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Male infanticide and defense of infants in chacma baboons

Introduction

Sexually selected infanticide is relatively widespread among primates, but has been documented primarily in one-male–multifemale reproductive units, e.g., in guenons (*Cercopithecus* spp.) (Butynski 1982; Fairgrieve 1995), langurs (*Presbytis* spp.) (Hrdy 1974; Newton 1988; Sommer 1994), howler monkeys (*Alouatta* spp.) (Crockett & Sekulic 1984), and mountain gorillas (*Gorilla gorilla berengei*) (Fossey 1984; Watts 1989). Although male infanticide has been invoked as a selective force in multimale–multifemale groups, such as in macaques (*Macaca fascicularis*) (van Noordwijk 1985), capuchin monkeys (*Cebus olivaceus*) (O'Brien 1991), and chimpanzees (*Pan troglodytes*) (Smuts & Smuts 1993), it has rarely been observed in these species (e.g., Valderrama *et al.* 1990; Camperio Ciani 1984) or follows patterns partly inconsistent with Hrdy's (1974) sexual selection hypothesis (Hiraiwa-Hasegawa & Hasegawa 1994). Thus current data suggest that the presence of multiple males in a primate group discourages infant-killing by other males.

Relative to one-male groups, the presence of additional, reproductively active males may both dilute the benefits of infanticide and increase its costs. Exploitation of the reproductive opportunity created by infanticide depends upon the perpetrator's ability to monopolize subsequent fertilizations, which is a function of social variables such as the number of males in a group, the intensity of male–male mating competition, and the potential for effective mate guarding. In multimale groups, defense of infants by other resident males may increase the costs of infanticide, while mating competition may decrease the benefits. The relative

contribution of these two processes in inhibiting infanticide in multimale groups remains unclear.

Nevertheless, infanticide is a suggested reproductive strategy in several primate species living in multimale groups: the red colobus monkey (*Procolobus badius*) (Leland *et al.* 1984; Struhsaker & Leland 1985), the hanuman langur (*Presbytis entellus*) (Borries 1997; Borries & Koenig, Chapter 5), the red howler monkey (*Alouatta seniculus*) (Clarke & Glander 1984; Sekulic 1983a) and the subject of this chapter, the chacma baboon (*Papio cynocephalus ursinus*).

Chacma baboons of southern Africa live in large, multimale–multifemale groups of 60–80 individuals. On the basis of their observations of a population inhabiting the Moremi Game Reserve in the Okavango Delta, Botswana, Busse & Hamilton (1981) were the first to argue that infanticide functions as a male reproductive strategy. Alpha males achieve greater mating success than other males in the group (Bulger 1993), but the duration of alpha tenure is brief relative to female interbirth intervals, averaging well under 1 year (Hamilton & Bulger 1990). Thus a male that has recently immigrated into a group and attained the alpha position in the dominance hierarchy may increase sexual access to fertile females by killing infants, thereby terminating lactational amenorrhea in their mothers sooner than if infants survived to weaning.

Collins *et al.* (1984) summarized observations of infanticides over a 3-year period at Moremi. This dataset comprised four cases: two directly observed attacks and two inferred infanticides based on circumstantial evidence. Two episodes in which infants survived injuries inflicted by males were also described (see Appendix 6.1). These data confirmed that infant death accelerated the resumption of cycling in mothers, suggested that infanticide was more common in the chacma baboon than among East Africa conspecifics such as the olive baboon (*P. cynocephalus anubis*), and directed attention at the much shorter tenures of alpha males in the Moremi population as a possible cause of this interpopulation difference. Nevertheless, the patterning of infanticidal attacks among the Moremi chacma baboons was also inconsistent with Hrdy's sexual selection hypothesis in some cases. For example, in one instance the infant injured by a male was already weaned (and presumably no longer inhibiting cycling in its mother); in another case, the attacking male was a low-ranking immigrant unlikely to fertilize the infant's mother subsequently. The data set and accompanying conclusions have been questioned on these grounds, as well as for other reasons (e.g., tranquilization of a mother via darting preceded the one directly observed infanticidal attack by a known male).

There is a clear need to re-evaluate the question of sexually selected infanticide in this baboon population. First, the implications of the inconsistencies in the Collins *et al.* (1984) record, which constitute a relatively large proportion of their observations, can be resolved only through consideration of additional data. Second, the assertion of systematic intraspecific variation in rates of infanticide among savanna baboons requires further supportive evidence. The possible generality of infanticide in chacma baboons is suggested by one observed and one inferred infanticide reported recently for a population inhabiting the Drakensberg Mountains, South Africa (Weingrill 2000; Appendix 6.1). Third, male infanticide has been argued to be a crucial selective agent behind the evolution of many features of the chacma baboon social system, such as infant-carrying by males (Busse & Hamilton 1981), the "tail-raising" visual display of females (Busse 1984a), triadic interactions involving males and infants (Busse 1984b), copulation calls (O'Connell & Cowlishaw 1994), heterosexual "friendships" (Palombit *et al.* 1997), and female–female social interactions (Palombit *et al.*, 2000). These arguments all presuppose the existence of infanticide as a sexually selected male reproductive strategy.

The occurrence of infanticide in chacma baboons has naturally directed attention to possible counterstrategies of females. Palombit *et al.* (1997) argued that chacma baboon friendships represent such a strategy. When they give birth, females typically establish and actively maintain close bonds with particular males, who presumably will defend their infants. Observational and experimental data suggest that friendships perform an anti-infanticide function, but Palombit *et al.* (1997) provided only limited descriptions of male responses to actual infanticidal attacks.

In this chapter we update the record for the Moremi chacma baboons by summarizing observations of infanticide over a 6-year period. We use these new data to test two predictions of the sexual selection hypothesis. First, a male will kill infants sired by other males. Second, a male will mate with females whose infants he has killed. Finally, we further evaluate the argument that males protect the infants of their female friends by examining the responses of males to actual and potentially infanticidal attacks, and by considering the implications of male defense for the sexual selection hypothesis.

Background and methods

Study area and subjects

The study site is situated in the Moremi Game Reserve in northwestern Botswana (23° 02′ E, 19° 31′ S). The Okavango Delta is a seasonal wetland comprising grasslands and raised "islands" covered with trees and shrubs. Descriptions of the study area are provided by Tinley (1966), Buskirk *et al.* (1974), Hamilton *et al.* (1976) and Ross (1987).

We summarize patterns of infant attack and mortality for the fully habituated study group, C troop, observed continuously from July 1992 to August 1998. Over this 6-year period, 31 adult (parous) females and 22 non-natal adult males resided in the group. At any given time, however, the group of 60–70 individuals generally comprised 3–8 fully adult non-natal males, 3–7 natal adult males (≥8 years), 22–26 adult (cycling) females, and their immature offspring. Maternal relatedness was known for all females and natal males because of the long history of prior observation (1977–1991) by W. J. Hamilton III and colleagues (e.g., Hamilton *et al.* 1976; Busse & Hamilton 1981; Hamilton & Bulger 1992).

