Reflections on Papers Past: Revisiting Hrdy 1974

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by Hari Sridhar

In a paper *(https://www.karger.com/Article/Abstract/155616)* *published in* Folia Primatologica *in 1974, Sarah Blaffer Hrdy* *(http://anthropology.ucdavis.edu/people/sbhrdy)* *reported the findings of her field study on Hanuman Langurs in India that suggested that infant-killing by male langurs was a reproductive strategy. Forty-two years after the paper was published, I asked Sarah Hrdy about the origin of this study, its reception when the paper was published, and what we have learnt since about infanticide in primates.*

Citation: Hrdy, S. B. (1974). Male-male competition and infanticide among the langurs (Presbytis entellus) of Abu, Rajasthan. Folia primatologica, 22(1), 19-58.

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Hari Sridhar: I would like to start by asking you what your specific motivation was to do the work presented in this paper. I realise that it formed part of your PhD dissertation. Could you place this research within the context of your PhD as a whole?

Sarah Blaffer Hrdy: I graduated from Radcliffe (then the women's part of Harvard) in 1969 and enrolled in a program on film-making at Stanford University. As an undergraduate, I had done ethnographic research in southern Mexico and also worked on summer medical projects in Honduras and Guatemala. I wanted to learn how to make educational films related to public health and community development. I soon became disappointed in the program, but while at Stanford began auditing a course on population ecology co-taught by the biologist Paul Ehrlich (https://en.wikipedia.org/wiki/Paul_R._Ehrlich). At that time (as he still is today) Ehrlich was talking about the challenges posed by human population growth. Listening to him, I recalled a remark made by a professor at Harvard (Irven Devore (https://en.wikipedia.org/wiki/Irven_DeVore)) in one of the first undergraduate courses taught on primate behavior which I had taken. Field primatology was then a very new field, and not much was known, but Devore mentioned that among these monkeys in India that I had never heard of before, males sometimes killed infants, supposedly due to the fact that they were living at very high population densities. This reminded me of John Calhoun (https://en.wikipedia.org/wiki/John_B._Calhoun)'s famous 1962 article in *Scientific American* (http://psycnet.apa.org/record/1963-02809-001) about pathological behavior in crowded rats which, rather randomly, I had encountered my senior year in high school. Although today I would interpret that study rather differently than Calhoun did then, at the time I accepted Calhoun's interpretation and decided to go to India to document what I (naively!) assumed would turn out to be a case study of crowding-induced social pathology in a primate. Just before Christmas, I dropped all my courses at Stanford and applied to graduate school at Harvard and the University of California, Berkeley, about the only places in the U.S. back that one could study primate behavior at that time. Harvard agreed to take me right away, starting spring semester, so I went. The following year as soon as summer vacation arrived, I used money my mother gave me to purchase an airline ticket and went to India to locate a place where I could watch langurs in a range of habitats. It was of course totally naïve to imagine I could just go to India and study infanticide, yet in retrospect it is not surprising that the first paper I published in graduate school was on this topic, since to understand why male monkeys sometimes killed infants was why I had gone to graduate school in the first place. In the course of trying to learn more about infanticide I became interested in the many other aspects of langur behavior covered in my PhD thesis, including female-female competition and bonding, shared care of infants, etc. But male infanticide was the beginning.

HS: If you don't mind my asking, how come your PhD supervisor wasn't an author on this paper? The reason I ask is because, by today's practice, that is somewhat unusual.

SH: Unless directly involved in data collection, analysis or writing, I don't see much justification for a supervisor to appear as an author. My advisor, Irven Devore, shared this view.

HS: Could you give us a sense of what your daily routine was like during the fieldwork for this study? Did you mostly work alone or did you have people to help you? How did you commute? Where did you stay? etc.

SH: My first visit to Mount Abu (https://en.wikipedia.org/wiki/Mount_Abu), I was accompanied by Daniel Hrdy. Dan was both a graduate student in Anthropology and a medical student, one of the first candidates in a new Harvard-MIT M.D.-PhD program, but at that time also working on Harvard's Solomon Islands Project. However, whenever his schedule permitted, he joined me in Mount Abu, as he did that first year. As has been the case for 45 years now, Dan's resourcefulness and unfailing support were invaluable. That first summer, we rented two rooms in the home of a local school master who together with his family became good friends. I still correspond with his daughter. Ideally, I would wake up before dawn, walk to the sleeping trees where I had left monkeys the evening before, and follow them on and off until evening.

