Habitat, Resource Utilization, Patterns and Determinants of Behaviour in Rhesus Monkeys

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INTRODUCTION

Study of ecology and behaviour of non-human primates has been of great interest to the naturalists and scientists. No other mammal has been studied as intensely as primates (Bearder, 1991). Until recently, non-human primates were studied mainly because of their phylogenetic proximity to man, their use as models for interpreting adaptations of early hominids; for reconstructing earlier phases of evolution and to understand human health and behavioural problems. Of lately, the importance of the study of non-human primates in the ecological context is being greatly emphasized. The researchers are showing more interest in studying the relationships among the animals and their environment. Behaviour studies of primates in the free-ranging conditions provides information not only about their social organisation, behaviour, and their relationship with each other and their environment but, also provides important information relating to their conservation and management. Adaptability and diverse expressions, complex interaction, ecological distinctiveness and behavioural distinctiveness of non-human primates make them a target of research on the principles that govern social organization in an ecological system (Smuts et al., 1987).

The study of the behaviour of non-human primates in the natural environment was first initiated by Psychologists and Zoologists during 1925-1935 (Yerkes and Yerkes, 1929; Nissen, 1931; Carpenter, 1934). Though there are several reports on various aspects of non-human primates in captivity, there are comparatively few reports on them in the free ranging environment. Social organisation, a product of social behaviour, is usually inferred through a synthesis of activity patterns and the individual interactions and response directions - who does what and to whom. Complete understanding of the organization requires a knowledge of the group in depth. Information, therefore, is required on group action and reactions under a multitude of conditions and challenges. The behaviour of monkeys can be regarded as representing a social phase through which man first passed in the prehuman stage of its development. Attempts have been made to collect data on the selected behaviours in rhesus monkeys and other macaques in free ranging conditions (Altman, 1962; Chopra et al., 1992a,b; Lindburg, 1971; Seth and Seth, 1985, 1986, 1993; Simonds, 1965; Southwick, 1967; Southwick et al., 1976) as well as in captivity (Bernstein and Ehardt, 1985a,b, 1986a,b; Bernstein et al., 1974a,b; Grewal, 1980a,b; Michael and Zumpe, 1970; Michael et al., 1968; Seth et al., 1992a).

FEEDING, LOCOMOTION AND RESTING

Feeding is the most important mode of subsistence in life. Food once in the possession of old world monkeys is rarely robbed even by a superior. The inhibition to steal is even sustained by the leader's supervision. As in spider monkeys, there are no sex differences in accepting food in rhesus monkeys (Pechtel et al., 1961). However, in competition for food, males succeed females (Wise et al., 1973). Among Japanese macaques, females catch more sweet potatoes than do males, when the sweet potatoes are thrown into a troop. Dominant males do not have to catch them since they keep the peripheral males away from them (Kawai, 1967). Maruhashi (1981) reported that Japanese macaque males spend less time in feeding and more time in resting or being inactive than females or juveniles. Further, he examined the intraspecific variations between troops in several regions of Japan and noted that the percentage of time devoted to feeding was similar in all areas.
If a new food is given to a Japanese macaque troop, the two to three year olds eat it first. Adult males are the last to acquire new food eating habit (Kawai, 1967). Japanese monkeys have a strategy to avoid noxious food on the basis of the novelty of the food (Matsumata and Hasegawa, 1983). In bonnet macaques, males usually lead the troop to the feeding ground (Rahaman and Parthasarathy, 1969). There is probably less competition among males for food in bonnets and lione tailed macaques (Sugiyama, 1968) than in rhesus and pig tailed. In food getting situations, among Japanese monkeys, threat responses are not seen very frequently in males than in females, however, there are differences in food acceptance in this species. Refusing food rarely occurs in females, but in males it does (Norikoshi, 1971).

Sussman and Tattersal (1981) reported feeding in crab eating monkeys, as the most common activity during the day. A few plant species were preferred more for the diet, of which fruit was the major component. According to Bernstein (1980), the stump tail macaques spent only 14.7 per cent of the time feeding but feeding followed the diurnal pattern with scores of only 2 per cent at sun rise whereas during afternoon and sunset sessions, feeding scores rose to 35 per cent and 25 per cent, respectively. Rhine and Kronenwetter (1972) observed only 6 per cent and 8 per cent feeding scores for their groups. A significant variation in feeding activity budget over months ranging from 35 per cent to 55 per cent was observed in green monkeys (Harrison, 1985). He further noted that diurnal rhythms of feeding and ranging were influenced by daily cycle of temperature; in the dry season, the activity was reduced if it was too hot or too cold while the temperature in the wet season did not affect activities. Feeding was also synchronised among individuals irrespective of the time of the day. Also, both, feeding time and distance travelled increased as food availability increased (Harrison, 1985). Changes of habitat, season and human contact did influence the activity day, affecting the feeding repertoire of free ranging rhesus monkeys (Chopra et al., 1992a; Seth and Seth, 1985, 1993).

Seasonal differences in dietary quality and the time spent feeding produced seasonal variations in rates of high energy social interactions, i.e., play, aggression and competition (Lee, 1984; Seth and Seth, 1992, 1993). Differences between groups in food availability and quality affected rates of social interactions. Both, between groups and seasons, low food quality reduced the frequency of interactions and increased the time spent in feeding.

Southwick and coworkers (1976) observed that artificial feeding resulted in significant increases in aggressive competition within the monkey groups. During feeding periods, the frequencies of aggressive threats, chases and attacks increased 2 to 6 times above those of non-feeding periods. Moreover, restricted access to available food appears to have been the most important determinant of the high frequency of aggression in the feeding area. Also aggression was increased when feeding on large fruits than on small fruits.

