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Male Infanticide in the Golden Snub-Nosed Monkey (*Rhinopithecus roxellana*), a Seasonally Breeding Primate

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Abstract In nonhuman primates, infanticide by adult males can occur when the leader male is ousted from a one-male, multifemale group, or when male dominance rank changes within a multimale, multifemale group. According to the sexual selection hypothesis, this behavior may be adaptive if perpetrators increase their reproductive success by killing unrelated, unweaned infants, thus shortening the interbirth interval of the mother, and then siring her next infant. Under an alternative hypothesis, infanticide is a byproduct of aggressive male–male competition and these predictions do not hold. Direct observations of the context surrounding infanticide in free-ranging primate populations that allow a test of these predictions are rare. Here, we document four cases of male infanticide and report paternity data for a group of golden snub-nosed monkeys (*Rhinopithecus roxellana*) at Shennongjia, China. Three cases of infanticide by new leader males supported the predictions of the sexual selection hypothesis, while another provides partial support for the sexual selection hypothesis, but can also be explained via a nonadaptive hypothesis. In this latter case, a male from an all-male

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group killed an infant during an aggressive episode that appeared to be accidental, as it took place 7 mo before a male takeover happened, and the perpetrator did not obtain any reproductive advantage. We conclude that most male infanticide events in golden snub-nosed monkeys are consistent with the adaptive selection sexual hypothesis.

Keywords Male infanticide · *Rhinopithecus roxellana* · Sexual selection hypothesis

Introduction

Infanticide has been observed in a variety of mammals, such as primates, carnivores, and rodents (Lukas and Huchard 2014) and is especially prevalent in primates (van Schaik 2000). The sexual selection hypothesis holds that male infanticide is adaptive (Hrdy 1974, 1979; Palombit 2012; van Schaik 2000). Under this model, infanticidal males improve their reproductive success by killing an unrelated and unweaned infant, thereby shortening the mother's interbirth interval. These males then sire the next offspring of the victim's mother (Hrdy 1979). As lactation suppresses sexual receptivity in many mammals (Bronson 1989), the death of an unweaned infant causes the mother to resume cycling, at least in nonseasonally breeding species. An alternative, the nonadaptive hypothesis holds that male infanticide is a byproduct of generalized male–male aggression (Bartlett *et al.* 1993) and occurs accidentally during aggressive episodes (Sussman *et al.* 1995). Under this hypothesis, the killer does not gain any reproductive advantage.

It has been assumed that the sexual selection hypothesis does not apply to seasonal breeders, because females will not resume cycling earlier as a result of the loss of an infant, so there is no reproductive advantage for the perpetrator (Wright 1995). However, two studies have shown that this is not necessarily the case (Borries *et al.* 1999; Soltis *et al.* 2000), and that if mean interbirth intervals are >1 yr, then killing a dependent infant may still reduce the interbirth interval, even in seasonal species, and therefore be advantageous for the male.

Although infanticide has been directly observed or inferred in a variety of primate taxa (Bellemain *et al.* 2006; Cords and Fuller 2010; Lukas and Huchard 2014; Palombit 2012; van Schaik 2000), few studies have presented the behavioral and molecular evidence needed to test the sexual selection hypothesis. In a study of Hanuman langurs (*Semnopithecus entellus*), the male was excluded as the father of the infant he attacked or killed in all 16 cases of attempted or successful infanticide where DNA samples were available for both adult males and infants; in the four cases of births following infanticides, the presumed killers were the likely fathers of these offspring (Borries *et al.* 1999). Male infanticide in Japanese macaques (*Macaca fuscata*) also met the conditions specified by the sexual selection hypothesis, because the study authors were able to exclude the attacker as the father of the victim in 22 of the 23 cases examined (Soltis *et al.* 2000).

The golden snub-nosed monkey (*Rhinopithecus roxellana*) is an Asian colobine that features a multilevel social organization in which a number of one-male, multifemale units (OMUs) form a stable and cohesive band numbering up to several hundred individuals (Grueter 2013). In addition to the constituent OMUs, one or several all-male units of up to 25 adult and subadult males associate closely with the band (Grueter

2013) but are usually prevented from mating (Xiang *et al*. 2014). Aggression between males is intense, especially during the mating season (Xiang *et al*. 2014; Zhao *et al*. 2005). Solitary males and males in all-male units periodically invade OMUs, replacing the former leader or mating with resident females (Qi *et al*. 2009; Yao *et al*. 2011; Zhao *et al*. 2005). Male OMU leaders cannot effectively monopolize access to resident females, and extra-unit males sire more than half of the offspring in the Qingling population (Guo *et al*. 2010). Copulations occur throughout the year, but particularly between May and November, and conception appears to be limited to the period from September to November with a corresponding birth from March to May (Xiang *et al*. 2014). Although infanticide has been reported in snub-nosed monkeys (*R. roxellana*: Zhang *et al*. 1999; *R. bieti*: Ren *et al*. 2011; Xiang and Grueter 2007), no study has yet tested evidence for whether this infanticide might be adaptive.

