Scatological clues lead to an intimate view

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Male sifaka with infant. Credit: Diane Brockman

The guys were all stressed out. There were new infants in the community, and the guys knew from experience that that's when invaders were likely to come and kill the babies, particularly the male infants. This annual threat was a defining moment in their lives -- it had more impact on everyone than the daily social struggle to be on top, or than any other community crisis, like defending the group against hostile neighbors. Nothing was more stress-inducing than having helpless infants around to protect from marauders.

This drama is wrenching to observe, yet until fairly recently, no one

knew it was happening. But then again, it is hard to get inside the head of a male sifaka, a large Madagascan prosimian primate which lives mainly high and unseen in the forest treetops. Sifaka have cryptic faces, devoid of the telling facial expressions of more advanced primates, like baboons, chimps or humans. At first glance, sifaka look thoughtless and simple, but the capacity for complex social drama is there. We can tell from their poop.

A finding published in the current issue of the *Proceedings of the Royal Society B* details how primatologists have found conclusive evidence of an annual, population-wide increase in anxiety and stress among male sifaka concurrent with birthing. Authors Diane K. Brockman of the department of anthropology at the University of North Carolina at Charlotte and Amy K. Cobden and Patricia L. Whitten of the department of anthropology at Emory University show that a significant rise in stress-related glucocorticoid hormones in male sifaka feces occurs annually and "reflects specific events related to reproduction rather than states or social context during the birth season."

These results, combined with recent evidence of male infanticide (largely directed towards male infants) suggest a more complicated social dynamic among the prosimians than primatologists traditionally believed to exist.

Verreaux's sifaka (*Propithecus verreauxi*), like other lemurs, are primates that are only found on the island of Madagascar and have long been considered to be generally more primitive than monkeys and apes. Sifaka, like many non-primate mammals, have clear annual estrous cycles where the females are only receptive for mating for a brief period once a year, and all the resulting infants are weaned by the following mating season.

However, the primitive appearance of the sifaka may be masking a more

sophisticated social animal. Brockman and colleagues have been studying a large population at Madagascar's Beza Mahfaly Special Reserve for two decades, where they have accumulated a substantial amount of data that points to more advanced social behavior.
"Prior to 1994, previous studies of wild populations of sifaka by Alison Richard and colleagues, supported the idea that sifaka males have little or no interest in newborns and they do not commit infanticide," Brockman notes.

"In 1994, we had our first incidence of a male at our study site invading a neighboring group, expelling the group's resident males, and mortally wounding an infant and likely killing a second infant," she said. "This new revelation fundamentally altered our perception of male social complexity, particularly the potential reproductive tactics males might employ during the birth season."

Seeing that a male sifaka was capable of such unpredicted behavior, the researchers examined the population again, looking for larger patterns.

"In 2000 when we began our current research on male dispersal tactics in sifaka, we decided to open our minds to all social possibilities with respect to these males - to jettison everything we thought we knew and start paying attention to every aspect of male social relationships, including those with infants, and by Jove, we saw that some males did interact with them!

"That year we recorded our first observations of a small subset of males holding, grooming, and carrying infants. In fact, one male carried an infant for two hours, just like a mother would, and groomed him," she noted. "You could have knocked me over with a feather!"

The researchers' observations implied a set of likely family and social relationships that was unexpectedly nuanced and perhaps as sophisticated

as the social relationships found in more advanced primates. Such implications are, however, difficult to substantiate without larger sets of hard data to test the ideas against.

In order to gather more definitive information about hormone-behavior interactions underpinning sifaka social dynamics, the researchers began to monitor physiological indicators of stress in the community by measuring glucocorticoid levels in the collected feces of individual animals. The level of stress hormone gave the researchers a measurable "signal" of the animal's physiological state and perhaps a way to determine its level of social anxiety.

Remarkably, the only statistically significant signal of stress the researchers found in the population as a whole was among the population's males at a time that coincided with the arrival of newborns- a puzzling correlation.

"The prevailing idea in the literature is that individuals should exhibit a stress response during periods of uncertainty, when they are faced with situations that are uncontrollable" Brockman noted. "This presented us with a conundrum—sifaka are seasonal breeders: from late June through late August, the infants appear: that's predictable. Then it dawned on me… what isn't predictable is whether or not a resident male is going to have his group invaded when newborns appear. We concluded that the predictability of the birth season signals the onset of the period of uncertainty for males (and females) when unpredictable events—invasions, increased infanticide risk—are likely to occur. That made perfect sense."

