

BARBARA B. SMUTS

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SEX AND FRIENDSHIP



IN BABOONS



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With a New Preface

**BARBARA B. SMUTS**

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# SEX AND FRIENDSHIP IN BABOONS

**In Memory of Alex and Daphne**



## PREFACE, 1999

When we say that we have a personal relationship with someone, we mean that we have a bond based on our individual identities, a relationship in which who I am and who you are makes a difference to how we are with each other. This book demonstrates that baboons also form such personal relationships. Adult females pair up with adult males in distinctive partnerships that stand out from the vast majority of female-male relationships. Sometimes these partnerships are intense but brief. Sometimes they last for much of an adult lifetime, sliding into an easy intimacy characterized by the freedom to ignore each other. Sometimes two adolescents, both new to the complicated world of adult sexuality and parenthood, become partners. Sometimes an old female, wise in the ways of males, bonds with a fierce, newly mature male who follows her around with puppy-like devotion. Sometimes two aging partners feed and rest in companionable silence, as they have done day in and day out for many years.

Some friendships are calm and low-key, leaving plenty of opportunity for each partner to socialize with other members of the opposite sex. Others are volatile, full of jealousy and periods of cold-shouldering, followed by reconciliations and good times. Some pairs spend much time together but rarely touch, while others groom frequently, embrace when their paths cross, and huddle together at night.

These relationships change as each baboon goes through different phases of life and matures into an ever-more idiosyncratic individual. Some relationships dissolve: the male leaves the troop for greener pastures; the female falls for someone else during a series of intense sexual encounters; the male gains in status and drops his adolescent friend for a new bond with the alpha female. Others settle into comfortable, relaxed familiarity.<sup>1</sup>

The reasons baboons form friendships with members of the opposite sex seem almost as diverse as the many forms these friendships take.<sup>2</sup> Young adult males who have just entered a troop in which strength doesn't guarantee sex cultivate bonds with females, both as a way to penetrate a complex network of interlocking ties and as a way to entice



females into mating with them later.<sup>3</sup> Older males that have already consorted with several females maintain bonds with some of them through the many months of pregnancy and lactation, long after the females have lost their sexual appeal.<sup>4</sup> These males befriend the females' tiny infants, protecting them from predators and from other baboons, perhaps especially against other males contemplating infanticide.<sup>5</sup> Maybe the male is protecting his genetic stake.<sup>6</sup> Maybe he is showing the female that if she consorts with him again the next time, he will stick around and help her. Maybe he is doing both.<sup>7</sup>

A female may go for a male because he invites her and her infant to forage near him, keeping other males and higher-ranking females away without asking much in return. Another female may prefer a recent immigrant because his ability to intimidate every other male in the group makes her feel relatively safe around him, even though he sometimes beats her up himself. Still another favors an especially calm male who grooms her infant and plays with it gently while she feeds in another tree. And another female, an adolescent, may hang out with a particular male because he is friends with her sister and her cousin, and she wants to keep on spending time with them.

Researchers will probably continue to debate for many years the reasons (in terms of evolutionary advantages) that baboon males and females form friendships. But more important, I think, than the exact reproductive advantages resulting from friendships is that they exist in every baboon troop that has ever been studied carefully and that they are so personal and so variable. The fact that this is so is not a coincidence, for it is the personal nature of the relationships that leads each one to be so distinctive, just as human marriages differ radically from one another. Discovering that baboons have friendships is just the beginning. This discovery opens the door to a vast series of questions about why this baboon ends up with that one, and another one with someone else, and about how and why the quality of each relationship is so different. These questions will yield answers that may ultimately be amenable to evolutionary analysis, but before that occurs, researchers must delve deeply into the richness of baboon lives and the nuances of their behavior. What do we know now, that we did not know in 1985, about how baboons relate to one another and why they do what they do?

