

Infanticide in ursine colobus monkeys (*Colobus vellerosus*) in Ghana: new cases and a test of the existing hypotheses

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Summary

During a 13-month study period on four groups of *Colobus vellerosus* at the Boabeng-Fiema Monkey Sanctuary in Ghana, we recorded all instances of male aggression to infants and mothers with infants using focal-animal and ad libitum sampling. Resident males did not attack infants, whereas new immigrant males who became high-ranking and those that immigrated as part of an all-male band did. During this period, three cases of confirmed infanticide, one case of likely infanticide, and three suspected infanticides were attributed to new males. Not all new alpha males attacked infants; however, after a takeover in Group B2, the new alpha male did not attack an eight-week old infant. Some resident males aided females in infant defence but were not successful. These new cases and previously reported cases of infanticide seem to best-fit predictions of the sexual selection hypothesis. Infant attacks were performed by seemingly unrelated males who gained mating access to mothers after their infants died. Loss of a previous infant shortened the inter-birth intervals of females ($N = 6$). Male infants may have been targeted preferentially at this site, which would support the 'eliminate a future sexual rival' hypothesis, although more cases are needed to reach a firm conclusion.

Keywords: colobines, black-and-white colobus, infanticide, infant defence by males, sexual selection hypothesis.

Introduction

Infant killing by males has a wide taxonomic distribution, having been observed in birds, rodents, artiodactyls, equids, carnivores, pinnipeds and pri-

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mates (Hausfater & Hrdy, 1984; Parmigiani & vom Saal, 1994; van Schaik, 2000a). The majority of infanticides occur in three orders of mammals: primates, carnivores and rodents, predominantly in species where lactation is longer than gestation (van Schaik, 2000a). Infanticide in non-human primates shows a relatively homogeneous pattern in that it is typically committed by adult males who are unrelated to their victim and who do not usually consume the infant after killing it (van Schaik & Janson, 2000).

There are eight hypotheses have been proposed to explain the incidence of infanticide (Table 1): (i) The hypothesis that has received the most support is the sexual selection hypothesis (Hrdy, 1974, 1979; Hausfater & Hrdy, 1984; van Schaik, 2000b), which proposes that male infanticidal behaviour has been selected for because it increases the performers' reproductive success, relative to other males. This hypothesis predicts that infanticidal males will kill unrelated infants that are young enough to shorten the mother's inter-birth interval (IBI) when the male has a possibility of siring her next offspring (Hrdy, 1979; Hausfater & Hrdy, 1984; Hrdy et al., 1995). (ii and iii) The 'eliminate the genes of current sexual rivals' and the 'eliminate the genes for future sexual rivals' hypotheses suggest that male infanticide could also be favoured by natural selection (even in the absence of shortened IBIs for females) because it increases the frequency of the actors genes in the population relative to those of other males (Hiraiwa-Hasegawa & Hasegawa, 1994; Enstam et al., 2002; Crockett, 2003). (iv) The 'by-product of adaptive aggression hypothesis', argues that the aggression shown by males when immigrating into a new group is adaptive, aiding him in male-male competition; infanticide is just a by-product of this aggression because infants are small and vulnerable (Alcock, 1993; Bartlett et al., 1993). (v) The social pathology hypothesis argues that animals living at high population densities in human modified habitats are 'socially crowded' and non-adaptive aggression by animals of either sex may cause the death of infants because they are more vulnerable than other individuals (Curtin & Dolhinow, 1978; Boggess, 1984). (vi) The cannibalism or exploitation hypothesis predicts that infants are killed to be used as a food resource (Hrdy & Hausfater, 1984). (vii) The resource competition hypothesis predicts that when food is severely limiting, individuals may commit infanticide to eliminate unrelated food competitors and, thus, increase their reproductive success through the improved survivorship of their young (Rudran, 1979; Agoramoorthy & Rudran, 1995). (viii) Finally, the parental manipulation hypothesis predicts that parents may stop

Table 1. Predictions of hypotheses for male infanticide.

Predictions for the occurrence of infanticide	Sexual selection ^a	Eliminate genes of current sexual rivals ^b	Eliminate future sexual rivals ^c	By-product of adaptive aggression ^d	Social pathology ^e	Cannibalism or exploitation ^f	Resource competition ^g	Parental manipulation (terminate investment) ^f	Prediction supported in this study?
1. Individuals do not kill their own offspring	++	++	++	+	-	+	++	-	Y
2. Young infants selectively killed (shortening inter-birth interval)	++	-	-	-	-	-	-	-	Y
3. Younger (more vulnerable) individuals likely to be killed	+	+	-	+	++	+	+	+	Y
4. Male infants targeted	-	-	++	-	-	-	-	-	Y
5. Killers are males (not females)	++	++	++	++	-	-	-	-	Y
6. Infanticide by individuals of reproductive age	++	++	++	++	-	-	++	++	Y
7. Killer has mating access to the mother after infanticide	++	-	-	-	-	-	+	-	Y
8. Average duration of reproductive tenure is as long as average age at puberty and potential victims do not disperse prior to breeding	-	-	++	-	-	-	-	-	N
9. Victims are eaten	-	-	-	-	-	++	-	+	N
10. Occurs only during times of heightened aggression around male invasions	-	-	-	++	++	-	-	-	N
or status changes									
11. Occurs when group size is limited by food resources	-	-	-	-	-	-	++	-	N

Table 1. (Continued).

Predictions for the occurrence of infanticide	Sexual selection ^a	Eliminate genes of current sexual rivals ^b	Eliminate future sexual rivals ^c	By-product of adaptive aggression ^d	Social pathology ^e	Cannibalism or exploitation ^f	Resource competition ^g	Parental manipulation (terminate investment) ^f	Prediction supported in this study?
12. Increased fitness to killer by killing own offspring	-	-	-	-	-	-	-	++	N
13. Victim closely related to infanticidal individual	-	-	-	-	-	-	-	++	N
14. Occurs in areas of human disturbance with artificially high population density	-	-	-	-	++	-	-	-	N
15. Removal of dominant male leads to takeover and infanticide without male-male aggression	++	+	+	-	-	-	-	-	Likely

Adapted from Crockett (2003). Ratings: ++, critical prediction of the hypothesis; +, consistent with hypothesis under some conditions; -, not predicted by hypothesis. References: ^a Hrdy (1974, 1979); Hausfater & Hrdy (1984); Hrdy et al. (1995); ^b Enstam et al. (2002); ^c Hraiwa-Hasegawa & Hasegawa (1994); ^d Alcock (1993); Bartlett et al. (1993); ^e Curtin & Dolhinow (1978); Boggess (1984); ^f Hrdy & Hausfater (1984); ^g Rudran (1979); Agoramoorthy & Rudran (1995).

investing in their young when this provides them with some other fitness benefit (Hrdy & Hausfater, 1984).

