

A “friendship” in wild chacma baboons of the Okavango Delta: adult male, adult female, and her infant. (Photo by Ryne A. Palombit.)



MALE INFANTICIDE IN WILD SAVANNA BABOONS: ADAPTIVE SIGNIFICANCE AND INTRASPECIFIC VARIATION

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INTRODUCTION

Infanticide by males is documented in insects, amphibians, birds, rodents, carnivores, and primates, as well as other mammals [Hausfater & Hrdy, 1984; Parmigiani & vom Saal, 1994]. Recognition of infanticide's widespread distribution has recently fostered a research program inspired by Hrdy (1979) and seeking to understand how aspects of a species' biology—and female biology in particular—may constitute adaptations to check the risk of infanticide [Ebensberger 1998; van Schaik & Janson 2000]. This shift in analytical focus towards the evolutionary consequences of infanticide significantly advances the study of this “protean and disturbing phenomenon” [Hrdy, 2000:xiii]. Nevertheless, there remains a crucial need to carefully document infanticide in the field; or, as Jolly et al. [2000:37] put it: “...there is no substitute for the slow accumulation of observations by collaborating observers, reported with enough detail to address the questions that may yet arise.” This is particularly so for data on nonhuman primates, which have generated much controversy without clarifying the proximate and ultimate causes of infanticide as successfully as research on rodents.

Infanticide in primates has been investigated primarily in groups comprising one breeding male and a few females, such as red howling monkeys, Hanuman langurs, and mountain gorillas [e.g., Crockett & Sekulic, 1984; Sommer, 1994; Watts, 1989]. Multimale societies have received far less attention, in part because infanticide appears to be less common in this social setting. It is now clear, however, that infanticide is not only a potential, but in some cases, a realized threat for females living in groups with multiple males [e.g., Hiraiwa-Hasegawa, 1987; Soltis et al., 2000; Borries & Koenig, 2000]. Comparative study of multimale social systems in which infanticide does and does not occur promises to illuminate the adaptive significance of this behavior.

This chapter has two objectives related to this larger question. First, I reevaluate the adaptive significance of male infanticide in savanna baboons (*Papio cynocephalus*), which live in large, multimale and multifemale groups. In their original review,

Collins et al. [1984:211] concluded that “no attempt can be made to refute either of the major hypotheses” explaining infanticide in baboons. Since then, new reports have more than doubled the sample of direct observations, as well as increased the pool of circumstantial evidence. I test the current competing hypotheses for male infanticide with these additional data. Hrdy [1974] proposed that infanticide is a reproductive strategy creating breeding opportunities for males whose sexual access to females is limited by intrasexual competition. A competing hypothesis argues that the killing of infants is largely an accidental side effect of generalized inter- and intrasexual aggression associated with replacement of breeding males in groups [Bartlett et al. 1993]. The nutritional exploitation hypothesis suggests that infanticide provides cannibalistic males with feeding benefits [Fox, 1975; Sherman, 1981]. The social pathology hypothesis that infanticide is an aberrant behavior arising maladaptively from human disturbance [Boggess, 1979] is now largely abandoned as a general explanation for primate infanticide [van Schaik, 2000].

Second, I use this larger data set to assess variation in male infanticide across populations of savanna baboons. Study of variation across populations of the same species provides a valuable means of examining the adaptive links between behavior and ecology [e.g., Clutton-Brock & Harvey, 1976; Martin, 1981; Jolly, 1985]. This has been particularly true for recent studies of the savanna baboon. Although significant gaps in our knowledge persist (particularly concerning the little-studied cape or Guinea baboon, *P. c. papio*, of west Africa), a relatively large body of data has accumulated from well-studied populations of yellow (*P. c. cynocephalus*), olive (*P. c. anubis*) and chacma baboons (*P. c. ursinus*). Analyses of baboon social behavior focus increasingly on intraspecific variation [Barton et al., 1996; Barton, 2000; Bulger, 1993; Cowlishaw, 1994, 1995; Dunbar, 1990, 1994; Hill et al., 2000; Silk et al., 1999].

Indeed, the savanna baboon is an excellent subject for such comparative work. The many subspecies share a close genetic relatedness [Jolly, 1993] that largely controls for the potentially confounding effects of phylogeny as well as basic features of life history and reproductive biology, but they otherwise differ considerably in ecology, behavior, and demography. Moreover, numerous researchers have emphasized “the breadth of the behavioral repertoire and capacity for social flexibility within contemporary savanna baboons” [Hamilton & Bulger, 1992:61], particularly with respect to male “behavioural flexibility to optimise reproductive strategies under changing conditions...” [Barton et al., 1996:328]. In this chapter, I extend these analyses to explicitly include interpopulation variation in infanticide by males.

There are compelling theoretical reasons to expect that infanticidal behavior will vary among males of the same population or species [Hausfater et al., 1981; Glass et al., 1985; Tuomi et al., 1997]. Although several primate studies have documented differences between groups of the same general population [e.g., Butynski, 1990; Crockett & Janson, 2000], it is only relatively recently that interpopulation variation in male infanticide has been examined [Arcadi & Wrangham, 1999; Borries & Koenig, 2000]. The potential for infanticide to increase male reproductive success in savanna baboons has long been appreciated [Altmann et al., 1978], and early data tentatively suggested at least one possible, but indistinct difference in this behavior between the chacma

baboon and the olive baboon [Collins et al., 1984]. The larger data set now available on infanticide by male savanna baboons allows a preliminary assessment of this question.

The Comparative Data Set: Published Reports of Males Injuring Infants

I evaluated the occurrence of infanticide by males by using several sets of data: (1) the distribution across study sites of reports of injurious attacks on infants by males; and (2) estimates of infant mortality due to infanticide; (3) the patterning of infanticide as it pertains to competing explanatory hypotheses.

Baboon systematics is “a tangle” [Groves, 2001:237] generating numerous taxonomic systems [see Grubb et al., 2002]. For the purpose of this review, I follow other workers in limiting a treatment of “savanna baboons” to the yellow, olive, chacma, and Guinea (or cape) baboons, which will be considered subspecies of a single species [Thorington & Groves, 1970; Smuts et al., 1987; Estes, 1991; Kingdon, 1997], and excluding the hamadryas baboon because of its “ecological/adaptive distinctiveness” [Jolly, 1993]. Although infanticide is documented among captive hamadryas [e.g., Gomendio & Colmenares, 1989], it has rarely been directly observed in the wild [Swedell, 2001].

Direct Observations of Attacks

In the last review of infanticide in wild savanna baboons, Collins et al. [1984] summarized eight directly observed attacks. I consider an additional 11 cases, most of which were published subsequently (Table I).

Unlike Bartlett et al. [1993], I include direct observations of males injuring infants that eventually survived (Table I). I include these episodes of nonfatal wounding for several reasons. First, in all cases the wounds sustained constituted a serious threat to infant survival, as reflected by their mode of infliction (by canines), their location (the head or torso), their immediate deleterious effects (e.g., impairment of locomotion), or a combination of these factors. Second, there is currently no theoretical or empirical basis for assuming that infanticidal aggression enjoys a success rate of 100%. Narrative descriptions of these attacks indicate that opportunities to fatally injure infants are ephemeral (see Tables I and II). This is partly because vigilant caretakers preemptively retrieve infants from dangerous situations before a male can initiate an attack. And this is partly because infanticidal attacks, once launched, elicit defense and even counter-attacks from others, which confront the attacker with potentially significant costs. Thus, males are predicted to dynamically adjust infanticidal behavior, selectively initiating, modifying, and even abandoning an attack in light of conditions. For example, even an infanticidal alpha male may benefit from avoiding confrontation with an infant’s adult male protector, since risk of injury in fights between male baboons is irrespective of the contestants’ competitive abilities [Drews, 1996]. The extensive distribution of wounds across infant victims’ bodies additionally supports the view that males commit infanticide opportunistically and rapidly: males apparently damage any body area they manage to seize during quickly executed attacks [Palombit et al., 2000; King & Steklis, in preparation; see Tables I and II, Figure 1].

Table I. Injurious attacks to infants by male savanna baboons: Direct observations.

Case	Site	Comments	Infant		
			Sex	Age	Injuries
<i>Papio c. cynocephalus:</i>					
1	Amboseli	During intergroup interaction, male from one group ran with live infant from other group in his mouth, pursued by screaming members of infant's group; infant found with wounds, after which it was handled by members of neighboring group and died; infant's mother also attacked by extra-group females	M	1 mo	two punctures and "gash" to head
2	Mikumi	"Aroused" subadult male seized infant and ran with it in mouth, pursued by screaming mother and other mobbing baboons; infant experienced difficulty walking after wounding, but survived	M	9 mos	to torso (side and back)
<i>Papio c. anubis:</i>					
3	Gombe	Male attacked infant with its mother; infant's wounds became infected, leading to death 11 days later	F	6.4 mos	to neck & torso
4	Gombe	Male attacked & bit mother carrying infant, was mobbed by numerous group members, then resumed attack, during which infant was killed from wounds (mother received cuts to head as well)	F	8.5 mos	to head & shoulder
5	Gombe	Infant approached and presented to male, eliciting two attacks during which he bit infant, inflicting wounds; other baboons, including mother and grandmother defended, the latter of which was injured by AC; infant died 22 min later	F	7 mos	bite to head, abdomen, & groin
6	Gombe	Vocalizing attracted observers to interaction in which male chasing nearby females and juveniles; male climbed tree with infant, inflicted bite wounds, and carried infant, screaming, in his mouth; infant died 15 min later	F	8.4 mos	chest & back
<i>Papio c. ursinus:</i>					
7	Moremi	Ten minutes after mother was darted by observer, male discovered with her dead infant, which he discarded partially eaten (after which male BF-see Case 11-ate)	?	4 days	not described
8	Moremi	Observer unfamiliar with group saw adult male bite infant at dusk; next morning infant was found dead of wounds	M	8 mos	bite to head
9	Moremi	Male bit infant; infant survived but showed incoordination for several weeks	F	11 mos	bite to head

Table I. (Continued)

Attacking Males						
ID	Immigration Date (mos before attack)	Rank	Sire of Victim? ^{ai}	Copulated with Mother?	Reproductive Benefit of Infanticide ^b	Ref ^c
<i>Papio c. cynocephalus:</i>						
-	Extra-group adult male	?	No	No	Low	1
-	Subadult (natal?) male	?	?	Not applicable (infant survives)	Low	2
<i>Papio c. anubis:</i>						
BR	9.5	Not alpha	No	Yes, but not as alpha (on day D-1) ^d	Moderate	3
FA	2.3	? (unhab- ituated group)	No	?	?	3
AC	8	Not alpha	No	No	Low	3
SG	Natal male	Alpha (recent)	Unlikely ^e	No (despite alpha rank)	Low	3
<i>Papio c. ursinus:</i>						
BB	2.5	Alpha 2.5 mos earlier	No	Yes, while still alpha (probably not in conceptive cycle?)	Moderate	3
?	?	?	?	?	?	3
BF	3.3 mos	Low-ranking	No	Not applicable (infant survives)	Low	4

