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Authors: Schoof, Valérie A. M., Wikberg, Eva C., Jack, Katharine M., Fedigan, Linda M., Ziegler, Toni E., et al.

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INFANTICIDES DURING PERIODS OF SOCIAL STABILITY: KINSHIP, RESUMPTION OF OVARIAN CYCLING, AND MATING ACCESS IN WHITE-FACED CAPUCHINS (*CEBUS CAPUCINUS*)

Valérie A. M. Schoof
Eva C. Wikberg
Katharine M. Jack
Linda M. Fedigan
Toni E. Ziegler
Shoji Kawamura

Introduction

In non-human primates, most infanticide cases (85%) occur during periods of social instability when a changeover of the top-ranking male occurs (van Schaik, 2000). In contrast, infanticides during periods of social stability have only been reported for a few species (Valderrama *et al.*, 1990; Murray et al., 2007; Gibson et al., 2008). The sexually selected infanticide (SSI) hypothesis (Hrdy 1974, 1979), proposes that infanticide is a male reproductive strategy in that males adopting this strategy benefit by gaining mating access to females who resume ovarian cycling prematurely following the death of their unweaned offspring. According the SSI hypothesis, infanticide is a male reproductive strategy if: 1) the attacker is unrelated to the infant, 2) the mother's time to conception is shortened by the infant's death, and 3) the infanticidal male has an increased probability of siring the mother's future offspring. Though other hypotheses have been suggested to explain infanticide, most reported cases occur during or after periods of social instability and thus appear to fit the SSI hypothesis (Hrdy 1974, 1979; van Schaik, 2000).

In white-faced capuchins *(Cebus capucinus*), infanticides are commonplace during periods of social upheaval resulting

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from alpha male replacements (Fedigan, 2003; Perry *et al.*, 2012; Jack et al., 2014). Using a combination of behavioral, genetic, and hormone data, we examine whether the first confirmed infanticides during a socially stable period without immigrations or changes in the male dominance hierarchy fit the predictions of the SSI hypothesis.

Methods

The study took place from July 2008 to November 2009 in the Santa Rosa Sector of the Area de Conservación Guanacaste, in northwestern Costa Rica (see Fedigan and Jack, 2012 for full description of the field site). Both confirmed infanticides occurred during observation of GN group by VAMS. Adult and subadult group composition was stable during the entire study period (4 adult males, 4 subadult males, 10 adult females, 12 juveniles, and 3-4 infants). We recorded data on male dominance interactions and sociosexual interactions using *ad libitum* and 10-minute focal animal follows on all eight resident males (>623 hours of focal data; 2575 contact hours). *Ad libitum* behavioral data were collected at the time of each infanticide. While alpha male white-faced capuchins are easily recognizable, dominance relationships among subordinate males are difficult to discern because agonistic behaviors are rare (Schoof et al., 2014). Therefore, we used the Elo-rating method to complement qualitative assessments of dominance rank, including that of the infanticidal male (Neumann et al., 2011).

To identify maternal resumption of ovarian cycling from progesterone (P) and estradiol levels, we collected fecal samples from LV and RM once every three days, beginning immediately after the infanticide until each female was visibly pregnant (LV: Mar 17, 2009) or she disappeared/died (RM: May 19, 2009; see Carnegie et al., 2011 for detailed methods). We defined the periovulatory phase as the day of the fP (fecal Progesterone) rise ± 3 days (Schoof et al., 2014).

Using DNA extracted from infant tissue samples and adult fecal samples, we amplified nuclear DNA at 20 loci via PCR (Apm01, Ceb01, Ceb02, Ceb03, Ceb04, Ceb07, Ceb08, Ceb09, Ceb10, Ceb11, Ceb105, Ceb115, Ceb119, Ceb120, Ceb127, Ceb128, Ceb130, d3s1210, d7s794, pepl4; see Wikberg et al., 2014 for detailed methods). Infant sires were assigned in CERVUS (Marshall et al., 1998; Kalinowski et al., 2007) at the 0.95 confidence level, and we used ML-RELATE (Kalinowski et al., 2006) to calculate estimated relatedness values (*R*) and evaluate kin relationships among adults.

Results

Case 1 - HW: At 17:55 on 30 August 2008, when the monkeys normally settle down, VAMS noticed something fall to the ground where some females were vocalizing nearby. After approaching slowly, an infant was observed (HW, 69 days old) lying on the ground, still breathing. VAMS immediately moved away so as not to interfere with the monkeys' behavior. The wounding incident was not directly observed, but it was assumed that a resident male was responsible because no extra-group individuals were in the area. On two occasions, the infant's mother (LV) came to the ground and made unsuccessful attempts to carry HW. Beginning at 18:15, in the dark, a single unidentified individual emitted lost calls (long distance contact calls) on and off for 30 min and moved away slightly for approximately 10 min before approaching again and being joined by a second monkey that emitted soft contact calls. At 18:19, the infant was no longer breathing. Examination of the remains confirmed the presence of a gash (~4 cm x 1 cm) in the lumbar/sacral region of the spinal cord, which was completely severed (Fig. 1). There were no other external wounds and no bones were visibly broken. Tissue samples were collected, and infant sex was confirmed as female.