We know that different males bring very different tools to the male-male psychological warfare I describe in this book. Some males have a knack for knowing when to pick fights they can win and for taking their frustrations out on someone else when they occasionally lose. These males tend to keep cool, internally, until and unless the situation demands a rapid response, and then they're ready for action ("fighters").



Other males concentrate on forming sexual consortships and are especially attentive to their sexual partners (“lovers”), while still others put a lot of energy into cultivating bonds with mothers and infants (“friends”). The males who successfully pursue any of these strategies experience lower stress than do males with less highly developed social skills.<sup>8</sup>

We also know that when a male olive baboon transfers to a new troop for the first time, he faces a complex series of social challenges that different males meet in very different ways. Some males concentrate on dominating resident males, whereas others tend to avoid aggression and focus instead on making friends with females. Some find a home in the first troop they enter, but others fail and try again in another troop.<sup>9</sup> After spending several years in a troop, each male must decide whether to remain for good or transfer once again. If he has lots of friendly interactions with females and infants, he’s considerably more likely to stay.<sup>10</sup>

We know that when a male forms a friendship with a female, he becomes highly attuned to her screams for help, especially if she has a young infant and especially if he hears the aggressive voice of a recently immigrated male at the same time. The screams of females who are not his friends are much less likely to stir his attention.<sup>11</sup>

We know that in some troops, at least some of the time, the highest-ranking male somehow manages to monopolize sexual access to most females right around the time they conceive, no matter with whom those females might want to mate.<sup>12</sup> Yet in other troops, many males, including lower-ranking males, consort with fertile females,<sup>13</sup> and it seems that females manipulate consort opportunities and often end up mating with their preferred partners.<sup>14</sup> In these contexts, different females choose different males as friends; they also differ as to which males they prefer as lovers.<sup>15</sup> This suggests that female preferences are not primarily based on attributes we can easily measure—like rank, age, or length of residence in the troop—but rather on specific characteristics of particular males and on the history of their relationships with those males. But we still haven’t a clue why a female prefers the male(s) that she does!

Finally, we also know much more about male-female affiliation in other primates than we did in 1985. Special male-female relationships reminiscent of baboon friendships occur among other primates, including rhesus and Japanese macaques, ringtailed and red-fronted lemurs, and perhaps even chimpanzees.<sup>16</sup> It also appears that in many primates, especially high rates of mutual, friendly interactions occur among particular female-male pairs, even though friendships may not necessarily occur with the regularity we see in baboons.<sup>17</sup> We know that both male



sexual coercion and infanticide are widespread in many primates, and in virtually all of these species, affiliated males protect females and/or their offspring from conspecifics, including infanticidal males.<sup>18</sup> And just as in baboons, males appear sometimes to invest in these relationships in order to enhance mating success, while at other times, they seem likely to be investing in their own infants.<sup>19</sup>

These recent findings provide some tantalizing glimpses into sex and friendship in baboons and other species, but we still know surprisingly little about differences between one friendship and another or how friendships develop and change over time, or how friends communicate their feelings and attitudes toward one another. Such matters remain mysterious because most research on male-female relations continues to focus on functional questions (such as whether males are the fathers of the infants they befriend) and overall patterns (such as whether friends spend more time together after the female gives birth), rather than on more proximate questions (how do friendships develop?) or variations within overall patterns (why do some males react more strongly to playbacks of their friends' screams than do others?).

Why is this so? Is it because most scientists find the functional questions and general patterns more interesting or more important? Is it because studying the subtle dynamics of social relationships is often more difficult and more time-consuming? Do young scientists feel that they are more likely to succeed in a competitive market if they focus on functional questions? Is it due to decisions about what gets funded, or what gets published? I don't know the answers to these questions, but I am convinced that scientists need to spend more time understanding how their subjects see the world, how and why their personalities differ, and what makes for an especially close or valuable relationship in a particular society.<sup>20</sup>

In the years since I wrote this book, this conviction has grown. I did not observe baboons again for any length of time until 1993, when David Gubernick and I spent five months studying and videotaping olive baboons at Gombe National Park, Tanzania. This occurred after an interval studying captive chimpanzees<sup>21</sup> and wild bottlenose dolphins<sup>22</sup>—perhaps the two most intelligent and socially complex nonhuman animals on the planet. Yet when I returned to baboons, their social sophistication did not pale in comparison with these brainy paragons; if anything, I saw more complexity among the baboons as a result of an eye better trained to look for it.