Table I. (Continued)

Case	Site	Comments	Infant		
			Sex	Age	Injuries
<i>Papio c. ursinus:</i>					
10	Moremi	13 min after baboons drove him off from an attack on a female and her ventral infant, the male attacked another infant while giving wahoo calls ^f , bit it, fled as defending baboons pursued him; infant died next day	F	6 mos	head puncture penetrating brain
11	Moremi	While wahooing & chasing other group members, male bit infant; mother had already resumed cycling two months earlier, and male had mated with her in these two cycles	F	1 yr	8 cm "gash" to back
12	Moremi	Male seen running through group with dead infant in mouth pursued by other screaming group members (including mother, sister, unrelated females, subadult natal males, and male "friend" of mother)	F	2 mos	not described
13	Moremi	Male seen running through group with dead infant in mouth as other group members screamed and male friend of mother chased him; attacking male partially ate body	M	3.7 mos	not described
14	Moremi	While wahooing, male attacked female carrying infant, obtained infant and instantly killed it, while mother and other females screamed; male partially ate body	M	1.8 mo	not described
15	Moremi	Male seen running with screaming infant in his mouth, as two subadult males pursued him and numerous baboons screamed loudly; male discarded dead infant with multiple wounds shortly thereafter	M	11.8 mos	to torso, head, & limbs
16	Moremi	Male seen running with infant in mouth; he was not pursued by defenders, but other group members screamed loudly; male ate body	M	2 days	not described
17	Moremi	While its mother was away at the site of a vervet monkey kill, a male rushed at her unattended infant, inflicting wound; a distantly-related, young adult natal male immediately retrieved infant and carried the rest of day; infant eventually survived after period of debilitation	F	9.3 mos	canine bites to torso
18	Drakensberg Mtn	While a female and her male friend were watching an intergroup interaction, a male of her own group attacked her nearby infant, biting and carrying by the head; she screamed and her male friend pursued the killer, but the infant was dead.	?	2 weeks	bite to neck & head
19	Drakensberg Mtn	In a group that is not studied, an adult male was seen killing an infant	?	?	not described

Table I. (Continued)

Attacking Males						
ID	Immigration Date (mos before attack)	Rank	Sire of Victim? ^a	Copulated with Mother?	Reproductive Benefit of Infanticide ^b	Ref ^c
<i>Papio c. ursinus:</i>						
CV	Natal male	Alpha 5 mos earlier	Unlikely	No (mother is dead)	Low	4
CV	Naatal male	Alpha 8 mos earlier	Unlikely	Not applicable (infant survives)	Low	4
WA	19	Alpha 2 mos earlier	Unlikely	Yes, while still alpha; during conceptive cycle	High	5
WA	22	Alpha 6 mos earlier	Unlikely	Yes, while alpha or beta ^d ; during conceptive cycle	High	5
DG	2.5	Alpha 2.5 mos earlier	No	Yes, while still alpha; during conceptive cycle	High	5
DG	2.5	Alpha 2.5 mos earlier	No	Yes, while still alpha; during conceptive cycle	High	5
DG	3.5	Alpha 3.5 mos earlier	No	Yes, while still alpha; during conceptive cycle	High	5
TM	3 (Natal male) ^b	Beta (Alpha 2.5 mos later)	No ^e	Not applicable (infant survives)	Moderate	5
DU	5	Alpha 5 mos earlier	No	Yes, while still alpha; during conceptive cycle	High	6
?	?	?	?	?	?	7

Notes for Table I.

- ^a “No” = refers to male absence from group when infant conceived; “Unlikely” refers to infant conceived while infanticidal male resided in group, but was low-ranking.
- ^b The potential for infanticide to have increased male sexual access to females in the subsequent conceptive cycle is determined by observations of subsequent mating patterns (in cases where infants died) or by male rank (in cases where infants survived injury) (see text).
- ^c Reference source: 1 = Shopland [1982]; 2 = Rhine et al. [1980]; 3 = Collins et al. [1984]; 4 = Buskirk pers. comm. to Collins et al. [1984]; 5 = Tarara [1987]; 6 = Palombit et al. [2000]; 7 = Weingrill [2000]; 8 = Lycett pers. comm. to Weingrill [2000].
- ^d “D-1” refers to 1 day before detumescence (or visible “deflation”) of the female sexual swelling; ovulation in savanna baboons is most likely on day D-3, but sometimes occurs on D-2 and D-1 (see text for references). Thus, male BR is a “possible father” of subsequent infant [Collins et al., 1984].
- ^e Natal male not related maternally to the infant he attacked.
- ^f The “wahoo” is a loud call typically given by male baboons [Buskirk et al., 1974; Byrne, 1981].
- ^g The infanticidal male had an unstable dominance relationship with a new immigrant male at the time the mother conceived her next infant, but he out-ranked all other males in the group.
- ^h Although a natal male, TM had previously emigrated from the study group into a neighboring group, where he remained for two years before returning to his natal group.

In light of this nature of male infanticidal behavior, it is expected that some proportion of targeted infants will survive, depending upon the severity of the injuries, their age and physical condition at the time, and the care they subsequently receive from conspecifics (e.g., one infant survived its injuries because it was immediately retrieved by a distantly-related natal male in the presence of its attacker and carried by him for the rest of the day). Therefore, inclusion of nonfatal but physically damaging attacks by identified males improves understanding of infanticide risk, its possible function, and its associated counterstrategies.

Inferred Attacks

Consideration of only directly observed cases is likely to underestimate the rate of infanticide [Janson and van Schaik, 2000]. Following Collins et al. [1984], but in contrast to Bartlett et al. [1993], I thus consider 19 reports of inferred infanticides in which the attacker was, by definition, unknown (Table II). These reports were based on circumstantial evidence of two sorts.

The majority, 15 cases (79%), were discoveries of infants with injuries of unknown but recent origin (which proved fatal in all but one instance). The nature of these wounds (e.g., deep punctures) precluded physical accidents as the cause (e.g., falling out of a tree or down a cliff). Predators, which for savanna baboons are primarily large carnivores such as leopards and lions, or, rarely, hyenas [Stelzner & Strier, 1981] and chimpanzees at some sites [Ransom, 1981; Wrangham & van Zinnicq Bergmann-Riss, 1990], were also an unlikely explanation for various reasons. Some injuries occurred among baboons inhabiting areas lacking predators (e.g., chacma baboons in the Drakensberg Mountains, South Africa). In 11 other cases (4, 6, 7, 8, 10-15, 17), infants were seen healthy and viable shortly before (sometimes minutes before) they were discovered with wounds. Researchers were thus with the study group when the rel-



Figure 1. The body of 2.5-kg infant chacma baboon minutes after it was killed by an adult male in an observed attack (Case 15 of Table I). The large dorsal posterior laceration has exposed underlying tissue and part of the pelvis and vertebral column. Other wounds are located on the head, left arm and (not visible) right leg. (Photo by Ryne A. Palombit.)

evant infant received its wounds. In all cases, predators were not only undetected, but baboons failed to show anti-predator behavior at the time, such as alarm calling, fleeing to refuges, and/or aggressive mobbing by adult and subadult males (common against leopards and smaller potential predators such as dogs and cheetahs in some populations). These conspicuous behaviors characterize observed contact between baboons and potential predators, especially during an actual attack in which a troop member is injured or killed [e.g., DeVore & Hall, 1965; Saayman, 1971; Cavallo, 1990; Bailey, 1993; Condit & Smith, 1994; Cowlshaw, 1994, 1997a; Palombit, unpublished data]; they were notably absent when these infants were wounded. On the contrary, it was an outburst of screaming and chases, as documented in directly observed infanticides, that often attracted observers' attention to the newly injured infant.

Together, these considerations implicate conspecifics as the likely source of the recent injuries to these infants. Reporting researchers tentatively offered this interpretation for all cases in Table II, although they could not, of course, specify with certainty the responsible individual(s).

Intragroup "kidnapping" or "aunting to death" [Hrdy, 1976] by adult or immature females is a possible, though unlikely cause of these injuries. Infants taken from their mothers are rarely injured (particularly lethally) by their female abductors, and starvation or dehydration is invariably the cause of death when it occurs, both in baboons



[Strum, 1974; Collins et al., 1984; Shopland & Altmann, 1987; Brain, 1992] and other cercopithecines [Bourlière et al., 1970; Schino et al., 1993; Muroyama & Theiry, 1996; Digby, 2000].

Thus, there are grounds for suspecting that males were likely perpetrators of the wounds summarized in Table II, particularly given the size and apparent depth of the wounds in some cases. Moreover, in several reports (6, 7, 10, 11, 12), the screaming of nearby baboons was directed at or elicited by particular male(s) in the vicinity of the injured infant.

The final four cases of inferred infanticide concerned formerly healthy infant baboons that either died in conditions preventing confirmation of wounds by observers (two cases) or that disappeared (two cases). Disappearance of viable young in conjunction with turnover or replacement of breeding male(s) is sometimes interpreted as indirect evidence for infanticide [e.g., Crockett & Sekulic, 1984; Pusey & Packer, 1994]. If the abrupt absence of a healthy infant from the group was the sole criterion for suspecting infanticide, the sample in Table II would be larger, since up to 40–45% of infant mortality in baboons comprises such disappearances, and some of these follow changes in the male dominance hierarchy [e.g., Collins et al., 1984; Palombit et al., 2000]. Rather, I consider disappearances additionally accompanied by circumstances suggesting infanticide. In one instance (Case 16), a healthy infant was found to be absent from the group after a three-hour break in observation, and the newly immigrant alpha male was simultaneously discovered with blood on his hands and face. This adult male had been directly observed to: (1) kill two other infants in the preceding six days (one of which he partially consumed); and (2) unsuccessfully attack the infant in question five days earlier (it was rescued by a sister [Palombit et al., 2000]). In the second instance (Case 17), an infant seen healthy disappeared during a violent intergroup interaction in which its mother was also wounded and during which observers were in continuous contact with the study animals. Likewise, the accompanying circumstances suggest infanticide for the two infants that were found dead but whose bodies could not be examined for wounds (Cases 1 and 18).

It is important to note that while these cases may improve understanding of demographic variation in infanticide, lack of descriptive detail limits their usefulness in evaluating competing hypotheses explaining infant killing. In other words, they help establish the occurrence of infanticide by conspecifics (probably males), without necessarily clarifying its proximate or purported evolutionary causes. Accordingly, the analysis of explanatory hypotheses below draws primarily upon the directly observed cases of Table I.

