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Engendered Primatology

Of Female Primates and Feminist Primatologists

Anindya Sinha and Sayan Banerjee

Abstract
In this chapter, we reflect on our readings of female/feminist primatologists' studies of female primates and our understandings of the gendered lives of bonnet macaques, a female-bonded nonhuman primate species, endemic to peninsular India. These two focal points provide us with insights into the complexities of individual identity in nonhuman societies and the situatedness of human and other-than-human gender identities in their lived worlds. We first discuss the beginnings of feminist philosophy of biology through the virtually forgotten Antoinette Brown Blackwell's remarkable critique of Darwinism and then trace the evolution of feminist primatology through the work of influential female primatologists. We consider how these feminist views have shaped our critical comprehension of gender roles in nonhuman primate societies and conclude by examining certain biological and sociocultural traits that are associated with biological sex and contribute to the social construction of gender in the lifeworlds of bonnet macaques and by extension, to those of other nonhuman primates.

Keywords: gendered lives, gender roles, sociocultural traits, individuality, philosophy of biology, bonnet macaque

'Primates existing at the boundaries of so many hopes and interests are wonderful subjects with whom to explore the permeability of walls, the reconstitution of boundaries, the distaste for endless socially enforced dualisms'.
– Donna Haraway, *Primate Visions*, 1989

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Introduction

Why do we study nonhuman primates and often so intimately? The principal answer would be that, given the position of humans in the tree of life, researchers in biology, anthropology, sociology, ethology, psychology, or the medical and veterinary sciences have traditionally been interested in comparative studies of human and nonhuman primates, giving rise, in the process, to the distinctly interdisciplinary field of primatology. At a more holistic level, such studies would then translate into the question of how *we*, human primates, evolutionarily came to be what we are today. A more deeply philosophical query, inherent in this, is that whilst much of our studies and ensuing thoughts about nonhuman primates over the years have definitely been shaped by our usually subconscious awareness of *them* being categorically different from *us*, it is only relatively recently that one has become acutely conscious of a strong belief that these imaginary, constructed lines have blurred and that *we* are actually in a continuum with *them*. And nowhere does this become more evident to us than when we begin to compare the complexities of individual and gender identities in human and certain nonhuman societies, especially when viewed from a feminist primatological perspective.

We thus reflect, in this chapter, on our reading of female/feminist primatologists' studies of female primates and our understandings of the gendered lives of bonnet macaques, a female-bonded nonhuman primate species, endemic to South India. These two focal points provide us with insights into the complexities of individual identity in certain nonhuman societies and the *situatedness* of human and other-than-human gender identities, both of which have been neglected in our natural sciences.

During its early years of development, field primatology, as pioneered in the United States of America, was a masculinist scientific enterprise, possibly given its perceived requirement of physically demanding fieldwork in far-flung tropical forests and yet unexplored foreign lands. This rendered its practice a subtly androcentric process, with a clear descriptive focus on the often more demonstrative and physically active males of the species, usually of the anthropoid apes. What has also remained unacknowledged in the larger Western scientific enterprise – and surprisingly, this has included primatology – is its failure to consider our own identities, in continuum with those of our study subjects, as gendered individuals. As a result, most of the discussions in the field – both discoveries and conceptual advancements – have overlooked the ways in which they have been influenced

by our self-identities.[1] This has become critically evident in the field of primatology, where a *female* researcher appears to be a completely different being from her *male* counterpart. Indeed, their discoveries in primatology, made relatively later in the chronological development of the field, have frequently completely reversed previous understandings of primate biology, of both human and other-than-human, by previous, usually male, primatologists. Through this process, we have also gained insights into our unique individual personalities and prospective gender identities, all of which, we believe, contribute to our positionality as primate researchers, shaping and reshaping our understandings, not only of the biology of different nonhuman primate species, but also of where we stand, as human primates, in this evolutionary continuum.

The androcentric approach to understanding nonhuman primates became most evident in the early primatological perspectives on the sexual differences between individuals in shaping the structure of primate societies. The males of most primate species populations observed, characterized as being powerful, competitive, and socially dominant, became the central node to understand the functioning of these societies. Moreover, a continuous focus on male primates, both in the wild as well as in laboratory settings, then gave rise to the view – almost an assumption – that a stable, dyadic, and linear male dominance hierarchy formed the basis of primate social organization. The females were predominantly regarded as docile mothers, who spent their time and energy in nurturing their young, and thus not contributing significantly towards the formation and maintenance of the societies, to which they belonged.[2]

Such an androcentric perspective was later challenged by comparably rigorous research – but conducted from a very different perspective – by female primatologists, giving rise to a distinctive *feminist primatology*.[3] These researchers focused their scientific attention on the hitherto unexplored lives of female primates, highlighting the importance of their behavioural roles in the construction, organization, and functioning of their societies.

1 Lynda Birke, Mette Bryld, and Nina Lykke, "Animal Performances: An Exploration of Intersections Between Feminist Science Studies and Studies of Human/Animal Relationships," in *Women, Science, and Technology: A Reader in Feminist Science Studies*, eds. M. Wyer, M. Barbercheck, D. Cookmeyer, H. Ozturk, and M. Wayne (Abingdon: Routledge, 2013), 495–506.

