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REVIEW

A HISTORY OF PRIMATOLOGY IN INDIA (IN MEMORY OF PROFESSOR SHEO DAN SINGH)

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A history of primatology in India (In memory of Professor Sheo Dan Singh)

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Abstract: India harbors a wide diversity of primates with 24 species that include lorises, macaques, langurs and gibbons. Systematic research on the primates in India started about 60 years ago. In order to develop a historical perspective, we recognize three broad phases of primate research: largely natural history and base line research, primarily behavioral ecology research, and increasingly question and hypothesis-driven research. We describe the old and the recent primate research in the country and suggest research areas for the future.

Keywords: Gibbon, Indian primates, langur, loris, macaque.

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Author details: MEWA SINGH is a renowned wildlife biologist at University of Mysore with over 45 years of research experience on Indian wildlife, especially primates. His interests are ecology, animal behavior and conservation management. He has trained a generation of students who are now excelling in many institutions all over the world. MRIDULA SINGH is a PhD in animal behavior and teaches psychology at Maharaja's College, University of Mysore. She carried out a long-term field study on maternal parental investment patterns in relation to dominance hierarchy in Lion-tailed Macaques in the Anamalai Hills. H.N. KUMARA is principal scientist at Salim Ali Centre for Ornithology and Natural History. His research interests encompass a large variety of taxa and topics in ecology, behavior and conservation. He initiated the first long-term studies on the Nicobar Long-tailed Macaques. DILIP CHETRY is a senior biologist with Aaranyak and carries out conservation research and action for wildlife, especially primates, in northeastern India. He also trains people in ecological research through various workshops and training programs. SANTANU MAHATO is a researcher at the University of Mysore and will be starting long-term studies on primates in the Anamalai Hills soon.

Author contribution: Mewa Singh conceptualized the article and other authors contributed to literature search and helped in article preparation.

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INTRODUCTION

India is home to at least 24 species of nonhuman primates that include two species of lorises, 10 species of langurs, 10 species of macaques, and two species of small apes, with several of them being threatened or vulnerable (Table 1) (Molur et al. 2003). Several species including the Slender Loris, Bonnet Macaque, and Assamese Macaque also have distinct subspecies making India very rich in primate taxa. Due to this diversity, research in primatology in India has made prominent strides. Although in the past, many researchers came to India from other countries and carried out pioneering studies on different primate taxa, most of the published research on Indian primates today is by Indian scientists, unlike in many other habitat countries. At a conference organized by the Association of Indian Primatologists, a group recently established by young primatology researchers, at Bengaluru in 2019, one of us (Mewa Singh) delivered the inaugural address on the development of primatology in India, and was surprised to know that many young scholars had not even heard the names of many of the pioneers. This fact motivated us to prepare this article so that the historical information is made available at one source before such valuable information becomes inaccessible or is forgotten. This will also provide a historical perspective for the development of primate research in India. Primates have been used in a wide variety of research in India. Classical paleontological and evolutionary studies have been carried out by S.R.K. Chopra and Ashok Sahni at Panjab University, Chandigarh. Research on primate physiology has been carried out by N.K. Lohia at University of Rajasthan, Jaipur, by N.R. Moudgal, M.R.N. Prasad, N. Ravindranath and Polani B. Sheshagiri at the Indian Institute of Science, Bengaluru, and by scientists at the National Institute for Research in Reproductive Health, Mumbai. At the Indian Institute of Science, Aditya Murthy studies neurophysiology of primates and Praveen Karanth works on primate taxonomy. In addition, primates have also been employed for biomedical research at the Central Drug Research Institute, Lucknow, National Institute of Nutrition, Hyderabad, National Institute of Virology, Pune, Post Graduate Institute of Medical Education and Research, Chandigarh, National Institute of Immunology, and All India Institute of Medical Sciences, New Delhi. In this article, however, we will focus only on research on primates in their natural habitats concerning ecology and behavior.

As it could probably be true for primatology globally, we recognize three phases of primatology research in

India to develop a historical perspective. These include: a largely, natural history and baseline research; primarily behavioral ecology research; and increasingly question and hypothesis driven research. It must, however, be made clear that these are not strictly discrete phases as all types of research have been carried out at all times, but it is only a working time frame to trace the research perspectives and developments. Further, since there has not been any institution in the country with the primary focus on primate research and conservation, most research has been individual initiatives scattered across different institutions. In this review, therefore, we will primarily refer to Ph.D. theses and only few references, and website(s) wherever available, of each researcher since the total number of references on Indian primates number in thousands. This will help readers to find other publications of the same researchers. To our knowledge, we have included all Ph.D. theses written on primates in India, either by an Indian or by foreign researchers. We clarify that this article is not a critical review of the contributions of Indian primatology, which remains another topic to work on, but a repository of information on the subject. It is, however, more than an annotated bibliography as the contributions of all the scientists are discussed briefly. A brief timeline of crucial developments in Indian primatology is illustrated in Figure 1.

A LARGELY NATURAL HISTORY AND BASELINE RESEARCH

Although a few short articles on Indian primates in their natural habitats were published earlier (McCann 1933; Nolte 1955), it was only in the late 1950s and early 1960s that systematic and relatively long-term studies were taken up. The main emphasis in those studies was on the natural history of the study species, and these descriptive studies provided a baseline for further research. The researchers, therefore, focused on the species rather than on specific research questions. The pioneers of that era are Charles H. Southwick, Phyllis Jay Dolhinow, Paul E. Simonds, Yukimaru Sugiyama, and Sheo Dan Singh.

Charles H. Southwick

Although short descriptions of the behavior of Rhesus Macaques and Hanuman Langurs were published before 1959 (McCann 1933; Nolte 1955), the first long-term field study on the distribution, population status, ecology and behavior was undertaken by Charles H. Southwick (<https://neurotree.org/neurotree/publications.php?p>

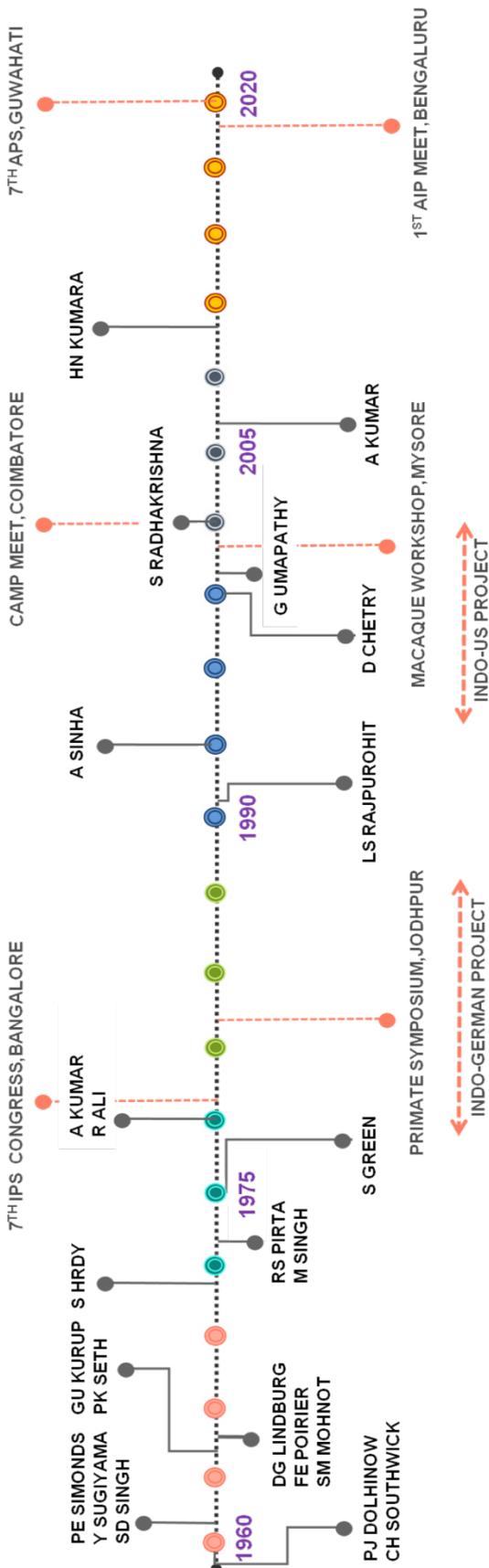


Figure 1. Illustration of the developments in Indian primatology with solid grey lines depicting initiation of field research by seminal primatologists pre-1980 and establishment of independent research groups focussed on primatology post-1990. Dotted red lines mark organization of crucial meetings, symposia and conferences and dotted red arrows trace the period of international collaborative projects. Colour designs of dots (that mark individual year on the timeline) are identical when they belong to the same decade.

id=56382&searchstring=&showfilter=all). Southwick conducted his studies from 1959 to 60 in Uttar Pradesh and in 1962 in West Bengal. The results of the surveys conducted on the Rhesus Macaque populations in 280 villages, 30 towns, and 200 Hindu temples revealed that 16% villages, 69% towns and 6% Hindu temples had Rhesus Macaques (Southwick et al. 1961a), and 406, 37, 84 and seven groups of macaques were located along roadsides, canal banks, railroads, and forest areas, respectively (Southwick et al. 1961b). The first detailed study on the ecology and behavior of the Rhesus Macaque was published in 1965 (Southwick et al. 1965). The group size was 15.1 individuals with an average of 3.5, 6.9, 3.8, and 0.9 adult males, adult females, infants, and juveniles, respectively. The study found a clear inter-group and within-group hierarchy and peaceful to violent inter-individual relationships. This study also laid foundations for further research in ecology and behavior of Rhesus Macaques. Southwick maintained his research collaborations with Indian primatologists and continued to publish on population trends in Rhesus Macaques until 2001 (Malik et al. 1984; Southwick & Siddiqi 1966, 1977, 1988, 2001).