The major concern with patterns of range use has been focused on how these patterns are affected by the distribution and abundance of resources especially food (Clutton-Brock, 1977); the optimal use of these resources (Menzel, 1973; Pyke et al., 1977); and the potential dangers (Altmann, 1974). However, these factors which influence the fitness of members of a group can affect the group's use of its environment. The patterns of range use were observed by a number of workers in different species of macaques. Various ranging parameters measured were daily travel distances, speed of movement, monthly range size and differential pattern of range used in both space and time. Harrison (1983) observed that range use was determined by the availability and distribution of important species of fruits and flowers, water in late dry season, habitat structure, sleeping site and by the presence of neighbouring groups competing for limited resources. McKee and Waterman (1982) also reported the same factors responsible for determining the use of range.

The group size played an important role in determining the home range (van Schaik et al., 1983; Seth and Seth, 1993). They noted that the length of the day journey, the time spent
travelling and searching for dispersed food items as well as social tension showed a monotonic increase with group size. They further elaborated that behavioural mechanisms behind these patterns is the "pushing forward" effect, i.e. foraging animals tend to move away when approached by others presumably because they reduced the availability of dispersed food items in patches they have searched. The per capita essential resource area is quite important in determining the population and range area (Furuichi et al., 1982). Primates have adopted behavioural strategies to maintain a range area much larger than usually necessary for bare subsistence. Rhesus macaques of Cayo Santiago showed both intergroup and seasonal variability in spatial defence (Lau, 1980).

Bernstein and Mason (1963b) found a definite relationship between temperature and the incidence of certain activities, for instance, resting increased with increasing temperature. They reported that animals spent 39 per cent of the time in resting or being inactive. Ruhayat (1983) observed in Presbytis aegyptia that animals spent more time in resting than other activities during a day.

GROOMING

Grooming behaviour is a very wide spread phenomenon in non-human primates during which animals behave as if they are carefully searching through the fur and scrutinizing the skin and occasionally transferring particles from the hair or the skin to their mouth. Monkeys may groom another animal as well as themselves. The first type of behaviour is called social grooming and the latter is referred to as self grooming. Goosen (1974) has shown that if social grooming is permitted it makes the groomer stay close to other animals longer. Animals groom others for longer periods of time than they groomed themselves (Boccia, 1983). Self grooming can occur in the presence as well as in the absence of another monkey. However, the duration of self grooming is increased by the mere presence of another monkey without the opportunity to groom other animal. In addition to inducing an increase in the duration of self grooming, the presence of another monkey also induced a tendency to stay close to the other and reduced locomotion (Goosen, 1974).

Because grooming accounts for such a relatively large portion of primate social behaviour, the distribution of grooming among individuals has often been used as a measure of social structure in different species (Kummer, 1968; Sade, 1965, 1972; Seyfarth, 1977a; Sussman and Tattersal, 1981). Seyfarth (1980) reported that high ranking females received more grooming than others. Social grooming was concentrated on areas which are inaccessible and/or invisible to a self grooming animal (Barton, 1985). In captivity, lion tailed monkeys, ring tailed lemurs and celebes black apes performed more social grooming of areas which are inaccessible to self grooming (Hutchins and Barash, 1976); thus suggesting that primate grooming may serve real utilitarian function in parasite removal in addition to its social function.

Rhesus female grooms more than rhesus males (Bernstein, 1970; Ruppenthal et al., 1974). In familial or kinship subgroups of free ranging rhesus, most of the kinship grooming involves mother-daughter grooming. Even when strangers were introduced to homosexual and heterosexual groups of rhesus, the introduced females display and receive more grooming than do the introduced males (Bernstein et al., 1974b; Hansen et al., 1966). Moreover, in rhesus housed in a single cage in the laboratory, self grooming occurs more frequently in females than in males (Cross and Harlow, 1965). Females reared in isolation display more self grooming and invitations to groom than do their male counterparts (Cross and Harlow, 1965) and normally reared subjects show more social grooming (Hansen et al., 1966). Mason (1960) has shown that early deprivation decreases grooming, particularly in male rhesus. Suomi and coworkers (1971) found that rhesus reared in social deprivation exhibited less grooming than socially reared macaques.

Both the sex and the dominant status of the groomee, but not the groomer were found to affect the body sites groomed and the posi-
tions assumed by animals during grooming bouts (Boccia et al., 1982). A stone was used by a mother to groom her infant (Candland and Weinberg, 1981). At times, a twig or a piece of chow was used in the same fashion.

Ovarian hormones administrated to a female increased the amount of grooming by males (Herbert, 1967). In addition, application of extracts of vaginal secretions from estrous females to the sexual skin of non-estrous females resulted in increased grooming of the non-estrous female by the adult males (Keverne and Michael, 1971).

In an overview of socializing function in many species of primates, Poirier and Smith (1974) state that females groom more than males. According to Sade (1972), the status of individuals in grooming networks correlates with dominance only in females. In summary, there is clearly a sex difference in grooming in rhesus monkeys and more importantly, the difference is felt to be at the core of the social organisation of the species.

Pig tail adult males do less grooming than adult females. Males do less grooming than they receive while females both groom and receive more grooming than do males (Bernstein, 1970, 1972; Rosenblum et al., 1966). Thus, the female pig tails spend a greater total time in social grooming than males. Bernstein (1972) views this as an indication of their stronger social binding. The grooming behaviour of crab eating monkeys resembles that of rhesus monkeys (Bernstein, 1970). Thompson (1967) found a much higher frequency of grooming in female-female pairs than in male-male or even male-female pairs of rhesus macaques.