Sarah Hrdy watching langurs at Mount Aby (© D.B. Hrdy; Anthro-Photo)

HS: You did your fieldwork in three stints of a few months each. Could you tell us what you were doing in the periods between these stints? Were you back in the US, analyzing and writing up your results?

SH: Keep in mind that these were early days in primatology. I doubt that my casual observational methods would be acceptable today. During the early years covered in that paper though, I was basically fulfilling course requirements for my PhD, which I earned in 1975, the year after that paper was published. That paper covered only one chapter of my thesis, which when revised and expanded to include two additional field seasons, was published as *The Langurs of Abu: Female and male strategies of reproduction* *(http://www.hup.harvard.edu/catalog.php?isbn=9780674510586)* (Harvard University Press, 1977).

HS: You mention many people in Abu – Mrs. Phiroze Merwanji, Nirmal Kumar Dhadlal, Aftab and Mona Ali and others – who helped you in your fieldwork. Could you tell us more about this "local informant network" that played such an important role in your study?

SH: Nirmal Kumar lived with his family right in the center of the home range of one of the troops of langur monkeys that I was studying. He was a dedicated and knowledgeable bird watcher who took great interest both in the monkeys themselves (some of whom he knew as individuals) and in my observations about them. Later, I also met Mona Ali, the wife of Aftab, a professor at the local police academy whose home fell within the home range of another of the groups. Nirmal Kumar and Mona are since deceased, but I remain in touch with Aftab, and his son Zefar, who recently visited the United States. Almost as important as their generous friendship to a stranger in a strange country, was their communications about unusual events in the lives of the monkeys I was studying that they happened to witness in their front yards.

HS: In the paper you say "Temporary identification was also facilitated by squirting the animals with coloured stains". This immediately brought to my mind the image of monkeys playing *Holi*! Could you tell us a little more about how you did this, i.e. what colours did you use and what did you use to squirt the colours?

SH: A number of the langur monkeys had distinctive traits (a bit of earlobe missing, or an odd tail) but others could be hard to identify. So I poured purple ink into a spray bottle and then sat quietly among the langurs, waiting for a chance to spray whoever I needed extra help identifying.

HS: The names you use for the troops is a series of 'B's. Why 'B'? Did it stand for anything? Also, you have given the monkeys some really interesting names (*see Table III on page 28*). Could you tell us how you decided on a name for a monkey?

SH: "B" just stood for "Bisexual" or breeding troop such and such as opposed to one of the all-male bands. I would also refer to these troops by some geographic landmark in their home range (Toad Rock Troop, Hillside House Troop; Bazaar Troop). As for names given to individual monkeys, they were based on some identifying trait in the monkey him- or herself, or else the name of a character I was reading about at the time, or just whimsy.

HS: Figures 3-6 show photos of langurs in different locations in Abu. Do you remember where exactly each photo was taken? When you look at these photos now, what memories do they bring back? Figure 5, especially, seems to have captured an important moment in your study.

SH: The hours I spent following monkeys at Mount Abu were among the most satisfying of my life, even though the events in Figure 5 were distressing at the time. It was almost evening when the adult male langur I called "Mug", who had been stalking this mother-infant pair for some days, caught hold of her infant and was running with him in his jaws along the rooftop of the Phiroze School, as two older females in the group ("Sol" and "Pawless") rushed at him to try and retrieve his victim. Years later, the self-sacrificing bravery of these old females at or near the end of their reproductive careers would play an important role in the development of my thinking about the roles group members other than mothers played in human evolution (for example in my 2009 book Mothers and Others: The evolutionary origins of mutual understanding).

Sol and Pawless charging Mug who had just attacked and injured Itch's infant (© S.B. Hrdy; Anthro-photo)

HS: In one place in your paper you mention making a super-8 film record? Do these films still exist? When was the last time you watched them?

SH: The super-8 films are stored in a box down at Dan's office here at the farm (http://www.citrona.com/) and I have long meant to go through them but no longer even have the right kind of projector. The 16 mm. films we made, along with the unedited footage, have been donated to the Peabody Museum at Harvard (https://www.peabody.harvard.edu/) for their archives.