One day, for example, two prime adult males, Apié and London, formed a coalition against another prime male, Randani. Randani was one of those males Robert Sapolsky describes as highly skilled in devel-



oping relationships with females and young—what I’ve labeled a “friend-type” male.<sup>23</sup> He was also chronically uninterested in getting into fights with other males. So Randani ignored the other males’ threats, and they continued to move closer, pant-grunting and flashing their canines at him while they stood close together, a seemingly invincible duo. Although Apié and London were trying to provoke Randani into a reaction, neither of them wanted to fight with him, so they frequently jockeyed for position, each trying to remain further away from Randani than his partner. Finally, as they got very close, Randani glanced nonchalantly at them and got up to walk away (consistently his favorite tactic whenever challenged by another male). His path of departure took him ever so slightly closer to Apié than to London, and just as Randani was near, London, standing to the side and slightly behind Apié, reached out and gave Apié a strong push, shoving his partner right into Randani’s path. Randani, whose position prevented him from witnessing this act, must have assumed that Apié was in the process of attacking him and so he attacked Apié. They fought briefly and then ran off down the beach. London, meanwhile, calmly sat down and watched the tension erupt between two males who would not be fighting each other but for his perfectly timed shove, a Machiavellian action worthy of a chimpanzee.<sup>24</sup>

My time at Gombe also sensitized me to the fragility of most friendships and made me marvel all the more at those few that survive social and demographic turmoil. The troop we observed at Gombe, “A” troop, had split into three subgroups shortly before we began our research. Many male-female friendships ceased as a result, since the partners ended up in different subgroups. Other friendships remained intact initially but faltered as one new male after another moved into the branch of “A” troop that we were studying. Some of these new males threatened old friendships directly by cultivating bonds with females. One male, Chongo (a “fighter-type” according to Sapolsky’s typology), persistently and ruthlessly attacked females whenever a male friend of the female was nearby, forcing the male to either fight or fail to protect his friend. (This strategy worked; Chongo was a superior fighter, and through this method he engaged every male, including the highly reluctant alpha male, in fights that Chongo won. As a result, he became the new alpha male within three months of entering the troop.) As I watched most friendships dissolve, or at least weaken, one stood out: the bond between the oldest male in the group, Bofu, and a late-middle-aged female, Santa Fe. In light of typical female behavior, Santa Fe should have given up her old friend, because she was in estrus and extremely attractive to the younger, stronger males. However, although



she consorted mostly with them, she also consorted often with Bofu (who very rarely paired up with any other females), and when she wasn't with another male, she hung out with him. Bofu, for his part, kept effectively coming to her defense and that of her offspring, even though his canines were worn. One day I stumbled upon them in a shady glade, sound asleep and curled up together in "spoon" position. Say what you will about scientific objectivity; I'm certain these two baboons loved each other.