The bonnet macaque, Macaca radiata, behaves differently from the other macaques (Rosenblum et al., 1966). Grooming is much less frequent between males than between female bonnet monkeys, whereas it is most frequent in adult male-adult female dyads (Koyama, 1973). Both, male and female macaques groom most with females. There is greater tolerance of males by males in bonnets than in rhesus (Sugiyma, 1971). Silk (1982) observed in a captive group of bonnet macaques that both kinship and dominance rank influence the distribution and rate of grooming and alliance formation. In lion tailed macaques, the female-female grooming dyads were commonly observed than male-male or male-female dyads (Seth et al., 1992a).

In stump tail macaques, Macaca arctoides, Gouzoules (1975) reports that the rank of the infant’s mother correlates positively with the amount of grooming the infant receives. The males groom females more when the females are in estrous (Blurton-Jones and Trollope, 1968). Rhine and Kronenwetter (1972) compared male and female stump tail macaques for the amount of grooming displayed and found that as marked variability and basic behavioural differences from the rhesus and other macaques, stump tail females groom more than males.

AGONISTIC BEHAVIOUR

Aggression within a group may serve multiple functions (Bernstein and Gordon, 1974) but aggressive conflicts have the potential to inflict injury on group members. Samuels and Henrickson (1983) reported severe aggression among females in a rhesus monkey group during breeding season.

The causes of aggression have been explored by Anderson and Chamova (1981); Boelkins and Heiser (1970); Drickamer (1975); Eaton et al. (1981); Maler (1976); Samuels and Henrickson (1983); and Southwick (1967). Packer and Pusey (1979) observed that female aggression towards male has an effect on male association with females in Macaca fasciata and Papio anubis. The aggression was increased by adult males with the increase in population density (Eaton et al., 1981). But Drickamer (1975) reported an inverse relationship of aggression with group size. When there is more competition for food in an urban environment, the level of aggression is higher than in forest dwelling troops of rhesus where food is more plentiful and more evenly distributed throughout the environment (Southwick et al., 1965). Artificial feeding of rhesus monkeys in rural and urban habitats, results in significant increase in aggressive competition within the group (Southwick
Many investigators have focussed attention on effect of season and gender on expression of aggressive behaviour. Significant differences exist in the frequencies with which age-sex classes of rhesus macaques engage in agonistic interactions with other age-sex classes. Bernstein and Ehardt (1986a) reported significantly more agonistic interactions within their own age-sex classes but adult females showed more aggression towards infants and young females whereas adult males directed more aggression towards subadult males. Moreover, group members showed more aggression to kin than non-kin members (Bernstein and Ehardt, 1986b). Eaton and coworkers (1981) reported that males were more aggressive during autumn and winter seasons and females were more aggressive during the spring and summer seasons. Juvenile agonistic interactions reached a peak during the weaning and birth period (Drickamer, 1975).

In Japanese macaques, the frequency of chasing females by males increased in the mating season (Enomoto, 1981). Walker and his group (1983) reported significant fluctuations in agonistic behaviour of females throughout the menstrual cycle.

Males have the greatest potential to inflict injury on others. But Mason and coworkers (1960) suggested that females were more aggressive than males. Whitten and Smith (1984) indicated than adult males received more serious wounds than other age-sex classes and low ranking animals were wounded more often than high ranking individuals. Higher testosterone levels in males produced higher aggression in them (Kling, 1975; Tiger, 1975).

Rhesus monkeys living within social groups seem to channel most of their agonistic encounters into episodes with minimal potential to inflict injury. The dominance relationships among individuals allow for the use of aggressive signalling in socialization process with minimal risk of injuries (Bernstein and Ehardt, 1985b).

In artificial group formation, animals are brought together without previously established social relationships. In these circumstances, extreme expressions are common and the frequency and severity of aggression are extraordinary (Bernstein, 1964; Bernstein and Mason, 1963a; Bernstein et al., 1974a,b). Levels of aggression decline rapidly as relationships are established (Ehrlich and Musicant, 1977; Rosenblum et al., 1968). Wolfe and Summerlin (1968) suggested that strangers introduce an element of social disorganization which is responsible for sharply increased agonistic behaviour. These responses are indicative of xenophobia (Southwick, 1967; Southwick et al., 1974). These initial aggressive responses serve to establish relationships with new comers and, therefore, aggression subsides (Mendoza and Barchas, 1983). Bernstein and Ehardt (1986b) supported the hypothesis that aggression is used as one of the mechanisms in socialization and that matrines are particularly active in the socialization of immature rhesus monkeys.

Aggression does function to establish and maintain social relationships (Bernstein and Gordon, 1974). Other animal's interference in agonistic episodes or the joint action of several animals against one or more was described as the control role (Bernstein, 1964, 1966) or benefits of established dominance relationships (Bernstein, 1981; Kaplan, 1978; de Waal, 1977). Control animals interfere in agonistic episodes within groups (Anderson et al., 1977; Erwin, 1977). Interference based on kinship has been described by Kaplan (1977), Kurland (1977) and Massey (1977).