Phyllis Jay Dolhinow

Though there were reports about the taxonomy of Hanuman Langurs, the first comprehensive field study on the demography, ecology and behavior of this species was published in 1965 by Phyllis Jay (Jay 1965, later known as Dolhinow, P.J.). Jay conducted an 18-month field study between October 1958 and April 1960 at Orcha, a small village close to a forest in Madhya Pradesh, and Kaukori, a village among agricultural lands in Uttar Pradesh. The two habitats of langurs varied with respect to availability of forest, food items of langurs, human density and human interactions, interactions with other primates and forest dwelling mammals including predators. The groups were largely bisexual with 1.5 to 2 adult females per male, but there were also all-male groups. The groups remained relatively stable. Activity peaked during dawn and dusk. The home ranges of the groups averaged from 1 to 3 square miles. The social interactions were usually peaceful and relaxed. There were no overt dominance interactions and activities such as grooming could occur for over five hours per day. The infants and juveniles were found to undergo a fairly long process of socialization. Jay also provided a detailed ethogram of langurs describing a multitude of gestures and vocalizations used by various age-sex classes. Dolhinow also carried out a survey on Rhesus Macaques from 1964 to 1965 covering 9,510

Table 1. Primate species in India with their IUCN and Indian Wildlife (Protection) Act status.

	Common name	Species	Conservation status	
			IUCN	IW(P)A
Lorises				
1	Slender Loris	<i>Loris lydekkerianus</i>	EN	I*
2	Slow Loris	<i>Nycticebus bengalensis</i>	EN	I
Langurs				
3	Himalayan Grey Langur	<i>Semnopithecus ajax</i>	EN	II
4	Bengal Hanuman Langur	<i>Semnopithecus entellus</i>	LC	II
5	Lesser Hill Langur	<i>Semnopithecus hector</i>	NT	II
6	Dark-legged Malabar Langur	<i>Semnopithecus hypoleucos</i>	LC	II
7	Coromandal Grey Langur	<i>Semnopithecus priam</i>	NT	II
8	Central Himalayan Langur	<i>Semnopithecus schistaceus</i>	LC	II
9	Nilgiri Langur	<i>Semnopithecus johnii</i>	VU	I
10	Capped Langur	<i>Trachypithecus pileatus</i>	VU	I
11	Golden Langur	<i>Trachypithecus geei</i>	EN	I
12	Phayre's Leaf Monkey	<i>Trachypithecus phayrei</i>	EN	I
Macaques				
13	Rhesus Macaque	<i>Macaca mulatta</i>	LC	II
14	Assamese Macaque	<i>Macaca assamensis</i>	NT	II
15	Stump-tailed Macaque	<i>Macaca arctoides</i>	VU	II
16	Pig-tailed Macaque	<i>Macaca leonina</i>	VU	II
17	Arunachal Macaque	<i>Macaca munzala</i>	EN	Not listed
18	White-cheeked Macaque	<i>Macaca luecongenys</i>	Unknown	Not listed
19	Tibetan Macaque	<i>Macaca thibetana</i>	NT	Not listed
20	Lion-tailed Macaque	<i>Macaca silenus</i>	EN	I
21	Bonnet Macaque	<i>Macaca radiata</i>	VU	II
22	Nicobar Long-tailed Macaque	<i>Macaca fascicularis umbrosus</i>	VU	I
Gibbons				
23	Eastern Hoolock Gibbon	<i>Hoolock leuconedys</i>	VU	I
24	Western Hoolock Gibbon	<i>Hoolock hoolock</i>	EN	I

*Schedule types under IW(P)A. Lower schedule types have higher protection than higher schedule types.

kilometers in rural and forest areas, and found one group per 11.6km in forests and 32.8km in rural areas (Dolhinow & Lindburg 1978).

Paul E. Simonds

After a short-term study by Nolte (1955), the first detailed study on the behavior of Bonnet Macaques was published by Simonds (1965). Paul Simonds (<https://anthropology.uoregon.edu/profile/simonds/>) conducted his study on Bonnet Macaque between October 1961 and June 1962 on the Mysore-Ooty road near Bandipur forests. The group size of Bonnet Macaques varied from >10 to 40–60 individuals. Simonds described the macaques as gregarious and

spending much time in grooming and play. Hierarchies within the group were found to be subtle. Females indulged in promiscuous mating with extreme male tolerance. Groups had overlapping home ranges. Simonds later visited India in 1963, 1970, and 1975 for subsequent research. Simonds (1965) became a base line for subsequent studies on Bonnet Macaques.

Yukimaru Sugiyama

A contemporary of Phyllis Jay Dolhinow was Yukimaru Sugiyama (https://www.researchgate.net/profile/Yukimaru_Sugiyama) from Kyoto University, Kyoto who conducted studies on Hanuman Langurs and Bonnet Macaques in Dharwad from April 1961 to

April 1963. Dr. D. Miyadi, Kyoto University, Kyoto was the project director and the Indian collaborator was Dr. M.D. Parthasarathy from Central College, Bangalore. Sugiyama reported the social structure of one-male groups and instances of infanticide in Hanuman Langurs for the first time and proposed that such a pathological behavior could be due to high population densities, and could occur to induce estrus in females (Sugiyama 1964, 1965, 1966). The process involved ousting the dominant male and other males of a langur group by an outside male who took over the group, and the ousted males formed an all-male group. He also carried out short-term studies on Lion-tailed Macaques (Sugiyama 1968) and Bonnet Macaques (Sugiyama 1971) during the afore-mentioned period. Later, Sugiyama made several visits to India in 1972–73 to study Himalayan langurs (Sugiyama 1976) and Rhesus Macaques, and in 1976, 1978, and 1997 to study Hanuman Langurs (Sugiyama 1984).

Sheo Dan Singh

When these field studies were going on in the 1960s, there was also experimental work carried out on Rhesus Macaques at the Department of Psychology, Punjab University, Chandigarh by Sheo Dan Singh that resulted in some exceptional findings which unfortunately have not found much mention in later literature on Indian primates. Singh captured monkeys from urban and forest environments and studied behavioral differences between them under laboratory conditions. When presented with novel stimuli, the urban monkeys were far more active and manipulated presented objects more than the forest monkeys (Singh & Manocha 1966) and were more responsive to stimuli of higher complexity (Singh 1968). Urban monkeys were more aggressive than forest monkeys whereas forest monkeys groomed more often than urban monkeys (Singh 1969). The urban and forest monkeys, however, did not differ in their problem-solving capabilities (Singh 1969) indicating that whereas the selection pressures of an urban environment have shaped many new adaptive patterns in urban monkeys, the basic intelligence does not seem to be affected. S.D. Singh was invited to head the Psychology Department at the newly established university at Meerut in 1971. At Meerut, he continued laboratory experiments on Rhesus Macaques primarily on selective lobectomy and learning, and also started experimental studies on these macaques in their natural habitats in Siwalik Hills in the Asarori Range forests near Dehradun. The Rhesus Macaque infants were separated from their mothers shortly after birth and were reared in social isolation