Randani and another male, Sherlock, also taught me much about the persistence with which a baboon will attempt to live out his or her own unique way of being in the world. Although I wrote about baboon personalities in this book, it was Sapolsky who really showed, in considerable detail, how adult male social behavior clusters according to different personality types, regardless of age. Because of my interest in friendships, I was especially intrigued with Sapolsky's description of the "friend-type." I thought about Sherlock, who transferred into Eburru Cliffs from the neighboring Pumphouse troop shortly before my study began. Shirley Strum's description of Sherlock's integration into Eburru Cliffs resembles Sapolsky's description of friend-type males.<sup>25</sup> Sherlock avoided interactions with other males but was very popular with females from the start. During my study, he had more female friends by far (six!) than any other male, even though he was still a relative newcomer. Six years later, Sherlock was still there, still had multiple friends, and was still actively consorting. At that point, he was at least thirteen years old (according to Strum's lower age estimate when he was an adolescent), which is definitely over the hill for a male baboon. But what really amazed me was my brief glimpse of Sherlock, seven years later, when I spent three days with Eburru Cliffs during a short visit to Kenya.<sup>26</sup> Although he looked much older, his distinctive face and tail were unmistakable. I was surprised to see him at the center of a cluster of females, and I was truly astonished when, the next day, I saw him contest a hot consortship. Sherlock, now twenty or older, was beyond the age at which most male baboons die, and well past the age at which they typically remove themselves from social center stage.

When I first met Randani in 1993 at Gombe, I kept thinking of Sherlock, but because they looked a lot alike, I attributed this to their physical resemblance. Then one day I was sitting with a small group of "A" troop females, who were resting beside a stream. Most of the troop were downstream, around a bend that made it impossible to see them. The only other baboons they, or I, could see were a few stragglers upstream who were moving toward us. I was looking at the females when, suddenly, all of their faces lit up. One by one, they began to make the



“come hither” face (illustrated on p. 6). I turned to look upstream and saw Randani, sitting about thirty yards away, tucking in his chin and shaking his head and shoulders in a way that most males do only when they are particularly excited (I later realized that all of Randani’s come hithers are of this intense type, and it makes me wonder whether this is true for friend-type males in general). Randani kept gesturing at these females for so long and with such enthusiasm that I was tempted to make a face back at him myself. In that moment, I was absolutely certain that he was a friend-type male, and later observations confirmed this strong intuition. Although he was not particularly high-ranking, especially for a prime-aged male and recent immigrant, Randani succeeded in forming a close friendship with the alpha female, Hans, during her pregnancy (a time when Hans was demonstrably wary of all the other males in the troop except her friend, Bofu). When Hans’s infant son was born, she made great efforts to remain close to Randani. Within a few days of the infant’s birth, she began to do something I had never witnessed before. She scorned Bofu and instead brought her infant to Randani, stuck around for a few moments until the infant, predictably, responded positively to Randani’s invitations to climb on him, and then trotted off to feed unencumbered, sometimes out of sight many meters away. Given the dangers of infanticide by recent immigrants at Gombe and the fact that there were half a dozen new males in “A” troop that ranked as high as or higher than Randani, this was an extraordinary act of trust.<sup>27</sup> It seemed to be justified. Randani never let the infant stray more than a foot or two away from him, and he kept all other males away. He even charged the new alpha male, the deeply feared Chongo, when he passed close to Hans’s infant.<sup>28</sup>

My appreciation for the vicissitudes of baboon relationships has been greatly enhanced by my studies of their greeting behavior. Greetings between pairs are by far the most common kind of social interaction among baboons, with some dyads greeting as often as twenty times in a single day. All baboons greet, including infants only a few weeks old. Greetings follow a standard pattern based on stereotyped elements derived from mother-infant interactions and mating behavior.<sup>29</sup> Two individuals come together, often exchanging grunts and come-hither expressions. One will usually present his or her hindquarters to the other, and the other will respond by touching the hindquarters with the hands or mouth, or even by mounting. When juveniles or females greet, they often hug. Embraces and other kinds of tender touching also occur between males and females and even, rarely, between adult males.

The anthropologist John Watanabe and I conducted a study of the Eburru Cliffs troop in 1983 that documented striking differences



among the greetings of different pairs of males.<sup>30</sup> Our most interesting finding concerned the greetings of Alex and Boz, two central characters in this book. These two constituted the tightest and longest-standing male-male alliance in the troop. They never competed, but instead took turns helping each other take estrous females away from younger, stronger males. This egalitarian partnership was mirrored precisely in their greetings, in which they took great pains to alternate in the subordinate, female-like role of presenting and the dominant, male-like role of responding.

