Proc. Indian Acad. Sci. (Anim. Sci.), Vol. 98, No. 2, March 1989, pp. 139–148.

Ontogeny of aggressive and submissive behaviour in free living rhesus monkeys (*Macaca mulatta*)

RAJBIR SINGH*
Department of Psychology, University of Rajasthan, Jaipur 302 004, India
*Present address: Department of Psychology, Kurukshetra University, Kurukshetra 132 119, India

MS received 27 January 1988; revised 1 July 1988

Abstract. Twenty rhesus monkeys of various age-sex classes were observed by focal animal and one-zero sampling technique for 12 months at Galta hillocks near Jaipur (Rajasthan). Behavioural elements sampled were screech, scream, bark, threat, chase, clasp-pull, bite, fear grimace, lip-smack and submit. These elements were categorized into aggressive and submissive behaviours by pooling the frequencies of elements. Mean per cent frequencies were derived and analysed by ANOVA, trend analysis, Kruskal Wallis one way ANOVA and Mann-Whitney 'U' test. It was found that submissive behaviour among females and aggressive behaviour among males changed with age. The findings have been interpreted on the basis of social conditions and the typical spatial position of the age-sex class within the group space/structure.

Keywords. Free ranging rhesus monkey; ontogeny; aggression; submission; trend analysis.

1. Introduction

Agonistic behaviour of primates in general and rhesus monkeys in particular is considered to be an important determinant of the organization of inter- and intra-group interactions. Although aggressive encounters occur with comparatively low frequencies (Bernstein and Mason 1963; Hall 1964; Post and Baulu 1978), the ability to handle attacks, displaying threatening and submissive gestures, agonistic aiding and fight interference are common situations in the social behaviour of rhesus monkey groups (Kaplan 1977; Bernstein and Carolyn 1985a). Failure in emitting such responses may lead to very high cost e.g. injury, physical disability, expulsion from the group, losing the rank and even death. Like play, affiliation and dominance, aggressive and submissive behaviours are shaped through socialization (Symons 1978).

Environment has been found to influence general aggressiveness of rhesus monkeys, e.g. urban monkeys are more aggressive than forest monkeys (Singh 1969; Lindburg 1971; Southwick *et al* 1976; Roonwal 1977). Age, sex, rank and kinship may also explain variability of agonistic behaviour in rhesus monkeys (Altmann 1968; Moller *et al* 1968; Hamburg 1971; Bernstein and Carolyn 1985b). Expression of aggressive behaviour is also influenced by internal physiological conditions such as reproductive cycle in females and seasonal changes in male hormones (Wilson and Boelkins 1970; Rowell 1972; Mallow 1981). The present study deals with ontogenetic changes in aggressive behaviours.

2. Methods

2.1 *Study area and group*

One group from a free ranging population of rhesus monkeys in Galta hillocks near

Jaipur (Rajasthan) was observed. Details of the characteristics of habitat, population and the study group have been reported earlier (Singh 1986).

2.2 *Focal animals*

Table 1 describes the number, transitional stage, approximate age, sex and duration of the 20 animals that served as subjects. Two animals of each sex in each of 6 developmental stages (except among young adults) were studied. Two old females were studied but old males could not be identified as age estimations within adult class is not possible for males as they continue to take part in breeding activities. In the sample, 12 animals were so selected that at the beginning they fell in one age class and after 12 months they entered the next age class, thus transition from one age class to the next could be studied. The month of May, the peak birth season, was considered as cut off point to decide age classes, i.e. progeny of the same year was considered 6 months old in November when the observations were started and similarly the progeny of the previous year was labelled as 1·5 years old and so on. Age status among adults was based on reproductive status or parity, dentition and colour of the skin of hindquarters or around callosities as size variation is obscured in the adult stage which is 4/5th of the life span of rhesus monkeys. The age of transition differed between the sexes.