and in peer-groups of six monkeys each. There were also mother-infant pairs in these experiments. The idea behind these experiments was to study the contribution of mothers, peers, and the group on the behavioral development of infant monkeys. Infants raised in peer groups when separated from others showed disturbed behaviors including 'protest' and 'despair' (Singh 1977). When these infants were exposed to strangers, they reacted aggressively just like the Rhesus Macaques in their natural groups (Singh 1980). S.D. Singh passed away on 26 June 1979 when he was less than 50 years old. The students trained by him continued their work and three of them, Waheeda Khan, Kiran Lata, and Suraj Bhan, submitted their theses under B.S. Gupta at Meerut. Waheeda Khan (Khan 1980) studied the effect of urban environment on social, emotional, and curiosity behaviors in Rhesus Macaques at different age levels. The urban monkeys were more aggressive whereas the forest monkeys were shy and timid. Urban monkeys also needed high levels of stimulation to satiate their curiosity. The same urban and forest monkeys were studied by Kiran Lata (Lata 1980) for development of cognitive behaviour. Environmental enrichment showed no effect on delayed response learning, object discrimination learning set, and oddity discrimination learning; however, the forest monkeys were slower to adapt to experimental situations than the urban monkeys. The above two studies were carried out in the Primate Laboratory at Meerut University. A field study carried out by Suraj Bhan (Bhan 1983) on the development of behaviour in Rhesus Macaque infants found developmental trends in play and social interactions at different age blocks, with male infants and juveniles being more playful than females. N.K. Chandel (Chandel 1981), though trained at Meerut, submitted his thesis at the University of Rajasthan, reported that patterns of affiliative behaviors in adult and adolescent Rhesus Macaques changed with age and mating season. Rajbir Singh (Singh 1981), who also went to Rajasthan from Meerut, reported that in free-ranging Rhesus Macaques, the social interactions among group members are not random but patterned by age, sex, and relative dominance in the social hierarchy.

Two other students of S.D. Singh, Raghubir Singh Pirta and Mewa Singh, made their careers in primatology and established many milestones in Indian primate research later. Pirta did his Ph.D. at Kashi Vidyapith University, his post-doctoral research at Utkal University, and later worked in Himachal Pradesh University till his retirement. Mewa Singh did his Ph.D. at the University of Mysore and continues to work there as Professor (for

Life) (The works of Pirta and Singh are discussed in later sections).

PRIMARYLY BEHAVIORAL ECOLOGY RESEARCH

This was the phase when baseline data were available on some Indian primates and researchers could now look at the ecology and behavior of their study species in greater detail. The approach still was primarily species-oriented.

Donald G. Lindburg

D.G. Lindburg came to India to study Rhesus Macaques in 1964. Of the 21 months that the study lasted, the first nine months were devoted to a field survey on Rhesus Macaques under the leadership of Phyllis Jay Dolhinow and during the remaining 12 months, Lindburg carried out an ecological and behavioral study of Rhesus Macaque at Asarori Forest, Siwalik Hills, at the Forest Research Institute, near Dehradun (Lindburg 1971). Prior to this study, only a few experimental studies were carried out on the behavior of Rhesus Macaques by S.D. Singh (cited earlier) and Lindburg's was the first account of Rhesus Macaque behavior from its natural habitats. The Rhesus Macaque is the most widespread non-human primate from 20°E in Afghanistan to 120°E in China, and from 18°N in India to 40°N in China. The habitat occupied by the species included *Sal Shorea robusta* dominated deciduous forest and the area was heavily grazed by domestic buffaloes. The mean group size was about 32 though it varied significantly from one habitat type to another. The groups were bisexual with adult male to female ratio being about 1:3 and the reproductive rate was about 90%. The home range of a large group was approximated to 15km². The Rhesus Macaque is largely frugivorous but occasionally feeds on insects and grasshoppers. Lindburg also provided detailed information on intergroup interactions, social behavior, and social organization and his article became the general reference for later research on the ecology and behavior of Rhesus Macaques. Lindburg continued his association with Indian primatologists (Singh et al. 1999) and also carried out conservation breeding of Lion-tailed Macaques at San Diego Zoo, San Diego, USA.

Frank E. Poirier

Frank E. Poirier (<https://anthropology.osu.edu/people/poirier.1>) studied Nilgiri Langurs in the Nilgiri Hills between September 1965 and August 1966. This was the time when base line studies were already published

on many Indian primates, and Poirier advanced the research to finer details of ecology and behavior. He published several articles in various journals from 1966 to 1970 but a detailed single report on the Nilgiri Langur was published in 1970 (Poirier 1970). The Nilgiri Langurs are distributed in the southern Indian states of Kerala, Tamil Nadu, and Karnataka. The home ranges of Nilgiri Langur groups overlapped with Bonnet and Lion-tailed macaques and occasionally with Hanuman Langurs, and varied from ¼ to 1 square mile. The average group size was 8–9 individuals in bisexual groups, and solitary and uni-sex male groups were also observed. The main food of Nilgiri Langurs were leaves, flowers, buds, seeds, and bark or stem. Poirier also reported other behaviors including social communication, dominance hierarchies, grooming, and play in detail. This report, therefore, provided an excellent background for analytical studies later.

Suraj Mal Mohnot

Though there were a few Indian primatologists including M.A. Beg, M.R. Siddiqi, M.D. Parthsarathy, and H. Rahman who carried out field work with the previously-mentioned foreign scientists, the first independent field study in India was undertaken by S.M. Mohnot at Jodhpur University. Mohnot started studying Hanuman Langurs near Jodhpur in 1965, obtained his Ph.D. in 1974 and became a faculty member at the Department of Zoology at Jodhpur University. In the years since then, Mohnot has carried out many long-term studies on primates, guided several Ph.D. students, hosted many foreign scholars, and made Indian primatology known to the world over. The duo of Roonwal and Mohnot also published the first comprehensive book on primates of South Asia (Roonwal & Mohnot 1977). The langur population near Jodhpur is unique in many ways, it is an isolated population since hundreds of years with no distribution of any other primates up to at least a hundred kilometers. The rocky and open nature of the region allows close day-long observations throughout the year (Mohnot 1984). The basic social system, social changes, and infant-killing were reported in the Jodhpur langurs (Mohnot 1971; Makwana 1979a). (More details on Mohnot's work will come later along with his students and collaborators).

Steven Green, Karen Minkowski, John F. Oates, Rauf Ali, and Jayashree Ratnam

Steven Green and Karen Minkowski (http://www.momentum2.miami.edu/donors_steven_green.html) from Rockefeller University collaborated with the

Bombay Natural History Society to carry out a long field study lasting 19 months from September 1973 to April 1975 on the Lion-tailed Macaque at Ashambu Hills in Tamil Nadu. Except for a short term study by Sugiyama (1968) and Karr (1973), nothing was published about the ecology and behavior of Lion-tailed Macaques till 1977 (Green & Minkowski 1977). Surveys by Green & Minkowski revealed that there were about 405 Lion-tailed Macaques in the wild in the states of Karnataka, Tamil Nadu, and Kerala. The Lion-tailed Macaque is an obligate rainforest dweller and primarily arboreal. The average group size is about 15 individuals. Sexual maturity in females is attained at about five years of age and very few infants are produced by a female in her lifetime. The primarily fruit diet of the species is supplemented with insects. Green & Minkowski also initiated long-term conservation plans for the endangered Lion-tailed Macaque. Green offered a post-doctoral fellowship to John F. Oates (<https://anthropology.commons.gc.cuny.edu/john-f-oates/>) to continue research on the Lion-tailed Macaques. The conservation initiatives taken up by Green & Oates finally resulted in a large area in Kalakad-Mundanthurai being maintained as a reserve primarily for the Lion-tailed Macaques (Sekhsaria 2015). Oates, however, shifted his focus to the Nilgiri Langur and commented on its geographical distribution and status (Oates 1979), and reported that most food items of the Nilgiri Langur had low fibre and condensed tannin content but the staple food items were highly digestible (Oates et al. 1980). As John Oates took over from Steven Green, Rauf Ali (<https://www.feralindia.org/user/78>) came to Kalakad-Mundanthurai to take over from John Oates. Ali was registered for Ph.D. at the University of Bristol with John Crook (Ali 1981) and reported for the first time that in the subspecies of Bonnet Macaques that he was studying at Agastyamalai, it was the females that emigrated and dispersed between the groups, a behavior not known in the other subspecies of the Bonnet Macaque or most other macaque species. Ali also observed that at the time of intergroup encounters, there was also heightened within-group aggression that he explained as the group males trying to prevent the females from crossing over to the opposite group. Years later, following Rauf Ali, Jayashree Ratnam (<https://www.ncbs.res.in/mscprogram/program-management>) arrived at the Mundanthurai forests to study Bonnet Macaques with a more pointed question about the foraging decisions in a social forager (Ratnam 2002). Ratnam analyzed foraging decisions in response to experimentally-induced variations in ecological and social variables. Social dominance determined which

individual fed at a given time, and social rank affected spatial distribution and the feeding rate of an individual.