In chacma baboons, both males and females are organized into linear dominance hierarchies in which all females are subordinate to males (Bulger 1993). Subjects were assigned dominance rankings based on the direction of agonistic interactions, i.e., "supplants," "grimace" visual displays, or overt aggression. The average tenure of alpha males in C troop was 6.6 months (SD = 4.2, $N = 9$ males), excluding several periods when the dominance relationship between the current alpha male and a contemporary new immigrant male was ambiguous to experienced observers. This estimate of alpha tenure duration corresponds roughly with the short mean of 5–6 months reported previously for the same population (Collins *et al.* 1984; Hamilton & Bulger 1990). Although males may remain in their natal groups into adulthood and eventually attain alpha status (Bulger & Hamilton 1988; Hamilton & Bulger 1990), all but one of the alpha males during 1992–1998 were non-natal individuals.

Infant wounding in Moremi chacma baboons

We describe below the directly observed and inferred cases of infant wounding. In some instances, observers were alerted to an infanticidal attack already underway by outbursts of intense screaming. The screaming associated with infanticides impressed observers as highly distinctive by virtue of its high amplitude and its patterning, i.e., sustained calling and widespread participation by large numbers of individuals of both sexes, many of whom were not involved directly in the interaction (for similar accounts, see Collins *et al.* 1984; Tarara 1987). Unless otherwise noted, all infants appeared healthy and lacked ostensible signs of illness or debilitation prior to attacks upon them. The cases described below are summarized in Table 6.1.

Direct observations

Directly observed infanticidal attacks on infants were by two non-natal adult males that had immigrated into the study group and/or had attained alpha status relatively recently. Male WA immigrated in April 1991, and attained alpha status for the second time during his residency in June 1992. Male DG immigrated into the group in June 1994 and became alpha male within a week. One non-fatal attack by a third male was also directly observed. Male TM was born in the study group in September 1985, emigrated in April, 1995 (entering a neighboring group), returned to his natal group in April 1997, and attained alpha status in October 1997.

Case 1

On 21 October 1992, loud screaming by multiple baboons directed observers' attention to male WA, who was running through the group with 61-day-old infant BR in his mouth. This infant had been seen alive 15 minutes earlier. Adult male TN, who was the friend of BR's mother, chased male WA, giving typical male loud calls ("wahoos") and screams. Several females including infant BR's mother, her 3.75-year-old daughter, and two unrelated high-ranking females also ran screaming at WA, followed by several subadult natal males unrelated to the mother; however, none of these individuals approached male WA closely or intervened directly.

Case 2

This infanticidal episode on 8 February 1993 essentially followed the same pattern as case 1. Loud screaming erupted and male WA was seen running with infant NK in his mouth. The 112-day-old infant had been seen unharmed in the previous 10 minutes. The adult male TO, who was the friend of NK's mother, ran over wahooing, approached WA, and appeared about to engage WA in a fight, but then withdrew. No other baboons

Table 6.1. *Summary of observed and inferred attacks on infant chacma baboons (1992–1998)*

Case	Infant	Date	Age (days)	Sex	Circumstances	Observer
Direct observations						
1	BR	21 Oct. 1992	61	F	Outburst of loud screaming by multiple baboons occurred and adult male WA was seen running through center of group with dead infant BR in his mouth. Male friend of BR's mother rushed over wahooing and screaming, but did not engage WA in fight	D.L.C., R.M.S.
2	NK	8 Feb. 1993	112	M	Outburst of loud screaming by multiple baboons as adult male WA ran through group with infant in his mouth. Male friend of NK's mother rushed over, but did not engage WA in fight. Male WA ate infant	D.L.C., R.M.S.
3	AR	13 Sept. 1994	54	M	Adult male DG attacked at close range female BL carrying infant AR. No males came to the aid of the female (but few were present at the time). Male DG ate the infant	R.A.P.
4	NH	15 Sept. 1994	353	M	Outburst of loud screaming occurred, and adult male DG was seen running with screaming infant in his mouth, pursued by two other baboons. Male DG dropped the infant, already dead, and ran off	R.A.P.
5	RB	20 Oct. 1994	2	M	Outburst of loud screaming and adult male DG was seen running with infant in his mouth. It was not clear whether the infant was already dead. Other adult males, including male friend of RB's mother, were >200 m away at the time of the attack	R.A.P.
6	CC	16 July 1997	280	F	While her mother was away at a vervet monkey kill site, CC was attacked and bitten twice in the torso by the adult male TM. The infant was retrieved by a distantly related, 8-year-old natal male. The infant became listless in ensuing days, but eventually recovered	D.L.C., R.M.S.
Circumstantial observations						
7	HI	13 Nov. 1997	29	M	During an intergroup interaction, an adult male of the study group (probably TM) attacked infant HI, biting him in the face and head. The infant died the next day	D.L.C., R.M.S.
8	JB	26 Aug. 1993	1	F	Outburst of screaming, chasing, and wahooing of adult male GL occurred. Infant JB was discovered dead with newly inflicted puncture wound to head	R.A.P.
9	HP	11 Oct. 1994	131	M	HP was seen alive and carried by his mother in early morning. When the group was recontacted in mid-morning, the mother was holding the dead body of HP, which had two bleeding puncture wounds in head	R.A.P.
10	MM	20 Aug. 1996	191	M	Outburst of screaming occurred. MM was discovered splattered with blood and with apparent canine punctures on left abdomen and left thigh, but still alive and carried by mother. He was dead the next morning	D.R.
11	SN	15 Nov. 1992	366	M	SN disappeared from the group during a violent, prolonged chase involving multiple baboons of both sexes, running about screaming and wahooing. Infant's mother was discovered the next day to have a wound on her left arm	D.L.C., R.M.S.
12	SU	19 Sept. 1994	156	F	SU was seen alive and carried by her mother in early morning. When the group was recontacted several hours later, SU was missing and adult male DG was found with blood on his face and hands, chewing on animal flesh	R.A.P.

Figure 6.1. An alpha male chacma baboon in the Moremi study group, minutes after he captured and killed an infant; case no. 3 (photo: Ryne Palombit).

entered the vicinity of male WA. Male WA ate the infant as male TO and NK's mother sat nearby. NK's mother was later found to have a new wound on her left arm.