2.3 *Description of recorded behavioural elements*

Seven behaviours and 3 vocalizations belonging to the agonistic category were defined as under:

(i) Screech—A marked rise and fall in pitch in single or extended serial vocalization. Occurs in submissive context.
(ii) Scream—A high pitched lacking rise and fall of screech. Occurs under severe attack.
(iii) Bark—A short, low and harsh vocalization, resembling a cough or louder sound which accompanies the threat.

Table 1. Characteristics of focal animals (n = 20).

Age class	Sex	n	Approximate age during study (yrs)	Animal codes	Duration of observation (h)
Transition-I	Female	2	0·5–1·5	FI_1, FI_2	16 each
Infancy to juvenilehood	Male	2	0·5–1·5	MI_1, MI_2	16 each
Transition-II	Female	2	1·5–2·5	JF_1, JF_2	13·33, 16
Juvenilehood to adolescence	Male	2	3·5–4·5	MJ_1, MJ_2	16 each
Transition-III	Female	2	2·5–3·5	AF_1, AF_2	16 each
Adolescence to adulthood	Male	2	4·5–5·5	SA_1, SA_2	13·33, 16
Within adulthood	Female	1	4·5–5·5	YF (nulliparous)	16
Young adult	Male	1	5·5–6·5	YM (Peripheral)	16
	Female	2	Multiparous (over 8)	MF_1, MF_2	16 each
Mature adult	Male	2	Central, fullsized (over 8)	MM_1, MM_2	16 each
Old	Female	2	Non reproductive (over 20)	OF_1, OF_2	13·33, 16

(iv) Threat—A varied facial communicating pattern, which may include more elements with increasing intensity of expression such as opening the mouth to expose only the lower teeth; thrusting the head forward; flattening the ears against the head; retracting brow; frowning; erection of hair; body is held stiff, upright and barking etc.
(v) Chase—Vigorous following of withdrawee while showing repeated threats and invariable attacks on the opponent upon capture.
(vi) Clasp-pull—Any brief nip, cuff, push, pull with closure of hand.
(vii) Bite—Common usage.
(viii) Fear grimace—A facial expression with lips retracted and teeth tightly clutched, generally accompanied by tenseness of musculature, withdrawal of upper and lower lips to expose teeth.
(ix) Lip smack—Rapid opening and closing of the pursed lips probably accompanied by tongue motions and producing soft clicking sound.
(x) Submit—Assuming motionless rigid posture to reduce the appearance in size in front of another animal.

3.1 *Procedure*

A time ruled check list was used to record codes of the above defined behaviours using focal animal and one zero sampling of behaviour (Altmann 1974). Each subject was observed for two sessions per week of 10 min each for 12 months covering all the social and climatic seasons. Observational sessions were randomly spread over all the diurnal hours from 5 am to 7·40 pm. Aggressive and submissive encounters during artificial feeding, interactions with other species and with animals of other groups were not recorded or scored. The interacting animal's age-sex class was recorded; however, for the infant the younger juvenile sex was not obvious and only age class was recorded. Aggressive encounters involving more than 4 animals were categorized as subgroup encounters and not scored. Due to the death of one juvenile female (JF_1), one old female (OF_1) and the migration of one sub-adult male (SA_1) in transition, 48 observation sessions could not be completed (table 1). The duration of actual recordings for all focal animals was 312 h.

3.2 *Scoring*

Observed frequencies of 10 behavioural elements were grouped into two behavioural categories. Aggressive behaviour included bark, threat, clasp-pull, bite and chase. Submissive behaviour included frequencies of occurrence for screech, scream, fear grimace, lip smack and submit. Since all the behavioural elements (except vocalizations) could be displayed by other animals towards the focal animal, frequencies of 4 behavioural categories were obtained for each animal, viz. submission to, submission by, aggression to and aggression by. To facilitate analysis the mean per cent frequencies for each age sex class were computed in two months age block by using the following formula:

$$\text{Mean per cent frequency} = \frac{\text{Observed frequency}}{\text{Maximum possible frequency}} \times 100.$$

Where, maximum possible frequency = number of animals in age class × number of

observed intervals in 16 sessions (480) × number of interactions in the behaviour element/category.