In a few primate populations, male infants may be targeted by infanticidal males more than females (*Alouatta palliata*, Clarke, 1983; *Pan troglodytes*, Hamai et al., 1992; Hiraiwa-Hasegawa & Hasegawa, 1994; *Semnopithecus entellus*, Sommer, 1994). Although the sexual selection hypothesis may still apply in these cases (if the mother's IBI is shortened and she mates with the attacking male), preferentially killing male infants has the additional benefit for infanticidal males of eliminating a future sexual competitor instead of a possible future mate (Hiraiwa-Hasegawa & Hasegawa, 1994).

When infants are targeted by infanticidal males, putative sires may defend infants in some primate species (i.e., *S. entellus*, Borries et al., 1999; *Papio cynocephalus ursinus*, Palombit et al., 2000; Weingrill, 2000; *Colobus vellerosus*, Saj & Sicotte, 2005), and males may base their dispersal decisions on whether or not they have offspring in the group (i.e., *S. entellus*, Borries, 2000).

In this paper we describe the occurrence of several infanticide cases following male immigration into three study groups of ursine colobus (*C. vellerosus*) at the Boabeng-Fiema Monkey Sanctuary (BFMS) in Ghana during a 13-month study period. We discuss these new and some previously reported cases of infant attacks at BFMS in terms of: (1) infant mortality due to infanticide; (2) the sex and age of victims; (3) the timing of attacks relative to male immigration and rank changes; (4) the effect of infant loss on IBI; and (5) male participation in infant defence, in order to test predictions of the available hypotheses for infant-killing by male primates (Table 1). This represents the second largest data set of infanticides for a colobine species (after *S. entellus*, see Sugiyama, 1965; Mohnot, 1971; Sommer, 1994; Borries & Koenig, 2000).

Methods

Research on *C. vellerosus* has been conducted at the Boabeng-Fiema Monkey Sanctuary (BFMS) in central Ghana (7°43'N, 1°42'W) under the direction of PS since 2000. This dry semi-deciduous forest is 191.6 ha in size, located 350 m above sea level in the Nkoranza district of the Brong-Ahafo Region. BFMS is surrounded by farmland but connects to several smaller

forest fragments in the area by a narrow, riparian forest. Fifteen bi-sexual groups of *C. vellerosus* (Wong & Sicotte, 2006) and a growing population of Campbell's mona monkeys (*Cercopithecus campbelli lowei*) are found in BFMS and are protected by a hunting ban (Saj et al., 2005).

The vegetation at BFMS is a mosaic of primary forest, regenerating farmland (secondary forest), and woodland (Fargey, 1991; Saj et al., 2005). Annually, there are two rainy seasons and two dry seasons. The long rains last from approximately March to July and there is a short rainy season in September. There is a short dry season in August and a prolonged one from November to February. The mean annual rainfall from 1985 to 1990 was 1250 ml (SD \pm 21.1, taken in Nkoranza, approx. 20 km from BFMS, Fargey, 1991).

Study species

C. vellerosus at BFMS is mainly folivorous, with an annual diet of 34% mature leaves, 40% young leaves, 8% seeds and seed pods, 8% unripe fruits, and 6% flowers and buds (Saj et al., 2005). There is no birth or mating season (Saj & Sicotte, in press). Group sizes vary considerably (range: 9–38, mean: 15.0, $N = 15$; Wong & Sicotte, 2006) as does group composition, which is multi-male, multi-female and uni-male, multi-female with the presence of all-male bands (AMB's) (Teichroeb et al., 2003; Saj & Sicotte, 2005). Between-group encounters are usually aggressive, with adult males as the main participants. Group males, solitary males, and males in AMBs also attack bisexual groups during male incursions (Sicotte & MacIntosh, 2004). Incursions seem to function in allowing males to assess nearby groups, to perhaps gauge the reproductive state of the females and the resistance they may encounter in immigrating into the group. Targeted aggression towards infants has been seen during both between-group encounters and male incursions (Sicotte & MacIntosh, 2004; Saj & Sicotte, 2005; JAT, unpubl. data). Males in AMBs sometimes approach and follow a group, intermittently attacking it and eventually immigrating into the group, usually in a matter of weeks. After immigrating they attempt to evict the resident males and one another (Saj & Sicotte, 2005; JAT, unpubl. data).

Study groups and data collection

For this research paper, four groups of *C. vellerosus* (WW, DA, B2 and RT) were studied for 13 months (July–November 2004, January–August 2005).

Table 2. Study group composition during the study.

Name	Group size	Adults		Subadults		Juveniles/infants
		M	F	M	F	
RT	13	1	5	1	1	5
B2	13–17	1–3	4	2–4	0–1	4–5
DA	21–31	3–8	9–10	3–5	1–3	4–5
WW	28–33	6–10	10–11	2–6	2–3	2–5
AMB	4–10	0–3	0–1	4	0–2	0

The size and composition of the groups during the study is provided in Table 2. All animals in the small study groups (B2 and RT) were individually recognized by features of the face and tail. All adult males and some adult females (DA, $N = 5$; WW, $N = 8$) were individually recognized in the larger study groups. An AMB was also followed briefly ($N = 9$ follow days, July–September 2004) after it formed and while the males were in the process of immigrating into DA group.

Each study group was followed for two 2-day periods per month from dawn to dusk (6:00 am to 6:00 pm) by JAT with the help of a research assistant. When rare events occurred, such as take-overs or infant attacks, the regular schedule of data collection was temporarily suspended to concentrate observations on the group where these events were taking place. Behavioural observations were done using 10-min focal samples (Altmann, 1974) that were alternated among adult and subadult individuals. The observer moved around the group and alternated focal-samples between males and females to insure that no individual was sampled more than once per hour. Ad libitum data collection was employed to record immigration events and rare behaviours such as infant attacks (Altmann, 1974).

