MALE MIGRATION IN LION-TAILED MACAQUES. <u>ANANDA KUMAR, M.,</u> SINGH, M., KUMARA, H.N., SHARMA, A.K. AND BERTSCH, C.

Key words: Lion-tailed macaque, male migration, Anaimalai Hills, habitat management, animal management

Abstract

Adult lion-tailed macaque males probably often migrate. Previous observations indicate the presence of solitary adult males in the forest and also the number of adult males in a group varying in repeated counts. This paper reports one fully documented case of a solitary male joining the study group. The resident male was first chased out and then allowed to reenter the group. One female conceived and delivered during the presence of migratory male. Almost all matings with that female were made by the migratory male. The other adult females in the group preferred the migratory male to the resident male in all social interactions including sexual present, approach, proximity, and grooming. The presence of two adult males resulted in a significant reduction in the frequency of social interactions among group members. The fact that the group females easily accepted the migratory male has significant implications for the management of this species inhabiting forest fragments.

Introduction

In social species of animals, a group is a stable unit. However, individual animals often disperse leading to immigration and emigration. In most of the social species, the dispersing animals are males. In a number of primate societies, the adult socionomic sex ratio is normally biased in favor of females. So, the adult sex ratio and shift direction results in non-random male shifts (DRICKAMER and VESSEY, 1973) and random male shifts (KOFORD, 1966; MELNICK et al., 1984). The male dispersal also can be classified as natal (from the natal groups) or secondary (later dispersal events) (BORRIES, 2000).

A number of aspects related to male dispersal that have attracted attention of researchers include the causative factors, the timing and the consequences of such dispersal.. Incest avoidance appears to be the most important causative factor for male dispersal (ITANI, 1972; SHIELDS, 1987). An adult male is probably rarely present in his group when his oldest daughter becomes reproductively mature in *Macaca mulatta* (MELNICK et al., 1984), in *M. sinica* (DITTUS, 1977), in species of *Presbytis* (RUDRAN, 1973; HRDY, 1974), and in *Cercopithecus aethiops* (HENZI and LUCAS, 1980). Another reason for male dispersal is competition among males and access to more estrus females (DOBSON, 1982; MOORE and ALI, 1984; PUSEY and PAC-KER, 1987; ALBERTS and ALTMANN, 1995). Obtaining a higher dominance rank by emigrating into another group emerged as another causative factor of male dispersal (BORRIES, 2000). As far as the timing is concerned, male dispersal often coincides with the mating season, especially in species that are characterized by strict breeding seasonality (SUGIYAMA, 1976; SPRAGUE, 1992; SUSSMAN, 1992). The major consequence of dispersal is the gene flow between/among groups, and as a result, a pattern favored by selection. In most studies, particular attention has been paid to the gains of dispersal for the male, and little is documented about the effect of such dispersal on the social interactions among the members of an established group. The implication of dispersal patterns for the management of a species has hardly been ever discussed.

We have been monitoring several groups of lion-tailed macaques in Anaimalai Hills and recording their demographic features over 5 years. Many groups are periodically visited for demographic data. During these repeated counts, we often observed that whereas the number of individuals of other age-sex classes would be constant, the number of adult males in a group would vary. Further, solitary adult lion-tailed macaque males were often encountered in the forest. A group of lion-tailed macaques usually has one adult male and cases of solitary males have been reported earlier (GREEN and MINKOWSKI, 1977; KUMAR, 1987; KARANTH, 1992). However, in these studies, the solitary males were neither identified nor followed, and hence, no systematic data exist on male migration in lion-tailed macaques. In this paper, we report a systematically documented male migration process, its effect on group social interactions, and its implications for the management of this endangered species.

Methods

Study area and group

The study area is Puduthotam Estate forest in Anaimalai Hills. This forest is less than 1 square kilometer and is inhabited by two groups of lion-tailed macaques. At the time of the study, the large group, PT-1 consisted of 46 animals, and the smaller group PT-2 consisted of 13 animals. All animals in PT-2 and many animals in PT-1 were individually identified for the past several years. PT-2 is our intensive study group. The methods of data collection included focal animal sampling (one-zero frequencies with 20-sec. intervals), focal behavior sampling and ad libitum notes. An animal was observed for an uninterrupted period of 5 minutes divided into 15 intervals of 20 seconds each. Each behavior that occurred was recorded only once during an interval. The total number of focal samples on adult individuals was 2871. Focal behavior sampling was made only with relation to swelling of the sexual skin and number of matings by different males. Other events related to male migration were recorded as ad libitum notes.

Observations

Migration related events

During 1996-97, a solitary adult lion-tailed macaque male, identified as BC, was often observed in this forest. The male was occasionally seen in PT-1 and was observed to mate with the females of that group. However, most of the times, it was a solitary male and remained away from both of the groups. This male entered our study group, PT-2, in September, 1997. The structure of the study group and the his-

tory of migration related events in shown in Table 1. In July, 1997, the group had two adult males (RM and LM) and one subadult male (SAM). LM left the group in August and joined the larger group. On September 22nd, BC, the solitary male, entered the study group. There was aggression between RM and BC, and RM was physically injured with a limping arm. Within few hours, RM was chased out of the group by BC, and from then on, RM kept wandering in the periphery of the study group. He made several attempts to enter the group but was attacked severely by BC. He never attempted to join PT-1. However, on October 11, '97, RM was once again seen inside the study group. From then on, the two adult males, RM and BC remained in the group until June 22nd, 1998. At that date, BC left the group and was again spotted as solitary male several times.