With respect to the olive baboons at Gombe, Collins et al. [1984] reported 12 infant deaths resulting from injuries of unknown origin but considered conspecifics likely sources in five cases (as opposed to other potential causes such as accident, chimpanzee predation, etc.). I (conservatively) consider only these five cases of inferred infanticide in Table II.

The data sets of directly observed attacks and inferred attacks did not differ from one another with respect to the median age (Mann-Whitney U-Test, $U = 146$, $N_1 = 17$, $N_2 = 18$, NS) or the sex ratio ($\chi^2 = 1.1$, $df = 1$, $N = 32$, NS) among the infants targeted.

With one exception (Gilgil, Kenya), studies producing circumstantial evidence for inferred infanticide have also been the sites of directly observed infanticidal attacks.

Infanticide Rate

I use the reported proportion of infant mortality due to infanticide to assess inter-population variation in the incidence of male infanticidal behavior. This measure, which Janson & van Schaik [2000] label the “relative infanticide rate,” is useful for comparative purposes, partly because it accounts for differences in infant mortality across the taxa of interest.

Patterning of Infanticidal Behavior

The patterning and circumstances of infanticidal attacks are used to test predictions of Hrdy’s (1974) sexual selection hypothesis. One prediction is already well supported empirically and is not subjected to further test: infant death significantly accelerates termination of lactational amenorrhea and the resumption of fertile cycling in mothers, thereby reducing interbirth intervals [Altmann et al., 1978; Collins et al., 1984; Smuts & Nicolson, 1989; Brain, 1992; Bentley-Condit & Smith, 1997; Palombit et al., 2000; Weingrill, 2000]. I assess how consistent each particular episode is with three other predictions of the sexual selection hypothesis.

Prediction 1: The aggressor male was unrelated to the infant victim (particularly, as father). Baboon field studies have yet to generate genetic data to test this prediction directly [cf. Gilbert et al., 1991; Borries et al., 1999]. Consequently, I indirectly assessed the male’s sire status in the following way: (a) “No” if he was absent from the group when the infant was conceived; (b) “Unlikely” if he resided in the group as a low-ranking male when the infant was sired; and (c) “Likely” if he resided in the group as a mid- or high-ranking male when the infant was sired.

Prediction 2: The infanticidal male was likely to sire the next infant of the female whose infant he killed. Again, the absence of genetic data necessitates use of indirect indicators, namely subsequent observations of copulation between the infanticidal male and the mother when she resumed cycling.

Using as much information as available for each case, I assessed the potential reproductive benefits of infanticide to the male. Admittedly, these were qualitative assessments, but they were not entirely arbitrary. I considered the following supplementary information to obtain them:

- (a) the reproductive state of the female at the time her infant was killed (had she recently resumed cycling already or was she still lactating?).
- (b) the timing of observed copulations with respect to the periovulatory period (indicated in baboons by de-tumescence of the sexual swelling [Hendrickx & Kraemer, 1969; MacLennan & Wynn, 1971; Wildt et al., 1977; Pope et al., 1983; Hodges et al., 1986] and/or the subsequent conceptive cycle, if known (calculated as one gestation period back from date of birth of the subsequent infant).
- (c) male rank at the time of copulation: following Bulger [1993] I assume that high rank in males (particularly alpha status) increases the probability of siring the offspring of consort partners. This assumption may not apply to some baboon populations,

however, notably the olive baboons of Gilgil/Chololo, Kenya [Strum, 1982; Bulger, 1993]. Male rank (at the time of infanticide) was the sole criterion used to assess the potential reproductive benefit of infanticide in cases where infants survived injuries and in cases where observers could not collect data on the subsequent sexual behavior of infanticidal males.

Prediction 3: Infanticidal males directed aggression primarily at infants, not other conspecifics. I used narrative descriptions to evaluate the contexts of male attacks on infants and the degree to which other individuals were targeted or otherwise involved in an attack.

The availability of relevant data for testing these predictions varied across published reports.

Caveats

Two important caveats should be kept in mind. First, although a relatively large number of baboon populations has been studied across Africa, usually only 1-2 groups are monitored in sufficient detail to generate meaningful data on male infanticide at each site. Thus, the total sample of individual baboons is limited.

Second, I assume that variation across study sites in the rates of injurious attacks on infants is not due to methodological differences affecting researchers' observation and/or reporting of this behavior. This assumption is most pertinent for populations generating few or no observations of infanticide: I tentatively interpret the rarity of reports as evidence for a relative rarity of male infanticide. Drawing inferences from negative evidence is problematical, but this assumption seems an acceptable starting point for an analysis for two reasons. First, most of the field sites considered have yielded data on infant mortality and its causes. Second, I focus particularly on long-term studies that were initiated in the 1970s or early 1980s, notably of: (a) yellow baboons at Amboseli (Kenya) by J. Altmann, S. Altmann, Hausfater, and colleagues [e.g., Altmann & Altmann, 1970; Altmann et al., 1977, 1988] and at Mikumi National Park (Tanzania) by Rhine and colleagues [e.g., Rhine, 1986; Rhine et al., 1988, Rhine et al., 2000]; (b) olive baboons at Gilgil (Kenya) by Harding, Strum, Smuts and colleagues [e.g., Strum, 1974, 1987; Harding & Gilmore, 1983; Bercovitch & Harding, 1993; Smuts, 1985], at Masai Mara National Reserve, (Kenya) by Sapolsky and colleagues [e.g., Sapolsky, 1993], and at Gombe National Park (Tanzania) by Packer, Collins and colleagues [e.g., Collins et al., 1984; Packer et al., 1995]; (c) chacma baboons at Moremi Game Reserve (Botswana) by Hamilton, Cheney, Seyfarth and colleagues [e.g., Hamilton et al., 1976; Bulger & Hamilton, 1987; Cheney & Seyfarth, 1999; Silk et al., 1999] and in the Drakensberg Mountains (South Africa) by Whiten, Byrne, Henzi and colleagues [e.g., Whiten et al., 1987; Henzi & Lycett, 1995]. Methodology and research goals differ among these field studies, but they share a relatively long period of demographic monitoring. It is possible that early reports of relatively frequent male infanticide at some sites stimulated collection and publication of additional data on injuries to infants (especially, perhaps, of a non-fatal nature), compared to other sites where infant mortality was initially attributed to alternative causes. It seems unlikely, however, that this would generally hinder documentation of conspicuous, injurious attacks on in-

fants by males. Nevertheless, this assumption remains provisional. Indeed, one goal of this chapter is to stimulate the reporting of relevant data.

Infant Victims

The sexes were equally represented among the infants attacked by males ($\chi^2 = 2$, $df = 1$, $N = 32$, NS) and among the subset that died from wounds ($\chi^2 = 0.33$, $df = 1$, $N = 27$, NS). The average age of infants attacked by males was 5.9 mos ($SD = 4.6$, $N = 35$) (a similar result is obtained when observed and inferred cases are analyzed separately).

Five infants survived attacks in which they were seriously wounded. Although infant sex did not influence survival versus mortality following injury ($\chi^2 = 0.43$, $df = 1$, $N = 30$, NS), infant age did. Infants reported to survive injurious attacks by males were significantly older (Mean \pm SD = 11.1 \pm 2.1 mos, $N = 5$) than those that died (4.8 \pm 4.2 mos, $N = 28$), across observed and inferred cases (but excluding the two infant disappearances, Cases 16-17 from Table II) (Mann-Whitney U-Test, $U = 10.5$, $N_1 = 5$, $N_2 = 28$, $p < 0.01$). The same result is obtained when only the directly observed injuries (Table 1) are considered (surviving infants: 10.3 \pm 1.4 mos, $N = 4$; dead infants: 4.7 \pm 3.8 mos, $N = 14$) ($U = 3$, $p < 0.01$). The greater survivorship of older infants has at least two possible causes. First, the advanced developmental state and larger body size of older infants may mitigate the deleterious consequences of wounds and thereby accelerate recovery. Second, these infants may sustain less damaging wounds, either because they are more successful at escaping from attacking males or because male assaults on them are less intense.

Does Male Infanticide Vary Across Baboon Populations?

The Distribution of Published Reports

Infanticide by males is widespread in savanna baboons. Thirty-eight published reports of observed and inferred attacks have come from six long-term studies of three subspecies (Tables I and II): yellow baboons at Amboseli (Kenya) and Mikumi (Tanzania), olive baboons at Gombe National Park (Tanzania) and Gilgil (Kenya), and chacma baboons at Moremi Game Reserve (Botswana) and the Drakensberg Mountains (South Africa).

Approximately 65% of the reported cases of observed and/or inferred infanticidal attacks (fatal or nonfatal) were of chacma baboons; roughly half of the reports have come from the Moremi population alone (Table III). With the exception of the olive baboons at Gombe, relatively few published reports have originated from east Africa. The major studies of yellow baboons at Amboseli and Mikumi, and of olive baboons at Gilgil, account for only about 10% of the reports of actually or potentially fatal wounds to infants. None has been published for olive baboons at Masai Mara or for yellow baboons studied for a shorter period at Tana River, Kenya [e.g., Bentley-Condit & Smith, 1997]. Gombe stands out among East African sites as the source of about one-fourth of all reported infanticidal injuries. More recent studies of chacma baboons inhabiting arid Namibia [Tsaobis Leopard Park: Cowlshaw, 1997a, b, c] and the Kuiseb River Canyon [Brain, 1992] have not yielded reports of male infanticide (although

Table III. Published reports of injurious attacks on infants by male savanna baboons^a

Site	All Attacks (%)		Fatal Attacks (%)	
	Observed (N=19)	Observed & Inferred (N=38)	Observed (N=15)	Observed & Inferred (N=33)
<i>P. c. cynocephalus:</i>				
Amboseli	5.3	5.3	6.7	6.1
Mikumi	5.3	5.3	0.0	3.0
<i>P.c.anubis:</i>				
Gombe	21.1	23.7	26.7	27.3
Gilgil	0.0	2.6	0.0	3.0
<i>P. c. ursinus:</i>				
Moremi	57.9	52.6	53.3	48.5
Drakensberg	10.5	10.5	13.3	12.1

^a “Observed” reports are taken from Table I. “Inferred” reports are taken from Table II.

apparent attempted infanticides have been detected [O’Connell & Cowlshaw, 1994]); these studies are of shorter duration than the Moremi and Drakensberg studies of chacma baboons, however.

