to individual reproductive success?—quickly become translated into a series of much more immediate, often compelling questions about phenomena of immediate concern to the baboon themselves. How does a friendship form? What makes it survive or, instead, falter in the early stages? Why does this male have half a dozen female friends, while that one has none? Even more basic, what exactly is friendship to a baboon? It was possible that the pairs I considered friends simply represented one end of a continuous distribution, with pairs who spent a lot of time together at one end and pairs who spent much less time together at another. However, it was my impression that interactions between friends differed not only in frequency but also in kind from interactions between other dyads, and that friends did indeed constitute a distinct category of relationships. The challenge was to reformulate this knowledge in a way that would permit both scientific scrutiny and objective communication to others without completely sacrificing the immediacy and vividness of the raw observations. Meeting this methodological challenge was a second major goal of the study.

The organization of this book reflects my two principal theoretical and methodological concerns. Research on any animal must begin with a general knowledge of the species' distribution and social organization, and Chapter 2 provides this information. It also introduces the EC baboon troop and the females and males who were the focus of this study. Chapter 3 describes what it is like to watch baboons and how I structured my observations in order to address the problems and questions discussed above.

Chapter 4 defines baboon friendships and considers how individual attributes like age and status affected the number and types of friends that an individual had. Chapter 5 investigates the role played by each sex in maintaining friendship and the ways in which the interactions of friendly dyads differed from those of other pairs.

Chapters 6, 7, and 8 turn to evolutionary questions by considering how baboon social relationships might contribute to individual repro-

ductive success. Chapter 6 analyzes the reproductive benefits of friendship from the female perspective, including male protection of female friends and affiliative relationships between males and infants. Chapter 7 investigates male–male competition for mates, and Chapter 8 considers the reproductive benefits of friendship from the male perspective. Through an analysis of the intimate connection between sex and friendship, Chapters 7 and 8 attempt to integrate information on male–male competition and female choice into a more unified model of male reproductive strategies.

Chapter 9 turns to some of the questions that to me are the most fascinating and frustrating ones raised by this study. Does the nature of friendship change through the life cycle? Are friendships disrupted by the female's sexual interest in another male? What roles do courtship and possessive behaviors play in establishing and maintaining friendships? Do baboons feel emotions like jealousy, ambivalence, and grief toward their friends?

These are fascinating questions because they concern issues of great relevance to human relationships, but they are also frustrating because they are the most difficult to answer—or even approach—in a scientific manner. Yet because I firmly believe that such questions can and should be addressed without abandoning scientific rigor, I make a preliminary attempt to do so here.

Chapter 10 considers male–female relationships in other primates, including ourselves, in light of issues raised by this study. It concludes by suggesting a different view of the evolution of human pair-bonds from the ones traditionally offered.

Although the first 5 chapters emphasize description and the last 5 interpretation, the two levels of analysis are not really separate. Many of the hypotheses about the evolutionary significance of friendships discussed in the second half of the book are the results of sudden insights that came to me while I was watching baboons. Conversely, the types of behaviors I paid the most attention to in the field were determined, in part, by the evolutionary framework I had adopted. This interplay between theory and observation, which was important at all stages of the research, is reflected in the presentation of information and ideas in this book. My goal in doing so is to convey a feeling for the process, as well as the results, of the study of primate behavior.

2 BABOONS

Eburru Cliffs troop moves away from the sleeping cliffs early in the morning. Some animals, still sleepy, rest quietly while their companions forage in the grass.

INTRODUCTION

Baboons and macaques are grouped together in the subfamily Cercopithecinae, which also includes the less well known mangabeys and guenons. Although there are important exceptions, in general mangabeys and guenons are forest-dwelling monkeys who spend the majority of their time in the trees, whereas baboons (in Africa) and macaques (in Asia) tend to live in more open country, spending much of their time on the ground. Baboons are found throughout sub-Saharan Africa from coast to coast and in the Arabian Peninsula.

Five types of baboons are grouped together in the genus *Papio*: the hamadryas, the Guinea, the yellow, the chacma, and the olive baboons. These five types were originally considered separate species (e.g., Jolly, 1966; Napier and Napier, 1967). Recent evidence, however, indicates that different types interbreed when they come into contact in the wild, suggesting that they are more appropriately viewed as racial variants of a single species, *Papio cynocephalus* (Nagel, 1973; Shotake, 1981; Jolly and Brett, 1973). According to this view, the olive baboons who were the subjects of this study are classified as *Papio cynocephalus anubis*. Throughout, the different types of baboons will be referred to by their common names.

Three of the five types of baboons, the olive, yellow, and chacma, have very similar social organizations. These three types, often grouped together under the name "savannah baboons," live in large groups of anywhere from 20 to 200 animals that contain several adults of both sexes. Savannah baboons are *promiscuous*, a term used by animal behaviorists to describe a breeding system in which both females and males tend to mate with several different members of the opposite sex. Hamadryas baboons, in contrast, are *polygynous*: One male mates exclusively with several females who belong to small, one-male social units. (Little is known about the social organization of Guinea baboons.)