Definitions

Infanticidal events are categorized as (following Watts, 1989): 1, confirmed infanticides (CI) where directed aggression (including chases and contact aggression) towards an infant or a mother-infant pair was observed leading to the infant being injured and dying from its wounds; 2, likely infanticides (LI) where directed aggression towards the infant or mother-infant pair was observed and the infant subsequently disappeared; 3, suspected infanticides (SI) where apparently healthy infants disappeared at the same time as a male

takeover or immigration of a male who became highest-ranking immediately or the infant's body was found with wounds that appeared to be caused by canines.

When the ages of infants were unknown, they were estimated depending on the size of the infant and the stage of its natal coat (Marteinson, 2004). Similarly, IBIs that were not known exactly were estimated based on infant characteristics when groups were re-contacted. Male dominance rankings were determined from the direction of aggressive displacements and submissive avoids and pant-grunts during focal samples and ad libitum data collection.

Data analyses

A binomial test was used to see if male–female birth ratios differed and a Fisher's exact test was used to see if there was a relationship between infant sex and whether or not immigrant males attacked them. A Spearman's rho was used to test whether the age at which infants were attacked was correlated with the mother's subsequent IBI. Tests were done using SPSS 13.0, significance was set at $p \leq 0.05$ and all tests were two-tailed.

Results

Two hundred and eleven full-day follows were conducted for the four study groups and the AMB. Contact and focal hours for each group is provided in Table 3. Fourteen males immigrated into three of the study groups during this period (Table 4). Three confirmed, one likely, and three suspected infanticides were attributed to new males in these three groups during this time period. Not all new males attacked infants and some previously resident males defended infants. A fourth study group received no male immigration and the five infants in this group did not suffer any male attacks. Resident males ($N = 22$) were not observed to attack infants in any of the groups. However, one formally resident, non-natal, subadult male (male *Lo*) did re-immigrate into group B2 as an adult and appeared responsible for two infant deaths (Cases 10 and 11, see below). Seventy-eight percent (7/9; Table 4) of new males that challenged dominants and increased their rank in their new group attacked infants, while only 20% (1/5) of new males that stayed low-ranking were seen to attack infants.

Table 3. Contact and focal hours for each study group.

Group	Number of follow days	Contact hours*	Number of focal samples	Focal hours
RT	48	567.5	639	106.5
B2	48	574.5	612	102
DA	48	574	599	99.8
WW	58	690	750	125
AMB	9	101	6	1
Total	211	2507	2606	434.3

* Including JAT and research assistants.

New cases of infant attacks at BFMS after male immigrations

Below is a description of the events leading to infant attacks after male immigrations in this study, as well as the outcomes. It is followed by brief accounts of the previous published attacks that have been seen at this site (Cases 1–4) and some analyses. All infanticides observed at this site are listed in Table 5.

Case 5: DA group, 1 LI, October 2004–January 2005

In July 2004, an AMB of seven males (3 adults and 4 subadults) began attacking the DA group, which contained three adult males and 10 adult females, the AMB stayed in proximity to DA and the males were tolerated by the members of DA by September 2004. Two subadult and one adult female left the group immediately after the AMB began attacking DA. They ranged with the AMB males for about a week, before forming their own group without a permanent male for several months. None of these females had dependent offspring and the adult female mated with several of the AMB males. It is unknown if any of these females were pregnant since we do not have data on subsequent births. At this site though, we have observed pregnant females soliciting copulations and mating in the first three months of their pregnancy ($N = 4$). By January 2005, the AMB males had evicted all of the original DA resident males. The new males did not direct aggression to four un-weaned female infants that ranged between 8 and 10 months of age, although the mothers of these infants did not begin to copulate with them until their infants were almost weaned (3–5 months later). They did, however, attack a male infant born to female *Pn* (infant *Pg*) between October 17 and 19, 2004. At least three of the seven new males were seen to attack

Table 4. Outcome of male immigration into focal groups at BFMS.

Male ID	Age	New group	Date of immigration	Part of AMB?	Challenge dominants?	Attack infants?	Rank outcome
<i>Wo</i>	Adult	B2	September 2004	N	Y	N	Takeover: Alpha for 3 months, becomes beta after <i>Lo</i> re-immigrates
<i>Lo</i>	Adult	B2	December 2004 or January 2005	N	Y	Y	After being evicted by <i>Wo</i> and absent for approx. 3 months, re-immigrates, becomes alpha over <i>Wo</i>
<i>Cy</i>	Adult	DA	July 2004	Y	Y	Y	Becomes alpha over <i>Wo</i> by October 2004, is injured and drops in rank below <i>Do</i> in early March 2005, disperses in late March 2005
<i>Do</i>	Adult	DA	July 2004	Y	Y	Y	Becomes beta by October 2004 and alpha by early March 2005
<i>Ca</i>	Adult	DA	July 2004	Y	N	N	Stays low-ranking, is evicted by November 2004
<i>Mo</i>	Older subadult	DA	July 2004	Y	Y	Y	Stays low-ranking, is evicted by January 2005
<i>Ma</i>	Older subadult	DA	July 2004	Y	Y	Y	Becomes beta by October 2004 and alpha by early March 2005
<i>Sh</i>	Older subadult	DA	July 2004	Y	Y	Y	Becomes gamma male by March 2005
<i>Js</i>	Young subadult	DA	July 2004	Y	N	N	Stays low-ranking
<i>Sc</i>	Young subadult	DA	October 2004	Y	N	N	Stays low-ranking
<i>Ha</i>	Adult	WW	September 2004	N	Y	Y	Becomes alpha by the end of October 2004
<i>Cl</i>	Adult	WW	December 2004 or January 2005	N	Y	N	Becomes beta by March 2005, is injured and drops to fifth-ranking in May 2005
<i>Ru</i>	Adult	WW	January 2005	N	N	N	Stays low-ranking
<i>Nr</i>	Adult	WW	June 2005	N	N	N	Stays low-ranking

Table 5. Social context of infant attacks & infanticides at BFMS.