Case 2 - RM08: During the afternoon of 24 January 2009, only the group's beta male (MM), a subordinate adult male, and two subadult subordinate males were present in the group. At 16:41, screams drew the attention of VAMS towards beta male MM and female RM, who were grappling, tangled and dangling by their tails. The beta male had RM's infant (RM08, 88 days old) in his mouth and seconds later he and RM08 dropped to the ground. The attack lasted no more than 20 seconds. The beta male was chased by RM and several other monkeys, and he disappeared out of sight. RM08 presumably died quickly thereafter because she did not make any further sounds or movements.

Approximately 15 minutes after the infanticide, beta male MM was again observed with the group and rested in proximity to a female and juvenile, and later carried an unidentified infant (>10 months of age). Subordinate adult male AD then approached the beta male and repeatedly engaged him in an aggressive coalitionary display against RM. The two males engaged in mutual play, AD sucked MM's tail, and then mounted him while duck facing and vocalizing. A few minutes later, the beta male was briefly chased by RM and several others, including male AD, although no contact aggression was observed. Two additional mounts between MM and AD occurred at 17:45, with the males taking turns. RM stayed with the dead infant long after the rest of the group moved off to a sleep tree. She tried several times to carry the corpse up into the tree with her and was eventually successful, but left the infant perched on a tree limb before heading off in the group's direction. Examination of the remains confirmed the presence of a large gash (~7 cm × 2.5 cm) at the thoracic/lumbar intersection of the spinal cord (directly below the last rib), which was completely severed. There were no other external wounds and no bones were visibly broken. Tissue samples were collected, and infant sex was confirmed as female.

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Kinship

Alpha male BG was assigned as the sire to both HW and RM08. Based on demographic data and genetic analyses, alpha male BG and beta male MM were likely full-siblings (R=0.64; full-siblings versus non-kin: P<0.001; full-siblings versus half-siblings: P=0.01; full-sibling versus parent-offspring P<0.001). The beta male had relatively low R-values with both mothers (LV, HW's mother: 0.13; RM, RM08's mother: 0.03), but we could not distinguish if they were non-kin or half-siblings (P=0.19 and P=0.11 respectively). LV subsequently conceived and gave birth to an infant (HP) who was also sired by the alpha, rather than the beta male. Based on the estimated kinship between the beta male and the infants' parents, he was most likely the paternal uncle of the three infants.

Sociosexual behavior and resumption of ovarian cycling

The conceptions of both HW and RM08 occurred prior to the start of this study, likely in January and May 2008 respectively (based on a mean gestation length of 157 days; Carnegie et al., 2011), and therefore we cannot evaluate male sexual access to the females at the time of conception. Prior to HW's infanticide, LV was observed copulating only with the alpha male BG. She had two periovulatory periods (POPs) beginning 88 and 109 days after the infanticide of HW. The second POP resulted in pregnancy and successful parturition of a subsequent infant on 22 May 2009, with an interbirth interval of 0.73 years (265 days). On 20 December 2008, during LV's conception POP, she and the alpha male engaged in sociosexual behavior (BG directed a duck face and dance display, behaviors that often lead up to a mount) and both engaged in sexual vocalizations but no copulations were observed. No other males were observed engaging in sociosexual behaviors with LV during this time. During the first two months of gestation, however, four other resident males engaged in sociosexual behaviors with LV, including beta male MM.

During RM08's gestation period, RM copulated (intromission observed) with a subordinate male and directed sexual vocalizations to the alpha male and was briefly mounted by him. In the four months following the infanticide and prior to her disappearance, sociosexual interactions – including some copulations – were observed between RM and all resident males *except* infanticidal male MM. RM had two probable POPs beginning 49 and 83 days after RM08's infanticide, and her hormone profile is consistent with the progesterone and estradiol fluctuations observed in ovulating females. RM did not conceive again before her disappearance in late May 2009 (she was presumed dead at 26 years of age).