Case 3

At 09:40 on 13 September 1994, the study group encountered lions while crossing a grassy field. Baboons fled, alarm calling, in either of two directions, and ascended the trees of wooded islands on opposite sides of this field. About 30 minutes later, the baboons returned to the ground and were relaxed despite the continued presence of lions 100–125 m away, which prevented reunion of the two subgroups that had formed during the initial flight. At 10:30, alpha male DG began wahooing and chasing females. He initially chased female LE (carrying her infant), and then female CD (whose infant was absent). When male DG came to within 20 m of primiparous female BL holding her 54-day-old infant AR, he terminated his chase of female CD and set upon BL. She ran away screaming, carrying her infant, but DG pursued her around an acacia bush, and when he emerged from the other side, he was already carrying AR in his mouth (Figure 6.1). Female BL continued to scream for about 30 seconds, along with several distant baboons. She then climbed into a small tree approximately 15 m from male DG, as he ate the infant. No baboons came to the aid of female BL, but this may have been partly because the subgroup she and DG were in, formed after the encounter with the lions, included only one of the other seven non-natal, adult males of the group. BL's male friend, a 9.5-year-old natal male who was second ranking in the hierarchy, was in the subgroup with BL, and had been last seen with her 30 minutes earlier. He failed to intervene against DG, though he appeared and sat 5 m from male DG soon after he had begun eating the infant.

Case 4

On 15 September 1994 intense screaming broke out and male DG was seen running with an infant in his mouth and pursued by two unidentified subadult males. At one point during the chase, DG stopped momentarily, sat down, and handled the infant, which was screaming and struggling to get loose. Male DG then resumed running with the infant in his mouth and, about a minute later, dropped its dead body and withdrew. The infant's wounds consisted of: (1) a laceration (6.5 cm × 5 cm) on the lower back exposing part of the pelvis and vertebral column; (2) minor lacerations on the top of the head and on left parietal region; (3) one bleeding puncture on the left arm above elbow; (4) one bleeding puncture on the leg, 5 cm above heel. The victim was the 353-day-old male infant NH.

Case 5

Female RS gave birth to her first infant RB on 18 October 1994. During this and the following day, the newborn infant grasped his mother weakly, prompting her to hold him in place on her ventrum with one hand when walking. On 19 October 1994, male DG made an apparent infanticidal attempt, but RS's male friend EG intervened successfully (see below). At 07:04 the next day intense screaming erupted and adult male DG was seen running with RS's neonate in his mouth. It was unclear whether the infant was still alive or already dead. DG ascended a tree and ate the infant. Male DG was unmolested by any of the group's adult males, all of whom, including the mother's friend EG, were several hundred meters away foraging on aquatic roots. Some of the intense screaming was by females that were also foraging down by the river and were too far away to have seen the attack transpiring on the other side of an intervening hill.

Case 6

On 16 July 1997, female infant CC was 150 m away from her mother, who was attempting to acquire a piece of a vervet monkey (*Cercopithecus*

aethiops) that had just been killed and was being eaten by an adult male. Adult male TM was with most of the other adult males of the group at the kill site, but he then returned to 280-day-old infant CC's location, seized her, and inflicted two canine punctures to her torso. Eight-year-old natal male MS rushed forward immediately, retrieved the wounded infant, and carried her into a tree. After searching unsuccessfully for her infant, the mother moved off with the rest of the group. Male MS attempted to follow after the group several times, leaving CC temporarily, but he always returned to her, for she was unable to keep up with him. About an hour after the group had left them, MS picked up CC and carried her back to the group, where she was reunited with her mother. By 19 July, CC was listless and appeared to be suffering from an infection. By 22 July, however, she was recovering, and, in fact, survived TM's attack. Although he was a natal male, TM was maternally unrelated to the infant CC. Male MS was the second cousin of CC.

Summary

In two instances (cases 3 and 6) infanticides were essentially observed from start to finish. In one case (number 4), the onset of the attack was unobserved, but the male was seen to kill the live infant in his possession. In the other cases, observers saw a particular adult male running with an infant in his mouth immediately after outbursts of screaming by multiple baboons. In five of the six cases, the infanticidal male was the current alpha male; in the sixth instance (case 6), the male attained alpha rank approximately 2.5 months after his non-fatal attack on an infant. Infants attacked by males DG and TM were conceived prior to these males' immigration into the group; the infants fatally wounded by male WA were conceived prior to his rise to the alpha position.

Circumstantial observations

The first four cases concern infants that were discovered with fatal injuries.

Case 7

During an interaction with a neighboring group on 12 November 1997, an outburst of screaming occurred from C troop baboons far from the interaction area and members of the other group. Observers arriving immediately found that the female LX's 29-day-old infant HI had received bite wounds on the face and head, but was still alive. Adult males AP, AU and TM were present, but the first two males were unlikely candidates for infanticide, since LX had established friendships with them when she gave birth to HI. On the other hand, several adult females present were directing intense screaming at alpha male TM, which suggested that he may have been responsible for the injuries. The infant died the next day of its wounds.

Case 8

On the morning of her birth on 26 August 1993, the infant JB appeared normal and healthy as late as 11:40. An hour later, many baboons began suddenly screaming intensely and several unidentified individuals were seen chasing one another through dense vegetation. The current alpha male MK was the subject of a focal animal sample at the time and was uninvolved, but adult male GL, who had immigrated into the group 3 days earlier and who would later become alpha, was seen wahooing and running from other baboons. Female JN was located 10 minutes later, grunting at a pregnant, 14-year-old female who was holding her now-dead infant. The infant's condition was characterized by the following: (1) a slightly bleeding, circular puncture approximately 3.5 cm above the left eye; (2) an exposed patch of scalp on the top of head; (3) multiple minor lacerations under the left eye, on the right hand, and around the nostrils; and (4) blood draining from its nostrils. Over the ensuing 30 minutes, JN unsuccessfully attempted to retrieve her infant's body from the other female, and finally withdrew. The pregnant female later abandoned the dead infant.

Case 9

At 06:45 on 11 October 1994, the adult female SH was seen carrying her 131-day-old infant, HP. When the group was contacted 45 minutes later, SH was found holding the now dead body of HP. The infant had a bleeding puncture wound on the temporal region of each side of its head. The current alpha male DG had attacked this infant and its mother several times in the preceding weeks (see below).

Case 10

In the late afternoon of 20 August 1996, an outburst of intense screaming occurred. The 191-day-old male infant MM, which had been seem healthy that morning, was found slumped on the ground near its mother. He was still alive, but had a non-bleeding puncture wound in the left abdomen and on the left thigh, as well as blood on his hair. Besides occasionally lifting his head and vocalizing, the infant hardly moved for the rest of the

day. Though still alive when the group entered its sleep tree that day, the infant was dead by 09:00 the next morning.

The last two cases concern disappearances of infants in circumstances suggestive of possible infanticide.

Case 11

On 15 November 1992, the 1-year-old male infant SN disappeared from the group during a violent, prolonged chase involving multiple baboons of both sexes. Many males were running about wahooing and chasing one another, and females were screaming at an intensity previously associated with observed infanticides. The interaction was observed from a distance, but the infant's mother was discovered the next day to have a wound on her left arm.