HS: When you were doing this work, who were the people you were discussing ideas with and seeking guidance from? Could you tell us a little more about how the people you list in the Acknowledgements helped?

SH: First and foremost, I needed to acknowledge Yukimaru Sugiyama (http://onlinelibrary.wiley.com/doi/10.1002/9781119179313.wbprim0319/abstract;jsessionid=B2AEBBE7FE3B7C1B1D071B537D282E61.f04t02?userIsAuthenticated=false&deniedAccessCustomisedMessage=) who along with Dr. Yoshiba, had first reported the occurrence of infanticide among langur monkeys in southern India, at Dharwar, as well as Professor S.M. Mohnot who studied the langurs at Jodhpur. It was S.M. who guided me around his study sites at Jodhpur and introduced me and Dan to free-ranging langurs for the first time. It was also S.M. who suggested that I go to Mount Abu. As mentioned, I first heard of langurs from Irven Devore when still an undergraduate. Later, Irv became my advisor, and along with Ed Wilson (https://en.wikipedia.org/wiki/E._O._Wilson) and Robert Trivers (https://en.wikipedia.org/wiki/Robert_Trivers), served on my thesis committee. It's hard to convey just how exciting a time it was to be in the Life Sciences at Harvard during the early 1970s. Wilson had just published *The Insect Societies* (https://www.amazon.com/Insect-Societies-Belknap-Press/dp/0674454901) (1971) and was working on *Sociobiology: The new synthesis (https://en.wikipedia.org/wiki/Sociobiology:_The_New_Synthesis)*, which came out in 1975. Meanwhile Trivers, an absolutely brilliant lecturer who introduced me to evolutionary theory, was working on his famous trilogy of papers on altruism (http://roberttrivers.com/Robert_Trivers/Publications_files/Trivers%201971.pdf), parental investment (http://roberttrivers.com/Robert_Trivers/Publications_files/Trivers%201972.pdf), and parent-offspring conflict (http://roberttrivers.com/Robert_Trivers/Publications_files/Trivers1974.pdf) published between 1971 and 1974. Even after my first brief stint in Abu in 1971, I had already realized that my starting hypothesis had to be wrong. Males likely to be the fathers of infants born in their group were quite tolerant of infants. Infants were only being attacked when males entered from outside the breeding system. Even if population density was a factor, it could not explain the behavior I set out to understand. What I needed was Darwin's theory of sexual selection derived from male-male competition for mating opportunities, a theory central to Sociobiology, as well as Sociobiology's all-important comparative method. Together, they allowed me to use recurring patterns to start to make sense of a puzzling jigsaw puzzle even before I had all the pieces in hand.

HS: Would you remember how long you took to write this paper, and when and where you did most of the writing?

SH: Professor Devore asked me to give a lecture on my work in one of his courses. I summarized the "lines of evidence" which led me to conclude that, far from pathological behavior (as I had initially assumed), infanticidal behavior by male langurs was an adaptive reproductive strategy. Only unweaned infants were being attacked, and by eliminating the source of lactational suppression of ovulation, the new male could compress the mother's fertility into the period he was likely to have reproductive access to her before another male replaced him. Afterwards, it did not take long to write up my observations and submit the paper. Trivers suggested I send it to *Folia Primatologica*

HS: Did this paper have a relatively smooth ride through peer-review? Was *Folia Primatologica* the first place this was submitted to?

SH: Since I don't recall anything special, the peer review must have gone smoothly.

HS: At the time when it was published, what kind of attention did this paper attract? Were the findings considered controversial at that time?