Case	Date	Group	Infant sex	Infant age ^c	ID of mother	Mother pregnant at male immigration? ^d	Event status	ID of attacking male(s)	Male defender present?	Male defender tenure ^e	Group comp. ^f	Attacker mating access?	Subsequent IBI ^g
1 ^a	April 2001	B1	M	7 months	G	No	A	AMB	Yes	>11 months	Multi-♂	MO	Approx. 17 months
2 ^b	August 2003	RT	M	Approx. 3 months	Je	No	SI	St?	No	—	Single-♂	Y	Approx. 11 months
3 ^b	August 2003	RT	M	Approx. 3 months	Fr	No	SI	St?	No	—	Single-♂	Y	Approx. 11 months
4 ^b	August 2003	RT	M	Approx. 3 months	Bl	No	CI	St	No	—	Single-♂	Y	Approx. 11 months
5 ^c	October 2004–January 2005	DA	M	2 days	Ph	Yes	LI	AMB	Yes	>17 months	Multi-♂	MO	Approx. 9 months
6	November 2004	WW	M	7 days	Jn	Yes	SI	Ha	Yes	>5 months	Multi-♂	MO	?
7	November 2004	WW	M	3 days	Lu	Yes	CI	Ha	Yes	>5 months	Multi-♂	Y	?
8	November 2004–April 2005	WW	F	14 days	Ch	Yes	CI	Ha	Yes	>5 months	Multi-♂	Y	?
9	November 2004	WW	?	3 h	Ml	Yes	CI	Ha	Yes	>5 months	Multi-♂	Y	8 months
10	December 2004–January 2005	B2	F	Approx. 5 months	Sf	No	SI	Lo?	No	—	Multi-♂	MO	?
11	January 2005	B2	F	Approx. 1.5 months	Rx	No	SI	Lo?	No	—	Multi-♂	MO	?

Abbreviations: A, attacks observed but infant lives; CI, confirmed infanticide; LI, likely infanticide; SI, suspected infanticide (see Methods for definitions); MO, mating observed between attacker(s) and mother; Y, mating not observed but new male(s) is resident in the mothers group after the infants death.

^{a,b} Cases previously described: ^a Saj & Sicotte (2005); ^b Sicotte et al. (2007). ^c Infant age at first attack or disappearance. ^d Mother pregnant at the time of the attacking male's immigration? ^e The known tenure in the group of the male defender. Mean tenure for males at BFMS is estimated at 15.8 months (range 3 months to >52 months, N = 29). ^f Group composition at time of infant attacks or disappearance. ^g Subsequent IBI after the loss of the infant.

the infant on different occasions. At the time of the attacks, only one of the original resident males (*Mc*) remained in the DA group. Following are the events that were observed.

Oct. 21, 2004, 16:12: An adult AMB-male grabs infant *Pg* as he is being transferred from female *Pn* to another adult female. The male brings infant *Pg* to its mouth. Female *Pn* and the other female lunge towards the male and he drops the infant. Infant *Pg* falls from a height of 25 m. Female *Pn* retrieves infant *Pg* from the ground. He had sustained a 3 cm cut to his right hip. Oct. 22, 04: 8:32: Adult AMB male *Ma* jumps toward female *Pn* and her infant *Pg*, who flee. Resident-male *Mc* places himself between male *Ma* and the mother-infant pair. Oct. 24, 2004, 15:01: Female *Pn*, infant *Pg* and male *Mc* are resting in proximity. An adult AMB-male threatens and grunts, repeatedly approaching (to 5 m), and displacing them over a period of 10 min. Male *Mc* remains between the AMB-male and the mother-infant pair (L. Brent, pers. comm.). Nov. 6, 2004. 13:44: Grunts are heard. Female *Pn* runs with infant *Pg* in ventral contact from an adult AMB-male, and is lost from sight. Fifteen minutes later female *Pn* and infant *Pg* are found 150 m from the rest of the group. The infant has a small, circular cut on the top of its head and a cut on its left hip (L. Brent, pers. comm.). Nov. 22, 2004–Jan. 25, 2005: No researchers are in contact with the DA group. Jan. 26, 2005: Infant *Pg* is missing and presumed dead.

Cases 6–9: WW group, 1 SI and 3 CI, November 2004

On Sept. 13, 2004, a new adult male (*Ha*) entered the WW group, which contained seven adult males and 11 adult females. Aggression involving male *Ha* and resident males of WW was frequent and by the end of Oct. 2004, male *Ha* had replaced male *Pc* as the alpha male (male *Pc* was evicted). Four females (*Jn*, *Lu*, *Ch* and *Ml*) gave birth two months after male *Ha*'s immigration. The females were not observed to mate with male *Ha* when they were pregnant and once the infants were born they began avoiding him. Male *Ha* was observed to attack three of these infants and is suspected of attacking the fourth (female *Jn*'s infant). However, male *Ha* did not attack an approximately 10-month-old, unweaned, female infant belonging to female *Cr*, although this female did not begin to mate until April 2005 (5 months later). Following are the events that were witnessed for each infant.

Case 6: SI, female Jn's infant. Nov. 14, 2004, 8:46: After several minutes of squealing, *Jn's* 1-week-old, male infant falls 22 m from a tree. It is unknown what caused the fall but male *Ha* was in the tree at the time. Female *Jn* immediately goes to the ground to retrieve the infant followed by several other adult and subadult females. Nov. 14, 2004, 8:58: Male *Ha* jumps to about 6 m above the individuals on the ground. Male *Jr* pant-grunts and approaches him, resting within 3 m of him. Nov. 14, 2004, 9:06: Female *Jn* comes up with the infant. No blood is visible. Nov. 14, 2004, 9:14: An unidentified adult male approaches female *Jn* and her infant. She lunges towards him, batting at him, and roars approximately seven times. The male flees. Nov. 15, 2004, 14:57: Female *Jn's* infant can no longer cling but is still alive. Nov. 17, 2004, 5:55: Female *Jn* does not carry her infant and is searching the ground. Nov. 17, 2004, 6:14: Female *Jn* returns to the high canopy without her infant. Nov. 17, 2004, 8:27: Female *Jn's* infant is found dead. It has an injury that is clotted and cleaned well. The flesh on its right shoulder is ripped open and the humerus is detached from the shoulder ball-and-socket joint. Nov. 22, 2004: Male *Ha* is seen to mate with female *Jn*.

Case 7: CI, female Lu's infant. Nov. 15, 2004, 10:52: Male *Ha* chases female *Lu* with her 3-day-old, male infant. She flees, leaps between two trees, and the infant falls approximately 10 m to the ground. Female *Lu* goes down and retrieves it. The infant's entire lower back and the top of its tail are bloody. Female *Lu* sits away from the group and when she moves at 14:49 the infant is clinging and squealing intermittently. Nov. 17, 2004, 9:37: Male *Ha* chases female *Lu* with her infant. She leaps to a branch that breaks and the infant falls approximately 10 m to the ground. Female *Lu* rushes to the ground to retrieve her infant. When she moves into the canopy again at 9:47, she carries the infant but it is now dead. Nov. 20, 2004, 14:17: After carrying her dead infant for three days, female *Lu* is last seen with it. Despite searches in the area, no body is found.