We here describe four instances of male infanticide that occurred during >8 yr of observation of a group of golden snub-nosed monkeys, with genetic analysis of paternity. We test the predictions of the sexual selection hypothesis: 1) killers are unrelated to the victims; 2) the victims' mothers conceived shortly after infanticide, and infant death shortens the length of the mother's interbirth interval; and 3) the killer sires the subsequent offspring of the victim's mother. We compare this adaptive hypothesis against the null mode, whereby infanticide occurs as a byproduct of aggression between a leader male and individuals from an all-male unit, and the infant is killed by a male that gains no reproductive benefit.

Methods

Study Site

We conducted the study on a free-ranging, provisioned group of golden snub-nosed monkeys at Dalongtan in Shennongjia Nature Reserve, Hubei province, China (coordinates: 31°29′N, 110°18′E). Reserve staff fed the monkeys two or three times a day at different sites with lichen, pine seeds, apples, carrots, oranges, and peaches; they did not herd the monkeys to the provisioning sites.

From January 2006 to March 2014, we conducted daily observations at distances between 3 and 50 m from 0800 to 1600 h in winter (December–February) and spring (March–May) and 07:00 to 19:00 h in summer (June–August) and autumn (September–November) so long as weather permitted (Xiang *et al*. 2014; Yu *et al*. 2013). We observed and recorded male infanticides *ad libitum* (Altmann 1974).

We collected the dead bodies of four infants attacked by males. We preserved tissue samples at −20°C in a freezer before use in paternity exclusion analysis. We collected hairs with attached roots from all reproductively mature adult males in the focal group and newborn infants of an infanticide victim's mother for paternity analysis (for details, see Xiang *et al*. 2014).

Data Analysis

We used 16 microsatellite loci to determine the paternity of the dead infants and the subsequent infant of the victim's mother, using all reproductively mature adult males (*N*

= 12) in the study group as candidate sires (Xiang *et al*. 2014; Yang *et al*. 2014). We used CERVUS3.0 to determine paternity (Kalinowski *et al*. 2007) with confidence levels of >80% (relaxed confidence) in one case and >95% (strict confidence) in four cases.

To determine whether the victims' mothers became sexually receptive shortly after infanticide, we estimated conception dates by subtracting gestation length from birth dates. As there are no accurate records of gestation length for wild individuals, we used the mean gestation of 202 days (SD = 1.1 days, $N = 5$) for captive individuals (Qi *et al.* 1995; Yan *et al.* 2003).

To test whether infanticide shortens the length of the interbirth interval, we used two-sample *t*-tests to compare the interbirth interval of females that lost infants to infanticide with those that did not suffer infanticide.

Ethical Note

All research methods adhered to Chinese legal requirements and complied with protocols approved by the State Forestry Administration of China. Because the field studies involved endangered and protected species, we obtained approval from the state and local governments. We collected data in a minimally invasive manner and recorded naturally occurring behavior.

Results

We observed three infants being killed by adult males, and inferred one further case of infanticide based on strong evidence (Table I). Autopsy confirmed that attacks by males contributed to the infant's death in all cases.

Infanticide Cases 1 and 2

Infanticide cases 1 and 2 occurred in the same OMU and the killer was the same adult male (male DD). Case 1 occurred 7 mo before the killer ousted the old leader male; case 2 took place 4 d after the killer became the new leader male.

In December 2006, the study group consisted of three OMUs with a total of 37 individuals and one all-male unit (five adults and three juveniles). Male CM was the leader male of an OMU that consisted of three adult females (JJ, HZ, and JZ), three juveniles, and one unweaned infant in December 2006. Adult males XY and DD from the all-male unit chased male CM together at 13:20 h on December 23, 2006. CM mounted a successful defense against XY and DD with the help of other leader males (HT and BT). However, during the aggressive incident, male DD was observed biting female HZ's unweaned infant (HZI06), who was aged 269 days. HZ106 bled from bites to the abdomen and the left thigh and died four days later (infanticide case 1).