2 Sherwood L. Washburn and Irven DeVore, "The Social Life of Baboons," *Scientific American* 204, no. 6 (1961): 62–71.

3 Linda Marie Fedigan, "Feminist Philosophy of Biology," in *Women, Science, and Technology*, eds. M. Wyer, M. Barbercheck, D. Giesman, H.Ö. Öztürk, and M. Wayne (New York: Routledge, 2008). 270–84.

The sophisticated complexity of female behavioural strategies and their decision-making, revealed during these studies, appeared to reflect the broader question of 'What can monkeys and apes teach us about being female on the planet or about being animals in complex and gendered societies?'[4] Feminist primatology, however, should not be conflated with the notion of female researchers simply researching primates, as was duly noted by when they wrote that '[m]any of the significant women in primatology would be reluctant to call themselves (or be labelled!) feminists'.[5] Rather, it is the *feminist standpoint* within primatological research that can be credited to have created this distinct philosophy.

Typically, such a feminist approach uses feminist philosophical methods to examine, often rather specifically, the categories of sex and gender. In the process of such analyses, feminist philosophers of biology have also been able to demonstrate that the philosophical inquiries within a specific scientific domain are frequently entangled with both ethics and politics. This is especially true for primatology. The first of the two general schools of thought on the philosophy of biology, promoted by feminist philosophers, thus concerns the biological notions of and knowledge claims involving sex and gender while the second school investigates the impact of gender values on biological research.[6]

Of Feminist Primatologists...

Charles Darwin presented an evolutionary explanation of the inherent differences between men and women in his book, *The Descent of Man* (1871).[7] He argued that, as men and women had different roles in the sexual division of labour and as men seemed to have evolved to be aggressive hunters while women had developed to be nurturing carers, the two sexes would typically have different needs and capacities. Darwin thus came to the conclusion that 'man has ultimately become superior to woman' and 'that if men are

4 Martha Ward, *A World Full of Women* (Boston, MA: Allyn and Bacon, 1996), 86.

5 Linda M. Fedigan and Laurence Fedigan, "Gender and the Study of Primates," in *Gender and Anthropology: Critical Reviews for Research and Teaching*, ed. S. Morgan (Washington D.C.: American Anthropological Association, 1989), 53.

6 Carla Fehr, "The Paradox of Feminist Primatology," in *The Stanford Encyclopaedia of Philosophy*, E.N. Zalta (Stanford, CA: Metaphysics Research Laboratory, Stanford University, 2018), https://plato.stanford.edu/entries/feminist-philosophy-biology/.

7 Charles Darwin, *The Descent of Man. and Selection in Relation to Sex* (New York: D. Appleton and Company, 1871), 643.

capable of a decided pre-eminence over women in many subjects, the average of mental power in man must be above that of woman'. Antoinette Brown Blackwell offered the first feminist critique of Darwin four years later, when, in her book, *The Sexes Throughout Nature* (1875), she contended that Darwin's own evidence did not support his conclusion.[8] She further asserted that the correct conclusion to draw from the observed biological facts was that the sexes are 'true equivalents – equals but not identicals' in all aspects of their physical and mental abilities. She claimed that because of his 'male standpoint', Darwin had misinterpreted the facts and that 'only a woman can approach the subject from a feminine standpoint'.[9] She also claimed that scientific knowledge of the realities of nature would serve as the final arbiter between these opposing viewpoints. The foundation of Blackwell's feminist argument thus rested, remarkably, on a contemporary biological interpretation of what has been referred to as ethical naturalism,[10] which contends that the correct social status of women would depend on what we understand about their nature.

Over a period of thirteen years, from 1956 to 1969, Louis Leakey, an influential and pioneering anthropologist, chose three women – Jane Goodall, Dian Fossey, and Biruté Galdikas – to study natural populations of three species of great apes – chimpanzees, gorillas, and orangutans, respectively – because he thought that the nurturing nature of women would make them more patient and perceptive in their direct observations of animal behaviour than would be men. Some feminists believe that the remarkable academic performance of these three women primatologists supports Sy Montgomery's suggestion (1991) that the feminine emphasis upon individuality, relationships, and empathy has scientific significance.[11] This also appears to hark back to Blackwell's advocacy of the *feminine standpoint* as integral to the natural sciences and her assertion that, as products of evolution, men and women were naturally comparable, if not identical, in their moral and intellectual qualities. We find support for this belief in our observation that female primatologists, who naturally focused their attention on female nonhuman primates, were able to subsequently demonstrate that the lives of female primates are far more complex and crucial to primate evolution

8 Antoinette B. Blackwell, *The Sexes Throughout Nature* (New York: Putnam and Sons, 1875).

9 Ibid., 22.

10 Larry Arnhart, "Feminism, Primatology, and Ethical Naturalism," *Politics and the Life Sciences* 11, no. 2 (1992): 157–70.

11 Sy Montgomery, *Walking with the Great Apes* (Boston, MA: Houghton Mifflin Company, 1991).

than many male scientists had previously imagined, investigated, or established scientifically.