3.3 *Analysis*

Obtained frequencies were subjected to single factor ANOVA to assess the significance of age changes upon behaviours, separately for each 3 age classes in transition of both sexes. In order to identify the trend or curve function of age and behaviour relationship, the trend analysis for those behavioural categories was attempted where the age had significant bearing on behaviour (Winer 1971). The linear trend hypothesized either an incremental or decremental straight curve function. The quadratic trend predicts the age function in terms of V or inverted V curve, showing incremental trend up to a particular age point followed by decremental trend or vice versa. The cubic trend defines such behavioural patterns which show once incremental then decremental and again taking incremental function or vice versa in a given age period, e.g. 'N' shaped curve. The trend analysis also yields a regression equation of age on behaviour.

Kruskal-Wallis one way ANOVA (Siegel 1956) was used to compare the frequencies among young, mature and old females to test the significance of within class behavioural changes.

Mann-Whitney 'U' test (Siegel 1956), suitable for comparison of two independent samples was used to assess the differences in behaviour between young and mature males.

A descriptive content analysis of the behavioural repertoire was also undertaken to see qualitative changes in terms of first or last occurrence of observed behavioural elements.

4. Results

A general survey of the occurrence of behaviour elements in the observation chart revealed a qualitative pattern in aggressive and submissive behaviours. Table 2 shows the first and last occurrence of the elements with age in both sexes, prepared by putting cross-sections of life span in terms of age classes in continuity. It was

Table 2. Duration of appearance of various behavioural elements during different stages in the life of rhesus monkey.

Behavioural element	Male	
Screech	1–3 years	2 years to old age
Scream	Never observed	3 years to old age
Bark	4·5 years to old age	Never observed
Threat	1 year to old age	1 year to old age
Chase	2·5 years to old age	3 years to old age
Clasp pull	1 year to old age	1·5 years to old age
Bite	3 years to old age	4 years to mature adulthood
Fear grimace	1–4 years	1 year to old age
Lip smack	Never observed	1·5 years to old age
Submit	3–4 years	1·5 years to old age

found that some of the behaviours developed during the juvenilehood while others did so during adolescence. At the same time, some of the elements were never observed after a certain age. Sex differences were also evidenced as males assumed an aggressive pattern with age advancement, while females exhibited aggressive as well as submissive behaviours. Adult males were never observed emitting scream and submit elements. Females were never seen barking but displayed all other elements throughout the ontogeny while males continue to display aggressive behaviours.

ANOVA applied to see the significance of age for 4 behavioural categories in both sexes under 3 transitional stages revealed that only 3 F values had associated probability equal to or greater than the confidence level (tables 3–5). It was found

Table 3. Mean per cent frequencies of submission toward others by females in transition stage-I, statistics for ANOVA and trend with regression equation.

Behaviour element	Toward	Mean % frequencies, Age blocks (K = 2 months)						
		1	2	3	4	5	6	Sum
Fear grimace	Female	Nil	Nil	0·05	0·10	0·10	0·05	0·30
	Male	Nil	Nil	Nil	Nil	0·05	Nil	0·05
	Juvenile	Nil	Nil	Nil	0·05	Nil	0·05	0·10
Lip smack	Female	Nil	Nil	Nil	Nil	0·05	Nil	0·05
	Infant	Nil	Nil	Nil	Nil	0·05	Nil	0·05
Submit	Male	Nil	Nil	Nil	0·05	Nil	Nil	0·05
	Female	Nil	Nil	Nil	Nil	Nil	0·05	0·05
Sum		Nil	Nil	0·05	0·20	0·25	0·15	0·65
Average		Nil	Nil	0·007	0·029	0·036	0·021	0·015

Summary of statistics.
(i) Between age blocks $F = 3{\cdot}14$, df = 5/30, $P < 0{\cdot}05$.
(ii) Linear trend $F = 16{\cdot}69$, df = 1/30, $P < 0{\cdot}01$.
(iii) Regression equation (X = behaviour and Y = age) X = 0·01 K − 0·01.