SH: The paper was published the year before the publication of Wilson's *Sociobiology: The new synthesis* and became caught up in what became known as "the science wars" over sociobiology and other topics. In terms of my own work, controversy focused on my proposal that infanticide might represent a general reproductive strategy among primates and really started to heat up in 1976 when I presented a paper at the American Anthropological Association meetings in Washington, D.C. and with publication of "Infanticide as a primate reproductive strategy (https://www.jstor.org/stable/27847641)" in the American Scientist in 1977, and publication of my monograph on *The Langurs of Abu*. My findings on infanticide were widely covered in the media, in *Time* magazine and elsewhere, sometimes more sensationally than I wanted. A grand old man of physical anthropology stood up and objected after one of my talks before storming out of the room. Meanwhile there were letters to the editors and articles in the American Scientist questioning whether "normal monkeys" could ever engage in such behavior since such destructive behavior could not possibly be adaptive (American Scientist vol. 65, p. 266), and this went on for years. Anyone interested, should consult British historian of science Amanda Rees (https://www.york.ac.uk/sociology/our-staff/academic/amanda-rees/)'s authoritative account of *The Infanticide Controversy (http://press.uchicago.edu/ucp/books/book/chicago/I/bo6925541.html)* published in 2009 by the University of Chicago Press.

HS: I notice, in the copy of the paper I downloaded from your website (https://reflectionsonpaperspast.files.wordpress.com/2018/01/3881d-male-malecompetitionandinfanticide.pdf), a couple of tables in which some words have been added later by hand, in the column titles. Could you tell us a little more about this?

SH: For sure! When I first published that 1974 paper, I failed to realize just how controversial it would be to suggest that infants who disappeared had been deliberately killed by incoming males as part of a reproductive strategy. I was not nearly as careful as I should have been in differentiating between infants who disappeared under suspicious circumstances, those where attacks were witnessed, and those whose deaths were confirmed. Later on, it became common practice to do this. Thus before xeroxing and mailing out reprints (this was in the days before internet) I added a qualification to the column heading so it read "Infants killed or missing".

HS: Today, 42 years after it was published, would you say that the main conclusions of this paper are still true, more-or-less?

SH: Although controversial at the time, my "sexual selection hypothesis", to explain why adult males sometimes attack and kill infants they are unlikely to have sired, has held up well. The killing of infants by males who are entering the breeding system from outside it, has been reported now for some 50 species of primates under remarkably similar circumstances, as well as among quite a few other creatures from lions to dung beetles. Although speculative at the time, my initial explanation is now widely accepted among evolutionary biologists and animal behaviorists. However, quite a few social scientists remain skeptical.

HS: Could you give us a sense of what kind of impact this paper had on your career and on the future course of your research?

SH: I did not set out to be a primatologist. Through my desire to explore a specific question – why male langurs were sometimes reported to kill babies – I was drawn into the then new field of primate behavior and from there into sociobiology. Once I started watching langurs in the wild, I also became increasingly interested in what females were up to. Over time, my focus expanded to encompass such then relatively under-studied topics as female-female competition and cooperation, female sexuality, infant-sharing etc. culminating in books like *The Woman that Never Evolved* and *Mother Nature* (http://www.hup.harvard.edu/catalog.php?isbn=9780674955394).

HS: When was the last time you visited your field sites in Abu? In what ways have these places changed since you worked there? Are the langur troops still there?

SH: I have not been back to Mount Abu since 1979, but about five years ago Dan and a colleague, Volker Sommer (http://www.ucl.ac.uk/anthropology/people/academic-teaching-staff/volker-sommer), visited. Dan said that the town is much more built up, the surrounding hillside forests also changed.

HS: One of the things that you couldn't do in your study is establish paternity of the infants that were killed. In subsequent work, was that done?

SH: I suspected early on that males were using the mother, not the infant, as their cue to either attack or tolerate the infant she carried, depending on whether he had previously mated with her. This hypothesis was consistent with the fact that infants borrowed (or "kidnapped") from another troop would not be attacked so long as they were carried by a familiar female. By 1980, when the paperback edition of the *The Langurs of Abu* was published, we were also beginning to get evidence that infanticide was a heritable trait among rodents, and I reviewed those studies in a brief preface to it. However it was 1999 before Carolla Borries (http://www.stonybrook.edu/commcms/anthropology/faculty-and-staff/borries.php) and her colleagues provided genetic evidence from their study population in Nepal that langur males there only attacked infants they had not sired. Carolla's paper was published in the Proceedings of the Royal Society volume 266, pages 901-904 with the title "DNA analyses support the hypothesis that infanticide is adaptive in langur monkeys (http://rspb.royalsocietypublishing.org/content/royprsb/266/1422/901.full.pdf)".

HS: This paper has been cited many times. Do you have a sense of what it mostly gets cited for?