Ajith Kumar

Ajith Kumar (<https://www.ncbs.res.in/mscprogram/program-management>) carried out a six-year-long study on the ecology and population dynamics of Lion-tailed Macaques in the Anamalai Hills and received his Ph.D. degree from University of Cambridge in 1987 (Kumar 1987). He examined variations in the demographic parameters and correlates of ecology and behavior. He reported delayed sexual maturity in females, long inter-birth intervals, low population turnovers but high infant survival rates. These macaques fed on fruits and insects. Larger groups had larger ranges than smaller groups. The low birth rate was explained to be due to high mating interference resulting in suppression of conception in many females. This study site in the Anamalai Hills became one of the most important centers for wildlife research in subsequent years.

INCREASINGLY QUESTION-ORIENTED AND HYPOTHESIS-DRIVEN RESEARCH

Although several researchers continued to focus on particular species, primate research, from the mid 1970s, became increasingly question-oriented and hypothesis-driven. Therefore, while discussing this phase of development of primatology research in India, we will not focus on the research by any individual but by several institutions where primate research was conducted or is still underway.

Jai Narayan Vyas University, Jodhpur

S.M. Mohnot (Mohnot 1974) established a major primate research program at Jodhpur where he trained a large number of Indian students and hosted several researchers from abroad. The unique Jodhpur population of Hanuman Langurs became a major focus of ecological research. Sarah Blaffer Hrdy (Hrdy 1975) (<http://www.citrona.com/hrdy>), a graduate student of Irvin DeVore and tutored by E.O. Wilson and Robert Trivers arrived in Jodhpur in 1971 and S.M. Mohnot advised her to study Hanuman Langurs at Mount Abu in Rajasthan. Infanticide in langurs, reported by Sugiyama and Mohnot, was just becoming a hot topic in primatology and it was generally being characterized as a 'social pathology' occurring primarily due to overcrowding. Hrdy observed many cases of usurping control of different groups of langurs and instances of infanticide. The females who lost infants

gave birth within 6–8 months after the death of their infants whereas the normal inter-birth interval was up to about 27 months. Infanticide could also occur in places where there was no overcrowding. Hrdy, therefore, proposed that infant killing was not a social pathology but a male reproductive strategy to garner reproductive access to females. In the years to come, sexual selection as an explanation for infanticide became the main focus of research on Hanuman Langurs. In 1977, the Indo-German project, conceptualized by Christian Vogel, was launched at Jodhpur to study interrelations between individual life-histories and troop histories (Vogel 1988). This project continued for many years and sponsored several German researchers who worked on Jodhpur langurs. These langurs feed on 35 species of plants, and a unique foraging 'invention' is feeding on the 'waternut' *Trapa natans* recently introduced to the region. The main food items of a large number of troops were *Prosopis juliflora* and the food provided by humans (Winkler 1981). The females reached menarche at the age of 29 months, cycled for 24 days, had gestation of about 200 days, and an inter-birth interval of 15.3 months. About 80% infants survived for six months but only 35.9% completed two years of life (Winkler et al. 1984). Volker Sommer (Sommer 1985) (<https://www.ucl.ac.uk/anthropology/people/academic-and-teaching-staff/volker-sommer>), a student of Christian Vogel at Gottingen, and hosted by S.M. Mohnot studied the Jodhpur langurs for his Ph.D. between October 1981 and December 1982, and again as a post-doctoral research fellow in 1986–1987. He witnessed and also inferred many cases of infanticide and discussed the male reproductive strategy with respect to three conditions, postulating that the infanticidal male is not the father of the killed infants, but actually sires the subsequent offspring, and infanticide shortens inter-birth interval, and found that these conditions were largely met (Sommer & Mohnot 1985).

Makwana (1979b) studied rhesus monkeys in Asarori, Siwaliks, and reported group size to vary from 6 to 90 with a male to female ratio of 1:2.7. Home range size varied with group size, and the daily range was about 1803 m. P.R. Ojha (Ojha 1979) observed that the tail carriage of the Rhesus Macaque alpha male with the basal half carried upright, distal part leaning forward and the tip forming a loop is unique and is not shown by any other member in the group. The upright posture is usually assumed in tense situations such as intergroup interactions or alarms. L.S. Rajpurohit (Rajpurohit 1987) (https://www.researchgate.net/profile/Lal_Rajpurohit2) reported that the ousted males did not achieve residency in

their natal groups and weaned sons follow their fathers after ousting. Emigrating males have a higher mortality than females resulting in female-biased sex ratios. G. Agoramoorthy (Agoramoorthy 1987) observed several cases of abortions in Hanuman Langurs happening probably due to stress after male take-over of a group and conjectured that an abortion may be a female reproductive strategy to avoid infanticide after the birth of the infant. Since the inter-birth interval in females whose infants were killed by the new males was shorter than other females, it appears that the male achieves higher reproductive success by infanticide. Hanuman Langurs are primarily folivorous but were also observed to spend considerable time feeding on insects, especially during the monsoon season, which supported the 'energy/nutrient maximization' hypothesis (Srivastava 1989). Carola Borries (Borries 1989) (<https://www.stonybrook.edu/commcms/anthropology/faculty-and-staff/borries.php>), a student of Christian Vogel, and hosted by S.M. Mohnot, studied competition in female langurs of Jodhpur from October 1984 to January 1986. She found that the young females occupied high ranks, and the hierarchical position of a female declined with age. Reproductive success was rank related that declined significantly from high, over middle, to low ranking females (Borries et al. 1991). In Kumbalgarh Wildlife Sanctuary, there were about 69% bisexual and about 31% all-male band groups of Hanuman Langurs, and their social organization was the same as in the Jodhpur langurs (Chhangani 2000) (https://mgsubikaner.ac.in/wp-content/uploads/2015/10/1396502908-2014Faculty_MemberDrAnilKumarChhangani.pdf). D.S. Rajpurohit (Rajpurohit 2005) determined dominance hierarchy and its role in social organization in Hanuman langurs, and G. Sharma (Sharma 2007) reported details of paternal care in these langurs. In 1994, S.M. Mohnot launched a mega research project (Indo-US Primate Project) for a period of five years, which was further extended by three years. Most of the research under this project was in northeastern India where Mohnot collaborated with P.C. Bhattacharjee at Gauhati University, Guwahati. Since most researchers were from the northeast, we will have a separate section for the research on northeastern Indian primates.

Hanuman Langurs being widespread have also been studied in different habitats in India. The Himalayas are a different ecological niche and the Himalayan Hanuman Langurs, though studied at different altitudes in Indian and Nepalese Himalayas, exhibit traits such as multi-male groups which are different from the langurs in the Indian plains that are largely uni-male (Bishop 1975).

Hanuman Langurs in Kanha Tiger Reserve are organized in mostly uni-male groups with an adult sex ratio of 1:7.9. In Kanha, an attack by a male band on the uni-male study group, resulting in killing of three infants, and the timing of takeover with respect to the birth season, supported the 'sexual selection' and not the 'social pathology' hypothesis (Newton 1984). At Morni Hill ranges of Siwalik Hills, 75% groups of Hanuman Langurs were uni-male with a sex ratio of 1:3.2, and these langurs shifted home ranges seasonally (Bala 2013). In Bidar District of Karnataka, there were 142, 55, and 28 uni-male, multi-male and all-male groups, respectively, with a total population of 6,384 individuals (Patil 2019). In the six study groups, the population size of 199 in 2012 increased to 270 in 2014.

University of Delhi and Vatavaran

Several studies were carried out on primates at the Department of Anthropology, University of Delhi by Praveen K. Seth. Though most of his work was on primate anatomy (which is beyond the scope of this article), Iqbal Malik (<http://www.vatavaran.org/>) and he carried out studies on population trends and behavior of Rhesus Macaques. The surveys conducted between 1975 and 1980 revealed that in several localities, the population of Rhesus Macaques increased by 66–79%, mainly due to human-provisioning (Seth & Seth 1983a; Malik et al. 1984). The populations, however, showed a declining trend in the later years (Malik 1989). Malik was also involved in translocations of urban Rhesus Macaques and found that most translocated monkeys appeared to exhibit normal behavior (Imam et al. 2000).