A prime example of such a misplaced focus is the male dominance hierarchy – traditionally considered to be the most important force governing nonhuman primate societies – right from the initiation of primate field studies till the 1970s (see, for example, Zuckerman 1932[12]). It was only during the 1960s that a few studies, primarily by female primatologists, brought into discussion the role of philopatric female primates in creating and maintaining the social bonds that bound their society together, rather than did the males, who tended to disperse in search of mating opportunities.[13,14] In 1971, Jane Goodall described the importance of mother–infant relationships and matrifocal family units in chimpanzee social organization, notwithstanding the male bonding, typical of chimpanzee society, during her long-term research on the chimpanzee communities of Central Africa.[15] Thelma Rowell conducted extensive studies of olive baboon societies and, in 1967, noted that the so-called male-hierarchy model did not seem to be as important as previously noted and that dominance appeared to be socially learnt independently by individuals females and males rather than being determined simply by age and sex.[16] The females in Rowell's studies seemed to perform the roles, apparently displayed by the dominant males in other investigations, including the determination of the daily movement routes by the older group females. Female baboons thus appeared to subtly regulate the group's social behaviour, forming, in essence, the nucleus of the group. Interestingly, Rowell's descriptions of female baboons and their roles in baboon society even gave rise, at the time, to a notion of 'contrariness', humorously also referred to as the 'Thelma Effect', in which certain animals behaved unexpectedly differently from what was expected from them from the oft-quoted literature![17]

Like Rowell, Barbara Smuts, in 1983, described the importance of male–female reciprocal friendships as a significant determinant of reproductive

12 Solly Zuckermann, *The Social Life of Monkeys and Apes* (New York: Harcourt, 1932).

13 Masao Kawai, "On the Rank System in a Natural Group of Japanese Monkey (I): The Basic and Dependent Rank," *Primates* 1 (1958): 111–30.

14 Syunzo Kawamura, "The Matriarchal Social Order in the Minoo-B Group: A Study on the Rank System of Japanese Macaque," *Primates* 1 (1958): 149–56.

15 Jane Goodall, *In The Shadow of Man* (Boston, MA: Houghton Mifflin Company, 1971).

16 Thelma E. Rowell, "Variability in the Social Organization of Primates," in *Primate Ethology*, ed. D. Morris (London: Weidenfeld and Nicholson, 1967).

17 Shirley C. Strum and Linda M. Fedigan (eds.), *Primate Encounters: Models of Science, Gender, and Society* (Chicago, IL: University of Chicago Press, 2000). 484.

success for both sexes in olive baboons.[18] In 1987, Shirley Strum, too, rejected the male-centric, aggression-based dominance model of baboon societies,[19] previously postulated by the studies of male primatologists, such as Sherwood Washburn and Irven DeVore,[20] reiterating once again that it was the females and their families that formed the stable core of the group and that baboon social structure was distinctively matrilineal. She also described how males and females took on complementary roles and relationships to construct and maintain their societies. Jeanne Altmann, one of primatology's most innovative leaders, working from the perspectives of a woman, a mother, and feminist, developed methodologies that encouraged the inclusion of female primates as subjects and allowed for the systematic study of the frequently low-key interactions among female primates and between mothers and their offspring, previously considered unimportant by largely male researchers.[21]

In 1993, Adrienne Zihlman argued that different species may exhibit sexual dimorphism in a variety of ways, including in their bone length and structure, propensities to accumulate muscle or fat, and/or canine size.[22] These various forms of sexual dimorphism may, in turn, be connected to variations in foraging tactics and aggressive propensities, both linked to evolutionary explanations of gender differences. Sarah Blaffer Hrdy developed her own unique approaches to study female grey langurs in Mount Abu in Rajasthan, northwestern India, during the 1980s and pioneered feminist primatology, when she noted that her shifting perceptions of female langurs was linked to her dawning awareness of male–female power relationships in her own life.[23,24] In 1982, Linda Marie Fedigan, apart from examining female-centric life-history strategies of monkeys in Costa Rica, also described thoroughly how the gender of researchers in anthropology and primatology could potentially affect their research

18 Barbara Smuts, "Dynamics of Social Relationships between Adult Male and Female Olive Baboons: Selective Advantages," in *Primate Social Relationships: An Integrated Approach*, ed. R.A. Hinde (Oxford: Blackwell, 1985). 112–16.

19 Shirley C. Strum, *Almost Human: A Journey into the World of Baboons* (New York: Random House, 1987).

20 Washburn and Irven DeVore, "The Social Life of Baboons."

21 Jeanne Altmann, *Baboon Mother and Infants* (Cambridge, MA: Harvard University Press, 1980).

22 Adrienne L. Zihlman, "Sex Differences and Gender Hierarchies among Primates: An Evolutionary Perspective," in *Sex and Gender Hierarchies*, ed. B.D. Miller (New York: Cambridge University Press, 1993), 32–56.