The model of social inheritance of dominance proposed by Kawamura (1958) and Koyama (1967) might operate through the differential interference of kin in interfamilial agonistic interactions. The role of mothers in the social inheritance of rank has been emphasized by Cheney (1977) and Watanabe (1979). Other animals in the group also support maturing females, targeting old female that she should out rank based on her family's rank (Ehardt and Bernstein, 1986). In this way, maternal survival is not a necessary condition for success (Altmann, 1980; Missakian, 1972; de Waal, 1977; Walters, 1980). Other group member's interference by more distant kin or
non-kin may serve to maintain stable inter- 
familial dominance relationships. So the 
defence of the victim will be strongly influenced 
by kinship relationships with the victim and 
since rhesus monkeys live in matrilineal 
groups, adult females are most active in 
defence of the victim. Bernstein and Ehardt 
(1985a) reported that agonistic aiding 
mostly favoured victims rather than aggressors and 
is much more likely to occur when matrilineal 
kin are involved. Females were more likely 
to aid and frequency of their participation 
increased with age. Reinhardt and coworkers 
(1986) observed that the rhesus α-female 
consistently interfered in favour of the victim. In 
contrast, males generally leave their natal 
groups and become less involved with their 
matrilineals as they mature. Adult males 
interfere in fights by supporting aggressors against 
their victim to establish and maintain alliances 
(Kaplan, 1978; Watanabe, 1979). Kaplan et al. 
(1987) observed that rhesus females aided 
relatives, interfered against target animals 
dominant to themselves, aided juveniles and 
aided victims more consistently and frequently 
than did males. Cheney and Seyfarth (1986) 
showed evidence of recognising that certain 
individuals associate regularly with each other.

Spontaneous self aggressive behaviours in 
adult male rhesus monkeys were observed by 
Pond and Rush (1983). The self aggressive 
behaviours included self clapping, self rubbing, 
and threatening of body parts. Wrist biting 
was observed by Grewal (1981) in Japanese 
monkeys. In several cases, wounds were 
inflicted. This type of behaviour occurred 
only when an animal was moved out of the 
cage, out of the room or during escape of 
other monkeys from their cage (Pond and Rush, 
reported increased self aggression in a group of 
 stump-tailed macaques in response to a temporarily impoverished environment.

**PLAY**

Much has been written about the primate 
play behaviour. Males play harder, begin play 
at an early age and cease play at a later age and 
play for longer periods of time than females. 
There appears to be qualitative and quantitative 
difference in play of young male and female 
primates (Poirier, 1989). Hinde and 
Spencer-Booth (1967a) noted that sex 
differences arise not so much in time of onset of 
play as in its expression. Harlow and Harlow 
(1966) distinguished the play of male and female 
laboratory rhesus at about two months of 
age. This difference is also observed in the 
field. Male baboons play rougher and more 
frequently (DeVore and Eimerl, 1965; Kum- 
mer, 1968; Rowell, 1972). Similar results are 
found in studies of vervets (Fedigan, 1972).

Rhesus macaque males play more frequently 
and rougher than females (Harlow and Lau- 
ersdorf, 1974). Social play in rhesus monkey 
begins at about one month of age, is of rough 
and tumble type (Hinde and Spencer-Booth, 
1967a), and usually involves two or three 
individuals of similar age (Kaufman, 1966; Loy 
and Loy, 1974; Seth and Seth, 1983, 1993). 
Infants, juveniles and adolescents/subadults, 
all engage in play. Juvenile play consists of 
chasing, wrestling and approach-withdrawal 
(Hinde and Spencer-Booth, 1967a). Juvenile 
play occasionally occurs in groups of 4-10 
animals (Southwick et al., 1965). Rhesus 
infants and juveniles frequently play with their 
siblings (Lindburg, 1971; Loy and Loy, 1974).

Male infants begin to play very early in life 
than female infants (Hansen, 1966; Seay, 
1966). One year old males, between infancy and juvenile period, play the most often, 
followed by two year old males and one year old 
females (Hinde and Spencer-Booth, 1967a; Loy and Loy, 1974). Two year old females are 
often busy playing mothering (Chamov et al., 
1967; Hinde et al., 1964). The removal of 
adults can increase juvenile play (Bernstein 
and Draper, 1964). Apparently, adults control 
the level of play exhibited by the immature 
monkeys.

Adult rhesus monkeys play far less frequently 
than juveniles and infants (Lindburg, 
1971; Chopra et al., 1992). Also in wild, 
mothers appear to play with infants more than adult 
males (Lindburg, 1971). When mothers are 
removed, adult males increase their interactions 
with infants and much of this increase is
in play (Spencer-Booth and Hinde, 1967; Redican and Mitchell, 1974). Two adults have not been seen playing together (Lindburg, 1971; Southwick et al., 1965; Hinde and Spencer-Booth, 1967a).

In rhesus macaques, sex differences in play have been reported under natural conditions, in captivity and under various degrees of social deprivation. For example, Anderson and Mason (1974) compared groups of socially deprived rhesus to socially experienced rhesus and found that, while rough and tumble play was significantly higher in experienced rhesus, in both groups, males were more often engaged in rough and tumble play than females. Similarly, Brandt and Mitchell (1973) found that male rhesus infants, when paired with preadolescents, played more than female infants. Males in a captive ‘nuclear family’ environment also played more than did females (Ruppenthal et al., 1974). In the same nuclear family environment, adult males but not adult females reciprocated play with infants. Male infants played more with older infants and adult males whereas female infants played more with younger infants (Suomi, 1972).

Play in the bonnet monkeys also develops very early in life. Four or more animals are often involved in play groups, involving chasing and grappling. Violent wrestling is usually confined to juveniles, subadults and adult males. Less vigorous wrestling is seen when adult males play with immature males (Nolte, 1955; Simonds, 1965; Sugiymama, 1971). Sex differences are apparent as early as two months of age (Simonds, 1974). Bonnet infants predominantly play with same sexed infants.