University of Mysore, Mysuru

Mewa Singh (<http://uni-mysore.ac.in/psychology/faculty/dr-mewa-singh>) started research on primates at the University of Mysore in 1975 and has studied Bonnet, Rhesus, Lion-tailed, and Long-tailed macaques, Hanuman and Nilgiri langurs, and Slender Loris. The group has carried out extensive studies on the ecology, behavior, and conservation management, both in situ and ex situ, on primates with over 150 publications (see <https://uni-mysore.ac.in/psychology/faculty/dr-mewa-singh>). Long-term field studies were initiated on Slender Loris (Singh et al. 1999, 2000; Kumara et al. 2006) and other primates (Kumara & Singh 2004) in various habitats. Population trends in Bonnet Macaques have been monitored in and around Mysuru for over 30 years showing a nearly 70% decline in the population (Erinjery et al. 2017a). Bonnet Macaques showed laterality in various activities as a division of labor

between the two hands (Mangalam et al. 2014, 2016). Sindhu Radhakrishna (Radhakrishna 2001) (<https://www.nias.res.in/professor/sindhu-radhakrishna>) carried out a 21-month-long study on the Slender Loris in the forests of Dindigul, Tamil Nadu. Most of the aggressive interactions among individuals were observed in the contexts of territorial defense and mating; individuals communicated through chemical and vocal signals, and immigrations were frequently seen in the study area (Radhakrishna & Singh 2002). Females were seen to be in estrus largely in October–December and births occurred in April–June; gestation lasted for 5.5 months and there was an inter-birth interval of seven months (Radhakrishna & Singh 2004). Anantha Krishna Sharma (Sharma 2002) (https://www.researchgate.net/profile/Ananthakrishna_Sharma) studied reproductive biology of the Lion-tailed Macaques in the Western Ghats and reported that there were two birth peaks in January to April and in September to December, which remained constant over the years and across forest fragments of different sizes (Sharma et al. 2006). In contrast, births in captive Lion-tailed Macaques occurred throughout the year. H.S. Sushma (Sushma 2004) (<https://www.sacon.in/adjunct-scientist/>) studied sympatric Lion-tailed Macaques, Nilgiri Langurs, Bonnet Macaques, and Indian Giant Squirrels and found that both macaque species had relatively narrow food niche breadth and high niche overlap resulting in co-occurrence of these species only in a few months of the year. On the other hand, Nilgiri Langurs had a low niche overlap with Lion-tailed Macaques and both langurs and squirrels had broad niches resulting in tolerance and co-occurrence of all three species (Sushma & Singh 2006). B.A. Krishna (Krishna 2007) studied maternal and parental investment patterns in Lion-tailed Macaques and observed that weaning occurs from five and a half months to about nine months of age of the infant (Krishna et al. 2008) and the weaning patterns indicated that the dominant females are positively biased towards their male offspring (Singh et al. 2007). Kuladeep Roy (Roy 2011) (https://www.researchgate.net/profile/Kuladeep_Roy) also studied sympatric primates in a different forest and found that though there was a high niche overlap between Lion-tailed and Bonnet macaques for about two months, it occurred at the time of resource abundance of the shared resources, and as a result, both of these macaques species and the Hanuman Langur which is a folivore, unlike frugivore macaques, could co-exist throughout the year (Singh & Roy 2011). Kavana T.S. (Kavana 2015) and Joseph J. Erinjery (Erinjery 2016) (https://www.researchgate.net/profile/Joseph_J_

Erinjery) studied individual differences indicating behavioral variability in macaques (Bonnet and Lion-tailed) and langurs (Nilgiri and Hanuman), respectively. Behavioral variability was higher in macaques than in langurs (Erinjery et al. 2017b). The ideal gas model approach showed that primates in the Western Ghats do not form active associations with each other (Erinjery et al. 2015). In context to langurs, Hanuman Langurs are more social than Nilgiri Langurs as the latter are more folivorous and require to spend much time in resting to digest leaves (Kavana et al. 2015). Prerna Singh (Singh 2017) observed abandonment of infants by Bonnet Macaque females after a group split, and reported that weaning may also occur without aggressive responses from mothers. Matthew Cooper from University of Georgia studied Assamese Macaques under the supervision of Irvin Bernstein in 1997–98 for his Ph.D. (Cooper 1998) and worked as a post doc in 1999–2001 at the University of Mysore on dominance style and relationship quality in Bonnet Macaques (Cooper et al. 2004a,b). Under the supervision of Clifford Jolly, Lisa Schlotterhausen (Schlotterhausen 2000) (<https://as.nyu.edu/departments/anthropology/graduate/alumni/doctoral-alumni/schlotterhausen-lisa.html>) from New York University, New York in affiliation with the University of Mysore reported that wild Bonnet Macaques moved and fed on more food items but engaged less in social activities than the commensal bonnets. Anna Nekaris (Nekaris 2000) (<https://www.brookes.ac.uk/templates/pages/staff.aspx?wid=&op=full&uid=p0029554>) from Washington University, Missouri under the supervision of David Tab Rasmussen, affiliated with the University of Mysore and observed that the Slender Loris was exclusively faunivorous feeding on insects and small vertebrates, and distributed their activity budget evenly between foraging and travelling. Cornelia Bertsch from Austria collaborated with the research group and studied Lion-tailed Macaques from 1998 to 2003 in the Anamalai Tiger Reserve.

National Institute of Advanced Studies, Bengaluru

At NIAS, primate research was initiated by Anindya Sinha (<https://www.nias.res.in/professor/anindya-sinha>) and joined later by Sindhu Radhakrishna. The group has been focusing on primate ecology, behavior, conservation, and cognition. After Simonds (1965), Sinha (2001) provided the first detailed description of distribution, ecology, and behavior of the Bonnet Macaque. Inarguably the best long-term field study on behavior of any primate species in India is Sinha's research on Bonnet Macaques in Bandipur National

Park, Karnataka, the study now covering a period of two decades. The Bonnet Macaques usually live in bisexual groups with each group having several adult males and adult females. Sinha, however, found that in Bandipur, 11 of the 21 groups of Bonnet Macaques were uni-male-multi-female groups (Sinha et al. 2005). The origin and evolution of this unique social organization in the Bonnet Macaque has been explained through a research-based model illustrating the following process (Sinha & Mukhopadhyay 2013). In deciduous forests, food becomes scarce and patchy in the dry season, and at the same time, tourists passing through the forest offer food which is rich and clumped. These two factors induce intense competition among females in a multi-female-multi-male group, leading to group fission, resulting in small groups of females. In such a situation, it becomes easier for a single male to monopolize reproduction, and consequently, the evolution of uni-male social organization takes place.

Sinha (Sinha et al. 2005) and his group also described a new macaque species, the Arunachal Macaque *Macaca munzala* from the forests of Arunachal Pradesh. Four students have carried out their Ph.D. research with Sinha. Rishi Kumar (Kumar 2012) (https://www.researchgate.net/profile/Rishi_Kumar24) reported the distribution, demography, and behavioral ecology of mixed groups of Bonnet and Rhesus macaques in peninsular India and observed that Rhesus Macaques were extending their range into the range of Bonnet Macaques, due perhaps to human intervention (Kumar et al. 2011, 2013). Mayukh Chatterjee (Chatterjee 2013) (<https://www.wti.org.in/members/mayukh-chatterjee/>) studied behavioral flexibility and social diversity in Bonnet Macaques with special reference to uni-male groups. Ecological differences can cause intra-specific and even intra-population differences in social systems which, in turn, produce flexibility and variability in behavioral strategies such as grooming and proximity. Narayan Sharma (Sharma 2013) (https://www.researchgate.net/profile/Narayan_Sharma3) studied effects of habitat fragmentation on primate populations in Upper Brahmaputra Valley where at least one species was lost in the last 30 years. Many, largely habitat specialist species, have shown decline in their populations whereas a more commensal and generalist Rhesus Macaque has become more abundant. Geographical distance, dissimilarity in spatial features and anthropogenic factors affected turnover in primate species composition. Shreejata Gupta (Gupta 2016) (https://www.researchgate.net/profile/Shreejata_Gupta2) found that Bonnet Macaques produce flexible and intentional gestures with context

variability. Gestures such as those used in play decrease with age and others such as those related to aggression and affiliation appear at the adult stage. Females had a higher repertoire of signals than males. Anindya Sinha also hosted Avanti Mallapur (<https://www.linkedin.com/in/avanti-mallapur-b9b2a615>), a Ph.D. student from the University of Edinburgh, Edinburgh (Mallapur 2005). Mallapur studied the effect of visitor presence on behavior of captive Lion-tailed Macaques and found that the visitor presence might adversely affect welfare of animals causing an increase in abnormal and other social behaviors (Mallapur et al. 2005).