Case 8: CI, female Ch's infant. Nov. 15, 2004, 15:39: A fight breaks out near female *Ch* and her 2-week old, female infant and one roar is uttered. Male *Jr* chases male *Ha* out of the tree. Nov. 18, 2004, 8:22: Three individuals are seen grappling and one roars 8–10 times. Female *Ch's* white infant falls 15 m to the ground and male *Ha* is chased from the site of the fall by male *Jr*. Female *Ch* runs to the ground to retrieve her infant. Nov. 18, 2004, 8:24: Female *Ch* climbs up to 5 m with the infant. It is clinging but it has

sustained an approximately 6-cm-long and 1-cm-wide wound across its left shoulder blade. Nov. 18, 2004, 8:26: Male *Ha* approaches female *Ch* with her infant. Male *Jr* chases male *Ha* back and four roars are emitted by one of them. Nov. 18, 2004, 8:27: Male *Ha* goes around male *Jr* and approaches female *Ch* and her infant from above. Male *Jr* blocks male *Ha*'s path. Nov. 21, 2004, 6:04: A male grabs female *Ch*'s infant off her ventrum, bites it and shakes it violently. Female *Ch* and another adult female dive towards him and one of them roars approximately 6 times. The male drops the infant and it falls 22 m to the ground. Female *Ch* runs to the ground and the other female lunges at the male again. He falls 5 m to a lower branch. Male *Ha* was known to be in that tree at the time. Nov. 21, 2004, 6:06: Female *Ch* comes up to 3 m holding the infant. It cannot cling with its back feet any longer and has a slash on its left lower back about 8 cm long. Nov. 23, 2004: Female *Ch* moves around carrying her paralysed infant. Nov. 27, 2004–Jan. 12, 2005: No researchers present at the site. Jan. 16, 2005: Female *Ch*'s infant is spotted, still alive and paralysed from the waist down. It is slowly changing to adult colouration. Mar. 25, 2005, 10:25: Female *Ch* pulls her infant off her ventrum and puts it down at a height of 15 m, turning away from it. The infant falls into the undergrowth and squeals. Female *Ch* and male *Jr* move down to the ground and are not seen for several hours. Mar. 25, 2005, 13:45: When the group moves on without the infant, JAT attempts to see where the infant is. JAT finds the infant's body but female *Ch* and male *Jr* rush back to the fall site, so the body is left. Mar. 25, 2005, 14:38: Male *Jr* leaves the body and returns to the group. Mar. 25, 2005, 15:38: Female *Ch* moves about 50 m away from the body. Mar. 25, 2005, 16:59: Female *Ch* moves >50 m away from the body so JAT is able to retrieve it. It was disembowelled in the fall. The wound sustained on Nov. 21, 2004 had reopened and shows where its vertebrae were pulled apart. All of the infant's body changed to adult colouration except the front of its calves, which remained grey. The infant lived for 123 days following the attack that paralysed it.

Case 9: CI, female MI's infant. Nov. 24, 2004, 15:01: Female *MI* is first noticed with a newborn infant. Nov. 24, 2004, 15:21: Male *Ha* moves towards *MI* and her infant. He lunges trying to grab the infant, they grapple, and 10 roars are emitted. Male *Ha* chases female *MI* and the infant falls 6 m to the ground. Female *MI* goes to the ground to retrieve it. Nov. 24, 2004, 15:22: Female *MI* moves up and sits 4 m above the ground with the infant. The base and end of its tail are bloody. Nov. 24, 2004, 15:24: Female *MI* stays

low attempting to lick the infant's wounds but it squeals each time. Nov. 24, 2004, 16:16: Female *MI* moves to sit near male *Jr*. Nov. 25, 2004, 8:31: Female *MI* is carrying her infant but it now appears to be dead. Nov. 25, 2004, 18:00: Female *MI* goes into the sleeping tree carrying her dead infant. Nov. 26, 2004, 16:53: Female *MI* is without the infant's body. It is never found.

Cases 10 and 11, Group B2, 2 SI, December 2004–January 2005

On Sept. 19, 2004, when B2 was contacted for a follow, a male take-over had occurred. All former resident adult males (*Lx*, *T* and *Le*) were missing and a new male was present (*Wo*). Male *Wo* directed aggression at the large subadult male *Lo*, until he also left the group (on approximately Sept. 21, 2004). Male *Lo* was seen alone and peripheral to the group on one occasion (Oct. 14, 2004), when he attacked male *Wo* and was again chased away. Male *Wo* never directed aggression to female *Sf*'s 8-week-old, female infant *Sm*, even though he had several opportunities to physically contact her. It is not known where male *Wo* came from or if he had any contact with female *Sf* before he took-over the group. In November 2004, female *Rx* was noticeably pregnant.

Male *Wo* was the only adult male of B2 until at least December 2004 (approximately 3 months). No researchers were present at BFMS for the month of December 2004. On the first day contact with B2 was re-established (Jan. 13, 2005), male *Lo* had re-entered the group and was dominant over male *Wo*. At this time, female *Sf*'s 20-week-old infant *Sm* was missing. In addition, a dead, female infant was found underneath a tree in which B2 was resting. The infant's legs, hands, ears and the top of the forehead had just started to change to adult colouration, indicating that it was approximately 6 weeks old (Marteinson, 2004) and likely belonged to female *Rx*. The infant had been disembowelled by a 4.7-cm-long cut to its ventrum and had a parallel laceration 1.9 cm from this major wound. Female *Rx* was seen without an infant and subsequently resumed cycling and began mating (by Jan. 28, 2005).

Male *Lo* was likely responsible for the deaths of female *Rx*'s infant and perhaps infant *Sm*. However, male *Lo* was known to be a member of B2 in June 2004. If gestation is estimated at six-months (Sicotte et al., 2007), he was likely a member of the group when female *Rx*, and perhaps female *Sf*, were inseminated. Whether or not he mated with them is unknown. He would have been competing with the three previous resident adult males in the group at that time (males *Lx*, *T*, and *Le*) when he was a large subadult. It also

cannot be ruled out that male *Wo* killed the infants; however, his indifference to infant *Sm* and his loss of alpha status to male *Lo* make this less likely.