Discussion

Predictions generated from the SSI hypothesis were only partially supported by the infanticides reported here. According the SSI hypothesis, the attacker should be unrelated to the infant. Genetic data confirm that both infanticide victims were sired by the alpha male BG, rather than by beta male MM who was the known attacker of infant RM08. However, the alpha and beta male are likely full-siblings who transferred between groups together at least twice (Wikberg et al., 2014). To our knowledge no studies have reported paternal kin bias between males and their sibling's offspring, and males may occasionally kill related infants (Gibson et al., 2008; Clarke et al,. 1994) if they have limited means to assess their relatedness to potential victims (Murray *et al.*, 2007; Widdig, 2007). Instead, males may rely on their mating history with the mothers to assess kinship (Sugiyama, 1965; Hrdy, 1974; van Schaik, 2000). However, the killing of close kin's offspring suggests that if cognitive links between mating history and paternity probability exist, these are not transferable to the mating behavior of others.



Figure 1. Photograph of lethal wound observed on HW (photo by Valerie A.M. Schoof). This characteristic wound was also observed on RM08's corpse.

The SSI prediction that the mother's time to conception would be shortened by the infant's death was generally supported. Capuchin infants are not fully weaned until 12 months (Carnegie et al., 2011; Fedigan and Jack, 2012). Given that both infants were under three months of age, the mothers were likely experiencing lactational amenorrhea at the time of the infanticides. Both mothers resumed ovarian cycling soon after the infanticide, and LV's interbirth interval was a mere 0.73 years, compared to the mean interval of 2.25 years for females whose infants survived to one year (Fedigan and Jack, 2012). The SSI hypothesis also predicts that the infanticidal male has an increased probability of siring the mother's future offspring. Following RM08's death, RM was observed engaging in sociosexual behavior with all resident males except the attacker MM. In the case of HW, the attacker was not identified, but the mother LV was observed copulating only with the alpha male during her conception period, and he sired the resulting offspring. Therefore, unless BG attacked his own infant (HW), the infanticidal male did not sire LV's subsequent infant. The probability of siring future offspring can also increase via an imminent or temporary increase in dominance rank, as was proposed for an observed infanticide in wedge-capped capuchins (Valderrama et al., 1990). We cannot discount

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this possibility since at the time of RM08's infanticide, the alpha male had been away for several hours.

The beta male may have committed infanticide despite a limited chance of siring the subsequent infant because the alpha male's absence may have minimized the risk of major repercussions. Alpha males and potential sires likely play an important role in infant defense as many infanticides occur after resident males, especially sires, disappear or die (van Schaik, 2000). While the role of protector male(s) is generally proposed as a response to threats from predators and non-resident conspecifics (van Schaik, 2000), potential sires may nonetheless protect infants from threats posed by co-resident males (Borries et al., 1999, Broom et al., 2004). Capuchin alpha males engage in infant defense during takeover attempts and intergroup encounters (Fedigan and Jack, 2013), and our analysis of long-term data shows that infanticide is just as likely to occur following rank reversals (where formerly subordinate males become alpha) as they are following takeovers by extragroup males (Jack et al., 2014). Although male vigilance is primarily directed towards predators and extragroup conspecifics (Rose and Fedigan, 1995), social vigilance appears to be related to the number of same-sex competitors (Jack, 2001). Thus, it is possible that alpha male absence, even if temporary, increases infanticide risk even in socially stable groups.

Conclusions

Few studies have included the genetic and hormone data necessary to evaluate if the SSI hypothesis can explain infanticides by male primates during periods of social instability (e.g. Borries et al., 1999; Harris and Monfort 2003; Murray et al., 2007). The current study includes unique observations of infanticides combined with genetic and hormonal data, allowing us to evaluate whether the SSI hypothesis might also explain infanticides during a period of apparent social stability. The hormonal data supported the rapid resumption of ovarian cycling and a shortened interbirth interval as predicted by the SSI hypothesis. In contrast, behavioral data did not support increased reproductive access to females. Finally, the genetic data provided mixed support for the predictions of the SSI hypothesis; although the attacker did not sire the infant(s), he was likely closely related to their sire, and he did not sire the mother's subsequent infant. Taken together, the SSI hypothesis was not well supported by these infanticides during a socially stable period.

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Valérie A. M. Schoof, Department of Anthropology, McGill University, 855 Sherbrooke Street West, Montreal, Quebec, Canada, H3A 2T7, E-mail: <vschoof@gmail.com; valerie.schoof@mcgill.ca> and Department of Anthropology, Tulane University, **Eva C. Wikberg**, Department of Integrated Biosciences, University of Tokyo, **Katharine M. Jack**, Department of Anthropology, Tulane University, **Linda M. Fedigan**, Department of Anthropology, University of Calgary, **Toni E. Ziegler**, Wisconsin National Primate Research Center, University of Wisconsin and **Shoji Kawamura**, Department of Integrated Biosciences, University of Tokyo

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