23 Sarah B. Hrdy, *The Woman that Never Evolved* (Cambridge, MA: Harvard University Press, 1981).

24 Sarah B. Hrdy, "Empathy, Polyandry, and the Myth of the Coy Female," in *Feminist Approaches to Science*, ed. R. Bleier (New York: Pergamon Press, 1986), 119–46.

on sexual differences in primate societies.[25] Based on all these female primatologists' work, several landmark volumes on female primate sociality were published in the 1980s, marking a paradigm shift in primatological research and its multifaceted understandings.[26] Finally, Donna Haraway, in 1989, through her own trail-blazing work on female primates and feminist primatologists, strengthened the then-upcoming theories of a *feminist standpoint* and *situated knowledges*, which, to this day, remain extremely influential and inspirational, and, we believe, rightfully so.[27]

...And of Feminist Primatology

Female researchers have remarkably impacted developments in primatology. Ruth Bleier has observed, for example, that: 'Primatology [...] serves as an example of the correction that a feminist perspective can effect in a field of knowledge [...] primatology is a lone example in the natural sciences of dramatic changes made under feminist viewpoints. This is related, in part, to the presence of a critical mass of women and feminists within the field [...]'.[28] A related, but important question of significant interest is whether primatology has indeed been deeply and academically influenced by women's movements, the political stance of feminism, and the feminist standpoint. According to Hrdy and Haraway, it cannot be a coincidence that a significant change in how people view female primates made its first appearance in the mid-1970s, at the same time that the second wave of Western feminism was urging scientists to consider the academic perspectives of women.[29,30] Based on her reading of Hrdy's research, Sue Rosser, a noted scholar of science studies, argued, in 1986, that the area of natural sciences that has

25 Linda M. Fedigan, *Primate Paradigms: Sex Roles and Social Bonds* (Montreal: Eden Press, 1982).

26 Hrdy, *The Woman that Never Evolved*; Samuel K. Wasser (ed.), *Social Behavior of Female Vertebrates* (New York: Academic, 1981); Fedigan, *Primate Paradigms*; Meredith F. Small (ed.), *Female Primates: Studies by Women Primatologists* (New York: Alan R. Liss, 1983); Evelyn S. Shaw and Joan S. Darling, *Strategies of Being Female* (Brighton: Harvester, 1984); Irene Elia, *The Female Animal* (Oxford: Oxford University Press, 1985); Bettyanne Kevles, *Female of the Species* (Cambridge, MA: Harvard University Press, 1986).

27 Donna Haraway, *Primate Visions: Gender, Race. and Nature in the World of Modern Science* (New York: Routledge, 1989).

28 Ruth Bleier, "Introduction," in *Feminist Approaches to Science*, ed. R. Bleier (New York: Pergamon Press, 1986).

29 Hrdy, *The Woman that Never Evolved*.

30 Haraway, *Primate Visions*.

been most significantly altered by a feminist viewpoint is primatology.[31] This analysis has been supported by Fedigan, who argued that primatology had demonstrated a high level of receptivity to critiques of androcentric language and interpretations, and a willingness to correct its past emphasis on male behaviour with its updated, contemporary perspectives on both sexes and their inter-relationship.[32] What is most apparent, however, is that, as primatologists, one can undoubtedly notice an increase in the efforts made to learn more about female lives and behaviours, as well as to create equal understandings of how female and male nonhuman primates perceive and act within, and interact with their specific socio-ecological environments.

It has occasionally been argued that women approach science differently from men, choosing different topics, framing different questions, favouring different theories and hypotheses, choosing different methodologies, and, generally, favouring different interpretations of scientific findings.[33] There is little data, however, to support or refute the claim that male and female primatologists conduct their investigations differently because there is scant research directly addressing this topic. A fundamental presumption, asserted particularly by Hrdy, Rowell, and Haraway, is that women are more inclined to view their social and physical environments from the perspective of female animals.[34] According to Strum and Fedigan, the primary descriptors used for female primates in earlier studies of primate behaviour, mostly by male primatologists, covered their roles as mothers and as sexual partners of the males in their social groups.[35] Over time, however, the image of female primates has expanded to encompass more dimensions. Numerous studies on the importance of female bonding through matrilineal networks, examinations of female sexual assertiveness and competition for reproductive success, their social strategies and underlying cognitive abilities, and their long-term knowledge of the group's local environment were extensively conducted in the 1970s and 1980s. Although this has not truly been proven, it has been hypothesized that women have perhaps

31 Sue V. Rosser, *Teaching Science and Health from a Feminist Perspective: A Practical Guide. The Athene Series* (New York: Pergamon Press, 1986).

32 Linda M. Fedigan, "Science and the Successful Female: Why There are So Many Female Primatologists," *American Anthropologist* 96, no. 3 (1994): 529–40.

33 Fehr, "The Paradox of Feminist Primatology."

34 Hrdy, *The Woman that Never Evolved*; Thelma E. Rowell, "Introduction: Mothers, Infants and Adolescents," in *Female Primates: Studies by Women Primatologists*, ed. M. Small (New York: Allan and Liss, 1984); Haraway, *Primate Visions*.

35 Strum and Fedigan, *Primate Encounters: Models of Science, Gender, and Society*.

contributed more, than have men, to the development of our current models of the canonical female nonhuman primate.