Previously reported cases of infant attacks at BFMS

Case 1: Saj & Sicotte (2005)

An AMB attacked and immigrated into group B in April 2001, severely wounding the resident male (*T*). The new males attacked the youngest infant in the group, a seven-month-old male (*Gi*), wounding it. The mother (*G*) stopped nursing the infant but defended it with other females and immediately began mating with the new males. When the previously resident male (*T*) recovered from his wounds he defended the infant and it survived.

Cases 2–4, Sicotte et al. (2007)

Evidence suggested that an AMB attacked RT group in August 2003 and the resident male (*Ne*) was killed. After the takeover a new alpha male (*St*) and subadult male were present and two male infants had disappeared. Male *St* continually attacked a third male infant and although the mother (*Bl*) and other adult females in the group defended the infant, it was eventually wounded and abandoned by its mother.

Infanticide as a source of infant mortality

Table 6 shows infant mortality in the four study groups over several study periods. Twenty-six infants were born during the study periods. Fourteen infants died (including all causes of death), indicating an infant mortality rate of 54%. Infant mortality from confirmed, likely, and suspected infanticide was 38.5%. Infanticide was the suspected cause of death for 71.4% of infants that died (10/14 deaths). If we include only confirmed infanticides, 29% of infants born were killed by males. During these time periods, changes in male group membership made 18 infants vulnerable to infanticide and at least 11 (61%) of these were attacked by new males (Table 7).

Sex and age of victims

The known sex ratio of infants born during study periods did not differ from a random distribution (16 males, 7 females; binomial test, $z = 1.67$, $p = 0.09$). In cases where sex could be determined and infants were killed by

Table 6. Infant mortality at BFMS.

Group	Time period	Known infant births	Infants disappear*	CI+LI+SI	Infant mortality (%)	Infant mortality from infanticide (%)
RT	March 2003–August 2005	8	0	3	37.5	37.5
B2	March 2000–August 2005	8	1	2	37.5	25
DA	June 2004–August 2005	2	0	1	50	50
WW	June 2004–August 2005	8	3	4	87.5	50
Total		26	4	10	54	38.5

* Cases where there was no evidence of infanticide; Time periods included for each group depend on when females were individually recognized.

confirmed, likely and suspected infanticide, victims have included six males and three females (Table 5), a proportion similar to the above proportion of newborn males and females in the study groups.

However, if all unweaned infants present in groups when the alpha male position was taken over by an immigrant (i.e., vulnerable infants) are included (7 males and 9 females), and if we include infants that were not fatally wounded, male infants were more likely to be attacked than female infants (Fisher’s exact test, $p = 0.011$, Table 7). Male and female infants may also be attacked differentially when they get older. For all infants for which sex was known, those under 6 months were attacked regardless of sex (9 infants: 6 males and 3 females); while of those above 6 months of age, one male was attacked and five females were not attacked.

Timing of infant attacks relative to male immigration and rank changes

In most cases, males that succeeded in taking over groups or attaining high rank attacked infants immediately (Cases 1–4, 10 and 11) and most infanticides (9/11 or 82%) were performed by the new alpha male but AMB males that challenged dominants also attacked infants (2/11 cases or 18%, Table 4). In Cases 5–9, the females were pregnant when the male(s) entered the group and infants were attacked soon after birth, within 2 months of the male(s) immigration (Table 5). In WW group, male *Ha* attacked four infants born within 2 months of his immigration (Cases 6–9) but was not seen to

Table 7. List of infants vulnerable to attacks after the alpha male position was taken-over.

Group	Date of alpha male change	New alpha male	ID of mother	Infant sex	Infant age ^a	Infant attacked?
RT	August 2003	<i>St</i>	<i>Je</i>	M	Approx. 3 months	S
		<i>St</i>	<i>Fr</i>	M	Approx. 3 months	S
		<i>St</i>	<i>Bl</i>	M	Approx. 3 months	Y
B1	April 2001	AMB male	<i>G</i>	M	7 months	Y
B2	September 2004	<i>Wo</i>	<i>Sf</i>	F	8 weeks	N
	January 2005	<i>Lo</i>	<i>Sf</i>	F	20 weeks	S
		<i>Lo</i>	<i>Rx</i>	F	6 weeks	S
DA	October 2004	<i>Cy</i>	<i>Pn</i>	M	2 days	Y
		<i>Cy</i>	<i>Mr</i>	F	Approx. 8 months	N
		<i>Cy</i>	<i>Np</i>	F	Approx. 9 months	N
		<i>Cy</i>	?	F	Approx. 8 months	N
		<i>Cy</i>	?	F	Approx. 10 months	N
WW	October 2004	<i>Ha</i>	<i>Cr</i>	F	Approx. 10 months	N
		<i>Ha</i>	<i>Jn</i>	M	7 days	Y
		<i>Ha</i>	<i>Lu</i>	M	3 days	Y
		<i>Ha</i>	<i>Ch</i>	F	14 days	Y
		<i>Ha</i>	<i>Ml</i>	?	3 h	Y

Abbreviations: Y, yes; N, no; S, attacks suspected.

^a Infant age at takeover or first attack.

attack an infant that was born 3 months after his immigration (to female *We*); however, this infant did subsequently disappear.

The effect of infant loss on IBI

When IBIs could be calculated, they were shortened when females lost their previous infant (Table 5). When infants were killed, the mean IBI was approximately 10 months ($N = 5$, range 8–11 month), much shorter than those estimated for other black-and-white colobus when infants survived (*C. polykomos*, 24 months, $N = 4$, Dasilva, 1989; *C. guereza*, 22 months, $N = 6$, Harris & Monfort, 2006). Males may benefit by shortening IBI's even when they do not succeed in killing infants. In Case 1, an older infant (7 months old) survived, but attacks seemed to have forced the mother (*G*) to wean the infant early (Saj & Sicotte, 2005), leading to an estimated IBI of 17 months. The same female had an IBI estimated at 22 months for a subse-

quent infant, when adult male membership in the group remained relatively stable. There was a positive correlation between known and estimated IBI and age of the infant when it was attacked or killed ($N = 6$, $r_s = 0.898$, $p = 0.015$).

Defence of infants

Mothers, often in coalitions with other females, defended infants, although this defence was ultimately unsuccessful (Saj & Sicotte, 2005; Sicotte et al., 2007). When resident males were still present in the group during infant attacks by new males they often aided the female(s) by intervening and chasing away attacking males or by placing themselves between the mother and the new male(s) (Saj & Sicotte, 2005). Male defenders were present in 55% of cases (6/11) of infant attacks reported here (Table 5). Male protection of infants was successful only in Case 1, when the infant was old enough to be immediately weaned and the mother mated with attacking males (Saj & Sicotte, 2005). In all other cases where a defending male was present, the infant was younger and could not be immediately weaned (Table 5).