Though the birth season was highlighted by the hormone data as unusually stressful for the males in the group, there was nothing occurring in that period that seemed likely to be as stressful as other events in a male's life - mating competition or changes in the

environment - with the exception of the increased risk of infanticide by males.

"The data thus pointed to the significance of the invasions for the physiological stress responses we observed in males---the likelihood for resident males of severe injury, or even death, and the killing of the group's newborns, " Brockman said.

Though seemingly abstract, the hormone data were key to understanding the primates' social world, Brockman notes: "The cryptic nature of sifaka facial expressions, the subtlety of their social relationships, and their often nuanced social lives present daunting challenges for those of use who want to understand better the role ecology and social environment play in shaping the reproductive and social careers of primates living in unpredictable environments such the lemurs inhabiting Madagascar.

"Being able to establish links between hormonal stress responses of individuals and populations to social and demographic events, including group take-over, male-male aggression, and infanticide in sifaka, affords us an opportunity to unlock some of the mysteries. It gives us a better idea of the coping strategies individuals employ to deal with the unpredictable events of day-to-day life in the forest," she said.

By understanding the daily realities of individual sifaka, the researchers can get a more accurate picture of larger social dynamics. "What we are learning about sifaka social complexity, and about males particularly, is a continuing source of wonder and amazement to me!" Brockman said. "This is field biology at it best, and it is absolutely thrilling!"

Infanticide by males has been increasingly observed in other species, where it is hypothesized to serve as, among other functions, a successful reproductive strategy for males (and females). By killing infants, males

cause females to go into estrus sooner then they would otherwise -- since nursing infants inhibits estrus -- thus allowing the infanticidial male to produce his own offspring sooner.

However, infanticide cannot serve this purpose in sifaka, since offspring are completely weaned prior to the next mating season, and the presence or absence of new sifaka does not affect the timing of the next breeding cycle. Instead, Brockman proposes that infanticide may function to help the invading male's offspring successfully reproduce by diminishing the number of male competitors an offspring might encounter in future mating seasons- an idea that is supported by observation that most of the infants killed at this site are male. Essentially, the invading males are clearing the way for their progeny to be successful fathers, thus insuring the future of their lineage.

The hormone-behavior interactions observed by Brockman and colleagues offer a glimpse into the social life of sifaka that resonates, perhaps painfully so, with humans and our own social struggles. An episode Brockman observed seems hauntingly similar to the foibles of humans and the tragedies they cause:

"We had one case of infanticide in a family group containing a couple and their infant. A male from a neighboring group came and joined the group. The two males began to hang out together and then the two of them left together and joined a third group, leaving the female alone with her infant.

"The female started 'lost-calling' - it's a plaintive contact call that resonates through the forest. We then observed the father of the infant chasing an unmarked (invading) male. By the time we caught up with them back in the couple's original home range, the unmarked male had disappeared and both parents were sitting on the ground with their infant, who was mortally wounded. We missed seeing the actual attack

by mere seconds, but the circumstantial evidence strong suggested infanticide. They remained there for the next two hours trying to pick up/hold their crying infant, but to no avail; they finally left the youngster and slowly moved into the forest. "

Brockman shook her head in wonder. "What was he thinking when he deserted his mate and newborn? I'm still at a loss to explain it."

Similarly, understanding the realities of life from a sifaka's-eye-view helps Brockman see possible explanations for other oddities in sifaka behavior, such as some anomalous observations concerning the sexuality of female sifaka.

"In my research, I have found that some a female sifaka will mate with an immigrant male during the birth season when she's not cycling," Brockman said. "Now this is not supposed to happen in a prosimian primate - it's called situation-dependant receptivity in higher primates, but animals with short estrus cycles are simply not supposed be receptive when they're not cycling.

"Now why would they do this? Well… it might be to establish a social bond with a male, perhaps keep him from committing infanticide…or an inducement to provide future infant care-giving services, but we do not yet have evidence to support either hypothesis…"

Though sifaka represent a fairly early stage of development on the primate family tree, Brockman notes that the results of this research yield surprising similarities with humans, who (along with cotton-top tamarin monkeys) also show elevated levels of stress hormones in males in anticipation of birth. Though sifaka are very different from humans in many ways, the research suggests that the ancestral roots of our social complexity may be far more ancient than we have previously believed.

Source: University of North Carolina at Charlotte