On 26 June 26 2007, male XY evicted leader male CM from his OMU and XY became the leader of the OMU, which consisted of three adult females (JJ, HZ, and JZ); three juveniles; and one unweaned infant, born on March 26, 2007. On August 5, male DD was observed chasing and stalking leader male XY. On August 6, a serious fight

Table I Circumstances and outcome of male infanticide in golden snub-nosed monkeys at Shennongjia, China (cases listed in chronological order)

Case no.	Date of occurrence	Victim and sex	Killer is a new leader male	Date of most recent male takeover	Age of victim (days)	Victim's mother	Estimated date of conception	Date of birth of next offspring	Interval between infanticide and conception (days)	Mother's inter-birth interval (days)
1	Dec. 23, 2006	HZI06♀	No	Aug. 6, 2007	269	HZ	Sept. 5, 2007	March 25, 2008	256	749
2	Aug. 10, 2007	JZI07♂	Yes	Aug. 6, 2007	142	JZ	Oct. 1, 2007	April 20, 2008	52	423
3	Aug. 20, 2012	HH3I12♂	Yes	May 15, 2012	166	HH3	Oct. 2, 2012	April 22, 2013	62	385
						XH[a]	Oct. 21, 2012	May 11, 2013	62	405
4	Sept. 20, 2012	XBI12♂	Yes	May 15, 2012	153	XB	Oct. 27, 2012	May 17, 2013	37	393

[a] The stepmother of HH3I12; for details, see text.

between males DD and XY resulted in XY leaving the unit and joining the all-male unit, and DD became the new leader of the OMU. At 13:10 h on August 10, DD attacked female JZ's unweaned infant (JZI07), aged 142 days, although females JJ and JZ attempted to protect it. The infant suffered serious injuries to the abdomen and neck and died several minutes later (infanticide case 2).

Infanticide Cases 3 and 4

Infanticide cases 3 and 4 occurred in the same OMU in 2012 after it was taken over by a male from the all-male unit (male NN).

In May 2012, the study group consisted of four OMUs with a total of 43 individuals and one all-male unit (four adults and seven subadults and juveniles). On May 15, 2012, male NN from the all-male unit evicted leader male DY and became the new leader of an OMU composed of three adult females (XH, XB, and HH3); two juveniles; and two unweaned infants. Female XB had given birth to XBI12 on April 19. Female HH3 gave birth to HH3I12 on April 2, but abandoned the infant at the age of 2 days due to a serious eye illness (to female HH3). Infant HH3I12 was adopted by its older sister female XH, who was lactating, but whose own infant had just died.

Infant HH3I12's biological mother, female HH3, could not keep up with her social unit and was separated from other members and usually associated with an adult male (CM) from the all-male unit from May 25, 2012. Leader male NN often tried to herd her to his social unit, but was unsuccessful. When her eyesight partly recovered female HH3 returned to nurse her baby from time to time after April 14, 2012 (16% of nursing time; Z. F. Xiang, *in preparation*). Female HH3 was observed to mate with leader male NN on July 3, 2012 and returned to her original OMU on September 22, 2012, when she again mated with leader male NN.

At 14:53 h on August 20, 2012, female XH was grooming female XB. Female XH's adopted infant (HH3I12) and XB's infant (XBI12), both unweaned, were playing with a juvenile in close proximity to their mothers; male NN, the new leader male, was also near them. Suddenly, male NN rushed toward and bit HH3I12. Females HH3, XH, and XB rushed toward male NN and retrieved their offspring. Male NN attacked infant HH3I12 again at 15:52 h on August 29 and at 15:22 h on September 3, but females XH and HH3 saved the infant. On the morning of September 15, infant HH3I12 was found dead at the sleeping site, with 13 punctures and slash wounds on the body, at least eight of them from teeth (infanticide case 3).

At 10:08 h on September 20, 2012, new leader male NN attacked and bit infant XBI12, although females XB and XH fought male NN. Female XB held infant XBI12 tightly against her chest, but the infant died within a few minutes (infanticide case 4). Female XB carried the corpse for 10 min, then abandoned it. The injuries were two obvious holes in the right abdomen (Fig. 1).

Predictions of the Sexual Selection Hypothesis

We could exclude the perpetrator as the father of the victims based on genotype in all four cases of infanticide (Table II). To assess potential effects of infanticide on interbirth intervals, we assessed all five mothers, including both the biological and foster mothers from case 3, and compared their interbirth intervals to those of other mothers. The mean

Fig. 1 An infant golden snub-nosed monkey with a fatal injury caused by a new leader male.

interbirth interval of mothers whose infant were killed by a male (N = 5) was significantly shorter than that of mothers with surviving infants (N = 37) (Fig. 2, $t_{4,36}$ = 4.06, P < 0.001). However, in case 1 the interbirth interval (749 days) was similar to that of a mother with a surviving infant, while in cases 2, 3, and 4, the interval was much shorter (Fig. 2). The victims' mothers conceived 53.2 ± 11.8 days (mean ± SD) after the infanticide and all gave birth in the following birth season (Table I). In cases 1, 2, and 4, the infanticidal male sired the next infant born to the victim's mother (Table II). In case 3, the adopted infant, the infanticidal male did not sire the next infant of the victim's biological mother. However, the infanticidal male did sire the stepmother's next offspring.