Infanticide as a Cause of Infant Mortality

The highest reported proportion of infant mortality attributed to infanticide comes from the chacma baboons of Moremi (Botswana): 29.4% reported by Collins et al. [1984] for a three-year period (N=17 infants death) and at least 37% reported by Palombit et al. [2000] for a six-year period (N=30 deaths). This rate is comparable to that reported for mountain gorillas [*Gorilla gorilla berengei*: 37%; Watts, 1989], and mantled howler monkeys [*Alouatta palliata*: 40%; Clarke & Glander, 1984]. A precise estimate of infanticide rate has not yet been published for the chacma baboons of the Drakensberg Mountains, but Weingrill [2000] reported “infanticide by males can be regarded as one of the main causes of death for infants in this population.” Although not quantitative, this assessment is noteworthy, for even qualitative statements of this sort are lacking from other long-term baboon studies.

In contrast to chacma baboons, male infanticide has not been identified as an important cause of infant mortality in long-term studies of east African olive baboons [Strum & Western, 1982] or yellow baboons [Altmann, 1980; Altmann et al., 1988; Rhine et al., 2000]. Among the yellow baboons of Amboseli, Kenya, longitudinal data re-

vealed that infanticide by males accounted for less than 5% of infant mortality [Altmann & Alberts, personal communication]. Likewise, Sapolsky (personal communication) has not obtained direct or indirect evidence of infanticide in his study of olive baboons in the Masai Mara. Alternative sources of mortality have been emphasized at these sites, such as disease, predation, nutritional/energetic stress (or some combination of these).

Once again, olive baboons studied at Gombe are distinctive among east African populations studied. Of 58 infant olive baboons that died over ten years at Gombe, four were killed by infanticidal males in observed attacks (Table I). An additional 12 deaths entailed injuries obtained in unobserved circumstances, of which Collins et al. [1984] judge that 5 were likely inflicted by conspecifics (Table II). Thus, infanticide by males accounts for at least 7.0-15.6% of infant mortality among these baboons.

The Patterning of Injurious Attacks: The Sexual Selection Hypothesis and Alternative Hypotheses

Prediction 1: Males are Unrelated to the Infants They Attack.

This prediction was supported in all 16 directly observed attacks for which relevant information was available. In 11 cases (69%) the attacking male could not have been the father due to his absence from the group when the infant was conceived. In the other 5 cases (31%) he was an “unlikely” sire because he was low-ranking at the time of conception and/or had not been observed to consort with the mother during that cycle. Moreover, in the cases where a natal male seriously injured an infant, researchers with relevant genealogical data also reported a low probability of maternal relatedness (due to factors such as previous group fission) (Table I).

Low probability of paternity between attacker and victim supports the sexual selection and nutritional exploitation hypotheses. The consistency of this result with one version of the generalized aggression hypothesis is ambiguous. If infanticide is the consequence of “the general mayhem accompanying male takeovers or escalated male conflicts for dominance” (van Schaik, 2000:46), then fathers may participate in some proportion of the male-male violence that inadvertently causes infant deaths. In other words, by emphasizing a definite stochastic component of lethal injuries to infants, the hypothesis allows for the possibility that a male’s fight with a rival might contribute to the accidental death of his own infant, but it does not specify quantitative predictions. The expected rate of such episodes relative to the current sample of observed attacks is therefore unclear, but in none of the relevant 16 cases did researchers implicate (likely) fathers in the deaths of infants, even indirectly. Additionally, male-male aggression did not precede infanticide in most instances (see Prediction 3 below).

In summary, the uniformly low relatedness between male baboons and the infants they injure neither clearly refutes nor supports the generalized aggression hypothesis, but it does endorse the two adaptive hypotheses.

Prediction 2: Infanticidal Males Obtain a Mating Benefit From Infanticide

Support for this prediction of the Hrdy model was low in a total of seven cases, or 44% of the 16 directly observed attacks with relevant information (or four of 13 [31%] of fatal attacks). These reports originated from all the study sites except the Drakensberg

chacma population; four came from east African (olive and yellow) baboons, while three came from the Moremi chacma baboons.

The seven reports varied in cogency. The sexual selection hypothesis does not explain infanticidal attacks apparently committed by non-resident, extra-group males (Case 1; possibly also inferred case 10 of Table II) or directed against infants whose mothers are either currently cycling (Case 11) or dead (Case 10). In these three cases (19%), infanticide not only failed to increase male sexual access to the (fertile) mother, it had little or no potential to do so. The other four cases are less straightforward because “low” consistency is based more upon inferences derived from negative evidence. Two cases (5 and 6) are based on the failure of researchers to document copulation with the mother when she resumed cycling (researchers note that sexual interactions may, of course, have gone unnoticed, and this may be relevant for the infanticidal male of Case 6, who was still alpha when the mother resumed cycling). In two final cases, the injured infants survived; the reproductive benefit potentially available to the attacking male was judged to be low due to his low dominance rank (Case 9) or subadult status (Case 2).

The probability that the infanticidal male sired the female’s next infant was “moderate” to “high” in 9 reports, i.e., 56% of all attacks and 69% of fatal attacks. “Moderate” consistency was defined primarily by any subsequent male copulation with the mother or, in one case where the infant survived, by the potential reproductive benefit in light of the high dominance rank of the attacker. “High” consistency referred to males that were both high-ranking (usually alpha) *and* known sexual consorts of the mother during her subsequent conceptive cycle.

These nine reports came from studies of olive baboons at Gombe, and of chacma baboons at Moremi and the Drakensberg mountains, but “high” consistency cases (N=6) were limited to the two chacma baboon populations. In chacma baboons, an adult male that has immigrated recently into the group and rapidly attained the alpha position in the male dominance hierarchy may commit infanticide. Not all new alpha males are known to kill infants, however. Observational data suggest that between one-half and one-third of newly immigrant alpha males at Moremi become infanticidal [Palombit et al., 2000]. Thus, infanticidal behavior varies within chacma baboon populations

Prediction 3: Infanticidal Males Direct Aggression at Infants Not Other Conspecifics.

The generalized male aggression hypothesis argues that infants are disproportionately vulnerable to accidental death from male aggression directed at others. Thus, injuries may be inadvertently inflicted to infants during prolonged or intense intra- or intergroup aggression. This reason may apply to two cases (Case 11 of Table I and inferred Case 17 of Table II). It is important, however, to place the intragroup aggression characterizing at least 11 instances (58%) of directly observed infanticidal attacks in the appropriate context (Cases 1, 2, 4-6, 10-13, 15, 16). Intragroup aggression involving multiple baboons was noted in these cases, but it did not precede infanticidal attacks. That is, the killing of an infant was not a consequence of ongoing male aggression to others. Rather, the precipitate outbreaks of screaming and/or aggressive chases

of multiple baboons were defensive responses to an attack that had just been initiated or even completed by an adult male. These chases were typically the mobbing of the attacking male (sometimes carrying an infant in his mouth) by other troop members. The qualitative and temporal patterning of these interactions was, therefore, inconsistent with the generalized aggression hypothesis. The intragroup “commotions” accompanying the circumstantial evidence of many inferred infanticides (Table II) should be interpreted in light of these patterns from directly observed attacks.

Similarly, intergroup interactions in savanna baboons are frequently “high arousal” situations during which males may not only chase extra-group individuals, but also conspicuously and aggressively herd females of their own group away from the rival troop [Buskirk et al., 1974; Cowlshaw, 1995]. Two directly observed infanticides coincided with intergroup interactions (Cases 1 and 18), and there is good evidence that four inferred attacks occurred in the same context (Cases 5, 6, 12, 17), thereby accounting for 18% of all fatal injuries to infants (N=33). Accidental injury to infants resulting from male aggression is possible in this context, but at least two episodes suggest that intergroup interactions may also provide opportunities for sexually selected infanticide (Case 18 of Table I and Case 12 of Table II). These infants’ deaths did not involve extra-group individuals or aggressive herding of their mothers by troop males. Circumstances surrounding Case 18 suggest that intergroup interactions may heighten the risk of within-group infanticide by distracting the attention of infant protectors. An analogous process may underlie Case 17 of Table I, in which a male attacked an infant after its mother had gone to the site of a recent vervet monkey kill. Baboon capture of prey are similarly “high arousal” events that rapidly attract numerous troop members [e.g., Harding, 1973, 1975].

The “considerable aggression to mothers” reported for two observed olive baboon infanticides at Gombe (Cases 3-4) has been offered as evidence against the sexual selection hypothesis [Collins et al., 1984], which predicts that attacks should be directed against infants rather than their mothers. This prediction requires qualification, however, if it is to prove useful in differentiating between the generalized aggression and sexual selection hypotheses. Hrdy’s [1974] model allows for male aggression to mothers because it may counter their protection of infants. Maternal aggression is a widespread potential female counterstrategy to male infanticide in mammals. Its effectiveness in forestalling infanticide is debated, partly because the costs, benefits, and variability of the behavior are poorly understood [Ebensperger, 1998]. This is particularly so for female primates, whose responses to infanticidal males range from “vehement counterattacks” to ostensibly impassive abandonment of infants [van Schaik, 2000]. Although female primates are known to individually or collectively attack actual or potential infanticidal males [e.g., Sugiyama, 1966; Mohnot, 1971; Hrdy, 1977; Pereira & Weiss, 1991; Borries, 1997], several researchers [Hrdy, 1979; Maestripieri, 1992; Palombit, 1999] have commented on their apparent ineffectiveness, at least compared to some rodents [e.g., Fleming, 1979; Wolff, 1985; Maestripieri & Alleva, 1991; vom Saal et al., 1995]. However, as Parmigiani et al. [1994] point out for rodent species in which females are similarly poor at deterring male assaults, the conspicuous protective behavior of mothers may successfully attract a male defender and/or delay killing long

enough for him or, in the case of baboons, other group protectors to arrive. Given the opportunistic nature of infanticidal attacks, such a tactic may potentially thwart an attack. This may be why female primates defend their infants even though their chances of single-handedly defeating a much larger attacking male may be low. Infanticidal males, however, can be expected to use direct aggression to thwart maternal protection. For example, one of the two above-cited attacks by infanticidal male baboons on mothers at Gombe was “apparently to prevent her from retrieving the infant” [Collins et al., 1984].

Thus, it is the patterning and intensity of male aggression to mothers (not its presence or absence) that usefully tests between the two competing hypotheses. Carefully developed quantitative predictions are necessary to test this aspect of the two competing hypotheses, but one important distinction is that the sexual selection hypothesis predicts that any male aggression to mothers will not negate the future reproductive advantage of infanticide. For example, males should not injure females so seriously that chances of mating with them are significantly reduced. Among the sample of directly observed attacks, mothers protected or attempted to protect infants in eight cases, but in only one (Case 4) did a mother sustain injuries (which were nonfatal and minor). This corresponds with the low incidence of serious wounds to mothers during infanticidal attacks in primates generally [van Schaik, 2000] (except in mountain gorillas and chimpanzees [Fossey, 1984; Goodall, 1986]). One inferred case (Case 1, Table II) is consistent with the generalized male aggression, however, because the infant’s death coincided with unusually “severe injuries” inflicted on numerous anestrous females during the period following a new male’s immigration into the group.

