



Infanticide in golden snub-nosed monkeys with multilevel society

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Infanticide, killing unweaned offspring in conspecifics, occurs widely among mammals, such as rodents, ungulates, and carnivores, especially in primates (Lukas and Huchard 2014). Such scenarios are often triggered by intruders that have replaced the former dominant males in nonhuman primates (Borries 1997). It has widely been viewed that infanticide is one of the solutions of sexually driven evolutionary selection: males kill infants to end lactational amenorrhea of the victim's mothers, forcing them to return to estrus and providing infanticidal males with the opportunities to sire their new offspring (Hrdy 1979). There is a broad spectrum regarding the patterns and mechanisms causing such events, referring to alternative breeding behaviors and mating systems—monogamy, polyandry, polygyny, and promiscuity (Qi et al. 2020). Initially, primate infanticide was reported on males with a polygynous mating system, featured by dispersed societies, multimale social structures, fission-fusion communities, hierarchically formed associations, and even monogamous pairs (Palombit 2015). Therefore, primates can offer ideal instructive models to understand the mechanisms driving infanticide. Male infanticide has been observed across many primate taxa, but the extent of its occurrence is not fully understood due to difficulty in observation and uneven reporting. Thus, the comprehensive report of infanticide cases will provide a complete chain of evidence for the sexual selection hypothesis to explain male infanticide.

Here, we reported two infanticide cases in a one-male unit (OMU) of golden snub-nosed monkeys *Rhinopithecus roxellana* in Qinling, China, by a bachelor (SZ, refer to Supplementary Table 1, for their social relationship) who had taken over the unit. We documented infanticide cases with the ad libitum sampling method, and the events were directly recorded. We integrated data based on behavior and genetic analyses of paternity to test the sexual selection hypotheses (refer to Supplementary Materials for details). These 2 cases

took place 9 months after SZ became a new dominant male; the first one was Yk's unweaned infant, ykb, 212 days old, and the second one was Yl's unweaned infant, ylb, 234 days old. The interval between the 2 cases was 2 days. The procedures are illustrated in Figure 1. After the events, the victimized mothers maintained a long distance from SZ, presenting diminishing social interaction with him than with other unit members. They stayed within the group of SZ rather than moving to other OMUs. At the beginning of December, a half month after the incidents, SZ mated them forcefully. What followed was that Yl began approaching an all-male unit (AMU) frequently, grooming individuals of the group (Supplementary Figure 1). She also accepted the grooming from the individuals in AMU, keeping an association with both AMU and SZ OMU. Several other females in SZ OMU also approached AMU, grooming individuals less frequently than Yl did. Yl, however, was not found to mate with the individuals in AMU; her interaction with the group gradually diminished, and she finally returned to her original SZ OMU at the end of the mating season. At the beginning of June 2022, 7 months after the infanticide, Yk was found with her newborn infant, ykb-2 (Figure 2). Paternity analysis indicates that ykb-2 is SZ's biological offspring (Supplementary Table 2), consistent with the gestation period of golden snub-nosed monkeys. Thus, Yk was pregnant and gave birth after mating with SZ.

In summary, the infanticide events reported in this study are characterized as follows: 1) SZ's takeover occurred before new infant birth, but cases happened after existing infants started to be independent. The mating season of this species is from September to November; females give birth from the following March to May, with a gestation between 6 and 7 months and a birth interval of 2 years (Qi et al. 2008, 2009). Our other study on the same species shows that male replacement was primarily associated with female



Figure 1. Two cases of male infanticide in *Rhinopithecus roxellana*. In the first case (A–I): (A) victim ykb (7 months), Yk's unweaned baby, solid and healthy; (B) ykb and his mother (Yk), a severe bleeding injury is seen on his waist; (C) feeble ykb due to the loss of blood; (D) SZ, the dominant male with blood on his hands; (E) ykb's broken, bent legs dragged after him; (F) A severe wound is in ykb's lower abdomen; (G) in the following day afternoon, the mother takes the dead ykb; (H) on the third day morning, the mother is grooming the corpse of ykb; (I) Yk takes the corpse and climbs up the tree. Other unit members gather with her and her dead baby. In the second case (J–L): (J) Yl puts the head of the dead infant (ylb) against her breast. ylb has a wound, as what has been on ykb; (K) conspicuous male tooth marks are seen on the dead baby; and (L) 2 dead infant bodies on the ground; Yl is grooming Yk.