In multi-male groups, not all long-term resident adult males defended infants. For instance in WW group, male *Jr* defended infants after male *Ha* entered the group, but resident males *Q*, *Be*, *Ac* and *Er* did little to help (Cases 6–9). Mothers approached males *Q* and *Be* in the presence of male *Ha* but direct chases and agonistic acts were only seen by male *Jr*. At the beginning of the study period (July 2004) male *Jr* was the third-ranking male under male *Pc* (alpha) and male *Q* (beta). It is unknown if male *Jr* was the sire of the infants he defended or if he was alpha male when they were conceived.

Discussion

In this paper, we report details of infanticidal attacks by new males that immigrated into three study groups. Males that became high-ranking and some males that immigrated as part of an AMB attacked infants and three confirmed cases, one likely case, and three suspected cases of infanticide were seen in a 13-month period. Some resident males and females defended infants but were not successful. For all cases observed at BFMS, male infants seemed more likely to be attacked than females. The applicability of current

hypotheses for infanticide are discussed in regards to these cases of infant attacks at BFMS.

A pattern of male immigration and attacks upon dependent infants after entering new groups has been documented in several colobine species (i.e., *Trachypithecus vetulus*, Rudran, 1973; *S. entellus*, Hrdy, 1974; Sommer, 1994; Borries, 1997; *T. cristatus*, Wolf & Fleagle, 1977; *Presbytis thomasi*, Sterck, 1995; *C. guereza*, Onderdonk, 2000; *C. vellerosus*, Saj & Sicotte, 2005; Sicotte et al., 2007). As in Hanuman langurs, the process of male replacement in *C. vellerosus* occurs quickly if the attacking male(s) ousts the resident male(s) immediately, or can occur gradually as new male(s) immigrate into a group and work their way up in rank, leading to some or all of the resident males leaving (Bogges, 1984; Newton, 1986). New males can also join the group and stay low-ranking or become high-ranking without previously resident males leaving.

As in several other species of primates (i.e., *Theropithecus gelada*, Dunbar, 1984; *Alouatta seniculus*, Crockett & Janson, 1993; *S. entellus*, Borries, 1997; *P. thomasi*, Steenbeek & van Schaik, 2001; *Cebus capucinus*, Fedigan, 2003), male immigration at BFMS was accompanied by high rates of infanticide. In this study, infant attacks were seen in all of the groups that received new males; however, not all new males attacked infants. New alpha males attacked infants most often while males that stayed low-ranking only directed aggression at infants if they immigrated as a member of an AMB (i.e., they were part of a group of males where several males alternated aggressing an infant). Committing infanticide might not have been as beneficial for low-ranking males, since they may not gain mating access to mothers after infants die. In addition, and perhaps more importantly, when resident males are still present in the group, their protection of infants may mean that infanticide is a risky behaviour for lower-ranking males. Only one immigrant male that attained alpha status in this sample did not attack infants (Table 4). Male *Wo* did not attack an 8-week old infant in B2 after he took over the group, even though he had several opportunities to physically contact it. It is possible that male *Wo* had previous contact with the mother of this infant (*Sf*), since extra-group copulations have been observed at this site (Teichroeb et al., 2005; JAT, unpubl. data).

It is generally thought that the frequency of infanticide should be lower in multi-male groups due to (1) putative sires being present in the group to protect infants; (2) males benefiting less from killing infants because they do

not have complete sexual access to the female afterwards; and (3) paternity uncertainty when females mate promiscuously (Hausfater & Hrdy, 1984; Leland et al., 1984; Newton, 1988; Newton & Dunbar, 1994; Borries & Koenig, 2000; van Schaik, 2000b; van Schaik et al., 2004). Broom et al. (2004) further suggest that low rates of infanticide are common in multi-male groups when new males enter at the bottom of the male dominance hierarchy and take several years to become high ranking, leading to large age and rank differences between resident males and immigrants. Infant attacks and disappearances in *C. vellerosus* at BFMS occurred in uni-male groups (27% or 3/11) and in multi-male groups (73% or 8/11) (Table 5), in proportions that are equivalent to the ratio of uni-male to multi-male groups in the population (3/13 groups or 23% uni-male, Saj et al., 2005). Indeed, males appear to be able to enter groups and attain high rank relatively quickly (or immediately if they manage to oust resident males), which probably allows infanticide to occur in multi-male groups (as suggested by Broom et al., 2004). New males that entered groups and stayed lower ranking in the BFMS population were less likely to attack infants than males that rapidly became alpha, an observation that supports Broom et al.'s (2004) suggestion.

Our findings suggest that male infants were attacked more often than female infants. However, our sample of infants above six-months of age included five females and one male. Although these female infants (aged 8–10 months) appeared vulnerable to attack because they were not weaned and their mothers did not begin mating until three to five months after the attacking males immigrated, we do have one case (Case 1) of forced weaning during attacks on an older infant (7 months). This differed from the normal weaning process (where weaning is slow, beginning at about one-year of age and taking several months before the infant is completely weaned) in that the mother immediately stopped feeding and associating with the infant, which was associated with a cessation of male attacks on the infant. Case 1 is the only case of forced weaning that we have seen after observing 13 infants go through the weaning stage. Thus, forced weaning does not seem to be frequent, although it can sometimes happen. The conditions under which it happens are not known at this point. The question also remains as to why the males in the cases reported here did not attack these five older, female infants in order to gain mating access to the females. These questions and whether or not male infants are truly targeted more than females can only be resolved once more cases of infanticide have been observed in this species.

Hypotheses for infanticide

The evidence for infanticide in *C. vellerosus* at BFMS is most congruent with the predictions for the sexual selection hypothesis (Hrdy, 1974; Table 1). In 8 of 10 occurrences, males that attacked infants were not formerly resident in the group, so likely did not have mating access to the females at the time they conceived. In the two cases (Cases 10 and 11) where the suspected attacker was formerly resident in the group, he was low-ranking (4th in the male hierarchy) and still subadult at the time when the infants were conceived and probably did not have mating access to the mothers, since mate-guarding by dominant males is common in multi-male groups (JAT, unpubl. data). Victims were young infants and IBIs were shortened when a female lost her previous infant (Table 5). Young infants were killed regardless of sex but males seemed more likely to be targeted when infants were over 6 months of age. Adult males were the aggressors and females were never seen to attack infants. In all cases, attacking males had mating access to the mothers after they lost their infants and in several cases, attackers were observed to mate with mothers after their infants died (Table 5).