In conclusion, current evidence raises the possibility that general male aggression to mothers may account for some infant deaths in baboons, without rejecting the sexual selection hypothesis in the majority of cases.

Nutritional Exploitation Hypothesis.

The hypothesis that males kill infants in order to gain a nutritional benefit [Fox, 1975; Goodall, 1977; Sherman, 1981; Kawanaka, 1981; Hiraiwa-Hasegawa, 1992; Hoogland, 1994] received support in four reports (21%) in which male chacma baboons (of Moremi) ate infants. These cases accounted for a larger proportion of the observed infanticidal attacks within the relevant population (4 of 8 fatal attacks), suggesting the possible importance of nutritional exploitation. Several other pieces of evidence weaken this interpretation, however. First, opportunities for males to cannibalize infants in their possession appeared to be more frequent than the observed rate of this behavior. Two of three cannibalistic males were observed to kill other infants, which they did not consume. This was not because other defending baboons chased them off; attackers simply discarded the bodies of infants.

Second, the nutritional exploitation hypothesis (but not the sexual selection hypothesis) predicts that male anthropoid primates will attack (and consume) newly orphaned infants, since vulnerability to infanticide is likely to rise significantly after mothers die [Rhine et al., 1980]. Two of the 33 fatally injured infant baboons (from both observed and inferred records) were orphans (Table I, Case 10; Table II, Case 2), al-

though neither was eaten by a conspecific. More generally, however, orphaned infant chacma baboons remained unharmed by adult males (N=11 orphans reported by Hamilton et al. [1982] and Palombit et al. [2000]). This result is consistent with the sexual selection hypothesis, since males obtain no mating benefit from killing orphans.

Finally, cannibalism does not oppose the sexual selection hypothesis, which makes no explicit predictions what males will do with the bodies of infants they have killed. Observations that three fatally injured infant baboons were eaten by the mother (Case 5, Table II), by a high-ranking female who obtained the carcass after it was discarded by the mother (Case 10, Table II), and by a low-ranking male after the infanticidal male abandoned the body (Case 7, Table I) underscore the possibility that cannibalism following infanticide simply reflects the opportunistic exploitation of a newly available source of energy and protein, not the adaptive reason for killing the infant. This hypothesis might be further tested, however, by analyzing inter-population variation in cannibalism in light of feeding behavior, protein intake, and local prey availability and consumption.

Conclusions

Adaptive Significance of Infanticide

The larger data set considered here clarifies and supports the patterns originally described by Collins et al. [1984]. All reports of injurious attacks to infants by male savanna baboons support two primary predictions of the Hrdy [1974] model: (1) males are unlikely fathers of the infants they injure; and (2) infanticide accelerates resumption of sexual cycling in females (Figure 2). The subsequent mating benefit of infanticide is absent or obscure in some reports, however. At least three reports (19%) unambiguously fail to support the sexual selection hypothesis in this regard. The other inconsistencies are more equivocal since they are based on negative evidence. Nevertheless, this result suggests that male infanticide in savanna baboons is not a unitary phenomenon with a single explanation. Other hypotheses, such as generalized male aggression or nutritional exploitation, are likely to apply in some cases.

Several caveats should be noted concerning the predicted mating benefit accrued by infanticidal males. First, a male's failure to subsequently copulate with a female does not necessarily mean that intrasexual selection is causally irrelevant to a particular episode of infanticide. The time lag of several months between the death of an infant baboon and male sexual access to its mother in her next conceptive cycle provides opportunities for demographic events to cancel the predicted reproductive benefit. For example, during this intervening period, a new male may immigrate into the group and challenge the killer's alpha status (possibly Case 13, Table I) or the female may die of other causes (Case 15, Table II). Although males are expected to adjust their infanticidal behavior in light of the average rates of male immigration and female mortality, individual cases may clearly be exceptional. Thus, the sexual selection hypothesis predicts that infanticide will increase a male's probability of siring the female's next offspring (relative to the costs and benefits of the alternative strategy of not committing infanticide); it does not predict that that probability is 1.0.

Second, an understanding of costs is critically important for predicting infanticide,



Figure 2. Loss of an infant accelerates resumption of ovulatory cycling in female baboons, thereby establishing a potential for infanticide to enhance male reproductive success (Photo by Ryne A. Palombit.)

but hindered by the paucity of relevant data. Theoretically, even a male with only moderate prospects of subsequently mating with the mother may seize an opportunity to commit infanticide if the accompanying costs are sufficiently low. This consideration underscores the importance of accumulating a large sample of detailed observations that allows quantitative modeling of male behavior. Currently available data for savanna baboons are insufficient for this purpose.

Third, study of the proximate “decision rules” [*sensu* Dawkins, 1980; Grafen 1991] underlying male infanticidal behavior will significantly improve functional analyses. For example, how do males “assess” their current (and future) reproductive options? A better understanding of the variables influencing male mating decisions would inform specific predictions about the mating success of infanticidal males and more fully test apparent exceptions. Although well studied in rodents, the proximate mechanisms underlying primate infanticide remain largely unknown.

In conclusion, current data are demonstrably more consistent with the sexual selection hypothesis than the smaller data set considered by Collins et al. [1984]. It is

clear, however, that this is due exclusively to new data on the chacma baboons of southern Africa. Over the last 17 years, field studies of east African baboons have not contributed any additional observations of male infanticide. With the possible exception of Gombe, the rarity of observations continues to obscure the adaptive significance, if any, of male infanticide in these populations.

Variation in male Infanticide

The wide distribution of reports across study sites suggests that male baboons in virtually all populations have the potential to commit infanticide. The behavior appears to be a general component of the (flexible) behavioral repertoire of male baboons. This suggests that female baboons are generally confronted with some degree of infanticide risk.

Nevertheless, the available data suggest that the degree and the patterning of male infanticide vary across populations. The evidence considered here supports the original suggestion of Collins et al. [1984] that infanticide is demographically more important among southern African chacma baboons (particularly in the Moremi population) compared to east African populations. The near absence of published reports of infanticide at many east African sites makes the contrast with Moremi baboons appear virtually qualitative.

Some of this variation may derive from differences in the methodologies and research priorities of individual studies. The data set from Moremi (47 infant deaths from 135 infants born over nine years; Collins et al. [1984] and Palombit et al. [2000]) is sufficient to doubt that small sample size has artificially inflated infanticide rate, however. Inferring the low frequency of infanticide at some sites from the rarity of (published) data is necessarily provisional. Again, however, there is no immediately obvious reason why male infanticide has been seriously underestimated (or under-reported) at active, long-term sites such as Amboseli, Gilgil, and Mikumi. If apparent population differences were solely the artifact of variable opportunities to observe infanticide, then one would expect higher, not lower, rates among east African baboons, where greater research effort has historically been invested in field studies of baboons. Thus, the data indicate a potential for biologically meaningful inter-population differences in baboon behavior, although the precise limits and significance of the differences are not clear.

Janson and van Schaik [2000] point out a possible bias affecting this measure of infanticide rate: the proportion of mortality due to infanticide may be especially high in populations with reduced infant mortality, e.g., due to unusually low predator pressure. This might apply, for example, to the Drakensberg chacma baboon population, in which male infanticide is purported to be a major (though unspecified) source of infant mortality [Weingrill, 2000], and both predator pressure and infant mortality are negligible [Henzi et al., 1997; Lycett et al., 1998]. However, this effect is unlikely to account generally for the variation observed across savanna baboon populations. Infant mortality is also insignificant among the olive baboons of Gilgil [Strum & Western, 1982], and yet infanticide is apparently much more rare at that site. Conversely, infant mortality is appreciable among both the yellow baboons of Amboseli [28%; Altmann 1980] and the

chacma baboons of Moremi [38-39%; Collins et al., 1984; Palombit, et al., 2000], but male infanticide is more common in the latter.

Moreover, the patterning of infanticide in chacma baboons is more clearly consistent with the sexual selection hypothesis than at most olive and yellow baboon sites. Given that males at no site have injured infants they were likely to have sired, consistency with the Hrdy model hinges primarily on the expected reproductive benefit of infanticide to males. This was low for four of the five directly observed attacks with relevant information involving olive and yellow baboons, but for only three of 11 of the chacma baboon observations. Accordingly, although researchers of east African savanna baboons have acknowledged the potential risk of male infanticide [most notably Smuts, 1985], students of the chacma baboon have more often explicitly identified infanticide as a likely selective agent behind the evolution of numerous aspects of its social behavior, such as infant carrying by males [Busse and Hamilton 1981; Anderson, 1992], the “tail-raising” visual display of females [Busse 1984a], triadic interactions involving males and infants [Busse 1984b], copulation calls [O’Connell and Cowlshaw 1994], heterosexual “friendships” [Palombit et al. 1997; Weingrill, 2000], intragroup spacing behavior [Cowlshaw, 1999], and female-female social interactions [Palombit et al., 2001].

Gombe merits special attention because fieldworkers have remarked upon “the dangers of infanticide by recent immigrants” among its olive baboons [Smuts, 1999:xiii]. The proportion of deaths due to infanticide is considerable (at least 7-15%), though apparently not as high as among the chacma baboons of Botswana (the rate at Gombe may be higher if infanticide did, in fact, account for more than the five of the 12 circumstantial cases that Collins et al conservatively attributed to it). Moreover, the consistency of the four observed infanticides ranged from low to moderate; no case was clearly as highly consistent as several of the episodes reported for chacma baboons. Thus, sexually selected infanticide is arguably more significant at Gombe than at other east African sites, but less so than in chacma baboons.

Clearly, the small sample sizes involved here temper the conclusions with caution. Methodological differences and small samples among studies will be more problematic for explaining *why* infanticide occurs (than for describing whether it happens at all). Tests of functional hypotheses rely on observations of often-subtle aspects of behavior. As noted above, however, some reports’ low consistency with the sexual selection hypothesis is not due to the absence or ambiguity of confirmatory evidence but to the presence of unequivocally contradictory data. Perhaps the most reasonable conclusion that can be drawn at present is that infanticide in chacma baboons is currently best explained as a sexually selected male reproductive strategy but that this cannot be said with as much confidence about infanticide in east African baboons.