Sindhu Radhakrishna joined NIAS in 2002 and continued surveys on lorises in northeastern India and Kerala. In Meghalaya, the Bengal Slow Loris was found in only two of the 16 sites surveyed and the habitat was found to be severely affected by anthropogenic activities (Radhakrishna et al. 2010). In Tripura, the encounter rate of the Slow Loris was 0.22 individuals (Swapna et al. 2008). The Slender Loris was found in 22 of the 36 forest ranges surveyed in Kerala with an abundance ranging from 0.02 to 1.44 individuals/km (Radhakrishna et al. 2011). She is also tracing human-monkey relationships in literature and folklore (Radhakrishna 2018). Asmita Sengupta (Sengupta 2015) (<https://www.atree.org/users/dr-asmita-sengupta>) studied seed dispersal as an ecosystem function by Rhesus Macaques in Buxa Tiger Reserve in 2012–2014. Macaques dispersed 84% of the 49 species they fed on. The macaque-handled seeds were largely deposited outside the tree canopy, were undamaged and had enhanced germination. Provisioning reduced the daily range of macaques and resulted in lesser seed dispersal than in unprovisioned macaque group. Shaurabh Anand (Anand 2019) (https://www.researchgate.net/profile/Shaurabh_Anand3) studied perceptions about human-Rhesus Macaque conflict in Himachal Pradesh. Whereas higher level forest officers proposed strict rules for management of negative interactions, the lower level officers agreed more with the farmers who actually suffered losses. Forest officers believed that sterilization and culling of monkeys were the effective interaction resolution measures, the farmers found these ineffective and against cultural and religious beliefs. Therefore, there appears to be higher human-human conflict than human-animal negative interactions (Anand & Radhakrishna 2020).

Northeastern India and Gauhati University

Northeastern India is an extremely rich region for primate diversity with 13 of the 27 Indian primate species including loris, macaques, langurs, and small apes found

there. Until the early 1980s, virtually nothing was known about these primates in northeastern India. Anwaruddin Choudhury (Choudhury 1989) (https://en.wikipedia.org/wiki/Anwaruddin_Choudhury) was the first person to begin primate research in northeastern India in 1986 when he reported that the Pig-tailed and the Stump-tailed macaques were restricted by the Brahmaputra River towards west of their range. He also discovered a new population of macaques which he described as a subspecies of *Macaca thibetana* but the same has now been described as a new species with the name *Macaca munzala*.

In one of the earlier studies conducted in 1987–1991 on the Golden Langurs (Dutta 1992), it was found that they were confined to the northwestern belt of Assam. The group had 7–13 individuals and shifted the home range seasonally. They fed on flowers, blossoms, leaves and fruits of 34 plant species. Atul Kumar Gupta (Gupta 1997) (<http://tdu.edu.in/governance/akgupta/>) observed that due to continuing loss of forests, primate populations in northeastern Indian region were being adversely affected.

Although a few field studies were carried out in the 1980s and 90s, it was in 1994 that long-term studies on several primate species in northeastern India were initiated under the Indo-US Primate Project with S.M. Mohnot of J.N.V. University, Jodhpur and P.C. Bhattacharjee of Guwahati University as the principal investigators. Prabal Sarkar (Sarkar 2000) (<https://www.ustm.ac.in/zoology-list-of-faculties/dr-prabal-sarkar/>) reported that in Assamese Macaques, a provisioned group spent more time on clumped resources than forest groups. As a result, the provisioned monkeys were more aggressive towards each other, and to reduce tension, also indulged more in grooming than the forest monkeys. Jayanta Das (Das 2002) found Gibbons in three and five reserved forests in Silchar and Karimganj divisions respectively with a median group size of three. In Borajan where the forest damage was extensive, Gibbons were forced to move on ground to cross between food patches and they showed many vigilance behaviors while walking on open grounds. Dilip Chetry (Chetry 2002) (https://www.researchgate.net/profile/Dilip_Chetry2) recorded altitudinal distribution range of Stump-tailed Macaques from 50–1,300 m in northeastern India with group size ranging from 2–63 individuals. Home range size was 336–587 ha. These monkeys fed on 200 food plants. Stump-tailed Macaques are terrestrial and non-seasonal breeders. Habitat loss, fragmentation, jhum cultivation, and traditional hunting were determined as the major threats. Rekha

Medhi (Medhi 2004) (https://www.researchgate.net/profile/Rekha_Chetry) studied the behaviour of a semi-provisioned introduced troop of Golden Langur outside its distribution range. Grooming played an important role in maintaining inter-individual relationship. She also reported development of neonate, neonate behaviour, intra-troop social dynamics and development of inert individual relationships. Jihosuo Biswas (Biswas 2004) (https://www.researchgate.net/profile/Jihosuo_Biswas) found that in Golden Langurs, the home ranges of the two study groups were 25 and 58 ha. Home range size correlated with group size and there was an overlap between ranges of different groups. There was a bimodal feeding peak in the mornings and evenings. These langurs spent about 44.75% of their time resting, probably to digest leaves which are their primary food items ingested. Joydeep Bose (Bose 2005) reported that Phayre's Leaf Monkey is found only in southern Assam, Tripura, and Mizoram. The home range size correlated with group size and varied from 2.7 to 17.6 ha with a day range of 304 to 592 m. Time-activity budgets differed between groups in plantations and forests. Leaves (54%), followed by shoots (23.2%) and fruits, flowers, and seeds were ingested. Dhiraj Kumar Borah (Borah 2010) studied ecology and behavior of Capped Langurs and found that though the time-activity budgets did not differ, the home range was larger and the day time length of movement was smaller in the undisturbed habitat than in the disturbed habitat. Langurs spent most time resting, followed by feeding, and grooming was the predominant social activity. Nabajit Das (Das 2013) (https://www.researchgate.net/profile/Nabajit_Das) found Bengal Slow Lorises in seven protected areas and two reserved forests in Assam with a density ranging from 2.78 to 9.21 animals/km². Lorises spent 42.59% of their time resting, followed by 27.46% in locomotion, and 21.28% in feeding. They used 44 trees and 12 lianas and the food consisted of 80.93% plant exudates and only 2.32% animal matter. The average home range size was 15.60ha.

PRIMATE STUDIES FROM THE NORTH-EAST IN OTHER UNIVERSITIES

University of Cambridge

Kashmira Kakati (Kakati 2005) (https://www.researchgate.net/profile/Kashmira_Kakati/research) found that in Hoolock Gibbons, the encounter rates were 0.09 animal/km, 0.23 animal/km, and 0.58 animal/km in small (<5km²), medium (20–30 km²), and large

(>100km²) forest patches, respectively. Likewise, the group size was 2.5, 3.29, and 3.9 in small, medium, and large fragments. There were fewer young in small fragments than in medium and large fragments.

North Eastern Hill University, Shillong

G.S. Solanki (Solanki 1987) and Awadhesh Kumar (Kumar 2006) (<https://nerist.ac.in/forestry/faculties/awadhesh>) studied the behavior of Capped Langurs in Pakhui Wildlife Sanctuary in Arunachal Pradesh and found that the langurs spent 54% time resting and 36% in feeding. Age-sex classes did not differ in their time-activity budgets. Most activities occurred between the heights of 10 and 15m. Langurs fed on 52 plant species, mostly of the family Moraceae, and 68% of their diet comprised leaves. Hunting for meat was the major threat for these langurs.

Mizoram University, Aizawl

Zothansiam (Zothansiam 2013) (<https://mzu.edu.in/department-of-zoology/>) found that Stump-tailed Macaques were scarcely distributed to the south bank of Brahmaputra River. In a captive group of Stump-tailed Macaques, copulations in females correlated with sexual attractiveness indicated by the bright red genital skin color. Males often indulged in homosexual behavior perhaps to regulate aggression. The forest study group fed on fruits, leaves, shoots, and flowers of 36 plant species. Pallab Deb (Deb 2015) studied the Western Hoolock Gibbon in southern Assam and Mizoram and found 51 individuals in 16 family groups with a mean group size of 3.1. Tree density varied among different habitats. Gibbons used tree from 5 to 30 m, though most of their activities were between the heights of 6 and 25 m. They fed on fruits, flowers, leaves and petioles of 32 plant species. Most of the habitats of Gibbons were under anthropogenic pressures.

North Orissa University, Baripada

Raju Das (Das 2012) (https://www.researchgate.net/profile/Raju_Das2) found that in the Chirang Reserved Forest, Golden Langurs fed on 91 plant species of trees and climbers. The spectrum of food plant species in the diet of langurs appeared to be determined by the floristic composition of the habitat.

Assam University, Silchar

Mofidul Islam (Islam 2015) (https://www.researchgate.net/profile/Mofidul_Islam) studied Hoolock Gibbons in the Inner-Line Reserved Forest in Assam and observed that gibbons mainly fed on *Ficus*,

Artocarpus, *Dysoxylum*, *Gmelina*, and *Syzygium*. Gibbon population positively correlated with canopy cover and tree density. The dramatically changing land cover due to reasons such as shifting cultivation is a major threat to the gibbons in the region.