Case 12

When the study group was first sighted on the morning of 19 September 1994, the adult female SY was carrying her 156-day-old female infant, SU. When recontacted several hours later, the infant SU was missing and the alpha male DG was simultaneously found with blood on his face and hands, chewing on a piece of animal flesh. Male DG had been observed to kill two infants in the preceding 6 days, one of which he had eaten (see above), and he had attacked the infant SU 5 days earlier (see below).

Summary

Although observations were defined as "circumstantial" when an infanticidal attack was not directly observed, it is clear that in four of these six cases, infant death coincided with newly inflicted, fatal wounding. There were two sources of injuries of these kinds: conspecifics or predators (such as lions or leopards). It seems unlikely that these wounds were inflicted by predators because of the absence of alarm calling or any of the flight responses typical of a predator encounter. Instead, the screaming and chasing of multiple baboons were consistent with an attack by a conspecific. The other two cases were instances in which the disappearance of an infant coincided with conditions associated with other observed infanticides.

The distribution of apparently canine-inflicted puncture wounds on the head (cases 7, 8, 9), torso (cases 4, 6, 10), and limbs (case 10) suggests that infanticidal chacma baboons deliver fatal bites on any body area they can seize, in much the same way as male hanuman langurs do (G. E. King & D. Steklis, unpublished data).

Other non-fatal attacks on females and infants

Besides the cases of infanticide describe above, we also observed a number of unsuccessful attacks on lactating females by the alpha male. Many of these interactions took the form of protracted chases of mothers with infants that contrasted sharply with the usually brief chases of cycling or pregnant females. We describe below several examples of such attacks and then summarize these and additional observations in Table 6.2. These *ad libitum* data provide further information on the response of males – friend and non-friend – to potentially infanticidal attacks.

Female SH and her infant HP

At 08:20 on 14 September 1992, alpha male DG appeared suddenly, wahooing, near female SH and her male infant HP, who fled screaming into a tree. DG followed and knocked SH and her infant to the ground by vigorously shaking the terminal branch she was hanging from. He jumped down after her, resuming his chase, whereupon an outburst of intense screaming and other calls from nearby baboons occurred. SH's male friend NP, the non-friend adult male WA, as well as several females ran over, but only NP moved in closely to DG. NP engaged DG in a fight, screaming and fear-grimacing as DG hit him, during which time SH escaped with her infant and climbed into the interior of a dense camelthorn acacia bush. Although DG pursued her, the density of branches and long thorns in the bush apparently prevented him from gaining access to her, and he eventually withdrew. Male NP and an adult sister of SH sat 5 m away from the acacia during this time.

On 22 September 1994, alpha male DG emerged from behind foliage and rushed at the infant HP, who was sitting near NP, the male friend of his mother. NP immediately grabbed the infant and, carrying him ventrally and screaming continuously, ran off pursued by DG. A non-friend adult male WA ran over from 25 m away, but DG immediately chased him off some distance and then resumed chasing NP and HP. Again screaming, NP carried the infant into a camelthorn acacia bush. Male DG followed, as did male WA and the infant's mother SH, both of whom sat outside the bush. DG then moved off.

Female AL and her infant AA

On 18 October 1994, alpha male DG chased the female AL and her infant AA from a wooded island into a grassy field. AL's male friend EG and her 9-year-old son ran over immediately after she began screaming. EG

Table 6.2. *Summary of non-fatal attacks on females and infants by alpha male DG*

Date	Target of attack	Response of mother's adult male friend	Response of other individuals
14 Sept. 1994[a]	Female SH and Infant HP	Friend NP ran over immediately; fought male DG, hitting, screaming, and fear-grimacing to him; then sat below acacia bush SH and HP had fled into until DG withdrew	Non-friend adult male WA and several females including the adult sister of SH ran over; these females and other females nearby screamed; male WA withdrew, but SH's sister remained with NP under the bush until the attacker DG withdrew
14 Sept. 1994	Female SH and Infant HP	Friend NP ran over and sat under the acacia tree SH and HP had fled into	An adult female maternally unrelated to SH accompanied NP, screaming, to the base of the acacia tree SH and HP had fled into
22 Sept. 1994[a]	Infant HP	Friend NP grabbed infant HP as DG rushed at it, and carried it ventrally while screaming and fleeing; NP entered an acacia bush with infant and remained there until DG withdrew	Non-friend adult male WA ran over, was chased off by DG, returned, and sat nearby; infant HP's mother SH accompanied WA
18 Oct. 1994[a]	Female AL and Infant AA	Friend EG ran over, fought DG, biting and hitting him; then chased DG several times; then sat near female and infant	9-year-old son of AL ran over immediately, but did not approach attacker
7 Nov. 1994	Female AL and Infant AA	AL with AA ran onto wooded island pursued by attacker DG; when recontacted 10 min later, (new) male friend TO was sitting below the tree AL and AA had fled into	None
8 March 1995	Female AL and Infant AA	Friend TO ran over, threatened DG visually, then gave roars and threat vocalizations; DG hesistated and withdrew, whereupon AL and AA descended and ran off with male TO	None
30 July 1994	Female BT and Infant BZ	Friend WA ran over, sat under the tree BT had fled into screaming, with BZ; then grabbed a nearby 19-month-old juvenile (unrelated to BT) and roared while looking at attacker DG	Non-friend adult male GL ran over and stood under the tree BT and BZ fled into
15 Sept. 1994	Female BT and Infant BZ	Friend WA ran over to within 15 m of acacia tree BT and BZ fled into; DG terminated chase of BT; BT descended with her infant and ran to WA	None
27 Oct. 1994	Female JN and Infant JK	Friend WA followed non-friend TO and sat under tree JN and JK had ascended; JN climbed down, joined WA, and followed him closely for 15 min	Non-friend adult male TO immediately ran over and sat under tree JN had climbed into
20 Jan. 1995[a]	Infant JK	Friend WA repeatedly threatened, hit, and grunted at infant JK when it approached alpha male DG and until it withdrew to its mother	None
14 Sept. 1994[a]	Infant SU	Friend GL ran over, chased DG; then sat below acacia tree into which SU's sister had carried it; while sitting under this tree, male GL grunted and looked at attacker DG and female holding infant	SU's 5-year-old sister grabbed infant, carried it pursued by attacking male into an acacia tree; SU's mother SY accompanied friend GL, screaming, and sat below the tree SU and her sister entered
19 Oct. 1994	Female RS and Infant RB	Male EG ran over, sat below tree RS and RB had escaped into; after 7 min, approached and presented genital region to alpha male DG, grunting; then sat near RS and RB in tree, barking occasionally.	None

Notes:
[a] These cases are described in greater detail in the text.

charged directly at DG, and both males slapped and bit at one another, though no obvious injuries were inflicted. DG then ran off wahooing and EG chased after him, but this failed to prevent DG from resuming his attack on screaming female AL and her infant. Again, EG engaged DG in a fight, which ended as DG ran away pursued by EG, though both males moved noticeably slower, the distance between them increased, and DG's rate of wahooing declined. After having chased DG in a wide arc, male friend EG moved off, whereupon DG rushed with renewed speed at a knoll of tall, dense grass within which female AL and her infant had remained in silence during the last male–male fight. She ran screaming from the grass carrying her infant, and DG chased them up a tree. Male friend EG immediately returned, climbed into the same tree, whereupon DG switched to chasing a young juvenile at the top of the tree. Thereafter, he sat stationary several meters from AL, AA and EG, while EG occasionally yawned. Several minutes later DG descended the tree and moved off.

