

**PROFILE**

## What's wrong with this picture?

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Research on wild primates was still a relatively new endeavour in the USA when I entered graduate school in 1970. Courses on primate behaviour were primarily taught in anthropology departments. I was drawn to the field because Japanese researchers had reported that adult male monkeys sometimes killed infants in a species of South Asian monkey known as the Hanuman langur *Semnopithecus entellus*, and I wanted to find out why. The summer after my first year in graduate school I went to Mount Abu, in Rajasthan, with this question in mind. At the time I had no special interest in female behaviour, which frankly struck me as boring.

According to the only available article on the subject, entitled 'The female primate', 'Her primary focus, a role which occupies more than 70 percent of her life, is motherhood ... A female raises one infant after another for her entire adult life ... Dominance interaction is usually minimal' (Jay 1963). This narrow view of female natures was the result of a combination of factors, including Victorian social biases left over from Darwin's day, the fact that earlier observations had focused on captive animals, often consisting of mothers caged individually with their young, and evolutionary theory itself. As then formulated, Darwin's remarkably original and quite powerful theory of sexual selection left out many sources of variation

affecting the differential reproductive success of females.

Darwin's theory that members of one sex (almost always males) were competing among themselves for access to the other (i.e. females) did a good job of explaining why langur males who usurped control of breeding females sought to eliminate unweaned infants sired by their competitors. The incoming male was essentially cancelling the last choice those mothers had made and, in doing so, reducing the time before he himself might have a chance to sire offspring. Except for specifying their role in choosing the 'best' male, however, sexual selection theory did not then ascribe active roles to females. They were viewed as essentially passive pawns in a brutal system. Yet the more I learned, the more interested I became in the females. Partly this was because, as a female myself, I could not help but empathise (Hrdy 1986). Here was a mother, and every 27 months on average some male, weighing almost twice as much as she did, equipped with canine weapons she did not have, would arrive in her troop intent on killing her baby. The more I watched them, the more fascinated I became by the flexible and often quite innovative strategies females employed to cope with the challenges posed by males.

The accompanying portrait of an 'all-male band,' 13 monkeys on a rocky crag, reminds me



Portrait of a Hanuman langur 'all-male' band. Photo: S. B. Hrdy/AnthroPhoto.

of my own dawning awareness of how opportunistic females can be. Hanuman langurs live in breeding troops composed of overlapping generations of females accompanied by one or more adult males who enter the troop from outside. The home ranges of these troops are traversed by all-male bands, containing anywhere from two to 60 or more males of all ages (Hrdy 1977). In the picture, the male I nicknamed 'Split-ear', long-time resident in the 'Toad Rock troop', grinds his teeth as he sits with eight juvenile and subadult males from his former troop, who like him have been driven out by a new male. For months, Split-ear and these possible-sons continued to skulk about their former home range. But take a closer look. The langur on the far right is a multiparous female. In her arms she holds her 13-month-old daughter. To her left, back to the camera, sits another female holding her infant. What were these females doing in what I assumed was an 'all-male band'?

Beginning with my first field season, I had occasionally seen females outside of their troops. But lacking any theoretical framework for interpreting their behaviour, I failed to attach any significance to them. As it happened, the very first wild langur I ever got a close look at was a lone female who had temporarily left the troop I had been searching for, and had probably (though I did not realise this at the time) gone off to solicit males in one of the roving all-male bands. Such polyandrous tendencies, it turns out, are typical of female primates, including langurs.

The highest incidence of extra-troop sexual solicitations was recorded for a troop in which an unusually successful alpha male had managed to remain in residence for many years. Since some females in his troop were likely daughters, there was a genetic rationale (inbreeding avoidance) for their extra-troop solicitations. However, on other occasions I saw females that I knew to be pregnant solicit unfamiliar males. Furthermore, I learned

that instead of being strictly cyclical, as non-human primates were assumed to be, langurs were capable of what I called 'situation-dependent' sexual receptivity. Unlike savanna baboons and some other monkeys, langurs do not advertise mid-cycle ovulation with conspicuous pink 'sexual swellings'. The only visible sign is their behaviour, presenting their rumps while frenetically shaking their heads. Only the resident male living with females month in and month out seemed to be much good at discriminating actual ovulation from non-fertile solicitations. Since langur males do not attack the offspring of females with whom they have previously mated, I hypothesised that females might be taking out an insurance policy in case one of these males usurped her troop one day, manipulating the information available to him about possible paternity.

The females 'out of place' in this photograph were pursuing yet another strategy. Shortly after this photograph was taken, one of the females left her partially weaned daughter in the band with the tolerant ousted males and returned to her former troop alone. This tactic for keeping her daughter safe might have worked, except that the daughter found her way back and rejoined her mother, and was attacked by the new male. The infant's wounds from the first attack were only superficial, but I feared she was doomed. Then, even though still years away from sexual

maturity, the 13-month-old began to solicit the usurping male. Although rump-presentation was a usual posture for a subordinate to assume before a dominant animal, combining it with frenetic head-shaking was not. It was as if this infant, at the margin of the age when an unweaned infant would be killed, strove to remind the new male 'I am a potential mate, not worth your killing'. Thereafter, his attacks ceased.

Decades later, my research still focuses on variation between females, and increasingly also between infants, and on how Darwinian selection acts on them (e.g. Hrdy 1999). I date my interest in maternal reproductive strategies to the days when I was puzzled by seeing females where they 'did not belong'.

## References

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