Table 4. Mean per cent frequencies of submissive behaviour by females in transition stage-II toward others, statistics for ANOVA and trend with regression equation.

Behaviour element	Toward	Mean % frequencies Age block (K = 2 months)						
		1	2	3	4	5	6	Sum
Fear grimace	Female	0·22	Nil	Nil	0·10	Nil	0·21	0·53
	Juvenile	0·06	Nil	Nil	0·21	0·78	Nil	1·05
	Male	0·06	0·05	Nil	0·10	0·20	0·10	0·51
	Adolescent female	0·06	Nil	0·05	0·05	0·29	0·10	0·55
Lip smack	Female	Nil	0·05	Nil	Nil	Nil	Nil	0·05
	Infant	0·06	Nil	0·05	0·47	0·20	Nil	0·78
Submit	Juvenile	Nil	Nil	0·10	0·05	0·20	Nil	0·35
Sum		0·46	0·10	0·20	0·98	1·67	0·41	3·82
Average		0·066	0·014	0·028	0·14	0·239	0·059	0·091

Summary of statistics.
(i) Between age blocks $F = 2{\cdot}71$, degree of freedom = 5/30, $P < 0{\cdot}05$.
(ii) Cubic trend $F = 8{\cdot}87$, df = 1/30, $P < 0{\cdot}01$.
(iii) Regression equation (X = behaviour and Y = age) = X = 0·02 K + 0·02.

Table 5. Mean per cent frequencies of aggression by others toward males in transition stage-II, statistics for ANOVA and with regression equation.

Behaviour element	By	Mean % frequencies						Sum
		1	2	3	4	5	6	
Threat	Male	Nil	Nil	Nil	Nil	0·10	Nil	0·10
	Juvenile	0·06	0·10	Nil	Nil	Nil	Nil	0·16
	Subadult male	0·11	Nil	0·16	0·05	0·06	0·21	0·59
	Female	0·06	Nil	Nil	Nil	Nil	Nil	0·06
	Infant	0·06	0·10	0·05	0·16	0·23	Nil	0·60
	Juvenile male-1	Nil	0·05	0·05	Nil	Nil	0·10	0·20
	Adolescent female	Nil	0·05	0·05	0·05	0·20	0·11	0·46
Chase	Female	Nil	Nil	0·05	Nil	Nil	Nil	0·05
	Juvenile	Nil	0·05	Nil	Nil	Nil	Nil	0·05
Clasp	Male	Nil	Nil	0·05	Nil	Nil	Nil	0·05
	Juvenile	Nil	0·10	Nil	Nil	Nil	0·42	0·52
	Female	Nil	Nil	0·10	0·21	Nil	0·21	0·52
Bile	Female	0 22	Nil	Nil	0·21	Nil	Nil	0·43
	Juvenile	Nil	Nil	Nil	0·10	Nil	Nil	0·10
Sum		0·51	0·45	0·51	0·78	0·59	1·05	3·89
Average		0·036	0·032	0·036	0·056	0·042	0·075	0·046

Summary of statistics.
(i) Between age block $F = 3{\cdot}40$, df = 5/70, $P < 0{\cdot}01$.
(ii) Linear trend $F = 4{\cdot}48$, df = 1/70, $P < 0{\cdot}05$.
(iii) Regression equation (X = behaviour and Y = age) $X = 0{\cdot}01\ K + 0{\cdot}02$.

that the submissive behaviour toward other animals by females in transition from infancy to juvenilehood differed significantly between age blocks (F 3·14, df 5/30, $P < 0{\cdot}05$). The rise and fall of observed frequencies depicted in figure 1 was tested by trend analysis, which was characterized by a significant linear incremental trend (F 16·69, df 1/30, $P < 0{\cdot}01$). Since the obtained equation was defined by a negative constant and a weak coefficient ($X = 0{\cdot}01\ K - 0{\cdot}01$), the submissive behaviour can be predicted as gradually increasing from infancy to juvenilehood among females (figure 1).