Possible Causes of Variation in Infanticidal Behavior

With the above caveats in mind, existing data warrant a preliminary assessment of underlying causes of inter-population variation in infanticide, but they are insufficient for quantitative correlational analysis [e.g., Borries & Koenig, 2000; Janson & van Schaik, 2000]. Thus, the following discussion seeks to develop functional hypotheses

for further testing. It is partly for that reason that I assume here that the purported behavioral differences among populations represent adaptations to contrasting social and, ultimately, ecological conditions. I do not presently consider in detail the null hypotheses that the differences are nonadaptive or even maladaptive consequences of recent history, but this is, of course, possible [Glass et al., 1985].

The economics of infanticide are the focal point of any discussion of adaptive variation in male infanticide. Infanticide may be more common in one population than in another because the associated costs of the behavior to males are lower or because the potential reproductive benefits of the behavior are greater (or both). In the discussion below I consider these two elements separately. In particular, I attempt to assess whether other suggested population differences in the biology of savanna baboons are potential causes of the observed variation in male infanticide.

Variation in Male Infanticide: Potential Costs

Protection of infants by other individuals has clear potential to increase costs of infanticide to males. Given the size and composition of savanna baboon groups, this defense may originate from various sources.

Maternal Aggression and Sexual Dimorphism

As noted above, female primates may actively defend their offspring against infanticidal males. The extreme body size dimorphism of savanna baboons [Plavcan & van Schaik, 1997], however, may create “a distinct power asymmetry” [van Schaik, 2000] that limits the effectiveness of maternal defense [see Flannelly & Flannelly, 1985]. Sexual dimorphism (male mass:female mass) in savanna baboon populations ranges from 1.36 to 2.07 [Dunbar, 1990; Barrett & Henzi, 1997] (for populations in which sample size exceeds one individual of each sex). This variation could potentially influence the effectiveness of maternal aggression, and therefore the rate of male infanticide.

Table IV summarizes body size data, where available, from the wild baboon populations in the above discussion of infanticide. The Moremi chacma baboons are among the most dimorphic, not only among the subset considered here, but also among all savanna baboon populations (in which more than one male and female have been measured). Although this finding is suggestive, the remainder of the small sample does not reveal an obviously substantive relationship between dimorphism and the qualitative differences in infanticidal rates across populations. East African yellow and olive baboons, in which infanticide is rare, are highly dimorphic; conversely, dimorphism is lower in the Drakensberg chacma baboons in which infanticide is reported to be an important source of infant mortality (clearly, a quantitative estimate of infanticide rate from the Drakensberg population would valuably elucidate this point). This result conforms with Janson and van Schaik's [2000] conclusion that sexual dimorphism is uncorrelated with infanticide rate in nonhuman primates in general. Part of the reason for this is that low sexual dimorphism does not preclude infanticide [Palombit, 1999], which is expected if males attack infants opportunistically when protectors are relatively distant and/or inattentive.



Female-Female Coalitions

Females may form alliances with one another to deter attacks or immigration of potentially infanticidal males [van Schaik, 2000]. Although this counterstrategy may be unattainable in species with female dispersal [Janson & van Schaik, 2000], it is potentially important in female-philopatric primates, such as savanna baboons. This benefit has, in fact, been offered as the adaptive reason for female gregariousness in primates generally [Brereton, 1995].

Female group size provides one means of assessing this counterstrategy. The positive correlation between female group size in Hanuman langurs (*Semnopithecus entellus*) and “conspecific threat” of infanticide (the number of nongroup males per bisexual group) may reflect the anti-infanticide function of larger coalitions of females [Treves & Chapman, 1996] (see below for an alternative interpretation, reversing causality). If relative infanticide rate reflects risk, this association is unapparent among the savanna baboons considered in this chapter (Table V). Chacma baboon populations have intermediate (Moremi) or small (Drakensberg) female group sizes compared to east African populations. Additional evidence against this explanation for variation in infanticide rate is the rarity of coalitionary behavior among female savanna baboons generally [Silk et al., 1999].

Male Protectors, Male Group Size, and Male-Male Coalitions

Infanticide appears relatively less common among primates living in multi-male versus uni-male groups [Hausfater & Hrdy, 1984; Parmigiani et al., 1994; van Schaik and Janson, 2000]. Similarly, studies of intraspecific variation have suggested that lower infanticide rates characterize groups containing more than one male [e.g., Newton, 1986; Robbins, 1995], although it is less clear if rates consistently decline with increasing male number once groups include more than one male. One interpretation of these patterns is that the presence of more males raises the costs of infanticide to restrictively high levels (see below for an alternative, benefit-oriented interpretation). These costs may derive from the active defense of infants by the attendant father and/or additional males, or from resident males’ prevention of immigration by intruder males. Suggestive data come from red howler monkeys (*Alouatta seniculus*), in which increasing male group size appears to discourage “incursion” infanticide by immigrating males (although male number had no inhibitory effect on “within-group” infanticide resulting from a long-term resident of the group rising to the alpha position) [Crockett & Janson, 2000].

Male group size varies among the savanna baboon populations for which data on infanticide are available, but again, no potentially causal relationship with infanticide rate is apparent (Table V). Cowlishaw and O’Connell [1996] and Henzi et al. [1999] found that although male group size was smaller in chacma baboon populations (primarily in South Africa and Namibia) than in other *Papio* subspecies. This does not apply clearly to the chacma baboons of Moremi, however. Indeed, Cowlishaw & O’Connell [1996] found that there was no statistically significant difference between chacma baboons and east African baboons when the Moremi population and one other chacma population were included in the analysis. Male group size in the Moremi chacma baboons is



comparable to that found in some east African populations (e.g., Gombe and Amboseli). Thus, the presence of fewer potential male defenders may promote infanticide in the Drakensberg chacma population, but it does not apply to the Moremi population. Moreover, differences in male membership also fail to account for temporal variation in infanticide within the Moremi study group [Palombit et al., 2000].

An alternative version of this counterstrategy is that the number of males per se is less important than the degree to which they cooperate in defending immatures against an infanticidal aggressor. In this regard, inter-population variation in the coalitionary behavior of males could differentially affect the coordination of infant defense and/or the prevention of immigration by intruder males, and thereby infanticide rate. Analogously, Robbins [1995:21] argues that uni-male groups of mountain gorillas suffer higher rates of infanticide than multi-male units partly because a single resident silverback will “lack possible partners for coalition formation during intergroup encounters.”

Notably, researchers of chacma baboons [e.g., Bulger, 1993; Henzi, 1996] have contrasted the striking (and currently unexplained) near absence of coalitionary behavior among adult males with its prevalence in east African baboon societies [e.g., Noë, 1992; Noë & Sluijter, 1995]. The possible implication of this difference for understanding infanticide remains undeveloped, since coalitionary support among males has generally been studied in mating rather than anti-infanticidal contexts. Nevertheless, observations of savanna baboons at virtually all sites reveal that aggressive attacks on infants frequently elicit ostensibly defensive responses from multiple males (Table D). This is true in chacma baboons as well, if “response” is defined as running to the vicinity of the attack. In this baboon, multiple males may move toward the attacker, but it is only the female’s male friend that mounts the most direct and active defense (i.e., protectively carrying the targeted infant, initiating and maintaining close proximity to the aggressor male, or engaging him with threats, vocalizations, appeasement gestures, chases, or, ultimately, fights). Although Palombit et al. [2000] suggest that the less active participation of “nonfriend” males may help deter infanticide in some circumstances (and may be facilitated by the existence of dyadic male-female friendships), the comparative data are unavailable for determining if male baboons in different populations coordinate anti-infanticide defense of infants in different ways (or if they coordinate defense at all and, instead, act independently). Clearly, this question deserves further empirical attention.

A final possible disincentive to infanticide in the savanna baboon is the male “friend.” Lactating females typically share cohesive associations (known as “friendships” [Strum, 1974]) with particular adult males. Palombit et al. [1997, 2000] present observational and experimental data suggesting that the benefit females derive from these social relationships is protection from infanticidal attacks by new alpha males, at least in chacma baboons. There are no qualitative differences in the occurrence of friendships that might be causally related to differences in infanticide: these relationships appear to be ubiquitous in savanna baboon populations [Ransom & Ransom, 1971; Seyfarth, 1978; Altmann, 1980; Strum, 1982; Anderson, 1983; Smuts, 1985; Collins, 1986; Bercovitch, 1991; Palombit et al., 1997]. Nevertheless, the nature and timing of

friendships vary considerably across female-male dyads [Smuts 1985; Strum 1987; Palombit et al. 1997]. The relative magnitude and importance of within- and between-population variation is unknown, however. It is possible, for example, that threat of infanticide varies less across savanna baboons than the effectiveness of male friends in deterring it. Tests of this hypothesis await new data.

Variation in Male Infanticide: Potential Benefits

Factors influencing the potential reproductive benefit of infanticide may promote population differences. Here I consider primarily variation in intrasexual competition among males and aspects of female reproductive biology.

Female Group Size

Crockett & Janson [2000] report that infanticide rate is correlated with female group size in red howler monkeys, presumably because infanticide generates greater reproductive benefits to males entering larger groups. Variation in female group size across the savanna baboon populations of interest (Table V) is inconsistent with this hypothesis, however. Female group size in chacma baboons ranges from small to intermediate, whereas infanticide has not been reported from east African groups containing more females.

Reproductive Skew

The potential benefit from infanticide largely depends upon a male's ability to exclude other males from mating with females during subsequent ovulatory periods. Low "monopolizability", or weak "reproductive skew" [Altmann, 2000; Borries & Koenig, 2000; see Hager, this volume], will discourage infanticide in two ways. First, it will increase the potential costs of infanticide for resident males by increasing the likelihood they will kill their own offspring. It is, of course, for this reason that female promiscuity offers potential as an anti-infanticide strategy [Hrdy, 1979; Harada & Iwasa, 1996]. This cost is relevant to low- or middle-ranking males that rise in rank in a group they have resided in for some time: they should be less infanticidal towards currently lactating females *if* previous alpha males had been unable to prevent them from copulating with these females when they were fertile. The fact that infanticide in savanna baboons is more common by males that have only recently immigrated into the group rather than by long-term residents suggests that this process operates to some extent. However, at least one long-term resident male at Moremi committed infanticide soon after ascending to the alpha position (Cases 12-13, Table I), indicating that it is indeed reproductive skew, rather than simply residency in the group, that affects infanticidal behavior. Second, reduced ability to monopolize matings will discourage infanticide by diluting the future reproductive benefit for males that kill infants. This factor may be another reason for the generally lower incidence of infanticide in multi-male primate societies (besides the above-cited costs of male defense).