Female JN and her infant JK

Though not involving overt aggression, an episode of 20 January 1995 suggested a potential threat to an infant. Infanticidal male DG moved to within 5 m of the 90-day-old infant JK, whereupon she approached to within 1 m of him twice in the space of a minute. Each time she did so, JN's male friend WA approached JK grunting, threatened her, and hit her, which caused her to scream and run back to her mother JN sitting 5 m away. When JK once again approached DG 4 min later, male WA grunted at her from several meters away and the infant immediately ran to her mother. Male DG then moved off.

Female SY and her infant SU

On 14 September 1994, DG appeared from behind a bush rushing silently toward the female infant SU, who was sitting on the ground. The mother SY was absent from the immediate vicinity, but her other 5-year-old daughter SR was nearby. SR grabbed her infant sister and fled, without screaming, pursued by DG. Having seen this interaction from a distance, SY ran forward, screaming continuously. Immediately, SY's male friend GL ran from 35 m away and chased after DG, who pursued SR and SU into a small acacia tree. GL arrived and sat below the tree, grunting continuously, glancing alternately at the female SR (holding SU ventrally) and at male DG. After about a minute, DG descended the tree and moved off.

Summary

Male friends interceded defensively in all 12 cases where the alpha male attacked or threatened infants but failed to injure them. Actual or potentially protective intervention was also observed by non-natal, non-friend males in four cases (33%), by subadult males once (8%), and by females (other than the mother) in three instances (25%). Thus, in seven cases (58%), baboons other than the male friend and mother became directly involved in the attack, but only male friends were ever observed to chase, threaten, physically attack or present to the alpha male, to carry infants in retreat, or to give roars, threat vocalizations, or wahoos.

Infant mortality

During the 6 year study period, 79 infants were born, of which one was stillborn, and 30 died or disappeared before the age of 15 months; two live infants were less than 1-year-old at the end of the study period. Thus, depending on the fates of these two infants, mortality among live-born infants was between 38% and 41%, which is equivalent to previously reported rates of 45% ($N=38$ infants) for C troop at a comparable group size, and of 39% ($N=28$) for a neighboring troop (Bulger & Hamilton 1987). Mortality rates, however, varied considerably over time. For example, during the 2 year period from July 1993 to July 1995, 76% of infants died ($N=21$). Such high levels of mortality are comparable with those observed in a population of desert chacma baboons (Brain 1992).

Sources of mortality for live-born infants are summarized in Table 6.3. Conservative estimates of mortality due to infanticide range from a frequency of 31% (if only observed cases of attacks are used) to 37% (if all 11 deaths described in Table 6.1 are considered). If disappearances of apparently healthy infants are included in this estimate, up to 76% of infant deaths may have been due to infanticide. Whichever estimate is used, infanticide is clearly a significant cause of infant mortality in this population. Its frequency is comparable with, if not higher than, that observed in mountain gorillas (*Gorilla gorilla berengei*) (37%; Watts 1989), howler monkeys (*Alouatta palliata*) (40%; Clarke & Glander 1984), and lions (*Panthera leo*) (27%; Pusey & Packer 1994).

Sex ratios among newborns and dead infants did not depart significantly from a 1:1 ratio. Of the 79 infants born, 42 were female, 35 were male and 2 were of unknown sex. Of the 29 infants that died, 18 were male, 14 were female, and 1 was of unknown sex. The mean age of infants

Table 6.3. *Mortality among live-born infants at Moremi prior to 15 months of age (1992–1998)*

Cause of mortality	*N*	%
Disease/debilitation	5	16
Disappear with mother[a]	2	7
Disappear (with no prior sign of debilitation)	12	40
Infanticide	11	37
Total	30	100

Notes:
[a] One case of infant disappearance with mother appears to have been due to leopard predation based on the presence of baboon hair, drag marks, and leopard spoor at the sleep tree site on the morning these individuals were discovered missing.

that were killed was 132.4 days (SD = 128, $N = 11$), which was statistically indistinguishable from infants that died of other causes or disappeared (Mean ± SD = 103.5 (±102.5) days, $N = 18$) (Mann–Whitney U-test, $U = 90.5$, $N_1 = 11$, $N_2 = 18$, $P > 0.10$), but was much less than the age of surviving infants at the time their mothers conceived their next infants (Mean ± SD = 710 (±148) days; $U = 0$, $N_1 = 11$, $N_2 = 26$, $P < 0.001$).

Infant births and deaths were distributed similarly across maternal age categories ($\chi^2 = 3.34$, df = 3, $P > 0.10$), suggesting equivalent rates of mortality among females of varying ages. Of the 11 cases of suspected and inferred infanticide in Table 6.1, six involved primiparous mothers and six involved multiparous mothers. Given that there were by definition fewer primiparous females in the group ($N = 20$ live births) than multiparous females ($N = 58$ live births), this suggests that primiparous female chacma baboons are more vulnerable to infanticide, as occurs among some birds breeding for the first time (Palombit 1999).

Variability in male infanticidal behavior

Alpha males differed considerably in infanticidal behavior. Three of the eight males that became alpha during the study period accounted for all observed infanticides, and were particularly implicated in most circumstantial cases. Moreover, two correlations among the data of Table 6.4 suggest that infant mortality varied with alpha male identity. First, levels of mortality among infants born before and after takeover were positively associated with one another across males ($r = +0.74$, $P < 0.05$, $N = 8$).

Table 6.4. *Mortality following male attainment of alpha status ("takeover") among infants already present in the study group and among infants born thereafter*[a]

Alpha Male[b]	Alpha tenure (mos)	Mortality of infants alive at takeover (%)[c]	*N*	Mortality of infants born after takeover (%)[d]	*N*
WA	8	33	3	25	8
ZR	3	9	11	0	2
MK	1	0	10	0[e]	4
WA	3	0	5	–	0
GL	8	0	6	0	1
DG	11	83	6	60	10
AU	6	0	4	6	18
AP	14	7	15	50	4
TM	5	0	9	13	8
AP	Current (>6)	0	6	–	0
Mean, SD		13%, 27	75	22%, 23	55

Notes:
[a] "Mortality" is defined here as death due to injuries (Table 6.1) or overnight disappearance *without* prior indication of illness.
[b] Alpha males are listed in chronological order.
[c] For males that attained alpha status more than once (WA, AP), infants that they may have sired (i.e., that were conceived during a previous alpha tenure) are excluded.
[d] Infants born later than one gestation period (5.5 months) into the tenure of a particular alpha male are excluded, since they are likely to have been sired by that male.
[e] Circumstantial infanticide case 8 is not attributed to male MK, since he was unambiguously uninvolved in the attack (see the text).