It is also important to note here that certain feminist and feminine ways of thinking have introduced new primatological conceptualizations and, in the process, uncovered the subjectivity that often remains ingrained in the practice of the biological sciences. An interesting example of this is the idea of situated knowledges, which was first put forth by Haraway (*Primate Visions*, 1989), and has since had a significant impact on feminist epistemologies. Haraway examined how primatology creates political narratives about and around the categories of nature, gender, and race, as well as how these categories are combined with specific viewpoints, uniquely located within particular social and physical settings. Her analysis clearly demonstrated how feminist epistemologies were able to forge new inquiries, yield novel perspectives on objects and beings, as well as on their categorizations, and allow for the development of new theories, all such endeavours benefitting from often-partial feminist perspectives, as opposed to completely impartial feminist perspectives. Finally, Haraway, in her exposition of how partial all viewpoints invariably were, pointed out that those who held relatively more dominant ideas did not feel the need to investigate alternatives because such viewpoints possessed long-held institutional and social authority, and the discipline was able to exclude authors, who had opposing viewpoints, which were proclaimed to be partial while the dominant paradigms were alone considered to be *objective*.

What are the apparent hallmarks of this feminist science of primatology? Could we return to the notion of *contrariness*, outlined above in the context of Rowell's studies, and argue, as has been done by certain science studies scholars, that the behaviour of animals, as often reported, are indeed guided by the expectations of those who study them?[36] Can the *Thelma Effect* then only be attributed to the observer's gender? Rowell claimed that Solly Zuckerman had himself suggested that '[…] among field workers the observer's own temperament and sex might be an important filter in determining, for example, the amount of agonistic behavior observed and reported in groups of primates'.[37] Some of the so-called *feminine* characteristics that have been believed to shape the way women *see* their primate subjects and make them ideal observers of their behaviour in the long term seem to be their

36 Vinciane Despret, "On a Useful Dualism," *Revue d'anthropologie des connaissances* 33, no. 3 (2009): 386–405.

37 Desmond Morris, *Primate Ethology* (Chicago, IL: Aldine Publishing Company, 1967), 222.

patience,[38] sensitivity, and their emotional connections to their subjects.[39,40] Fedigan has also speculated that such beliefs have stemmed from and, in turn, supported 'the myth that primatology is a type of mothering activity' and that women are naturally better observers of nonhumans because they have a particularly close relationship with nature.[41]

Strum and Fedigan, on the other hand, attribute this paradigmatic change in primatological vision not to the researcher's gender but to a shifting focus on the *particular* rather than to the *general*, when they argue that: 'We have moved from a general vision that primate society revolves around males and is based on aggression, domination, and hierarchy to a more complex array of options based on phylogeny, ecology, demography, social history and chance events'.[42] Haraway adopts a somewhat similar viewpoint, when she succinctly describes this alternative *feminist* perspective thus: '[…] the unifying theme in the primatology done by women has been their high likelihood of being skeptical of generalizations and their strong preference for explanations full of specificity, diversity, complexity, and contextuality'.[43] Finally, we return to the classic study of Fedigan on why there are so many successful women in primatology, in which she hypothesizes that women are possibly drawn to this discipline primarily because of '[…] the nature of the subject matter itself: the primates'.[44] She goes on to suggest that this attraction could potentially be due to two reasons, the first of which is the almost ubiquitous importance of sociality across virtually all simians and apes, and the female bondedness that pervades most nonhuman primate societies. And given the crucially significant roles played by female primates in their social organizations, it is possible that women primatologists could be curious about such feminine success stories.[45] Fedigan's second argument concerns the observation that nonhuman primatology invariably draws attention to human lives and human behaviour, and the possibility of examining the origins and evolution of human behavioural attributes from comparative, cross-species perspectives. She then refers to the work of Aisenberg and

38 Londa Schiebinger, "Has Feminism Changed Science?," *Signs: Journal of Women in Culture and Society* 25, no. 4 (2000): 1171–75.

39 Haraway, *Primate Visions*.

40 Vinciane Despret, "Sheep Do Have Opinions," in *Making Things Public: Atmospheres of Democracy*, eds. B. Latour and P. Weibel (Cambridge, MA: MIT Press, 2005), 360–70.

41 Fedigan, "Science and the Successful Female," 536.

42 Strum and Fedigan, *Primate Encounters*, 5.

43 Haraway, *Primate Visions*, 397.

44 Fedigan, "Science and the Successful Female," 536.

45 Ibid., 530.

Harrington[46] and suggests that women are particularly attracted to subjects that allow them to '[…] examine human nature, experience, capacity, and values' and those that '[…] touch experiences vital to the human experience of the world'.[47] More than men, Aisenberg and Harrington further argue, women scientists appear to search for a professional life that offers opportunities for personal transformation and nowhere is this more apparent than in academic disciplines that involve understandings of human nature, such as the science of nonhuman primatology.[48]

Of Female Nonhuman Primates…

But what does the science of nonhuman primatology actually tell us about the *nature* of other-than-human primates? A close examination of the lives of female nonhuman primates, to choose an example of relevance to this essay, provides fascinating insights into their unique lifeworlds, '[…] full of specificity, diversity, complexity, and contextuality'.[49] Such a statement, intuitive as it may sound to close observers of nonhuman primate sociality and the behavioural profiles of individual females, however, flies against the grain of most natural science programmes, accustomed as they are to classical notions of innately determined, species-typical biological traits that unhesitatingly incorporate, within them, definitive patterns of sexually dimorphic behavioural repertoires characterizing the *typical* other-than-human primate *male* and the *female*, often in that order of importance.