Although our research on male-male greetings was rewarding, it was also frustrating because I sensed that we were missing important behaviors that occurred too quickly for us to record accurately in real time. I was therefore very excited by the opportunity to document baboon behavior on videotape at Gombe. We captured 100 hours of "A" troop's interactions on tape, with a focus on greetings among all age-sex classes.

After watching hundreds of these videotaped interactions, I've discovered that, indeed, when interactions are seen only once, in real time, we miss much. I've found, for example, that my conclusions about which baboon started a fight often change when I watch the interaction in slow motion. I've discovered that baboons touch each other (especially brief, light touches on the torso) and also exchange fleeting facial expressions much more often than I could document in real time. My strong subjective impression that greetings vary in "tone" is being confirmed by our ability to quantify such subtleties as tail posture, mutual eye contact, synchrony of movement, frequency of intimate touching, and the overall pace (slow and smooth versus fast and jerky) of gestural exchanges.

Preliminary analyses suggest that greetings between males and females who are friends tend to involve more eye contact and slower pacing than greetings between non-friends. But of even greater interest to me is the possibility of using these tapes to explore how one friendship differs from another. We have found, for instance, that when Santa Fe and Bofu (the devoted couple described above) come together, they often dispense with the formal hindquarter presentation used by other friend pairs and instead greet face to face. It is my hope that detailed analyses of male-female greetings, as well as greetings involving other age-sex classes, will do much to elucidate how baboons communicate their feelings, attitudes, and perhaps even future intentions in their relationships with one another.

What is the purpose of delving so deeply into the details of social relationships in other species? One reason is scholarly, the sort of rationale scientists put in grant proposals to try to convince funding agencies that



their work holds relevance for humans. Indeed, I believe that a rich understanding of social relationships in other species (especially primates and other large-brained, long-lived, highly social species like dolphins, elephants, lions, mongooses, and other social carnivores) is very important to understanding ourselves. We've spent more than ninety-nine percent of our history as a species living in small, face-to-face groups like those of wild primates, which means that, just as for baboons today, virtually all of our social relationships have involved a few dozen individuals. This, in turn, implies that human evolutionary social psychology largely reflects the sorts of situations described here for baboons: making, keeping, and losing friends whose aid is critical to survival and reproductive success.<sup>31</sup> Still in its early days, evolutionary psychology has tended to focus on dramatic adaptive problems, such as finding and competing for mates, often by investigating short-term relationships among college students largely unfamiliar to one another and removed from their families and communities. More recently, evolutionary psychology has begun to focus increasingly on the sorts of questions addressed in this book and in other nonhuman research: relationships in community and group settings, long-term bonds, and the motivations and emotions that underlie these long-term commitments.<sup>32</sup> As this happens, evolutionary psychologists will find studies of other animals increasingly relevant since they are often the source of important new discoveries that also apply to humans.

Although these contributions to human understanding are, in my view, very significant, I believe there is an even more important reason for conducting detailed research on animal relationships and animal personalities. I began this introduction by noting that baboons form *personal* relationships just as we do and that what makes these relationships personal is the fact that individual identities matter. I have recently discussed in some detail what this means to us as a species that holds the fate of other animals in our hands.<sup>33</sup> If baboons (and dolphins and lions and many other species) are capable of relating to one another as individuals, this implies that they are also capable of relating to us that way; my experience and that of many other people proves this is so. This means that our world is replete with nonhuman beings with whom each of us could potentially form personal relationships, each with a unique flavor stemming not just from the characteristics of the two species we represent but also from the unique attributes of each individual.<sup>34</sup> Although rare people exist who are devoted to the welfare of other species in principle, for most people, a sense of caring and responsibility for other species depends on feeling directly connected to them. Jane Goodall and Dian Fossey proved that research that makes other animals



come alive as individuals, with whom we could in principle have personal relationships, contributes immensely to this kind of awareness. We scientists are privy to a rare and precious opportunity when we come to know intimately nonhuman animals living in their own worlds. We have a responsibility to those animals to show other people who they *really* are—sentient beings who matter to one another, living lives as full of drama and emotion and poetry as our own. To perceive the planet as populated with billions of such creatures staggers the imagination, but it is true, and if we want the world of the future to retain this richness, we need to become ever more conscious of this reality before it is too late.