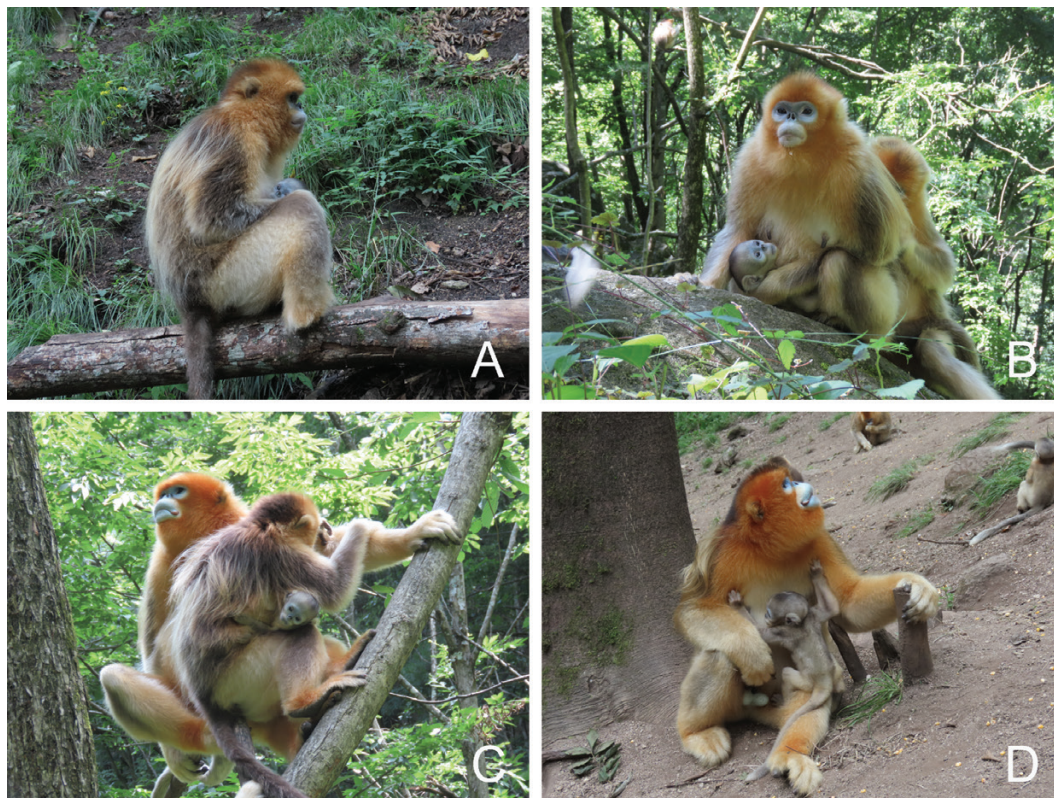


Figure 2. Newborn infant of Yk, and responses of other unit members in SZ OMU. (A) Yk holds ykb-2 (10 days) with breastfeeding; (B) Yk holds ykb-2 and is groomed by other members in the same OMU; (C) Yk carries ykb-2 and grooms SZ; and (D) SZ holds ykb-2 in the feeding area.

choices. Moreover, male replacement tends to occur randomly throughout the year, while females do not have young infants (less than 1-year-old). However, for females who have infants under 1-year-old, such a replacement tends to occur between December and March, after the mating seasons have ended (Fang et al. 2018). Such a phenomenon seems to be related to the fact that the new dominant male may kill infants to increase the mating chance. Thus, it is dangerous if a takeover occurs while Yk and Yl are pregnant in January, implying that these 2 mothers may lose their infants by infanticide from birth to the end of the mating season. That was why 9 months after SZ took over, in November 2021, before the end of the mating season, SZ killed ykb and ylb successively. On the other hand, infants were old enough to leave their mothers away, providing opportunities for SZ to attack them. Moreover, another study on the same species over the last 17 years indicates that not a single infanticide case occurred in a semi-provisioned group (Qi et al. 2020). Such stability was established under a unique environment featured by proximity exchange between OMUs and AMU; females have increased opportunities to engage in extrapair matings (EPMs) with more than one sexually mature male in both OMUs and AMU. It has been reported that females mating with multiple partners in primates can effectively prevent infanticide (Lukas and Huchard 2014). SZ was a bachelor from a new AMU that had not previously been present in our study herd. The mating season had passed before he took over these females at the end of January. That means these 2 mothers may lose their infants by SZ infanticide in the period of birth-mating season. Another study of the same species in Shennongjia shows that only a tiny number of infanticide cases (1/4) happened in the mating season, and half cases (2/4) happened immediately after the takeover in August (Yao et al. 2016). 2) Females in SZ OMU were noticed to be agonistic to SZ. Such a coalitionary defense may have delayed or reduced the events to some extent. A recent publication based on a 15-year study on the same species at Shennongjia, which focused on the female counterstrategies against male infanticide, indicates that females developed a set of the behavior to avoid infanticide (Xiang et al. 2022). However, as for the 2 infanticide cases reported in this study, females did not show such behavioral patterns, such as establishing a relationship with the ousted males or moving to other OMUs. They, however, formed a joint defense with other females in the same OMU against male attacks. Unfortunately, such a mechanism seemed to fail to avoid the events. 3) Infanticide may cause females to move to other units before a perpetrator has a chance to mate (Supplementary Figure 1). 4) The females with unweaned infants (Yk, Yl) refused to mate with SZ may be the trigger of SZ's killing their infants. Thus, the results reported in this study provide complementary evidence to understand the sexual selection hypothesis associated with animal infanticide. It suggests that the middle mating season might be the prime time for male infanticide in seasonally breeding species.

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Conflict of Interests

The authors declare that they have no competing interests.

Authors' Contributions

WL, CLW, and BGL conceived and designed the study; WL, FN, and NLL collected the data; SXD analyzed the data. WL wrote the manuscript with input from the other authors; and RLP, BGL, CLW, PZ, and ZYS revised the manuscript. All authors read and approved the final version of the manuscript.

Statement of Ethics

Our research adhered to the regulatory ethics requirements issued by Guanyinshan National Nature Reserve, China. All applicable institutional, national, and international guidelines for the care and use of animals were followed.

Supplementary Material

Supplementary material can be found at <https://academic.oup.com/cz>.

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