SH: My suggestion that infanticide might represent a male reproductive strategy coincided with major transformations within both evolutionary biology, and the social sciences generally, as evolutionists moved away from "group selection" models to thinking in terms of "genetic selfishiness" and selection at the level of individuals rather than groups. In 1990, I became one of the younger women to be elected to the National Academy of Sciences and no doubt my role in these ongoing paradigm shifts was a factor. Ironically though, some forty years later I find myself far more interested in cooperative than self-serving behaviors, especially shared care of infants and the special roles played by allomothers such as those two selfless old langur females, of Sol and Pawless! But this is the fun part of science, we can keep on asking new questions, growing, learning new stuff.

A matrilineal grouping of female langurs and their infants (© S.B. Hrdy; Anthro-photo)

HS: Have you ever read this paper after it was published? When you compare this paper to ones you write today do you see any striking differences?

SH: I have reread it, but not in a while. The answer to both questions is yes.

HS: Would you count this as one of your favorites, among all the papers you have published?

SH: At the time I wrote this paper, women were not that well represented in evolutionary biology. My undergraduate honors thesis on *The Black-man of Zinacantan: A Central American legend (https://www.amazon.com/Black-man-Zinacantan-Central-American-legend/dp/0292707010)* was published as a book in 1972, but it was in another field (Cultural Anthropology). In 1973, I also wrote a seminar paper for Ed Wilson on *The care and exploitation of infants by conspecifics other than the* *mother* *(http://www.sciencedirect.com/science/article/pii/S0065345408600832)*, which he submitted to *Advances in the Study of Behavior*, but since publication was delayed until 1976 this paper in *Folia Primatologica* was my first scientific publication related to evolutionary biology. As such it opened doors for me and established my credentials in a field I was eager to learn more about.

HS: What would you say to a student who is about to read this paper today? What should he or she take away from this paper written 38 years ago? Would you add any caveats?

SH: I would remind anyone reading the paper today that infanticide is a widespread and protean phenomenon, with sexually selected versions being just one of various forms that it takes (see summary table below). I would urge them to read what I wrote about possible similarities, but also important differences, between human and nonhuman primate infanticide when I returned to the topic 25 years later, in *Mother Nature* *(https://www.amazon.com/Mother-Nature-Maternal-Instincts-Species/dp/0345408934)* (pages 237-250).

Predictions generated by five explanatory hypotheses for infanticide*

Class of Infanticide	Age and sex of killer	r^{o}	Age of infant	Nature of gain
1. Exploitation as resource	Either sex at any age large enough to subdue victim	Distant	Size and vulnerability more important than age	Nutritional gain by killer
2. Competition for resources	Either sex usually (but not always) breeding adults	Distant	Vulnerability more important than age	Increased resources for killers and their kin
3. Sexual selection	Adult of sex investing least in offspring typically male	Distant	Unweaned (but specifically younger than age at which lactational amenorrhea ends	Additional breeding opportunity
4. Parental manipulation	Either sex, but most likely an individual of the sex investing most, typically female	$\approx .5$	Just after birth	Increased inclusive fitness
5. Social pathology	Adult of sex most likely to respond to social disturbance with increased aggressiveness	Relationship not critical	Size, proximity, and vulnerability more important than age	None directly, although may result in decreased population

*Adapted from Hrdy 1979; Hrdy & Hausfater 1984

Table describing different hypotheses for infanticide (source: adapted from Hrdy 1979 and reprinted from Table 1 on page xx of Hrdy and Hausfater's introduction to the 1984 volume edited by Hausfater and Hrdy (pp. xiii-xxxv) entitled Infanticide: Comparative and evolutionary perspectives, republished as a paperback by Transaction Publishers in 2008)

Author Biography: Hari Sridhar is a post-doctoral researcher studying heterospecific sociality at the Centre for Ecological Sciences, Indian Institute of Science, Bangalore. Since early 2016, he has been interviewing authors of well-known papers in ecology and evolution, to find out about: 1. the making of the paper 2. the impact the paper had on the author's career and research and 3. the author's current stand on what was said in the paper. Through these interviews, Hari wants to construct 'shadow papers', which capture the past and future of the original published articles. His interviews are archived at https://reflectionsonpaperspast.wordpress.com/ (https://reflectionsonpaperspast.wordpress.com/)