Of the other hypotheses for infanticide listed in Table 1, 'elimination of the genes of a current sexual rival' (Enstam et al., 2002) also receives some support, however this hypothesis is based on sexual selection (i.e., it involves male–male competition) and only the proposed benefit varies (elimination of a rivals genes rather than proliferation of your own) (Crockett, 2003). Contrary to the evidence here, this hypothesis does not predict that infants young enough to shorten the mother's IBI will be targeted or that the attacking male has sexual access to the mother after the infant is killed. Some critical predictions of the social pathology (Rudran, 1979; Agoramoorthy & Rudran, 1993) and the 'by-product of adaptive aggression' (Alcock, 1993; Bartlett et al., 1993) hypotheses were also met in this study (predictions 3, 5 and 6, Table 1); however these predictions are also congruent with the sexual selection hypothesis. Social pathology is refuted though because while BFMS is a forest fragment with some human disturbance, *C. vellerosus* do not take food from human sources and the population density (119 ind./km², Wong & Sicotte, 2006) is not artificially high compared with black-and-white colobus in other forest fragments (*C. guereza* range: 138 ind./km², Shalla, Ethiopia, Dunbar, 1987; to 1250 ind./km², Border of Kibale NP, Uganda, Onderdonk & Chapman, 2000). The 'by-product of adaptive aggression' hypothesis is

refuted in that at BFMS males directly targeted infants and mothers with infants and aggression stopped once infants had been fatally injured or killed (Cases 1, 4, 5–9). No directed aggression by new males towards females without infants was seen. Moreover, in Cases 5–9 the victims were born after the infanticidal male(s) had already been in the group for 2 months, so the generalized aggression that followed these males' immigrations was settled.

Besides the sexual selection hypothesis, the only other explanation for infanticide that may be supported in this study is the 'eliminate a future sexual rival' hypothesis (Hiraiwa-Hasegawa & Hasegawa, 1994). There are two critical predictions for this hypothesis, one of which (prediction 4) seems to be supported in this study. In this data set, male infants seemed to be targeted preferentially. However, the other critical prediction (prediction 8) was not supported in this study. Thus far our data indicate that the average duration of reproductive tenure for males is not as long as the average age at puberty for male *C. vellerosus* and potential victims would likely disperse prior to breeding (Table 5; Teichroeb et al., data not shown). Nonetheless, males in this population do appear to move between groups frequently and it may be advantageous to them to eliminate a future sexual rival even if he is unlikely to mate in his natal group.

Infant defence in C. vellerosus

Some resident *C. vellerosus* males defended infants although it is not known if they were the sires. Male defence was only successful in Case 1, when the infant could be immediately weaned (Saj & Sicotte, 2005; Table 5). In all other cases, infants were too young to feed on their own (*C. vellerosus* infants normally suckle for more than 12 months after birth; JAT, unpubl. data). Cooperative defence by females and a protector male may work to delay infant death (as in Case 5, where the infant disappeared approximately 2 months after it was first attacked); but given the long nursing period in *C. vellerosus*, it is unlikely that defenders could keep new males from having contact with very young infants long enough for them to be weaned. Infant defence may only be a viable strategy when infants are old enough that they can be weaned within a short time period.

Infanticide in the black-and-white colobus

Thus far, infanticide in the black-and-white colobus seems most prevalent in *C. guereza* and *C. vellerosus* (Oates, 1977; Onderdonk, 2000; Harris &

Monfort, 2003; Saj & Sicotte, 2005; Sicotte et al., 2007), the two species that are thought to be the most recently evolved and closely related (Grubb, 1982; Oates & Trocco, 1983). Infanticide has yet to be recorded in *C. polykomos* despite two long field studies being done on this species (Tiwai Island, Dasilva, 1989; Tai Forest, Korstjens, 2001). Nor has infanticide been seen in *C. satanas* or *C. angolensis*, although in comparison to the above species, little behavioural research has been done on them.

For *C. guereza*, which do not appear food limited despite living in small groups, Chapman & Pavelka (2005) have suggested that the formation of small groups may be a counterstrategy to infanticide since larger female groups are more of a target for incoming males (Crockett & Janson, 2000; Steenbeek & van Schaik, 2001; Koenig & Borries, 2002). *C. vellerosus* groups are generally composed of more females than guereza groups (*C. guereza*: mean from 13 sites = 2.9, Fashing, 2007; *C. vellerosus*: mean from BFMS and Bia = 5.5, Oates, 1994; Saj et al., 2005), and at least at BFMS the risk of infanticide appears relatively equal for single-male and multi-male groups (or for small and large groups), so females may not benefit from lower infanticide rates in smaller female groups of this species. Infanticide occurs in multi-male groups because males can become high-ranking immediately upon immigrating, making this a beneficial and relatively risk-free behaviour. Infants may only be safe from infanticide if the resident male(s) is strong enough to prevent male immigration (as was the case for male *St* in group RT in this study). The strength of resident males is likely related to their age and *C. vellerosus* groups may have periods of stability that are dependent on the tenure stage of the resident male(s) (as seen in Thomas langurs, Steenbeek et al., 2000). It remains to be seen if other characteristics of groups, such as size, influence the capacity of the resident male to resist immigration attempts by extra-group males.

Conclusions

During the sampled periods, infant mortality from infanticide for *C. vellerosus* at BFMS was high (71.4%) when compared with some other species (i.e., *S. entellus*, 31%, Borries & Koenig, 2000; *A. seniculus*, 44%, Crockett & Janson, 2000; *Papio cynocephalus ursinus*, 31–37%, Palombit et al., 2000). Further study will confirm if infanticide rates are always high for this

population or if the study periods represented here were particularly unstable. Furthermore, future study on *C. vellerosus* in a continuous forest would be ideal to compare rates of infanticide in an area less disturbed than BFMS. Infanticides in this population conform best to the sexual selection hypothesis (Hrdy, 1974). Our data also suggest that male infants may be targeted more often than females though, which would lend support to the 'eliminate a future sexual rival' hypothesis (Hiraiwa-Hasegawa & Hasegawa, 1994).

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