Submission by females also increased significantly when juveniles became adolescents (F 2·71, df 5/30, $P < 0{\cdot}05$). However, the observed frequencies changed their direction thrice which was significant as a cubic trend in statistical terms (F 8·87, df 1/30, $P < 0{\cdot}01$). Observed frequencies plotted upon age blocks in figure 2 shows that submissive behaviour decreased initially then increased till 5th age block, but returning to the initial level in the 6th block. The derived linear regression equation in general predicted fast additions in submission as entering into adolescence because the constant was positive and the regression coefficient was also substantial for each age block ($X = 0{\cdot}02\ K + 0{\cdot}02$).

The frequencies of aggression by others toward males in transition from juvenilehood to subadult class significantly differed between age blocks (F 3·40, df 5/70, $P < 0{\cdot}01$). Age dependent changes in frequencies was best characterized by a linear incremental trend (F 4·48, df 1/70, $P < 0{\cdot}05$). Figure 3 shows that during juvenile period (i.e. in first 3 age blocks) the aggression received was less varied, however, during subadult stage males received more aggression. Such pattern was expressed by a linear regression equation in the form of gradual increase in aggressive behaviours by other animals toward male subadults ($X = 0{\cdot}01\ K + 0{\cdot}02$).

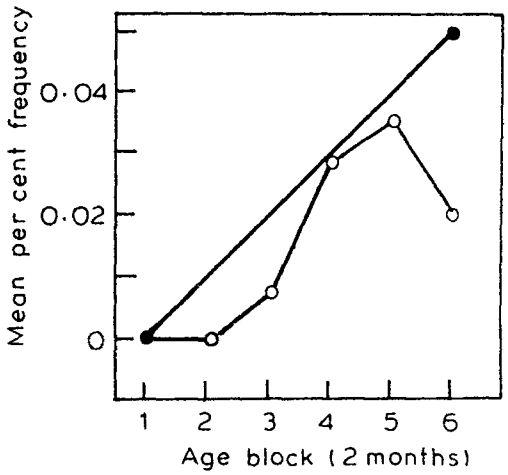

Figure 1. Mean per cent frequencies of submission to others by females in transition from infancy to juvenilehood. Straight line defines the best fit linear equation as $X = 0{\cdot}01\,K - 0{\cdot}01$ (age from 6–18 months).

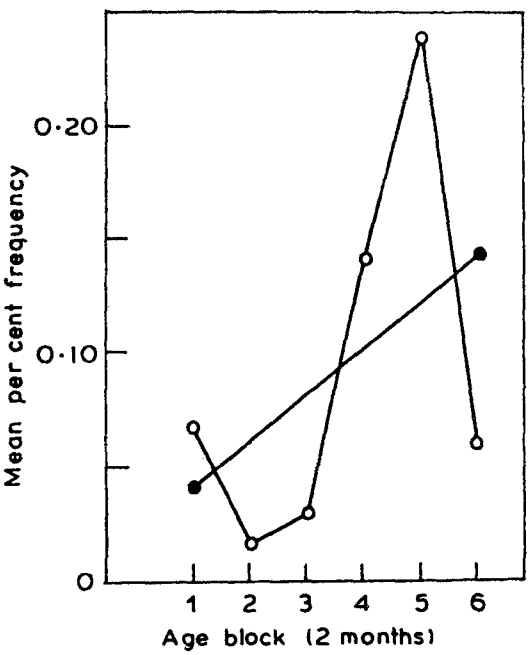

Figure 2. Mean per cent frequencies of submission to others by females in transition from juvenilehood to adolescence. Best fit linear function is by equation as $X = 0{\cdot}02\,K - 0{\cdot}02$ (age from 18–30 months).