Reproductive skew might be expected to decrease with increasing male membership in groups, as alpha individuals encounter greater costs in preventing more males from copulating with females. As noted above, differences in male group size in the

populations considered here do not support the prediction straightforwardly. Although the (infanticidal) chacma baboons of the Drakensberg show the predicted smaller male group sizes, the Moremi chacma baboons do not. This pattern underlies Bulger's [1993] conclusion that differences in group demography do not clearly account for intergroup variability in the mating skew among male baboons.

Evidence that mating is more strongly skewed in the chacma baboon than in other baboons comes from various measures of male mating success (Table V). Among chacma baboons, alpha males account for a greater percentage of mating success than other males. Moreover, non-alpha males have been observed to achieve higher mating success than resident alpha individuals at Gilgil and Amboseli, but not at Moremi or the Drakensberg. Consequently, Bulger [1993], Henzi [1996], and Weingrill et al. [1999] have argued that alpha male chacma baboons monopolize periovulatory copulations more successfully than alpha males in other populations. In contrast, among the olive baboons of Gilgil, turnover in male consorts is frequent and male rank is a poorer predictor of mating success, in part because it is difficult to discern dominance relationships among males in the first place (Strum, 1982; Bercovitch, 1986). A compelling pattern emerges for Gombe: mating success among the olive baboons at Gombe is demonstrably more skewed than at Amboseli or Gilgil, but less so than among chacma baboons, and the incidence of male infanticide at Gombe appears similarly intermediate. On the other hand, male mating success at Mikumi and Masai Mara appears less variable and more skewed than at Amboseli and Gilgil, suggesting a potential for infanticide that is unrealized in the published reports from those sites. In conclusion, however, these data do suggest that variation in reproductive skew is likely to be an important determinant of variation in male infanticide in savanna baboons.

Why alpha male chacma baboons are apparently better able to monopolize copulations is unknown, but the absence of male-male coalitions is almost certainly relevant. Among east African baboons, male coalitions occur in mating contexts, bring about changes in consort status, and thereby disrupt high-ranking males' sexual access to fertile females. Ecological considerations may also be important. Moremi chacma baboons live in the Okavango Delta, a wetlands habitat of high primary productivity [Tinley, 1966; Ross, 1987]. Thus, the mate guarding of alpha male chacma baboons may be less constrained by foraging demands than it is among baboons inhabiting other habitats [*sensu* Altmann et al., 1996; Alberts et al., 1996]. An analogous argument, incidentally, concerns the monitoring or "shadowing" of mothers, infants, and their protectors by infanticidal males. The possibility that ecological conditions proximally constrain or facilitate opportunities for infanticide has not been explored in detail.

Male Immigration, Alpha Tenure, and Population Density.

Relative infanticide rate is likely to be higher in populations in which females are exposed to larger numbers of strange males [Hrdy, 1979; Leland et al., 1984]. In female-philopatric species, this is primarily a function of the rate at which immigrant males replace current breeding male(s). The rate of male immigration among Moremi chacma baboons is 3.8 ± 3.1 males/yr ($N = 8$ years; Cheney, personal communication), but directly comparable data are unavailable from other sites.

Population density may indirectly reflect incursion rate by potentially infanticidal males, as well as a measure of male-male competition generally. The chacma baboons of Moremi have the highest population density reported for savanna baboons (24 individuals/km²), compared to yellow baboons at Amboseli (6 individuals/km²) [Cheney, 1987], olive baboons at Gombe [15-23 individuals/km²; Ransom, 1981], and chacma baboons in the Drakensberg Mountains [2.5 individuals/km²; Henzi & Lycett, 1995]. These data are consistent with the notion that higher densities lead to more frequent male immigration and infanticide in savanna baboons. Likewise, higher population density may intensify intrasexual mating competition among males, although at very high densities, mating competition may decline [e.g., Jirotkul, 1999]. The extremely low density reported for the chacma baboon of the Drakensberg Mountains opposes a simple relationship between population density and infanticide. This result has at least two interpretations. First, population density may not accurately reflect the rate of male intrusions in these baboons. In Ugandan blue monkeys (*Cercopithecus mitis*), for example, influxes and infanticide by males were more frequent in a low-density population than in a nearby higher-density subpopulation [Butynski, 1990]. Alternatively, it is possible that additional intervening variables account for the presumed high incidence of infanticide in the Drakensberg (see below).

Another indicator of male replacement is tenure length of alpha males. The high population density and male immigration rate among Moremi chacma baboons are associated with extremely short alpha tenures, averaging 6-7 months [Palombit et al., 2000]. This association contrasts with multi-year tenures reported at Amboseli and Gombe [Collins et al., 1984] as well as the Drakensberg [Weingrill, 2000].

Alpha male tenure, along with female reproductive physiology and the costs of infanticide, may importantly influence the role of male reproductive skew in promoting infanticide (see above). When brief alpha tenure is combined with high mating skew, infanticide is likely to be more beneficial than a non-infanticidal strategy. These males are confronted with a brief period of exclusive sexual access to females, after which their reproductive options are severely limited (by rival males, who themselves monopolize fertilizations). As alpha tenure lengthens, however, (keeping mating skew constant), the net benefit of infanticide declines. This is because alpha tenure persisting long enough to allow currently lactating females to resume cycling will provide the male with sexual access to these females, without his having to incur the costs of infanticide. Clearly, the reproductive physiology of females is critical here, particularly the time required to fertilize a female after loss of her infant and reproductive rate in general. If these vary across savanna baboon populations, then variation in tenure may have differential effects on the reproduction of males.

Females in various savanna baboon populations seem to respond similarly to loss of infant: cycling typically resumes within a month, and several cycles are necessary for subsequent fertilization [Altmann et al., 1978; Collins et al., 1984; Smuts & Nicolson, 1989; Brain, 1992; Bentley-Condit & Smith, 1997; Weingrill, 2000]. Reproductive rate, as measured roughly by interbirth interval, varies across savanna baboon populations: olive baboons: 26.5 mos (Gilgil) and 25 mos (Gombe); yellow baboons: 24 mos (Amboseli), 21 mos (Mikumi), 28 mos (Tana River); chacma baboons: 24.6 mos (Moremi)

and 38 mos (Drakensberg) [Hill et al., 2000]. Although this variation is substantial, the values for savanna baboons from Gombe, Gilgil, Amboseli and Moremi are similar to one another, in spite of apparently large differences in male infanticide. Thus, variation in male alpha tenure should have broadly similar effects on reproductive opportunities for males. The exception is the chacma baboon of the Drakensberg, which has conspicuously longer interbirth intervals than other populations, suggesting more restricted breeding opportunities for alpha males (see below).

CONCLUSIONS AND PROSPECTS

Although variability in the defense of infants by adult males (either collectively or individually) may account for some of the differences in infanticide rates across baboon populations, factors influencing the reproductive benefit of infanticide appear to be especially important. Notably, the ability of males to monopolize matings and the duration of alpha tenure relative to female reproductive rate possess particularly great potential to influence the expression of sexually selected infanticide.

These factors have apparently interacted in different ways to promote male infanticide in two populations of baboons with purportedly high rates of infanticide. It would not be surprising that male chacma baboons at Moremi and the Drakensberg have arrived at infanticide as a reproductive strategy via slightly different “routes” given the substantial demographic and ecological differences between them. The Drakensberg chacma baboons (Figure 3) combine the longest known interbirth intervals for savanna baboons with one of the lowest known rates of infant mortality [7%; Lycett et al., 1998], possibly because of extremely low predation pressure. These conditions reduce the number of offspring an alpha male may produce for a given unit of tenure. In spite of tenures typically exceeding 20 months and ranging from 12-42 months [no mean published; Weingrill, 2000], opportunities for alpha males to fertilize lactating females will be lower compared to males in east African populations, in which female reproductive rates are higher, infants die more frequently due to other causes (making their mothers available for fertile mating), and alpha tenures are comparable (if not longer). If additionally combined with high male mating skew (as seems to be the case in Drakensberg chacma baboons), these conditions will select for male infanticide as a reproductive strategy (Figure 3).

The interaction of these variables is similarly complex in the Moremi chacma baboons (Figure 4). Infant mortality (due to causes other than infanticide) is substantial in this population, and female reproductive rate is moderate. Both of these conditions characterize east African baboons with low infanticide rate, however. The factors that differentiate the Moremi chacma baboons from these other baboons are extremely skewed mating and the shortest reported alpha tenures. Thus, males are faced with a transient period of high mating exclusivity, followed by a long period offering few, if any, mating opportunities. This combination of conditions should select strongly for infanticide.

Given the reproductive physiology of females, however, the extreme brevity of tenures in chacma males raises the theoretically contradictory possibility that an alpha male who kills an infant will himself be displaced by another male before its mother

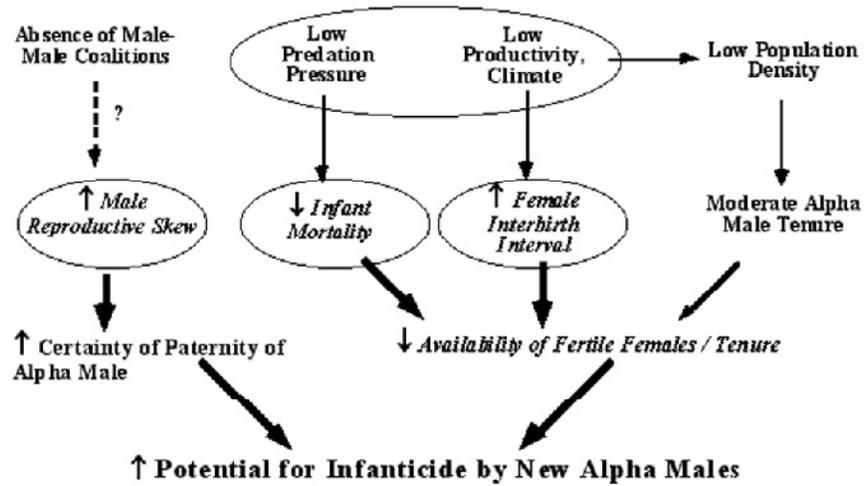


Figure 3. Diagram of proposed factors influencing the evolution of male infanticide in chacma baboons of the Drakensberg Mountains. Bold-faced areas indicate factors with proposed special importance for this population (cf. Figure 4).