Support for the Nonadaptive Hypothesis

In case 1, the infant was killed by an adult male from the all-male unit 7 mo before the killer took over the mother's OMU, while in cases 2, 3, and 4, infanticides occurred after the new male leader evicted the older one.

Table II Kin relationship between the killer male, the victim, and the subsequent infant of the victim's mother in four cases of infanticide in *Rhinopithecus roxellana* at Shennongjia, China

Case no.	Killer	Victim	Victim's mother	Victim's sire	Sire of the mother's next infant
1	DD	HZI06	HZ	CM (>95%)	DD (>95%)
2	DD	JZI07	JZ	CM (>95%)	DD (>95%)
3	NN	HH3I12	HH3[a] (biological mother)	HED(>95%)	CM (>80%)
			XH (adoptive mother)		NN (>95%)
4	NN	XBI12	XB	DY (>95%)	NN (>95%)

Paternity is assigned with confidence levels of >80% (relaxed confidence) or >95% (strict confidence)

[a] Infant HH3I12 was adopted and nursed by female XH (see text for details).

Discussion

In this study, we documented four instances of male infanticide in a group of golden snub-nosed monkeys. Our results support the sexual selection hypothesis in three cases, but although the fourth provides partial support for the sexual selection hypothesis, it can also be explained via a nonadaptive hypothesis.

In two cases (2 and 4), the context in which the behaviors were observed and the genetic data support the sexual selection hypothesis. The infanticidal male killed an unrelated, unweaned infant; the infant death resulted in a shorter interbirth interval than in females with surviving infants; and the killer sired the next infant of the victim's mother's (Table II). These findings are consistent with both observed and inferred incidents of male infanticide in other primates, such as Hanuman langurs (Borries 1997; Borries *et al.* 1999).

In case 3 the killer did not sire the subsequent offspring of the victim's biological mother although she resumed cycling. At first glance, this result does not support the sexual selection hypothesis. However, the victim was adopted and nursed primarily by its older sister, the death of the infant led to that female resuming cycling, and the killer did sire the adoptive mother's next infant, supporting the sexual selection hypothesis.

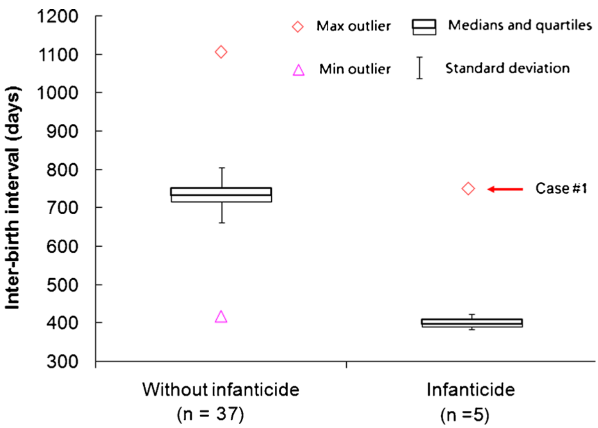

Fig. 2 Median interbirth interval in females with and without infanticide.

In case 1, the killer killed an unrelated infant and sired the subsequent infant of the victim's mother, but infanticide did not shorten the interval to that infant's birth (Table I, Fig. 2), so the killer did not increase his reproductive success beyond that accrued as new leader male. This case offers only partial support for the sexual selection hypothesis. It is also consistent with the byproduct of aggression hypothesis, as the infant's death resulted from male–male aggression well before the infanticidal male's eventual takeover of the unit 7 mo later. In this case, killing a female infant may also have harmed the killer's future reproductive success, as he was the leader of the victim's OMU from August 2007 to October 2013 (Z. Xiang, *unpubl. data*). If the female infant had survived and reached maturity within the unit, she could have mated with him and given birth between 2010 and 2013.

In sum, three of four male infanticide events in golden snub-nosed monkeys are consistent with the adaptive selection sexual hypothesis, while another provides partial support for the sexual selection hypothesis, but can also be explained via a nonadaptive hypothesis. These results provide further evidence that sexually selected infanticide can occur in seasonally breeding primates and provide the first evidence for sexually selected infanticide in a species with a multilevel social organization.

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