Burton (1972) reported that Barbary macaques started social play at the age of three months. Barbary macaque infants preferred age mates over aged play mates (MacRoberts, 1970). Contact between adult males and younger animals was frequent (Deag and Crook, 1971) but very little of it was play. Adult females had never been seen playing (MacRoberts, 1970; Burton, 1972). Pig tailed macaques display a sex difference similar to that in rhesus. Bernstein (1967, 1970, 1972) has reported that all age classes of pig tailed macaques play but play is most common among juvenile males. Pig tails engage in less social play, but more non-social play than bonnet macaques. The total percentage of time spent playing is greater in one year old bonnets than in one year old pig tails (Kaufman and Rosenblum, 1969).

Dolhinow and Bishop (1970) suggested a powerful endocrine influenced sexual differentiation in play behaviour. Administration of gonadal hormones prior to adulthood, decreases bonnet play behaviour and activity levels drastically (Rosenblum and Bromley, 1976). Females exposed to androgens during a critical period of early development become masculinized as pseudohermaphrodites (Goy and Phoenix, 1962; Goy and Resko, 1972; Phoenix et al., 1968). These masculinized animals tend to develop play patterns approximately half way between typical male and female patterns. Other factors also affect the differential expression of play according to sex. Males are usually physically larger and stronger than females; this alone may explain some differences between the frequency and duration of play. This, plus the endocrine influence, increases the likelihood that females experience less novelty and more aversive contact during exploration in social play than do males (Poirier, 1987). This may be partly responsible for shaping the quiet, withdrawn, gentle activities of females and the tendency for females to orient to object manipulation play rather than social contact play typical of males (Baldwin and Baldwin, 1977).

DOMINANCE HIERARCHY

The individuals of a group can be arranged in a linear hierarchy based on dominance relations that exist in each group (Bernstein, 1976; Deag, 1977). In most cases, males are dominant over females and both can be ranked in separate hierarchies. Immature females generally assume their mother’s rank (Walters, 1980). In rhesus, each female rises in rank above her elder sister and this also is occasionally observed in baboons (Moore, 1978). Bernstein and Williams (1983) studied dom-
inance relationships in a rhesus monkey group. They observed that male dominance relationships were most stable. Adult female dominance relationships were also quite stable but immature females slowly achieved dominance over sisters and females subordinate to their mothers. Old age and deteriorating physical condition of mothers appear to be associated with mother-daughter rank reversals (Silk et al., 1981b). Seasonal changes in dominance rank for adolescent and subadult males in semi free ranging rhesus monkey group were reported by Tilford (1982). Subadults dropped in rank in the mating season and this decrement was related to concomitant drop in their alliances.

The hierarchy is based on the transition matrix of the direction of the outcome of a number of interactions between different individuals (Dawkins, 1976). Such linear hierarchies are often based on only one or a few types of interactions (fights or supplants over food) and their predictive value is limited (Richards, 1974). Seyfarth (1977b,c) and Cheney (1978) gave a model wherein dominance determines the distribution of friendly behaviour among the members of the group and subordinates are often excluded from receiving benefits of such behaviour.

During immaturity, competitive dominance rank is acquired through a variety of interactions with others in the social group. In many species, the rank of the young females and in some cases that of the male depends on that of their mothers and is a result of the support given during aggression and competition (Cheney, 1977; Kawai, 1958; Lee and Oliver, 1979; Sade, 1967). The dominance rank of an immature may also depend upon individual aggressiveness which increases at a particular time during development, such as first estrous (Walters, 1980) or just before the transfer from the natal group (Packer, 1979). Fedigan (1972) observed that immature vervets in a captive group had the social dominance ranks as their mothers.

O’Keeffe and coworkers (1983) determined dominance ranks of free ranging stump tail macaques on the basis of competitive food tests and there was positive correlation between dominance ranks and ranks for the variables such as groomed by, overall affiliation, and pair proximity scores. Similar results were reported by Singh (1984) in free ranging rhesus monkeys. Furuichi (1983) observed in Japanese monkeys that dominant subordinate relationship restricted the feeding behaviour of subordinates i.e., either the dominant drives away the subordinate through agonistic interactions or the subordinate avoids approaching the dominant without any agonistic interaction. These occurred only when the personal space or individual distance was less than a certain distance called tolerance/intolerance distance.

**SEXUAL BEHAVIOUR**

During the period of heightened sexual activity, the females of many primate species actively approach males and perform specific behaviour patterns that elicit mounting by males (Chopra et al., 1992b). Of these behaviours, sexual presentation whereby the female exposes the anogenital region to male appears to be common to many old world monkeys and apes. It has been observed under laboratory conditions that female rhesus monkeys also use three other gestures to initiate mounting by males, namely, the hand-reach, head-duck and head-bob (Michael and Zumpe, 1970). Different females vary greatly in the frequencies with which they perform these four types of sexual invitations. But all four tend to covary with changes in hormonal status of females, being facilitated by estrogens and inhibited by progesterone (Zumpe and Michael, 1970). The frequency with which a female makes sexual invitations to a male is affected by the presence and dominance rank of a second female (Everitt and Herbert, 1969; Goldfoot, 1971). Males also compete with each other for access to mates (Southwick et al., 1965).

Furthermore, the behaviour of the male may influence the number of invitations made by the female during the test. Michael and Zumpe (1970) demonstrated that the female’s invitations ceased for a period of 10-30 minutes after the occurrence of the male’s ejacu-
lution. It has been observed that administration of testosterone to ovariectomized female rhesus monkeys increased their invitations without markedly affecting the sexual activity of their male partners (Trimble and Herbert, 1968; Michael, 1971). In contrast, administering small doses of estrogen intravaginally increased the sexual activity of their male partners without markedly affecting females's invitational behaviour (Michael and Saayman, 1968). Anderson and Mason (1977) observed that, the laboratory female squirrel monkeys, receiving estradiol, increased their affiliative interactions with males, while females receiving progesterone decreased their contacts with males. Zumpe and Michael (1977) demonstrated that tests without ejaculation following those in which ejaculation occurred were associated with increased number of invitations.