Kruskal-Wallis 'H' was applied to assess the significance between young, mature and old females (statistically parallel to chi-square distribution) aggressive and submissive behaviour (table 6). The obtained statistics were non-significant for both categories of aggressive behaviour, but significant for submissive behaviour by

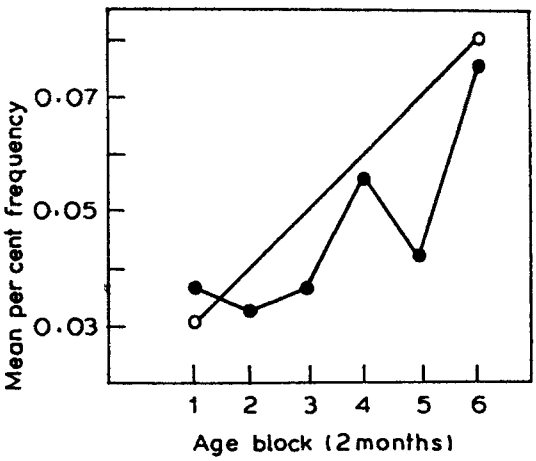

Figure 3. Mean per cent frequencies of aggression by others towards males in transition from juvenilehood to subadulthood. Linear equation for straight line was X = 0·01 K + 0·02 (age from 42–54 months).

Table 6. Mean per cent frequencies of young, mature and old females for 4 behavioural categories of agonistic behaviour and Kruskal-Wallis ANOVA for significance between them.

Behaviour category	Mean per cent frequencies Young	Mature	Old	χ^2 (df = 2)	*P*
Aggression to others	0·07	0·06	0·05	2·69	NS
Aggression by others	0·07	0·03	0·03	1·23	NS
Submission to others	0·18	0·08	0·17	12·67	< 0·01
Submission by others	0·11	0·08	0·02	6·79	< 0·05

NS, Non-significant.

others (*H* 6·79, df 2, $P < 0·05$). Mean per cent frequencies show that with increasing age females received less submission by others. Others submit to old females least (mean = 0·02%) and maximum to young female (mean = 0·11). Mature females submit less to others (mean = 0·08) than young (mean = 0·18) and old females (mean = 0·17).

Significant differences between young and mature adult males tested by Mann-Whitney 'U' test (table 7). It showed that mature males were significantly higher in aggression to, aggression by and submission by others than the young adult stage. In either stage, they rarely emitted submission toward other animals.

5. Discussion

Overall ontogenetic pattern of rhesus females was that submissive rather than aggressive behaviour should emerge as a characteristic feature. Their submission toward other animals slowly increased during transition from infancy to juvenilehood which further increased during way to adolescence. However, during mature adult years it decreased and again increased in old age. The pattern may be interpreted as a function of increased pressure from other animals in the core area

Table 7. Mean per cent frequencies of young and mature males for 3 behavioural categories and Mann-Whitney 'U' for difference between them.

Behaviour category	Mean % frequency Young	Mature	*U*	*P*
Aggression to others	0·05	0·07	3	<0·01
Aggression by others	0·08	0·21	0	<0·01
Submission by others	0·03	0·10	0	<0·01

of the group, as the females have to be integrated in the central space of the group. Similarly, females received less submission by other animals as they mature, because they themselves were less aggressive to others. Less submission during mature adulthood may be due to strong affiliation with males and support of kinship.

Aggressive behaviour among males increased linearly when they become sub adult from juveniles because juvenilehood among rhesus males is generally peripheral and solitary, whereas sub-adult males start taking interest in group activities to secure a place in group space. Interestingly, mature males received and emitted more aggression than young adults; this may have been due to the role of mature males in intragroup strifes. Typically, as males advance in age, the submissive behavioural elements are dropped from their behavioural repertoire. It seems that apart from other factors, the most important factor to influence the quantitative expression of aggressive and submissive behaviour may be age dependent spatial position of the animal in the group space, i.e. a consistent and stable dispersion of group members in an area. Assuming central position in the group is a motivating force for animals which enhances the likelihood of aggressive and submissive behaviours. Moreover, these patterns are not only susceptible to changes during growing years but also during adulthood. Old animals become more submissive and display a general disengagement in group activities, as reported by Hauser and Tyrrell (1984).