A critically important question that we thus raise here, and which appears to us to have been largely ignored in primatology is, in the words of Letitia Meynell and Andre Lopez, '[are …] there […] good, scientifically credible reasons for thinking that some nonhuman animals might have genders […]?'[50]

Early critical responses to such species-constrained stereotypic suppositions, especially concerning the development of gender in nonhuman primates, come from the noted anthropologists, Frances Burton and Susan Sperling. Burton[51] examined the roles that the two biological sexes played

46 Nadya Aisenberg and Mona Harrington, *Women of Academe: Outsiders in the Sacred Grove* (Amherst, MA: University of Massachusetts Press, 1988).

47 Fedigan, "Science and the Successful Female," 536.

48 Aisenberg and Harrington, *Women of Academe*.

49 Haraway, *Primate Visions*, 397.

50 Letitia Meynell and Andrew Lopez, "Gendering Animals," *Synthese* 199 (2021): 4287–311.

51 Frances D. Burton, "Ethology and the Development of Sex and Gender Identity in Non-human Primates," *Acta Biotheoretica* 26, no. 1 (1977): 1–18.

across nonhuman primate societies and the responsibilities that individuals took up with regard to the most important group-maintenance and individual-survival tasks faced, including the obtaining of food, reproduction and rearing the young, moving the group to sleeping sites, resting areas, food sources, or away from danger, protecting the group, and maintaining group cohesion. Her survey and her studies on the Barbary macaque in Gibraltar allowed Burton to conclude that, apart from being a progenitor or progenitrix, there was no evidence that the basic social roles that individuals of either sex assumed in nonhuman primate societies were 'biologically determined'.[52] She thus argued, rather strongly, for the contributions made by developmental histories, social learning, individual experience, and goal orientation in shaping individual behavioural profiles, their variability, and the social roles performed by different individuals to varying extents in primate societies.

Criticizing the various theories of ultimate causality that had dominated primatological models for the origins of gendered behaviour, including feminist sociobiology, Sperling[53] asked for more accurate and coherent approaches to define and describe primate gender differences. Following Burton, she hypothesized that the bewildering diversity of data on gender-role dimorphism in primates could perhaps best be explained by emphasizing the contextual development of behavioural profiles, rejecting the biological essentialism of gender dualism, and focusing attention on the complex interactions between organisms and their environments of development.

From another, radical perspective, a clear articulation of a species-inclusive sex/gender distinction is reflected in Rebecca Jordan-Young's concept of gendered norms of reaction[54] and Sara van Anders' Sexual Configurations Theory.[55] In a novel approach that allows sociocultural parameters to integrate with biological factors, Jordan-Young proposed the consideration of the sexes as different ecotypes in a cultural environment, suggesting that different cultural and culturally mediated environmental inputs may lead to a wide variety of outcomes for a particular sex. She also notes that gender develops in a crucially interactive manner and that gender norms that shape individuals in early development may have physiological outcomes, which, in adulthood, may appear to be more biologically driven

52 Ibid., 13.

53 Susan Sperling, "Baboons with Briefcases: Feminism, Functionalism, and Sociobiology in the Evolution of Primate Gender," *Signs* 17, no. 1 (1991): 1–27.

54 Rebecca Jordan-Young, *Brain Storm: The Flaws in the Science of Sex Difference* (Cambridge, MA: Harvard University Press, 2010).

55 Sara van Anders, "Beyond Sexual Orientation: Integrating Gender/Sex and Diverse Sexualities via Sexual Configurations Theory," *Archives of Sexual Behavior* 44 (2015): 1177–213.

than that of cultural origin. This, then, raises the potential difficulty of distinguishing biological from cultural causes – sex from gender – in organismic development and ignores gender/sex considerations in accounting for traditionally described sex-typical behaviours.

Sari van Anders' Sexual Configurations Theory considers sex and gender as different components of a larger sexual configuration and rejects the simplistic identification of rigidly defined categories, such as a *woman* or *homosexualit*y. She conceptualizes a sexual diversity continuum, identifying multiple axes along which different individuals could potentially vary in both character and strength. Sex and gender are then two distinct axes within this larger sexual configuration, evolving over a lifetime and interacting with other intersectional identities, such as race or class in the case of humans, during their underlying processes of development. Individual primates could thus be positioned along different independent parameters within a visually represented, conceptual space representing their multidimensional sexual configuration.

Acknowledging Jordan-Young and Van Anders' contributions of a comprehensive theoretical account of sex and gender, grounded in modern biology but incorporating within it distinctive sociocultural influences that provide for flexibility in gender expression and sexuality, Meynell and Lopez[56] generalize this framework to actively include nonhumans and operationalize gender to make it empirically tractable, defining, in the process, three categories:

> Sex: A cluster of traits that are highly correlated with or physically integrated with differential gamete size within the species and that have biological causes, both proximately by various means – like genetic causes and fetal development – and ultimately through evolution;
> Gender: A cluster of traits that are highly correlated with or culturally integrated with sex in the species – typically, behavioral, psychological, and social traits but in some cases, morphological and physiological traits – and that have sociocultural and historical causes, both proximately by way of social learning and ultimately by way of tradition;
> Gender/sex: Traits related to sex and gender whose etiology cannot be identified, or traits in which sociocultural and biological causes are so closely inter-related (consider surgical interventions) that the distinction cannot be drawn (whether in the lived experience of individuals or, as is more salient for the study of nonhuman animals, by external observers).[57]