Second, mortality among infants born after a takeover increased with the duration of an alpha male's tenure ($r = +0.83$, $P = 0.01$, $N = 8$). These data indicate that attributes of alpha males or conditions of their tenure may explain some of the variation in infant mortality rates.

The sexual selection hypothesis

The sexual selection hypothesis predicts that males are unrelated to the infants they kill. In the six directly observed cases, the alpha male was unlikely to be related to the infant he attacked because it had been conceived prior to his immigration into the group (males DG and TM) or while he was lower ranking (male WA). Although the identity of the infanticidal individual was unknown in the six other attacks, in all cases

the current alpha male was a recent immigrant who had been absent from the group when the infant was conceived. In one instance (case 8), the suspected perpetrator was a new immigrant who shortly became alpha male.

A distinction is sometimes made between the killing of infants already present in the group and "prospective infanticide", in which a male kills infants conceived prior to his attainment of alpha status but born soon afterwards. The latter suggests that males must somehow evaluate paternity, but the former variant is assumed in economic models of infanticide (Chapman & Hausfater 1979). Prospective infanticide is known in hanuman langurs (*Presbytis entellus*), lions (*Panthera leo*), and tropical house wrens (*Troglodytes aedon*) (Freed 1987), but nevertheless occurs rarely. For example, in hanuman langurs, 66% of infants born after male takeover were unharmed, compared to 44% of those infants already present when a new male entered the group (Sommer 1994).

Prospective infanticide, however, was common in the C troop chacma baboons. In five of the six (83%) directly observed cases, the infant attacked by the alpha male had been born after he had achieved alpha status but before he had copulated with their mothers. More generally, mortality due to wounding or sudden disappearances (unrelated to illness or predation) was roughly equivalent, if not more common, for infants born after a new male became alpha (22%) than for those born before (13%) (Table 6.4).

The sexual selection hypothesis predicts that an infanticidal male will mate with the female whose infant he kills. Female chacma baboons resumed cycling within 1–3 months of their infants' deaths, in accordance with numerous data demonstrating that loss of an infant significantly accelerates resumption of cycling in savanna baboons (Altmann *et al.* 1978; Collins *et al.* 1984). In all five directly observed cases of infanticide, the attacking male copulated with the mother when she resumed cycling (Table 6.5). Moreover, in four of these five cases, the infanticidal male was the alpha individual both at the time of the attack and subsequently, when the mother conceived her next infant. In the fifth instance, the attacking male's alpha position was ambiguous with respect to a new immigrant. Given that alpha males in the study group generally achieve greater mating success with females around the time of ovulation (Bulger 1993), these data support the hypothesis that infanticide increases male sexual access to fertile females.

The identity of infanticidal males was unverified in the circumstantial

Table 6.5. *Reproductive patterns following observed and suspected infanticides*

Case[a]	**Known** or *suspected* infanticidal male[b]	Did infanticidal male copulate with mother when she resumed cycling?	Alpha male when mother conceived her *next* infant
1	**WA**	Yes	WA
2	**WA**	Yes	Ambiguous alpha: WA or new immigrant NP
3	**DG**	Yes	DG
4	**DG**	Yes	DG
5	**DG**	Yes	DG
7	*TM*	Yes	AP
8	*GL*	Yes	GL
9	*DG*	Yes	Ambiguous alpha: DG or new immigrant AU
10	*AP*	Not applicable[c]	Not applicable[c]
11	*WA*	Yes	Ambiguous alpha: WA or new immigrant NP
12	*DG*	Yes	DG

Notes:
[a] Case numbers are from Table 6.1. Case 6 is excluded because the injured infant survived.
[b] Known male attackers in directly observed infanticides are indicated by **boldface**. Suspected infanticidal males in circumstantial attacks are indicated by *italics*. In all cases of the latter except case 8, the suspected infanticidal male is operationally defined as the current alpha male. In case 8, the current alpha male was uninvolved in the infanticidal attack, but new immigrant male GL was observed wahooing and running at the time (see text).
[c] The female died shortly after her infant was killed.

cases, but in only one of five cases did the alpha male at the time of the infant's death unambiguously fall in rank before the mother subsequently conceived her next infant (Table 6.5). Even without positive identification of the attacker, this pattern is striking in light of the short tenure of alpha males in general.

Other hypotheses for male infanticide are less supported. The possibility that males killed infants in order to exploit them nutritionally is suggested by partial consumption of infants' bodies in three of the five directly observed infanticides. This finding by itself does not invalidate the sexual selection hypothesis, which makes no explicit predictions concerning what males will do with the bodies of infants they have killed. Moreover, orphaned infant chacma baboons were unharmed by resident adult males even though they presumably were especially vulnerable to

cannibalism at that time ($N = 2$ orphans during this study; $N = 9$ reported by Hamilton *et al.* 1982).

The hypothesis that the killing of infants is a largely an accidental side effect of generalized inter- and intrasexual aggression (Bartlett *et al.* 1993) receives only limited support, primarily from two inferred infanticides. In case 11, an infant disappeared during a prolonged intragroup aggressive interaction involving multiple baboons. In case 7 an infant was mortally wounded during an intergroup encounter, in which group arousal and aggression are indeed generally heightened. This case does not necessarily disqualify the sexual selection hypothesis, however, since it remains to be determined whether this context provides infanticidal males with opportunities to kill infants. The actual onsets of infanticidal attacks were unobserved in most cases, but it is important to note that the intense screaming generally associated with them usually erupted spontaneously from individuals otherwise silent and relaxed in the immediately preceding moments. These outbursts of screaming were thus not part of escalating aggression, but appeared to be the vocal response to an apparently precipitous infanticidal attack already in progress or, in fact, accomplished.

In summary, the sexual selection hypothesis best accounts for the currently available data on infant-killing in the Moremi population.

Infanticide as a facultative strategy

Theoretical models (e.g., Chapman & Hausfater 1979; Hausfater *et al.* 1981) have assumed that "infanticide" versus "non-infanticide" may be a pure evolutionarily stable strategy (ESS) pursued by two different types of male or a mixed strategy pursued by individuals at some probabilities p and q, respectively. The data for Moremi baboons are few, but the fact that three of eight alpha males accounted for all observed woundings of infants, and were also implicated in most of the suspected infanticides, suggests that males vary in infanticidal behavior.