North Eastern Regional Institute of Science and Technology, Nirjuli, India

Kuldip Sarma (Sarma 2015) studied the Eastern Hoolock Gibbon in Lower Dibang Valley and Lohit districts of Arunachal Pradesh and found 77 groups and three solitary individuals with a mean group size of 3.04. He estimated the presence of 6,953 groups of gibbons with 21,710 individuals in the state. Groups in protected forests had larger home ranges than in unprotected forests.

Tezpur University, Tezpur

Mrigankhi Borah (Borah 2016) found that Hoolock Gibbons in Hoolongapar fed on 54 plant species in which *Ailanthus*, *Ichnocarpus*, *Trichosanthes*, and *Ficus* were the most preferred species. Fruits comprised 51.14% of the diet. *Vatica lanceaefolia* and *Artocarpus chaplasha* grew and survived better in the gaps than in understory whereas *Artocarpus chaplasha* grew better in the understory.

SOME OTHER CENTERS OF PRIMATE RESEARCH

Salim Ali Center for Ornithology and Natural History, Coimbatore

Ajith Kumar initiated a study to explore the impact of habitat fragmentation on various taxa including primates. G. Umapathy (Umapathy 1998) (<https://www.ccm.res.in/People/Research-Group/G-Umapathy>) found that in forest fragments, tree density and canopy height best predicted occurrence of primates, and it is suggested that arresting further degradation, and improving quality, of habitats along with retention of jackfruit orchards may help primate conservation in the fragmented landscape (Umapathy & Kumar 2000). An Indo-German Project funded by the Volkswagen Foundation with Werner Kaumanns from German Primate Centre, Gottingen and Ajith Kumar from SACON as Principal Investigators was launched to further study the effect of forest fragmentation. Though not based at SACON, the effect of forest fragmentation on the behavior of Lion-tailed Macaques was also studied by Shaily Menon (Menon 1993), a student of Frank Poirier from The Ohio State University. Menon

studied groups of Lion-tailed Macaques in 1989–91 in a degraded forest fragment near Valparai and in an undisturbed forest at Varagaliyar and reported that the monkeys in fragments spent more time in ranging than resting or feeding, and were more terrestrial than the macaques in undisturbed forest. R. Krishnamani (Krishnamani 2002) (https://www.researchgate.net/profile/Krishnamani_Ramanathan) reported that of the 190 woody plant species in the study area, Lion-tailed Macaques used 74 as food trees. The relative density of these species being 57.1% indicated that the habitats in Karnataka could support a good population of Lion-tailed Macaques. H.N. Kumara (<https://www.sacon.in/division/conservation-biology/#ffs-tabbed-12>) joined the institute in 2010 and continued studies on primates. Surveys were carried out on Lion-tailed Macaques, Nilgiri Langurs, and Slender Loris in the unexplored forests, and several conservation actions were initiated, resulting in the formation of Sharavathi Lion-tailed Macaque Wildlife Sanctuary. K. Santhosh (Santhosh 2017) (https://www.researchgate.net/profile/K_Santhosh2) reported that in the Lion-tailed Macaque in its northernmost population in the Western Ghats, the mean monthly day path length correlated positively with the number of fruiting trees, and tree density and fruit tree density also correlated positively with habitat use (Santhosh et al. 2015). Kumara initiated long-term studies on the Nicobar Long-tailed Macaque (NLTM). This island population surveyed earlier (Umapathy et al. 2003) suffered a heavy loss to the 2004 Indian Ocean tsunami, however, in the following decade or so, the population of these macaques has not only recovered but increased (Velankar et al. 2016). Arijit Pal (Pal 2018) (https://www.researchgate.net/profile/Arijit_Pal4) found that in NLTM, the number of births correlated with the monthly rainfall, and about 71% of the births occurred in the rainy season (Pal et al. 2018a). These macaques showed six extractive foraging behaviors, including some being tool-aided, and teeth flossing (Pal et al. 2018b). Partha Sarathi Mishra (Mishra 2020) (https://www.researchgate.net/profile/Partha_Mishra3) found reciprocity, though not equitable, in grooming among NLTM males, but no rank-related differentiation of affiliation, indicating lack of social bonds in this subspecies (Mishra et al. 2020a). Females directed grooming towards high ranking males, though dominance hierarchy was less steep than expected in *Macaca fascicularis* (Mishra et al. 2020b).

University of Rajasthan, Jaipur

It was found that multi-male Hanuman Langur groups split only after a takeover by a male from an all-

male band, and the split resulted in formation of two uni-male groups (Mathur & Manohar 1990). In another study, Mathur & Manohar (1992) demonstrated that population density and not habitat disturbance was correlated with takeover in Hanuman Langurs. Reena Mathur (https://www.researchgate.net/profile/Reena_Mathur2) at the University of Rajasthan also hosted Linda D. Wolfe who arrived from the USA in 1984 on an NSF grant and studied feeding ecology of Rhesus Macaques. The monkeys in a town group foraged more, moved less, engaged in fewer aggressive acts, and slept less during the day than the monkeys in a forest/temple complex (Wolfe 1992).

Himachal Pradesh University, Shimla

R.S. Pirta (https://www.researchgate.net/profile/Raghubir_Pirta) carried out his Ph.D. research at Kashi Vidyapith University, Varanasi where he studied cooperative behavior in Rhesus Macaques and reported that adult females were the main groomers, and grooming duration increased during the mating season; play was largely restricted to infants and juveniles (Pirta 1983). In cooperative attacks, adult females were help-givers in both forest and urban groups, though cooperative attacks were more among the latter (Pirta 1984). Human disturbance caused more detrimental effects on Hanuman Langurs who were largely restricted to broad-leaf forests than Rhesus Macaques who often visited towns too (Ross et al. 1993). Anita Chauhan (Chauhan 2009) (https://www.researchgate.net/profile/Anita_C Chauhan5) reported that the Rhesus Macaques subsisting in temple areas interacted more aggressively with humans than the macaques in a marketplace and the Hanuman Langurs, due possibly to the heavy dependence of the temple macaques on human resources. Santosh Kumar Sahoo (Sahoo 1993) carried out a study from 1988 to 1991 in Shimla and found that the Rhesus Macaques engaged in agonistic interactions more than the Hanuman Langurs, and most of these agonistic interactions occurred during human feeding. Pramod Kumar (Kumar 1992) studied Rhesus Macaques and Hanuman Langurs in Shimla between 1987 and 1991 and found that populations of both species increased 26.61% and 25.86%, respectively, during the study period. Rhesus Macaques were more urban than langurs and the adult sex ratio in the two species was 1:2.3 and 1:5.6, respectively. As Shimla gets very cold in winter, there were significant seasonal variations in the behavior of both species.

Kerala Forest Research Institute, Peechi

K.K. Ramachandran (<http://www.kfri.res.in/whois.asp?ID=10&sub=1>) initiated primate research at KFRI, primarily on Lion-tailed Macaques and Nilgiri Langurs and supervised Ph.D. research of two students. Gigi K. Joseph (Joseph 1999a) (<https://nirmalacollege.ac.in/department-faculty/dr-gigi-k-joseph/>) reported the presence of 14 groups of Lion-tailed macaques and 85 groups of Nilgiri Langurs in Silent Valley. The food of Lion-tailed Macaques comprised 91% plant and 9% animal matter. The average group size of Nilgiri Langurs was 5.89. R. Suganthasakthivel (Suganthasakthivel 2011) (https://www.researchgate.net/profile/R_Suganthasakthivel) found a total of 13 groups with an average group size of 15.4 of Lion-tailed Macaques and 23 groups of Nilgiri Langurs with an average group size of 6.5 in the Nelliampathy forests. The relative abundances of diurnal arboreal mammals ranged between 1.2 and 12.6 individuals per 10km.

Centre for Cellular and Molecular Biology, Hyderabad

After his Ph.D. from SACON and post-doc from University of Mysore, G. Umopathy joined Laboratory for the Conservation of Endangered Species (LaCONES) at CCMB, Hyderabad and continued his studies on effects of habitat fragmentation on demography, genetic status, hormones, and endoparasites in primates in the Anamalai Hills. Sustained habitat fragmentation and exposure to human and livestock increased the prevalence of endoparasite in Lion-tailed Macaques (Hussain et al. 2013) and Nilgiri Langurs (Tiwari et al. 2017). M.S. Ram (Ram 2018) (https://www.researchgate.net/profile/Ram_M_S2) constructed phylogeography of the Lion-tailed Macaque across its range and found that these macaques in forest fragments had depleted mitochondrial diversity and that the Palghat gap in the Western Ghats separated their populations into two almost 2.11 million year ago (Ram et al. 2015). In the Endangered Golden Langur in Assam, though the genetic diversity was high, populations in smaller forest fragments showed lower nucleotide diversity than in larger fragments (Ram et al. 2015).