By and large, the observation support the findings of Altmann (1968) reporting that the agonistic behaviour of adult males is somewhat more likely to be aggressive than that of adult females, while the behaviour of adult females is more likely to be submissive.

References

Altmann J 1974 Observational study of behaviour: sampling methods; *Behaviour* **49** 227–265

Altmann S A 1968 Sociobiology of rhesus monkeys IV: Testing Mason's hypothesis of sex differences in affective behaviour; *Behaviour* **32** 49–69

Bernstein I S and Carolyn L E 1985a Agonistic aiding: Kinship, rank, age and sex influences; *Am. J. Primatol.* **8** 37–52

Bernstein I S and Carolyn L E 1985b Age-sex differences in the expression of agonistic behaviour in rhesus monkey (*Macaca mulatta*) groups; *J. Comp. Psychol.* **99** 115–132

Bernstein I S and Mason W A 1963 Activity patterns of rhesus monkeys in a social group; *Anim. Behav.* **11** 455–460

Hall K R L 1964 Aggression in monkey and ape societies; in *The natural history of aggression* (eds) J Carthy and F Ebling (New York: Academic Press) pp 51–64

Hamburg D A 1971 Psychological studies of aggressive behaviour; *Nature (London)* **230** 19–23

Hauser M D and Tyrrell G 1984 Old age and its behavioural manifestations: A study on two species of macaque; *Folia Primatol.* **43** 24–35

Kaplan J P 1977 Patterns of fight interference in free ranging rhesus monkeys; *Am. J. Phys. Anthropol.* **47** 249–288

Lindburg D G 1971 The rhesus monkey in North India: An ecological and behavioural study; in *Primate behaviour: Developments in field and laboratory research* (ed.) L A Rosenblum (New York: Academic Press) vol 2, pp 1–106

Mallow G K 1981 The relationship between aggressive behaviour and menstrual cycle stage in female rhesus monkeys (*Macaca mulatta*); *Horm. Behav.* **15** 259–269

Moller G W, Harlow H F and Mitchell G D 1968 Factors affecting agonistic communication in rhesus monkeys; *Behaviour* **31** 339–356

Post W and Baulu J 1978 Time budgets of *Macaca mulatta*; *Primates* **19** 125–140

Roonwal M L 1977 Urbanization in primates and comparison with man; *J. Sci. Ind. Res.* **36** 179–187

Rowell T E 1972 Female reproductive cycles and social behaviour in primates; in *Advances in the study of behavior* (eds) D S Lehrman, R A Hinde and E Shaw (New York: Academic Press) vol 4, pp 69–105

Siegel S 1956 *Non parametric statistics for behavioural sciences* (New York: McGraw Hill)

Singh R 1986 Ontogeny of play behaviour in free ranging rhesus macaques (*Macaca mulatta*); *Proc. Indian Acad. Sci. (Anim. Sci.)* **95** 605–612

Singh S D 1969 Urban monkeys; *Sci. Am.* **221** 108–115

Sonthwick C H, Siddiqi M F, Farroqui M Y and Pal B C 1976 Effects of artificial feeding on aggressive behaviour of rhesus monkeys in India; *Anim. Behav.* **24** 11–15

Symons D 1978 *Play and aggression: A study of rhesus monkeys* (New York: Columbia University Press)

Wilson A P and Boelkins R C 1970 Evidence for seasonal variation in aggressive behaviour by *Macaca mulatta*; *Anim. Behav.* **18** 719–724

Winer B J 1971 *Statistical principles and experimental design* (New York: McGraw Hill)