If some males commit infanticide at significantly higher rates than others, an important goal of future research is to discover why. Existing data can only suggest potentially important variables meriting further study. Reduced opportunity for reproduction, as reflected by the ratio of estrous to anestrous females, is one of these. For example, male DG attained alpha rank at a time when only one of the group's 18 females was

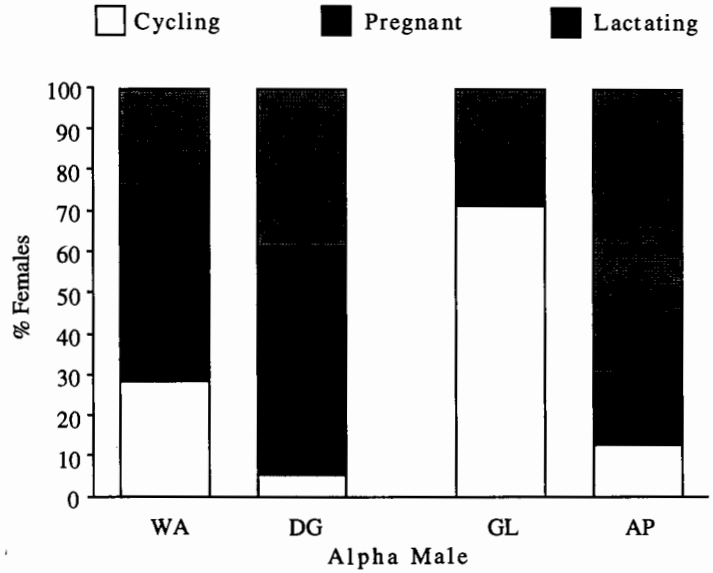

Figure 6.2. Distribution of reproductive conditions of resident females chacma baboons at the time of attainment of alpha position. Males DG and WA were responsible for a relatively large number of infanticides, whereas few infanticides were attributed to males GL and AP.

cycling. More generally, available data show that anestrous females, particularly pregnant females, were more abundant when males DG and WA each became alpha and embarked upon a series of infanticidal attacks, than when the males GL and AP became alpha and committed few, if any, infanticides (Figure 6.2). Because of long interbirth intervals and short alpha tenures, females that are pregnant at the time a new male becomes alpha are especially unlikely ever to become available as fertile mates to him, unless their infants subsequently die *in utero* or postnatally. Another possible reason for variation in infant-killing by males is the number of adult males in the group, since infanticide may be more costly in groups with more adult males. The case of male DG opposes this hypothesis, however, at least in its simplest version. He achieved alpha status at a time when male membership of the study group was at its highest level, including seven non-natal adult males and eight natal adult males (≥9 years old); the abundance of males failed to prevent male DG from killing a large number of infants. Finally, currently unidentified attributes of

individual males may also contribute to variation in infanticidal behavior upon reaching alpha rank.

Clearly, more data are necessary to elaborate the causes of variation in infanticidal behavior of male chacma baboons. These data additionally promise to clarify the source of interpopulation differences, i.e., the notably lower incidence of infanticide in East African savanna baboons. At present, our data endorse the conclusion of Collins *et al.* (1984) that the brevity of alpha male tenure in Moremi chacma baboons (<7 months) is a likely proximate cause of infanticide in this population. The success of alpha males in monopolizing copulations with fertile females, which Bulger (1993) described as "the most striking aspect of male mating patterns" in Moremi chacma baboons, may further distinguish them from East African conspecifics (e.g., Bercovitch 1987; Altmann *et al.* 1988, 1996), although direct comparative data are needed to determine this. If so, male chacma baboons may be more likely to reap the reproductive benefits of infanticide. The reasons for the shorter tenures and possibly greater mating exclusivity of alpha male chacma baboons, however, remain obscure.

Friendships and male defense of infants

Palombit *et al.* (1997) argued that heterosexual friendships in chacma baboons are female counteradaptations to deter male infanticide. There were few opportunities to observe the responses of males to actual or potentially infanticidal attacks, although some preliminary patterns emerge. A protective role of male friends is suggested by their direct intervention in all attacks in which infants escaped injury, and their absence in two-thirds of the attacks in which infants were severely or fatally wounded. Male friends do not always act alone. In over half of attacks on infants, other individuals became involved in the interaction, including maternal relatives of either sex, and non-friend adult males.

The participation of both non-friend and friend males in defense is noteworthy because experimental data suggest that male friends are more predisposed than control males to aid females and dependent infants under attack (Palombit *et al.* 1997). There are at least two interpretations of this result. First, it should be kept in mind that it is sometimes difficult to identify "aiding" of females, let alone its relevant proximate causes, from the aroused running about and screaming of

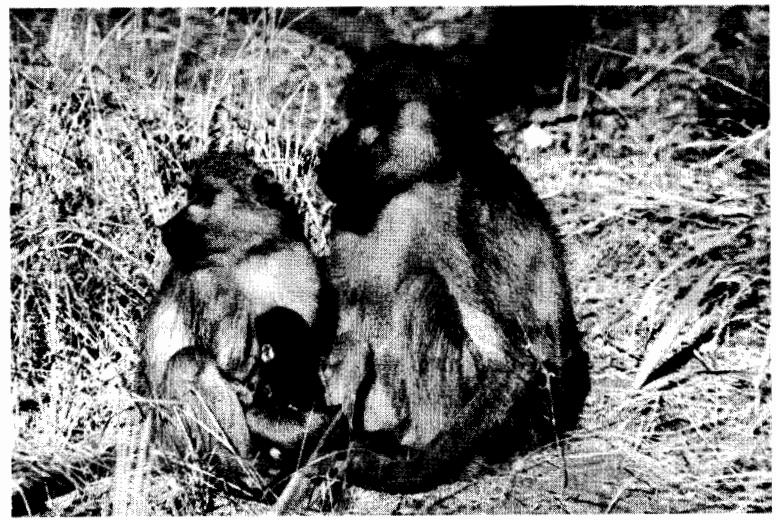

Figure 6.3. A friendship in chacma baboons: a lactating female with her infant and an adult male (photo: Ryne Palombit).

multiple baboons following actual or potentially infanticidal attacks by alpha males. Indeed, it was precisely this problem, combined with the rarity of such attacks, that prompted Palombit *et al.* (1997) to use playback experiments to evaluate this question systematically under more controlled circumstances. Thus, interpretation of the *ad libitum* observations is complicated by the possibility that some baboons may not be "involved" in the sense implied here.

Alternatively, the few available data suggest that male friends invested more heavily than non-friends in defense of lactating females and infants under attack (Figure 6.3). This was variably expressed as reactions that were more direct and sustained, uniquely involving the protective carrying of targeted infants, initiating and maintaining close proximity to the aggressor alpha male, or engaging him with threats, vocalizations, appeasement gestures, chases, or, ultimately, fights. Non-friend males responded less conspicuously, but nevertheless actively, by rushing to the site of an attack and remaining there in a state of aroused vigilance. The possible benefit of their presence is suggested by the fact that their intervention occurred in one-third of attacks in which infants escaped injury but was absent in all cases where infants were wounded or killed (even though male friends defended in one-third of these). Participation of sub-

adult males and females, however, was broadly similar in both injurious and non-injurious contexts (or, perhaps, slightly more common in cases where infants were seriously wounded). How non-friends specifically influence the outcome of attacks remains unclear, but deterrence may operate through elevated costs of attempted infanticide in the company of several adult males. The threat of more active defense by non-friends is implied, but in practice simply the presence of these males may be sufficient to modify alpha male aggression. Notably, however, non-friend males intervened in alpha male attacks on infants only when the mother's male friend interceded as well. In summary, the data from Moremi implicate the critical role played by male friends in protecting infants, but also hint at an important, though conditional, contribution to deterring infanticide by non-friend, adult males.