Either sex can initiate consort by approaching the other. However, females initiate about 70 per cent of all close physical contacts (Lindburg, 1971). Males lip smack towards females and females initially grimace and withdraw. The females are some what more apprehensive than the males. Once established, a consort can last for a single copulatory sequence or for each receptive period for years depending upon the individual or the dyad (Agar and Mitchell, 1975). During breeding season, males can influence female choice by advertising their locations with branch shaking (Wolfe, 1981).

According to Lindburg (1975), female choice plays an important role in the formation of mating associations, and preferences of the females for certain males is related to factors other than male dominance. Males contacted the unfamiliar females more often than they contacted the familiar females (Chambers and Phoenix, 1982). Zumpe and Michael (1984) suggest that the familiar partner phenomenon was not restricted to the males and was associated with increased social affinity and decreased agonistic tension between partners. Under natural conditions, this phenomenon encourages troop transfers and out breeding.

The regulation of sexual breeding in captive and free-ranging rhesus macaques has been linked to environmental and behavioural cues that trigger the hormonally mediated physiological changes which initiate and confine receptivity to a specific period of the year (Carpenter, 1942; Koford, 1965; Southwick et al., 1965; Vandenbergh and Vessey, 1968; Lindburg, 1971; Vandenbergh, 1973; Drickamer, 1974; Varley and Vessey, 1977; Gordon, 1981; Herndon, 1983; Smith, 1984; Chopra et al., 1992a,b). A consistent relationship between the onset of mating and decreasing day length has been reported by Van Horn (1980), but the correlational evidence for photoregulation of reproductive function in macaques has not been confirmed experimentally (Riesen et al., 1971; Gordon, 1981; Wehrenberg and Dyrenfurth, 1983). Differences in photoperiod have not been considered sufficient to act as a proximate cue for mating (Koford, 1965) and changes in daily temperatures are not large enough to influence breeding (Koford, 1965).

Rawlin and Kessler (1985) observed photoperiod as a function of latitude, set the temporal limits of seasonal reproduction in rhesus macaques, while the onset of spring rains regulate reproductive activity within that range.

Loy (1971) reported estrous behaviour both intermenstrually and perimenstrually in free ranging rhesus monkeys. A female who failed to conceive during the autumn breeding season showed cyclic estrous behaviour throughout the entire annual cycle. Rhesus and bonnet non-mothers participated in courtship earlier in the breeding season than mothers (Small, 1983). Females without infants cycled earlier and conceived earlier than mothers having dependent offspring (Scuccchi, 1984). This might be due to the reasons that some mothers are still lactating during breeding season and lactation may induce secondary amenorrhea, and presence of an infant decreases the frequency of sexual activity for mothers. Heavier females reached sexual maturity at an earlier age than lighter females (Frisch and Revelle, 1970; Mori, 1979; Nieuwenhuijzen et al., 1985; Wolfe, 1979).

However, studies in rhesus monkeys (Wilen and Noftolin, 1976) and bonnet monkeys (Silk et al., 1981a) did not support the criti-
cal body weight hypothesis. Young sexually mature female rhesus monkeys copulate on more days prior to conception than older females (Wilson et al., 1984).

Rhesus males also masturbate more often than rhesus females (Agar and Mitchell, 1975). Males, in wild, sometimes masturbate even when females in estrous are available. Female homosexual behaviour also occurs in rhesus monkey but less frequently than male homosexual behaviour (Carpenter, 1942). Fairbanks and McGuire (1977) noted that contact aggression directed by females towards females is correlated with female homosexual behaviour. But male like mounting is part of the normal repertoire of female rhesus and this behaviour increases in females if males show no interest in them. It occurs in one third of the rhesus females (Michael et al., 1974).

Among rhesus macaques, there is an inhibition of mating between mother and son (Sade, 1968; Loy, 1971). Itoigawa and co-workers (1981) reported no observed instances of mother-son mating in Japanese monkeys. But Kortmulder (1974) observed some sexual activity with the mother when the son is sexually immature or is a young adult. The incidence of brother-sister mating is also low and is only among young animals (Missakian-Quinn and Varley, 1977). Missakian (1973) recorded 5.4 per cent of all mount series and populations involved mother-son pairs and 12 per cent between brothers and sisters. All mother-son and brother-sister matings involved males from 3-5 years of age group.

The avoidance of mating among relatives is also maintained by the migration of maturing males from their natal group (Duggleby, 1977). Moreover, the original mother-infant bond persists into the adult relationship between the mother and the offspring, which results in incompatible roles for the son.

**PARTURITION**

Despite considerable number of field studies of free ranging primates, studies relating to the number of births observed in the wild are few. The reason is, almost all the primate births occur at night (Jolly, 1972), which makes observational studies difficult. However, cases of day time delivery and behaviour have been reported (Lindburg, 1971). Jolly (1972) has pointed out the advantage of night time births in the more mobile higher primates, since the infant is then at less risk during the initial period when its ability to cling to mother's fur is at its weakest. Dunbar and Dunbar (1974) also confirmed Jolly's conclusions that most primates give birth during night.