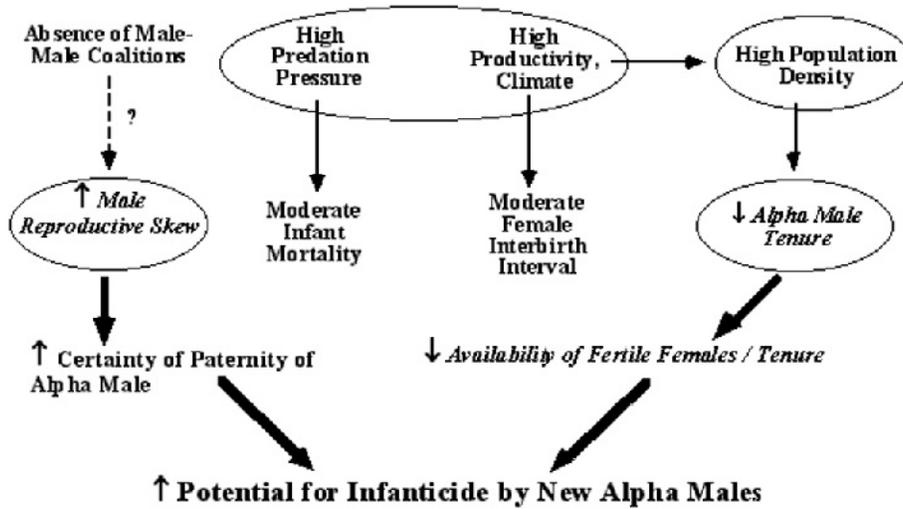


Figure 4. Diagram of proposed factors influencing the evolution of male infanticide in chacma baboons of the Moremi Game Reserve, Botswana. Bold-faced areas indicate factors with proposed special importance for this population (cf. Figure 3).

resumes cycling and can be fertilized. Resolution of this problem ultimately lies in improving our understanding of variation in male infanticidal behavior in this population. As noted above, infanticide appears to be a facultative strategy adopted by one-third to one-half of new alpha males [Palombit et al., 2000]. These males predictably obtain sexual access to the females during their subsequent conceptive cycles partly because their alpha tenures are longer than the average of 6-7 months (although their tenure still falls short of values for other baboon populations, exceptionally exceeding one year).

Another impediment to infanticide arises when an infanticidal male's offspring are themselves vulnerable to attacks by the *next* alpha male [e.g., Hausfater et al., 1981]. Addressing this factor in the Moremi chacma baboons will require at least two sets of data. First, an understanding of variation in infanticidal behavior of alpha males is again critical. As noted above, although most alpha males are potentially infanticidal, they vary considerably in rates of attacks on infants [Palombit et al., 2000]. Thus, a former infanticidal alpha male's offspring are not invariably attacked by his successor. The facultative nature of infanticide—and the implied possibility of behavioral polymorphism among males—may, in fact, be a necessary condition for the maintenance of sexually selected infanticide in this population. We do not yet know, however, if such a polymorphism is expressed as a pure or mixed strategy [*sensu* Dawkins, 1980]. Second, data are needed on variation in the effectiveness of male friends in deterring infanticide. Although males of all ranks are involved in friendships [Palombit et al., 1997], they compete with one another for access to high-ranking males as friends [Palombit et al., 2001]. It is likely that males vary in the ability and/or willingness to incur costs in the defense of infants, and some males (*former* alpha males?) may be better at deterring infanticide than others. Thus, again, the new alpha male does not necessarily eliminate the offspring of a formerly infanticidal alpha male.

The conclusion that emerges is that a subtle and complex interplay of numerous factors is likely to account for variation in infanticide in baboons. The two critical variables in promoting infanticide appear to be high reproductive skew in males and low availability of fertile females per unit time of tenure. The causes of the former are unknown, although variation in male-male coalitionary behavior is implicated. The latter may arise in at least two different ways that focus either on the female or male contributions to this process. First, cycles of female fertility may be lengthened by low rates of reproduction and (non-infanticidal) infant mortality (as in the Drakensberg chacma baboons). Second, male access to females with relatively usual cycles of fertility may be severely constrained by truncated alpha tenures arising from high rates of immigration. Ultimately, all of these processes are influenced by demography and ecology. Although the intriguing patterns are insufficient to test these hypotheses rigorously, they do clearly establish a rationale for careful, quantitative analysis of male reproductive strategies in general and infanticidal behavior in particular across baboon populations.

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Table II. Reports of inferred infanticidal attacks in savanna baboons

Case	Site	Infant			Comments	Ref ^a
		Sex	Age	Injuries		
<i>Papio cynocephalus cynocephalus:</i>						
1	Amboseli	M	1 mo	??	Approximately two weeks after an adult male immigrated into group and became alpha, a mother found carrying her (formerly healthy) infant; infant death coincided with unusually high rates of "severe injuries" to anestrous females and abortion among pregnant females	1
2	Mikumi	F	4 mos	to neck	Infant discovered dead with bloody wounds 1-2 days after orphaned	2
<i>Papio cynocephalus anubis:</i>						
3	Gombe	F	14 days	six small wounds to head	Dead body discovered with wounds; possibly killed during "major fight" previous evening	3
4	Gombe	M	8.5 mos	Yes (not described)	Discovered dying where 2 min earlier loud vocalizations of males had been heard	3
5	Gombe	M	2.0 mos	to lower back	Died during break in observation and intergroup interaction; mother ate body	3
6	Gombe	M	16.2 mos	to torso, penetrating body wall	Wounded during intergroup interaction; died 8 days later	3
7	Gombe	M	8.3 mos	Yes (not described)	A "commotion" attracted observers' attention to adult male SG (Table 1) very aggressively chasing other baboons, notably a female in the vicinity of her "severely wounded", bleeding infant, which died within minutes	3
8	Gilgil	F	4 mos	deep punctures to head & thigh	While an adult female was "searching frantically" for her separated infant, sounds of male fighting and infant screaming heard; infant then discovered with wounds; died 3 hrs later	4
<i>Papio cynocephalus ursinus:</i>						
9	Moremi	F	11 mos	to head & lower back	Formerly healthy infant found alive but with wounds, which resulted in loss of leg use; disappeared by 3 days later.	3

Table II. (Continued.)

<i>Papio cynocephalus ursinus</i> ::							
10	Moremi	M	1 day	multiple lacerations & punctures	Mother discovered carrying her dead infant with injuries; both seen healthy 30 min earlier; after mother discarded carcass, it was partially eaten by high-ranking female.	3	
11	Moremi	M	14 mos	3 cm cut to head	Outburst of screaming directs observers' attention to infant (seen healthy moments before with bleeding laceration; baboons found mobbing an extra-group male; infant survived attack.	3	
12	Moremi	M	1 mo	multiple bite wounds to head	Outbursts of intense screaming directed observers' attention to wounded infant with sounds; adult female present directed screaming at new immigrant adult male TM (see Table I, Case 17; infant died the next day; attack occurred during an intergroup interaction, but members of the other group were uninvolved.	5	
13	Moremi	F	1 day	puncture and laceration to head	Outburst of screaming directed observers' attention to baboons chasing adult male GL from site where a previously healthy infant was simultaneously found dead, with bleeding puncture wounds; infant seen healthy 1 hr earlier; male GL had immigrated into group 3 days earlier, and he achieved alpha status 3-4 mos after attack.	5	
14	Moremi	M	4.5 mos	two punctures to head	Observers found mother carrying dead infant with bleeding wounds 45 min after it was seen healthy	5	
15	Moremi	M	6.4 mos	punctures to abdomen & thigh	After outburst of screaming, formerly healthy infant found alive, but with bleeding wounds; it was carried by mother, but died by the next day	5	
16	Moremi	F	5.2 mos	?	Mother seen with her infant in early morning; when re-contacted 3 hrs later, infant was gone and known infanticidal alpha male DG (see Table 1), who had previously attacked this infant, simultaneously found with blood on hands and face	5	
17	Moremi	M	12.2 mos	?	Infant disappeared during prolonged, violent intergroup interaction immediately prior to which seen healthy; mother also wounded during intergroup interaction	5	
18	Drakensberg Mtn	?	1.8 mos	? ^b	Infant seen alive previous day discovered dead, carried by its mother; mother had blood on her chest; lack of predation in population suggests infanticide	6	
19	Drakensberg Mtn	?	?	Yes (not described)	Infant from a non-study group found dead with wounds possibly inflicted by male canines	6	

^a Reference Source: 1= Pereira [1983]; 2= Rhine et al. [1980]; 3= Collins et al. [1984]; 4 = Smuts [1985]; 5 = Palombit et al. [2000]; 6 = Weingrill [2000]

^b Observer(s) could not determine if the body of dead infant carried by its mother bore wounds.

Table IV. Sexual dimorphism in body size in selected savanna baboon populations

Population	Male Mass (kg)			Female Mass (kg)			Dimorphism (male/female)	Source
	Mean	Range	N	Mean	Range	N		
<i>P. c. cynocephalus</i>								
Amboseli (Kenya)	25.8	-	20	11.9	-	18	1.96	Altmann et al. [1993]
<i>P. c. anubis</i>								
Gilgil (Kenya)	24.4	21.2-29.0	11	12.8	9.8-15.2	30	1.91	Smuts [1985]
Gombe (Tanzania)	26.5	23.0-28.0	6	-	-	-	-	Packer [1979]
Masai Mara (Kenya)	27.1	21.8-32.0	54	14.0	10.9-18.0	23	1.94	Popp [1983]
<i>P. c. ursinus</i>								
Moremi (Botswana)	28.8	25.8-35.0	19	13.9	12.2-15.5	17	2.07	Bulger & Hamilton [1987]
Drakensberg Mtns (S. Africa)	23.0	20.5-26.4	6	15.9	-	1	1.45	Barrett & Henzi [1997]

Table V. Comparative social and male mating data for selected savanna baboon populations^a

Population	Female Group Size		Male Group Size		Male Mating Success ^b		
	Mean	Range	Mean	Range	%Mating by Alpha Male ^c	Alpha Mating ^d	Rank of "Top Male" ^e
<i>P. c. cynocephalus</i>							
Amboseli (Kenya)	15	11.5-18.5	7.7	6.5-8.5	8, 8, 9	3, 7, 5	2, 2, 5
Mikumi (Tanzania)	36	-	13	-	19	1	1
<i>P. c. anubis</i>							
Gilgil (Kenya)	25.4	19-34	8.6	5-13.5	8, 8, 14, 17, 36	1, 1, 5, 6	1, 1, 5, 12
Gombe (Tanzania)	14.5	13-16	7.3	6.5-8	40	1	1
Masai Mara (Kenya)	13	10-16	11	10-12	42	-	-
<i>P. c. ursinus</i>							
Moremi (Botswana)	18.1	16.1-20	7.2	5.4-9	56, 59	1, 1	1
Drakensberg Mtns (S. Africa)	9	-	4	-	70	1	1

^a Data from Bulger [1993]

^b In some cases, multiple values are provided for measures of male mating success. These refer to research conducted at the given study site on different study groups or at different times (see Bulger [1993] for details).

^c Percent mating success of alpha individual relative to other males

^d Mating rank of alpha individual relative to other resident males

^e Dominance rank of the male with the highest mating success in the group