The distribution of savannah baboons is continuous, so that olive baboons, the most northerly species, are replaced by yellow baboons further south; yellow baboons, in turn, are replaced by chacma baboons whose range extends to the tip of southern Africa (Napier and Napier, 1967). Olive baboons, the subjects of this study, are darker, stockier, furrier, and altogether more bearlike than the paler, more gracile yellow baboons, and many chacma baboons are even larger and darker than olive baboons. It is possible that these differences in appearance are also paralleled by differences in social organization and behavior, but our knowledge of the three species is still too imprecise to tell. For

this reason and because of their continuous distribution and close genetic relationships (Cronin and Meikle, 1982), observations from all three types of savannah baboons will be treated equally whenever results from different baboon populations are compared.

My study was based on a troop of olive baboons named "Eburru Cliffs," which is part of a population of baboons living near the small town of Gilgil in the Great Rift Valley of Kenya, about 100 km northwest of Nairobi. Further details about the Gilgil baboons and the study troop are given below, but a brief review of the social organization of savannah baboons is given first.

BABOON SOCIAL BEHAVIOR: A BRIEF SUMMARY

Social Organization

Most baboon groups, or "troops" as they are often called, contain several adult males, and because males are almost twice as large as adult females, they tend, at least initially, to capture the observer's attention. Partly for this reason and partly because of androcentric biases, early research on baboons (and many other primates) tended to emphasize the role adult males play in maintaining group cohesion (e.g., Hall and DeVore, 1965). Only after groups were studied for several years did it become obvious that it was the adult females who formed the core of the social system in savannah baboons—a pattern previously described for Japanese macaques (e.g., Kawai, 1958, 1965; Kawamura, 1958, 1965) and rhesus macaques (e.g., Sade, 1965).

In savannah baboons, macaques, vervet monkeys, and most other Old World monkeys, females remain in their natal groups throughout their lives, whereas males generally move to another group as adolescents. The females in a baboon troop are therefore related to one another through common ancestors. Closely related females—mothers and daughters, sisters, and sometimes even grandmothers and granddaughters or aunts and nieces—tend to associate with one another, forming kin-based subgroups within the larger troop. This pattern of association with kin also holds for immature males who have not yet left their natal group (Johnson, 1984). In addition to frequent exchanges of friendly behaviors like grooming and sitting close together, members of the same matriline also support one another during aggressive encounters with other troop members.

Female baboons frequently avoid other females during foraging, and exchanges of threatening and submissive gestures between them are common. Fights also occur, but they are less frequent than threats or submissive behavior. Primatologists use these types of interactions,

often referred to as "agonistic behaviors," to determine dominance or "agonistic rank." If, for example, baboon B consistently avoids and shows submission toward baboon A, and A consistently threatens B but does not avoid her, then A is considered dominant to B. Among female baboons, dominance relationships are clear-cut (reversals of outcome are rare), linear (if A ranks above B and B ranks above C, than A also ranks above C, and so on), and relatively stable over many years (Hausfater *et al.*, 1982; but see Smuts, 1980 and in preparation). Adult daughters usually rank just below their mothers, so that whole matrilines can be ranked with reference to one another. These patterns are very similar to those found in macaques (Kawai, 1965; Kawamura, 1965; Sade, 1967; Silk *et al.*, 1981b) and vervets (Seyfarth, 1980; Bramblett *et al.*, 1982).

Many researchers have suggested that in female baboons, macaques, and other Old World monkeys with similar social organization, female dominance rank is an important determinant of female reproductive success, because higher-ranking females often have priority of access to resources that affect reproduction, such as food and water. Sometimes higher-ranking females do score higher on various measures of reproductive success (Dittus, 1979; Dunbar, 1980; Sade *et al.*, 1976; Silk *et al.*, 1981a; Whitten, 1983), but in other cases they do not (Cheney *et al.*, 1981, 1985; Gouzoules *et al.*, 1982). Although long-term effects of female rank are controversial, there is abundant evidence to show that, in the short-term, female rank affects a wide variety of behaviors. For example, high-ranking females are groomed more often by other females (Seyfarth, 1977, 1980) and by immatures (Cheney, 1978; Silk *et al.*, 1981c), are less vulnerable to harassment by other females when they are caring for young infants (Altmann, 1980; Silk, 1980), and have greater access to the best feeding and drinking sites (Cheney *et al.*, 1981; Wrangham, 1981; Whitten, 1983). Because female rank has been shown to have important effects on female behavior, I often include it as a variable in my analyses of male–female interactions.