Aligarh Muslim University, Aligarh

Ekwal Imam (Imam 2000) (https://www.researchgate.net/profile/Ekwal_Imam) monitored populations of Rhesus Macaque near Aligarh. In the study region, 963 monkeys in 1993 increased to 1337 in 1995 with a birth rate of 0.81 infant/female/year and high infant survivorship. These observations agree with general trends in population increase in Rhesus Macaques in

several places in 1980s and 1990s.

University of California, Davis

Uma Ramakrishnan (Ramakrishnan 1999) found that in the wild bonnet macaques, discrimination of predators, and anti-predatory responses, develop ontogenetically as juveniles, subadults and adults respond to the stimuli differently.

University of Burdwan, Bardhaman

Sangita Mitra (Mitra 2000) studied behavior of Assamese Macaques near Darjeeling during 1996 and 1999 in broadleaf forests up to 2,500m, though the macaques were found mostly between 200 and 500 m. The adult sex ratio was 1:2.88 and the ranges varied from 0.6 to 3.5 km².

University of Calicut, Kozhikode

Arboreal mammals with special reference to the Nilgiri Langur were studied in the high ranges in Kerala (Joseph 1999b). A surprising finding was that Nilgiri Langurs were observed to feed on fruits (50%) more than on leaves (30% and flowers (20%). More carbohydrates containing food were used by langurs in summer and more protein and lipid were consumed during rainy season and winter.

Maharaja Ganga Singh University, Bikaner

Rhesus Macaques in the Aravali Hills were active during mornings and evenings in summer, but more active during the day in winter (Sharma 2009).

Indian Institute of Science, Bengaluru

Though taxonomy research on primates has been going on in the Indian Institute of Science for long, it is only recently that an ecological study by Mehreen Khaleel (Khaleel 2020) (https://www.researchgate.net/profile/Mehreen_Khaleel) has shown that Hanuman Langurs in Kashmir Himalaya are distributed wider than previously thought. These langurs show seasonal variations in home ranges and diet in accordance with the energy maximizing strategy.

University of Madras, Chennai

R. Sasi (Sasi 2018) provided the status and distribution pattern of lion-tailed macaque and slender loris for the less explored regions including Parambikulam landscape and Megamalai-Srivilliputhur-Tirunelveli hills in the southern Western Ghats.

Bharathiyar University, Coimbatore

Shanthala Kumar (Kumar 2019) (https://www.researchgate.net/profile/Shanthala_Kumar) reported that the relocation of Bonnet Macaques from urban areas to a wild habitat facilitated the spread of alien endoparasites to Lion-tailed Macaques where these parasites were otherwise absent. Even on an isolated island system, the increased use of human-dominated spaces by Nicobar long-tailed Macaques has resulted in an increased endoparasite richness and prevalence.

FUTURE

National survey of primates

There have been some attempts in the past to census primates in different regions of the country. The earliest surveys were on the Rhesus Macaques in certain parts of northern India initiated by Charles Southwick (described earlier in this article). Zoological Survey of India undertook surveys in northern India under the leadership of R.P. Mukherjee (Mukherjee & Mukherjee 1972), in southern India by G.U. Kurup (Kurup 1984), and in the northeastern India by J.R.B. Alfred (Alfred & Sati 1990; Alfred et al. 2004) and some others at localized places the details of which are available with ZSI at <http://faunaofindia.nic.in/>. Primates in northeastern India were also surveyed under the Indo-US Primate Project (Srivastava 1999). Ullas Karanth (Karanth 1985) surveyed Lion-tailed Macaques in the state of Karnataka. Most of these surveys are now outdated and were largely localized. It is only recently that a systematic survey on Rhesus Macaques has been carried out in Himachal Pradesh (Kumara & Singh 2020). There have been several status assessments of primates by Zoo Outreach Organization including PHVAs for the Lion-tailed Macaque (Kumar et al. 1995), primates of South Asia (Molur et al. 2003) and Hoolock Gibbon (Molur et al. 2005). There is, therefore, an urgent need to take up a nationwide survey of primates in India.

Population monitoring

Population dynamics can be studied if a population is monitored for decades. Most research studies are of two to three year durations, and hence cannot bring out the stochasticity of primate populations. A lesson is learnt from the monitoring of Bonnet Macaque populations around the city of Mysore for over 30 years now by Mewa Singh and his team which has shown a ~70% decline in these macaques (Erinjery et al. 2017a). We need to identify populations that are representatives

of each species in different habitats and monitor them at least once in three years for several decades to comprehensively know the trends.

Taxonomic studies

Several species of primates in India are classified into subspecies. In order to prioritize conservation, it is necessary that genetic studies are carried out on all subspecies to determine whether there are more distinct species. For example, the Hanuman Langur was considered as only one species but it is now shown that there are many distinct species of this langur (Ashalakshmi et al. 2015). Morphologically similar populations of the Lion-tailed Macaque north and south of the Palghat gap have been genetically differentiated for the past 2.1 million years (Ram et al. 2015).

Ecological and behavioral research with long term field studies

There are many subspecies of few primate species in India for which even baseline ecological and behavioral information are not yet available. There is therefore a need to not only study these subspecies, but also all species across varied habitats. There are hardly any long-term field studies carried out in India. The one carried out by Anindya Sinha and his group on Bonnet Macaques at Bandipur brought out excellent results about evolution of sociality (Sinha & Mukhopadhyay 2013). A study on the Himalayan Grey Langur near Chamba by the Wildlife Information Liaison Development / Zoo Outreach Organization has been going on since 2012 (<https://www.speciesconservation.org/case-studies-projects/himalayan-grey-langur/9744>) though the results are yet to be published.

Conservation and management

Many species of primates, because of their threatened or vulnerable status, require active intervention for in situ management. Wildlife Trust of India has been carrying out rehabilitation of Eastern Hoolock Gibbon from small and isolated forest fragments to large forest complexes (Roy et al. 2015). Since different species inhabit different ecological settings and experience anthropogenic pressures, Singh (2019), for example, has provided approaches to management of urban- and forest-dwelling species. Likewise, appropriate management strategies need to be synthesised through dialogues between primate biologists and wildlife managers.

Conservation breeding

Several species of primates in India are threatened. An expert group of primatologists and wildlife managers should decide which of these species require conservation breeding in order to develop sustainable captive populations for restocking or rehabilitation, if required in the future. An initiative has already been taken for conservation breeding of Lion-tailed Macaques but it has not yielded desired results. Perspectives for systematic management on the basis of analysis of conservation breeding programs in various countries have been provided to aide planning (Kaumanns et al. 2005, 2013, 2020).

National Primate Research Centre

There is a long pending demand of primatologists to have a National Primate Research Centre that should be managed both by primate biologists and wildlife managers, and funded by the Ministry of Environment, Forest and Climate Change and Ministry of Science and Technology, Government of India. This Centre would not only initiate new research but will also coordinate among various institutions and governmental agencies in the country that are engaged in primate research and management. The Primate Centre could also host a National Primate Museum to showcase primate taxa, educate people and build awareness for their protection and conservation.

A Platform for Interactions

A Primatological Society of India was established in the late 1970s but it became inactive in the 1980s. Since then, there has not been a single platform for Indian primatologists to meet and exchange information except a CAMP meeting conducted by Zoo Outreach Organization (Molur et al. 2003). An enthusiastic group of Indian primatologists have established a new platform named, Association of Indian Primatologists (<https://www.indianprimates.org/>) in 2019 and conducted its first national workshop at Indian Institute of Science, Bengaluru in November 2019. This platform needs to be strengthened.

International Cooperation

Only three important international meetings have been held in India: the 7th Congress of the International Primatological Society at Bengaluru in January 1979, International Symposium on Primates at Jodhpur University in February 1982, and the 7th Asian Primate Symposium at Gauhati University in February 2020. The proceedings of the Bengaluru and Jodhpur meetings led



to seminal publications (Seth & Seth, 1983b, 1989a,b; Roonwal et al. 1984, respectively). We encourage the research groups in India to become more active in developing international cooperation so that expertise from different countries could be integrated in research and conservation. A successful example of such a cooperation has been the conduct of an international workshop on macaques at the University of Mysore that resulted in the publication of an outstanding volume with contributions from prominent primatologists from several countries (Thierry et al. 2004). This cooperation also helped develop strategies for conservation management, both in situ and ex situ, of the endangered Lion-tailed Macaque (Singh et al. 2009; Kaumanns et al. 2013).

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