56 Meynell and Lopez, "Gendering Animals."
57 Ibid., 4297–98.

Another perspective from which the analyses of gendered behaviour in nonhuman primates can be advanced, but which has largely remained ignored in Western primatology, is that of phenotypic flexibility, a form of context-dependent variation in behaviour, which includes reversible, phenotypic, usually behavioural transformations, shown by single individuals in response to variations in their ecological and social environments.[58,59] Importantly, this variation could represent or may have the potential to become integral to the life-histories of particular individuals and, subsequently, be subject to natural selection, allowing them to accrue a selective advantage over others, a point previously made by Burton.[60,61]

Most nonhuman primates live in social environments that often change unpredictably due to various socio-ecological factors but which, in turn, significantly affect their group composition and social structure. Are individual primates capable of exhibiting developmental behavioural flexibility under these circumstances as well? And, if they are, is it possible that such flexibility could then be incorporated into their long-term life-history strategies and, in the process, significantly impact their dynamic, occasionally gendered, life-worlds? Furthermore, could such behavioural flexibility then be horizontally, vertically, or obliquely transmitted to other individuals by social learning, particularly with the extended adult–juvenile contact periods, so typical of primate societies, thus providing ample opportunities for such cultural transmission?[62,63] Is it then conceivable that the phenotypic behavioural flexibility that we are increasingly encountering in nonhuman primate societies – primarily as a result of dynamic organism–environmental interactions – and its transmission could ultimately establish distinctive behavioural traditions and other-than-human cultures, with the evolution of its own novel evolutionary rules?[64,65] What is nevertheless of greatest relevance in the context of our current discussion is whether our comprehensive knowledge of phenotypic

58 Theunis Piersma and Jan Drent, "Phenotypic Flexibility and the Evolution of Organismal Design," *Trends in Ecology and Evolution* 18, no. 5 (2003): 228–33.

59 Anindya Sinha, "Not in Their Genes: Phenotypic Flexibility, Behavioural Traditions and Cultural Evolution in Wild Bonnet Macaques," *Journal of Biosciences* 30, no. 1 (2005): 51–64.

60 Burton, "Ethology and the Development of Sex and Gender Identity."

61 Sinha, "Not in Their Genes," 52.

62 Ibid., 56.

63 Luke Rendell and Hal Whitehead, "Culture in Whales and Dolphins," *Behavioral and Brain Sciences* 24 (2001): 309–82.

64 Eva Jablonka, "Inheritance Systems and the Evolution of New Levels of Individuality," *Journal of Theoretical Biology* 170 (1994): 301–09.

65 Eva Jablonka and Marion J. Lamb, "Epigenetic Inheritance in Evolution", *Journal of Evolutionary Biology* 11 (1998): 159–83.

flexibility and other-than-human behavioural traditions could potentially contribute to a more nuanced grassroots-level understanding of nonhuman gender and its performance within and across nonhuman primate societies.

...And of Female Bonnet Macaques

In the concluding section of our essay, we provide a preliminary narrative of the phenotypic flexibility and other-than-human behavioural traditions, both of which contribute to gendered behavioural expression, encountered during our long-term study of several populations of free-ranging bonnet macaques *Macaca radiata*, a cercopithecine primate species endemic to peninsular India.

Various populations of the bonnet macaque and their constituent individuals appear to be unusual in exhibiting remarkable social flexibility and a wide variety of behavioural strategies at different stages of their life histories, all of which enable them to adapt successfully to very different socio-ecological habitats.[66] This female-bonded species usually lives in large multimale-multifemale groups in which adult females develop strong affiliative relationships with one other and often with the adult and subadult males of the group. In recent years, however, increasing anthropogenic influences appear to have led one particular population of the macaques in the dry deciduous forests of Bandipur and Mudumalai National Parks in South India to have evolved a new form of social organization in which small unimale groups are occasionally formed by a few adult females and their offspring taking an unprecedented decision to leave their natal groups, usually accompanied by an adult male.[67] These unimale troops are strikingly different from the typical multimale troops in the nature of the unique social relationships that develop between the single male and the resident females, as well as within the females of the troop.[68]

In a relevant instance of phenotypic flexibility, displayed by a group, BM15, of this population, individual adult females of different dominance

66 Anindya Sinha, *The Monkey in the Town's Commons: A Natural History of the Indian Bonnet Macaque*, NIAS Report R 2-01 (Bangalore: National Institute of Advanced Studies, 2001).

67 Anindya Sinha et al., "Ecology Proposes, Behaviour Disposes: Ecological Variability in Social Organization and Male Behavioural Strategies among Wild Bonnet Macaques," *Current Science* 89, no. 7 (2005): 1166–79.