Females give birth to a single infant at a time and the period of infant dependence can last for a year or more (Altman, 1980; Rhine et al., 1985). Breeding patterns of genus *Macaca* range from strictly seasonal to non-seasonal. *Macaca arctoides* does not exhibit the seasonal cyclicity (Smith, 1984). Booth (1962) reported births throughout the year in *Cercopithecus* monkeys. Females without infants from a previous season begin breeding earlier (Drickamer, 1974; Kaufman, 1965; Small, 1983; Wilson et al., 1978) than those with infants. Females without surviving infants have a greater probability of birth the following year (Anderson and Simpson, 1979; Takahata, 1980). Late seasonal birth is associated with decreased likelihood of birth in the following season and increasing parity is associated with increased likelihood of birth (Casebolt et al., 1985).

Kemp and Timmermans (1982) demarcated three distinct phases in the parturition process viz., prepartus, partus and postpartus. The first signs of eminent child birth are hollow postures of the back, stretching of legs, walking to and fro and touching the vulva. The characteristic postures were demonstrated with cyclic regularity (about 2-4 minutes), 35-210 minutes prior to actual parturition (Adachi et al., 1982). Teas and her group (1981a) reported that in free ranging rhesus monkeys the parturition behaviour was characterised by general lack of contact with other troop members and by overall conspicuousness.

Many factors have been shown to influence the reproductive performance of female rhesus monkeys. Studies of female age and parity have yielded conflicting results. Koford (1966) did not find any variations in birth rates with female age. In other studies, higher birth
rates were observed in females 4-7 years old (Wilson et al., 1978) and in females 7 years and older (Drickamer, 1974). Smith (1981) reported a significantly greater number of offspring of high ranking males born earlier during the birth season than those of low ranking males.

MOTHER-INFANT RELATIONS

During the past decade, many studies have been conducted into the effects of social rearing conditions on maternal rearing behaviour. Examination of the relationships between the time an infant spends off and at a distance from the mother, the frequency with which it is rejected by its mother and the relative role of mother and infant in maintaining spatial proximity indicates that the mother plays a large part in the increasing independence of the infant during the early months (Hinde, 1969). The mother provides a secure emotional base for the infant by passively affecting contact-comfort and warmth. The infant was able to regulate its own interactions with the mother, gradually achieve independence and develop appropriate social skills with peers by seeking stimulation from the environment (Harlow and Harlow, 1965). The mother also regulates its interactions with others, by interacting both with the infant and with other members of the group (Hinde and Spencer-Booth, 1967b; Spencer-Booth, 1968). Most of the infants, who lost their mothers before the weaning period, could not survive, while young animals over one year could survive their mother’s death (Hasegawa and Hiraiwa, 1980).

According to Seay and coworkers (1964) and Harlow and Seay (1966), rhesus mothers reared under conditions of complete social deprivation are incapable of rearing their young. These mothers are hyper aggressive towards their offspring (Arling and Harlow, 1967; Harlow and Harlow, 1965). Rhesus monkeys, brought up with surrogate mothers only, also display inadequate maternal behaviour (Harlow and Harlow, 1969). After growing up without their mothers, but among peers, rhesus females can still become adequate mothers (Chamove et al., 1973). Young females brought up in a group of natural composition who have not suffered from social deprivation in any form, are competent mothers (Hinde, 1974). When living in a group of natural composition, the macaques gain considerable experience with infants through observation of the mother with young and perhaps also through carrying infants around (Hinde, 1974).

Another factor affecting the quality and character of maternal behaviour is the number of deliveries accomplished. According to Kemp and Timmermans (1984), pluriparous proved more capable in looking after their young than primiparous. Others observed that pluriparous rhesus females display more adequate maternal behaviour than primiparous, even after growing up in partial social deprivation (Harlow et al., 1966; Ruppenthal et al., 1976). Orphaned mothers and old mothers showed different type of maternal care from typical multiparous mothers. The primiparous rhesus mothers protected their daughters more, whereas sons received more maternal protection from multiparous mothers (Hooley and Simpson, 1981). But Baker-Dittus (1985) observed no difference in the amount of time mothers invested in carrying and nursing male and female infants. Captive rhesus mothers are more protective and less encouraging to early independence in their infants than free ranging mother (Berman, 1980).

POPULATION DYNAMICS

The general trend is one of continued logging activity, dramatically increased forest products extraction and sporadic primate hunting. With the increase in human population, the area needed for subsistence and cash crops increases. This increase in forest conversion coupled with extensive logging activities dramatically decreases the available habitat for non-human primates. Although isolated pockets of monkeys may survive, many of these would be forced into suboptimal habitats and thus, be easier prey for occasional human predation (Fuentes and Ray, 1996).

For several years, field primatologists have
been concerned about the rapid depletion of wild non-human primate populations. At the same time, there has been growing awareness that non-human primate populations are valuable biological resource (Seth and Seth, 1986).

The censusing of primate species in their natural habitat is of great importance in the determination of priorities for primate management and conservation. Attempts have been made to evaluate the status of primates in certain critical areas and national parks (Cant, 1978; Neville et al., 1976; Struhsakar et al., 1975; Fieese, 1975; Wilson and Wilson, 1975). Most long term studies of monkeys and apes have shown either declining populations due to environmental deterioration, trapping or changing human attitude (Southwick and Siddiqi, 1983) or have shown increasing populations (Seth and Seth, 1992, 1993; Seth et al., 1992) due to special protection and husbandry as in macaques of Japan or rhesus monkeys of Cayo Santiago and La Pareguera (Drickamer, 1974). With reasonable protection and good habitat, rhesus populations often increase at a rate of 10-16 per cent per year whereas in deteriorating and exploited conditions, they may show comparable rates of decline (Southwick et al., 1970). But Teas and her group (1981b) observed that totally protected population of rhesus monkeys in Kathmandu valley has shown relatively stable number over a period of several years. Clark and coworkers (1986) also observed no change in total number, location of the groups and age-sex composition in howler monkeys, over a period of 14 years.