## NOTES

1. These descriptions are based on olive baboons I observed at Gilgil, Kenya, from 1976 to 1979 and in 1983 and on those I observed at Gombe National Park, Tanzania, in 1993.
2. "Reasons" refers both to evolutionary explanations (in terms of reproductive benefits) and to more immediate motivations of the baboons themselves.
3. Shirley C. Strum, "Agonistic Dominance in Male Baboons: An Alternative View," *International Journal of Primatology*, 3 (1982): 175–202, *Almost Human* (New York: Random House, 1987), and "Reconciling Aggression and Social Manipulation as Means of Competition. 1. Life-History Perspective," *International Journal of Primatology*, 15 (1994): 739–765; and Debbie L. Manzolillo, "Intertroop Transfer by Adult Male *Papio anubis*" (Ph.D. diss., University of California, Los Angeles, 1982).
4. During pregnancy and lactation, female baboons cease to cycle and males show no interest in mating with them until they resume, which in the Eburru Cliffs troop occurs, on average, about fourteen months after birth if the infant survives. See Barbara B. Smuts and Nancy A. Nicolson, "Reproduction in Wild Female Olive Baboons," *American Journal of Primatology*, 19 (1989): 229–246. Toward the middle of each estrous cycle, females form sexual consortships in which they pair up with particular males for anywhere from a few hours to several days. During consortships, females mate only with their consort partners. See Glenn Hausfater, "Dominance and Reproduction in Baboons," *Contributions to Primatology*, 7 (1975).
5. Ryne A. Palombit, Robert M. Seyfarth, and Dorothy L. Cheney, "The Adaptive Value of 'Friendships' to Female Baboons: Experimental and Observational Evidence," *Animal Behaviour*, 54 (1997): 599–614.
6. Jeanne Altmann, *Baboon Mothers and Infants* (Cambridge, Mass.: Harvard University Press, 1980); David M. Stein, "Ontogeny of Infant-Adult Male Relationships during the First Year of Life for Yellow Baboons (*Papio cynocephalus*)," in David M. Taub, ed., *Primate Paternalism* (New York: Van Nostrand Reinhold, 1984), pp. 213–243; Michael E. Pereira, "Agonistic Interac-



tions of Juvenile Savanna Baboons. II. Agonistic Support and Rank Acquisition," *Ethology*, 80 (1987): 152–171; Ronald Nöe and Albertha A. Sluiter, "Reproductive Tactics of Male Savanna Baboons," *Behaviour*, 113 (1990): 117–170; and Fred B. Berkovitch, "Mate Selection, Consortship Formation, and Reproductive Tactics in Adult Female Savanna Baboons," *Primates*, 32 (1991): 437–452.

7. In this book I proposed that males gain two main benefits from friendships with females: enhanced chances of mating with the mother in the future ("mating effort" hypothesis), and opportunities to contribute to the survival of their own offspring ("paternal investment" hypothesis). I suggested that the relative importance of these two benefits varied with male life history: new immigrants or recently mature natal males tend to form friendships as a way to enhance mating opportunities, but as a male's tenure in a troop increases, his friendships tend to reflect previous mating activity so that he ends up affiliating with infants he could have sired (pp. 164–169 and 198–200). In some cases, male-infant affiliation may simultaneously enhance the survival of a male's own infant *and* increase his chances of mating with the mother the next time she conceives. Thus, both hypotheses may apply, sometimes to different males, sometimes to the same male with different females or at different points in time.