Although rank and kinship are important determinants of female–female relationships, they are by no means the only significant factors. Unrelated females of disparate ranks sometimes form close bonds (personal observation), and because baboon females are strongly attracted to mothers carrying young infants, all females go through periods of intense social interaction with other females (Seyfarth, 1976; Altmann, 1980).

Unlike females, adult male baboons rarely associate with members of their own sex. Close proximity between adult males is rare, and

grooming almost never occurs. With rare exceptions, males come together only to greet, fight, form alliances against other males, or compete over the same resource (Smuts and Watanabe, in preparation). Male dominance relationships are not so clear-cut or stable as those of females (Hausfater, 1975), although in some troops temporary linear hierarchies can be identified (e.g., Packer, 1979b). Male–male relationships are discussed in greater detail in Chapter 7.

Development

Baboon births occur throughout the year, although in some populations there may be seasonal birth peaks (Altmann and Altmann, 1970). Baboons are born with a dark, velvety coat that is replaced by the browner adult pelage by around 7 months. These babies are generally referred to as "black infants." Infants cling to the mother's belly and later ride on her back until they are at least 1 year old, and weaning is completed between 1 and 2 years (Nicolson, 1982). By this time, infants are spending a great deal of time away from the mother, often playing with peers, but they tend to return to her when frightened, during the rest periods that punctuate the day, and at night.

Both females and males reach puberty at about 4–6 years of age, although there is great individual variation in rates of development (Altmann *et al.*, 1977; Scott, 1984). Females continue to grow for only 2 or 3 more years after puberty, but males do not reach full adult size until they are around 9 or 10. Fully grown males have much longer and sharper canines than adult females, the hair around the neck and shoulders is much longer, forming an impressive mane, and they weigh about twice as much as adult females.[1]

By the time growth has stopped, most males have left their natal troop to join another. In the Gilgil population, however, some males remained in their natal troops (Strum, 1982; Manzolillo, 1982; personal observation; see Chapter 7). Partly because males reach full adulthood at a later age than females, the typical baboon troop contains many more adult females than adult males. Mortality rates may also be higher among subadult and adult males than among females of comparable age. It is difficult, however, to obtain accurate information on male mortality, because when a male disappears from a troop, observers often have no way of knowing whether he has died or transferred to another troop.

[1] Mean adult male weight in Eburru Cliffs: 24.4 kg (s.d. 2.4), $N = 11$; mean adult female weight: 12.8 kg (s.d. 1.3), $N = 30$.

Estrous Cycles and Mating Behavior

Female baboons, like human females, undergo menstrual cycles once they reach puberty, but these cycles are normally referred to as *estrous cycles*, a term applied to the reproductive cycles of many other mammals. Females who are experiencing estrous cycles will be referred to as "cycling females" to differentiate them from *anestrous* (noncycling) females.

Wild female baboons usually have their first estrous cycles when they are 4–6 years old but do not conceive until 1 or 2 years later (Altmann *et al.*, 1977; Strum and Western, 1982; Scott, 1984). Gestation lasts about 6 months. Following the birth of an infant, the mother undergoes a period of amenorrhea when she does not cycle. If the infant dies before being weaned, the mother resumes sexual cycling within a few days or weeks. Otherwise, cycling does not resume for from 5 to 21 months after birth, with a mean of 14 months for EC troop (Nicolson, 1982). Females typically have several cycles before they conceive. The length of the interval spent cycling before conception varies considerably among females of the same troop. It can be as short as 1 month or as long as 15 months; the mean for EC troop was 6 months. In EC, the mean interbirth interval for mothers whose previous infants survived was 26.5 months (Nicolson, 1982).

The estrous cycle lasts for about 35–40 days (Scott, 1984). After 2–3 days of menstruation, the perineal area begins to swell, reaching maximum tumescence within 1–2 weeks. The perineum remains fully swollen for about 7–10 days. A rapid and obvious decrease in the size of the swelling marks the onset of detumescence. The swelling continues to decrease in size for several days and then disappears. About 10 days later, the female menstruates (if she has not conceived), and the cycle begins again. Ovulation occurs about 1–4 days prior to detumescence (Hendrickx and Kraemer, 1969; Wildt *et al.*, 1977; Shaikh *et al.*, 1982). Following Hendrickx and Kraemer (1969), and Hausfater (1975), the day of detumescence is labeled "D-day"; the first day preceding D day is labeled "D-1"; the second preceding day "D-2," and so on. Cycle days that follow the onset of detumescence are labeled "D + 1," "D + 2," etc.

As soon as their perineums begin to swell, adolescent and adult females are sexually receptive, and they will solicit copulations from males of all ages, including infants. Immature males are eager to copulate with any sexually receptive female, but fully adult males are much more discriminating (Hall and DeVore, 1965; Hausfater, 1975; Collins, 1981; Scott, 1984). They show the greatest sexual interest