Surveys of rhesus monkey populations in India have been carried out by Southwick and his colleagues since 1959 (Southwick et al., 1961a,b; Southwick and Siddiqi, 1966, 1968; Siddiqi and Southwick, 1977). Also Dolhinow and Lindburg (1983) assessed the abundance of rhesus monkeys in the forest areas of Asarori. In another roadside survey of northern India during 1964-65, a total of 83 groups were counted (Mukherjee and Mukherjee, 1972) and reported a tendency to decline in Indian rhesus monkey population. But Seth and Seth (1983, 1992, 1993) studied rhesus monkey populations in Asarori forests and Rajasthan and reported an increase in population over a period of 5 years. In another study, Seth and coworkers (1992b) conducted surveys of rhesus monkeys in seven states of northern India, from 1981-1986, inhabiting eight habitats and reported a population of about 16,000 animals in 400 groups. They observed an increase in population of free ranging rhesus monkeys in all the habitats over this period (Seth and Seth, 1992, 1993).

Singh and coworkers (1984) conducted a survey of bonnet macaques inhabiting urban, forest, roadside and village habitats. They reported that forest and urban areas tend to have smaller groups than the other habitats. This observation, to some extent, supports the conclusion drawn by Crook and Garlan (1966) regarding group size in non-human primates. Tiwari and Mukherjee (1983) conducted nationwide surveys of rhesus monkeys in India, estimating rhesus population at 153,000 and Southwick and Siddiqi independently estimated rhesus number at 160,000 to 200,000 (Southwick et al., 1986).

Displacement behaviour has been studied in naturally occurring primates and is recognized as an important facet of their life and well-being (Bradshaw, 1993; Cardinal and Kent, 1998; Sade, 1967). Self grooming is an important behaviour in all primates. Animals tending to their own coats show no interest in their own well-being (Cardinal and Kent, 1998). Foraging requires time and patience and is usually performed by a contended monkey (Chamove, 1989).

Many of the strategies developed for enhancing the environment of captive primates involve providing opportunities for foraging behaviour (Boccia and Hijazi, 1998). In the wild, foraging involves spending significant amounts of time finding, obtaining, and processing food (Boinski, 1988; Chamove et al., 1982). However, in captivity, this time is typically reduced to the time necessary to consume the easily accessible, provisioned food. Manipulation of food distribution and availability has shown profound effects not only on foraging behaviours, but also affects a range of other behaviours, from stereotyp-
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...ies to agonism to infant development (Andrews and Rosenblum, 1991, 1992; Boccia and Hijazi, 1998).

Relevant information available on the free-ranging rhesus monkeys, living under different ecological constraints, has initiated comparative studies on the dynamics and the adaptability characteristics of these populations, the consequences of the demographic changes on their diverse habitats, and their genetic endowments in relation to the habitats occupied.

Population studies are of great value in various fields of applied ecology and in conservation and management of non-human primates; they occupy a pivotal role in current field studies of non-human primates. From a practical standpoint, demographic data provides information necessary to evaluate the overall status and health of non-human primates (Mitani, 1990). Implementation of effective conservation measures depend on the understanding of demographic processes and patterns. Population studies also provide information about the factors which are responsible for the structure of social groups, a central issue of primate behavioural ecology (Mitani, 1990). Looking from conservation and management point of view, there is hardly any information about the perceptions of the people vis-a-vis non-human primates. Since people are directly or indirectly associated with non-human primates, their attitude or perception about these species directly influences their survival. Conservation and management programs, therefore, cannot be formulated and implemented without people’s participation. Lande (1988) has recently shown that the demographic and behavioural considerations should be of greater immediate importance than the genetic factors in the formation of the conservation plans. Individuals in many populations show decreased reproduction at low population densities for non-genetic reasons such as lack of social interactions for breeding difficulty in finding mates, or other densities dependent ecological factors collectively known as the Allee effect (Andrewartha and Birch, 1954).

An increase in the ecological diversity of the free-ranging rhesus monkeys has resulted from the deliberate changes in the environment. Human analogues of natural communities have emerged from the replacement of the wilderness by a multiplicity of new micro-habitats characterized by a kind of environmental diversity different from that of the original environment, which may have been somewhat monotonous (Dubos, 1978). The management and conservation of non-human primates should be done by transforming the natural ecosystems into humanized ecosystems which are biologically diversified, ecologically stable and productive of new human values (Seth and Seth, 1993). Efforts to maintain the diversity of the biological resources, especially of the macaques, are urgently required at the local, national and international levels.

Though the development of detailed understanding of the habitat mosaics (both physical and biological) and their consequences for troop and population attributes constitutes the central problem in population ecology, assessment of the habitat requirements, the ecological changes (if any), and their population dynamics provides the insight, data and information necessary for optimum conservation of the taxa.


ABSTRACT Study of ecology and behaviour of non-human primates has been of great interest to the naturalists and scientists. No other mammal has been studied as intensely as primates (Bearder, 1991). Until recently, non-human primates were studied mainly because of their phylogenetic proximity to man; their use as models for interpreting adaptations of early hominids; for reconstructing earlier phases of evolution and to understand human health and behavioural problems. Of lately, the importance of the study of non-human primates in the ecological context is being greatly emphasized. The researchers were showing more interest in studying the relationships among the animals and their environment. Behaviour studies of primates in the free-ranging conditions provides information not only about their social organisation, behaviour, and their relationship with each other and their environment but, also provides important information relating to their conservation and management. Adaptability and diverse expressions, complex in-
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