68 Sunita Ram, Suri Venkatachalam, and Anindya Sinha, "Changing Social Strategies of Wild Female Bonnet Macaques during Natural Foraging and on Provisioning," *Current Science* 84, no. 6 (2003): 780–90.

ranks significantly changed their behavioural strategies, as they regularly alternated between bouts of natural foraging and feeding on provisioned foods.[69] Provisioning was marked by a sharp increase in feeding competition, accompanied by severe aggression and feeding supplants, but individual females were also able to adopt different, but appropriate, strategies aimed at reducing social tension within the group, behaviour never exhibited by adult males. Moreover, a comparison between the affiliative relationships displayed by adult females in two groups – the aforementioned BM15 and GK2 – in two geographically separated populations also revealed striking differences that could potentially be ascribed to ecological differences in their food availability and distribution. In BM15, where the adult females periodically foraged on limited and patchily distributed human-origin foods and competition was strong, individuals directed their allogrooming up the dominance hierarchy, with subordinate females grooming dominant individuals at relatively higher levels than they groomed those subordinate to them.[70] In contrast, individual females of GK2 foraged only on natural food sources, competition for resources was relatively low, and individual females preferentially allogroomed those subordinate to them. What is also noteworthy is that the patterns of allogrooming between the originally observed adult females of GK2 remained strikingly similar to that observed a decade later in the group, although there had been a significant change in its feeding ecology over this period – from complete natural foraging initially to a regime where the feeding was largely on provisioned human foods. Such a longitudinal maintenance of similar behavioural patterns in this macaque group suggests a process of intergenerational transmission of maternal social networks, implying direct mother–daughter transmission mechanisms of behavioural practices in this species[71] – a striking example of a gendered behavioural tradition in nonhuman primates. Yet another example of sociocultural behavioural flexibility was that displayed by several adult, subadult, or juvenile females in the unimale troops of Bandipur–Mudumalai, who, faced with a lack of mate choice and/or female companionship, emigrated to other neighbouring unimale or multimale troops, either singly or in small associations.[72] Such migration by juvenile and adult males was, however, of more regular occurrence in this population and possibly represented a primarily innate biological trait.

69 Ram, Venkatachalam, and Sinha, "Changing Social Strategies."
70 Ibid.
71 Sinha, "Not in Their Genes," 59.
72 Sinha et al., "Ecology Proposes."

A search for gender-specific behaviour amongst individuals could perhaps meet with greatest success in situations that require a uniquely gendered response from the community. During the course of our study, we thus observed three adult female macaques – RI, TU, and BECA – from three different populations – GK1, CAMP2, and DV, respectively – to perform a rather unusual tool-assisted, self-directed manipulative behaviour, best described as *vaginal grooming*, wherein they inserted short sticks or twigs into their vagina and scratched vigorously, possibly in response to an infection in their genital organs. What is remarkable is that while all the three females used physically similar objects – short twigs, dry sticks, or grass blades – as tools, they used individual-specific objects, possibly because they best met the needs of the situation. RI was, however, the only female to actively modify her tools for the purpose.[73] The diversity and complexity of such tool manufacture thus varied across the three females from the three populations but could reflect a form of self-motivated learning of object affordances, leading to a gender-specific, goal-oriented usage, possibly underlain by causal inferences. It is also noteworthy that this object-aided self-grooming remained idiosyncratic and failed to propagate within the performer's respective groups, possibly given the specificity of individual need, and hence the difficulty of an observer to grasp the actual intent of the actor while observing such tool-assisted behaviour. It could thus be argued that certain kinds of gendered behaviour, with the potential to become a gender-specific behavioural tradition, may not spread simply because of the narrow window of its applicability.

Finally, although many bonnet macaque groups live in close association with humans, most adult and juvenile individuals of either gender fail to display any kind of affiliative interactions with people. Another notable exception in this regard were four juveniles – two females, BO and SH, and two males, MI and DO, again of the group GK1, who regularly interacted with and displayed contact affiliative behaviours with human observers. Remarkably, all these individuals, ranging in age from one to four years, were offspring of an adult female, SU, who was unique among the eleven adult females of this group in her high degree of tolerance of human observers, even – unusually – requesting food from them on occasion. It is thus possible that SU's offspring may have learnt to be tolerant of humans by observing her behavioural interactions with them, another example of parent–offspring

73 Anindya Sinha, "Complex Tool Manufacture by a Wild Bonnet Macaque, *Macaca radiata*," *Folia Primatologica* 68 (1997): 23–25.

transmission of behavioural traits.[74] BO and SH continued to display such affiliative behaviour towards humans in their adulthood while MI and DO stopped doing so; such interactions were thus unusually gender-specific in nature and capable of being transmitted socially to emerge as a gendered behavioural tradition in later years.

In conclusion, the varied interactions between individual genotypes and specific environmental components that can generate such behavioural flexibility in bonnet macaques, often of a gendered nature, need to be elucidated and understood further. What is clear, nevertheless, is that social lability and individual behavioural variability of this nature could enable individuals of a species to evolve novel and innovative, often gendered, behavioural strategies that could promote more effective survival and reproduction under periodically changing, but challenging, socio-ecological situations.

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Anindya Sinha, primarily based at the National Institute of Advanced Studies in Bangalore, India, had early research interests in the molecular biochemistry of yeast metabolism, the social biology of wasps, and the classical genetics of human disease. His principal research over the last three decades has, however, been on the behavioural ecology, cognitive ethology, population and behavioural genetics, evolutionary biology, and conservation studies of nonhuman primates. His current research interests in the natural philosophies, urban ecologies, and performance and heritage studies principally concern ethnographic explorations of human–nonhuman

74 Sinha, "Not in Their Genes," 58.

relations and the lived experiences of other-than-humans, with their promise of unique understandings of more-than-human lifeworlds, in the past, today and in the future.

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