The hypothesis that emerges from the combined, if unequal, participation of both friend and non-friend males is that heterosexual friendships effectively deter infanticide partly because they facilitate communal defense of infants by several adult males. That is, a lactating female's male friend may or may not be capable of single-handedly preventing infanticide, but his immediate and substantive commitment to defending her may increase the probability of involvement by other males who otherwise eschew costly engagements with the alpha male on their own, and whose participation may be crucial in some circumstances. This hypothesis predicts that non-friend males' coalitionary support involves fewer costs (e.g., risk of injury) than the male friend's, and that they benefit from the interaction for reasons that may or may not be related to infant defense per se. For example, non-friend males may undermine the current alpha male's dominance status by supporting another male's aggressive confrontation with him. The importance of a particular male's defensive commitment is further corroborated by patterns of female competition for friends. When establishing friendships, lactating females routinely overlook several "unbonded" adult males available in favor of a male that already possesses a female friend, even though the ensuing competition with the rival female results in diminished sociospatial access to the male and a weakened friendship (Palombit *et al.* 2000). Some probability of paternity may be the crucial variable underlying female preferences for particular males, since 68% of friendships involved a male with whom the female was known to have copulated during the cycle in which she conceived her current infant (Palombit *et al.*, 1997) and since the strength of male response to playback of female screams is positively correlated with male rank at the time the female conceived her infant (Palombit *et al.* 2000).

Conclusions

Although our data considerably augment the previous summary of Collins *et al.* (1984), they remain limited (e.g., are taken from a single group) and dictate a need for further testing of the conclusions offered here.

As in one-male primate groups, the social context of infanticide in chacma baboons is broadly related to replacement of the primary breeding male, in this case, the alpha male. Typically, the new alpha male in a chacma baboon group is also a recent immigrant, but this is not strictly necessary. Even a long-time resident of the group may attempt infanticide upon attaining (or resuming) the alpha position in the male hierarchy. These were the two situations in which we observed infanticide. A third context for infanticide is possible in multimale groups and does not involve male replacement: if two females are simultaneously ovulating and the alpha male can sexually consort only with one of them, then the other female's infant might be vulnerable in future to infanticide by this same alpha male. Infanticide did not occur in this context, however, among Moremi chacma baboons.

In general, existing data support the sexual selection hypothesis more than alternatives. The systematic flexibility and ontogeny of male infanticidal and defensive behavior provides compelling evidence in favor of Hrdy's (1974) hypothesis. During attacks directed at infants, some males consistently defend particular infants, while aggressors are generally new alpha males likely to benefit reproductively from the target infant's death. The stability of this pattern opposes the view that infant fatalities are the consequence of erratic male–male aggression. Moreover, the transformation of male behavior illustrates how male mating strategies apparently involve an adaptive suite of behaviors, beginning with immigration and attainment of short-lived alpha status, leading directly to infanticide in some cases, followed by accelerated fertilization of females, then by resistance to new incoming males, an eventual fall in rank from the alpha position, and, notably, continued membership in the group and protection of infants. One of the most striking features of

chacma baboon social behavior is that infanticidal alpha males later become the friends of females and the ardent defenders of young against infanticide.

Females' friends are the principal defenders against infanticide, but the responses of adult, non-friend males to attacks may also help to alleviate immediate danger to infants in some circumstances. The patterns of non-friend intervention in chacma baboons suggest that communal infant protection is fostered by one particular male's disproportionately active investment in defense. Such a mechanism may operate more generally in multimale primate groups to lower frequencies of infanticide in this social setting. Another possible deterrent arising in a multimale setting is suggested by the co-occurrence in alpha male chacma baboons of both infanticide and high mating exclusivity (see above). Where alpha males are less successful in monopolizing copulations with fertile females (e.g., Altmann *et al.* 1996), infanticide will offer them fewer advantages. In summary, preliminary data from the Moremi population suggest that the presence of multiple males in a primate group can discourage infanticide both by increasing its attendant costs and by decreasing its future benefits. If so, an important implication is that female primates can potentially alter the economics of sexually selected infanticide in their favor by manipulating male membership in groups (Altmann 1990; Packer & Pusey 1983) and their social relationships with males (Palombit *et al.* 1997). How and when they do so remain unclear.

Currently available data are remarkably consistent with the predictions of Hrdy's (1974) sexual selection hypothesis and suggest that infanticide and defense of infants are elements of an adaptive reproductive strategy of male chacma baboons.

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Appendix 6.1. *Previous observations of infanticide in chacma baboons* (Papio cynocephalus ursinus)

Population	Date	Observation Type	Infant age	Infant sex	Comments	Source
Moremi (C troop)	1 Sept. 1979	Direct	4 days	?	Newly immigrant alpha male BB seen eating infant after mother had been tranquilized	Collins *et al.* (1984)
Moremi (C troop)	8 Sept. 1979	Direct	8.1 mo	M	Infant bitten by unidentified adult male at dusk was found dead the next day with canine puncture wounds in skull	Collins *et al.* (1984)
Moremi (W troop)	6 Feb. 1980	Direct	2 days	?	Newborn infant was somehow taken from its low-ranking mother by a pregnant female; when seen again 2 days later it was dead	Collins *et al.* (1984)
Moremi (W troop)	16 Feb. 1979	Circumstantial	10.8 mo	F	Infant found with lacerations on its head and lower back; 4 weeks later, it received a second wound and then disappeared 3 days later	Collins *et al.* (1984)
Moremi (C troop)	29 June 1980	Circumstantial	1 day	M	Female discovered carrying her dead newborn infant, which had multiple lacerations and punctures (both had been seen healthy 30 min earlier)	Collins *et al.* (1984)
Moremi	Nov. 1982	Direct	6 mo	F	Natal male that became alpha in previous June attacks infant that is alone and inflicts fatal wound to head	Tarara (1987)
Drakensberg Mtns	?	Direct	2 weeks	?	Newly immigrant alpha male fatally wounds infant in the neck during an intergroup interaction	Weingrill (2000)
Drakensberg Mtns	?	Circumstantial	7 weeks	?	Mother with dried blood on her chest seen carrying a dead infant	Weingrill (2000)

Notes:
M, male; F, female; Mtns, mountains.