Several subsequent studies, however, have treated these hypotheses as mutually exclusive by arguing that male friendships with females always, and only, involve paternal investment. Berkovitch ("Mate Selection") rejected the mating-effort hypothesis for the neighboring Pumphouse troop because males found in proximity to infants were subsequently equally likely to consort, or to fail to consort, with the infants' mothers. His conclusion is based on the assumption that if friendship enhances consort activity, then males will have a greater than 50 percent chance of consorting with their female friends. This assumption is not valid because there is enormous variation among male baboons in the frequency with which they consort, and many factors other than friendship contribute to this variation. For this reason, the mating-effort hypothesis does *not* predict that males will have a greater than 50 percent chance of consorting with friends (as Berkovitch assumes), nor that females will consort more often with friends than non-friends (as Manzollillo assumes in "Intertroop Transfer"). Rather, as I emphasized (p. 168), it predicts that being friends with a female makes a male more likely to consort with her *than he would be otherwise* (e.g., in my study friendship on average roughly doubled a male's chances of consorting). To evaluate *this* prediction one must compare each male's consorting activity with friends with what is expected given his consorting activity overall. This method controls for the variation across males in how frequently they consort. None of the studies claiming to reject the mating-effort hypothesis frames the hypothesis in these terms and none provides a rationale for framing it in another way. Thus, unfortunately, this hypothesis remains untested for other troops or populations.

Berkovitch ("Mate Selection"), Pereira ("Juvenile Baboons"), and Nöe and



Sluijter ("Reproductive Tactics") argue that since the males who affiliated with females and their infants were usually in the troop when the infants were conceived, these relationships must reflect paternal investment. This is an odd argument since, prior to these studies, several researchers, including myself, had already shown a significant positive relationship between consorting activity with *particular* females (as opposed to simply presence in the troop) and subsequent male-female and male-infant affiliation (p. 163). These data, along with recent evidence for chacma baboons (Palombit et al., "Friendships"), provide much stronger support for the paternal-investment hypothesis than evidence that the friend was present in the troop when the infant was conceived. However, other results indicate that it is unlikely that *all* affiliation between males and infants reflects paternal investment. First, males occasionally affiliate with infants they could not have sired since they were not present in the troop when the infants were conceived. For example, Nöe and Sluijter ("Reproductive Tactics") report that "some significant [male-infant proximity] scores were found for infants conceived before a male's arrival" (Figure 3 shows five such pairs for one troop and eight for another). Second, many cases exist in which two or three males simultaneously affiliate with the same infants (Altmann, "Baboon Mothers," Stein, "Ontogeny," Nöe and Sluijter, "Reproductive Tactics," Palombit et al., "Friendships"). Since only one of these males could have fathered the infants, the other male (or males) must be investing in someone else's infant. This could result from male inability to accurately estimate paternity, especially when the mother mated with more than one male around the time of conception, but my data suggest that this explanation cannot account for all, or even most, such instances. (Table 8.1 lists nine females with two or more friends [excluding all subadult males] for whom I also had data on mating during the preceding conception cycle. In two of these cases [PH and HH], both male friends were seen consorting with the mother. In the other seven cases, at least one of the friends was never observed consorting with the female, and in one case, neither friend was observed consorting with her.)

As far as I know, only one study since mine has investigated whether females with more than one friend mated with both males during the conception cycle. Palombit et al. ("Friendships") list five females who had two friends and one female who had three friends. For two females, mating information was available for both friends, and in these cases, both friends were seen copulating during the conception cycle. When data from the other females with more than one friend are combined, we find four friends who copulated and five friends for whom data were unavailable. Although the missing data preclude a definitive conclusion, these results suggest that friendship may be more closely tied to prior copulation in this baboon population than in my troop. This result is consistent with other differences between the Okavango chacma baboon population and the Gilgil olive baboon population. Okavango males typically achieve alpha rank soon after migration and quickly monopolize matings with estrous females until another male enters and the process is repeated,