Fig. 1: Migratory males, a typical phenomena in wild lion-tailed macaques. (Photo: W. Kaumanns)

Table 1: The structure of study group, and the summarized history of migration related events.

Period	Males	Females	Young
Jul-Aug '97	RM, LM, SAM	5	3
Aug '97	LM leaves; Joins PT-1		
Sep 22, '97	BC immigrates; RM chased out		
Oct 11, '97	RM rejoins group		
Oct '97-Jun '98	RM, BC, SAM	5	3 new births
Jun 22 '98	BC emigrates		

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Breeding status of the group females

Table 2 presents information on the breeding status of the adult females in the group. The female FAC has not reproduced during the study period. Two other adult females, BRE and NIP delivered their infants on February 24th and January 2nd 1998 respectively. They must have conceived during August and July of 1997. The migratory male BC was not present in the group at that time and RM was the dominant adult male. BUL delivered her infant on May 1, 1998 and she must have conceived around the end of October, 1997. She, therefore, becomes the focus of attention. BC joined the group during September and ousted RM. BUL was frequently reaching 2nd and 3rd degrees of swelling during October and was being frequently mated.

Female	Conception	Male(s) present	Delivery
FAC	-	-	-
BRE	Aug '97	RM	Feb 24 '98
NIP	Jul '97	RM	Jan 2 '98
BUL	Oct '97	RM & BC	May 1 '98
SAF	-	-	-

Table 2: BC's migration and the breeding status of group females.

Mating with BUL

Table 3 provides a summary information about mating with BUL by the two adult males during different months. The most interesting month is October when conception would have taken place. RM mated with her only 4 times as against 66 matings by BC. Further analysis showed that of the four matings by RM, only one occurred at the 3rd degree of swelling. Only one ejaculation was seen by RM and that too when BUL had 2nd degree of swelling. On the other hand, BC mated with her 38 times at 2nd degree of swelling with 6 ejaculations, and 28 times at 3rd degree of swelling with 5 observed ejaculations. It can, therefore, be presumed that BUL would have conceived by BC. During November, BUL mated only 7 times with BC and never with RM. In the subsequent months, there was no considerable occurrence of mating with BUL, and there was no difference between the two males for their frequency of mating with BUL. BUL delivered in May, and in June, BC again left the group and became a solitary male.

Table 3: Summary information about matings with BUL by the two adult males during different months.

Month	RM mates	BC mates	October data				
Oct	4	66	RM mates				
Nov	0	7	Deg	Mate	Eja		
Dec	0	1	2	3	1		
Jan	2	3	3 1 0				

Month	RM mates	BC mates	Oc	October data					
Feb	1	2	BC mates						
Mar	0	2	2	38	6				
Apr	1	0	3	28	5				
May	0	0	May 1 delivery						
Jun	0	0	Jun 22: BC leaves						

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Social behavior

In the following section, the data are presented on social behavior under four conditions:

- when RM was the only adult male in the group,
- when BC migrated to the group and pushed RM out,
- when RM again joined the group and RM and BC were together in the group, and
- when BC left the group and RM was again the only adult male.

The values presented in data tables (4-10) refer to the occurrence of a social interaction in per cent of 20-sec. Intervals during one-zero sampling.

Approach behavior

When RM and BC were the lone males in the group, they had a mean occurrence of female approaches to them in 0.585 and 0.22 per cent of 20-sec intervals respectively (Table 4). However, when the two males were together in the group, females approached males in 0.039 per cent of intervals combined for both males. The female approaches towards the migratory male were about 2.5 times more than towards the resident male. This value remained as low as 0.008 per cent of intervals even when BC left the group and RM was the only adult male in the group. The data about male approaches to females give a slightly different picture. When RM was alone, he approached females in 0.63 per cent of intervals. This value was only 0.10 per cent in the case of BC, the migratory male, when he was alone in the group. However, when the two males were together, although individually each one had a low occurrence of approaches, if the values for the two males were added, approaches towards females occurred in 0.11 per cent of intervals. This value also remained at 0.11 per cent when RM was the only adult male again. In other words, not a considerable change was observed in the case of male approaches to females. The most notable point here is that most of these approaches by males were accounted for by the approaches to FAC who was the most dominant female in the group. There were only 5 instances of females following BC, the migratory male. The resident male was never followed.

Table 4: The occurrence of approaches in percent intervals when adult males were lone males or together in the groups.

Female	(1)*	(2)*	(1)**	(2)**	(1)^	(2)^	(1)^^	(2)^^	(1)*	(2)*
FAC	0.17	0.87	0.36	0.09	0.01	0.07	0.06	0.19	0.01	0.40
BRE	0	0.17	0	0.11	0	0.01	0.02	0.03	0	0
NIP	0.57	0.57	0	0	0.01	0.02	0.01	0.04	0.02	0

Female	(1)*	(2)*	(1)**	(2)**	(1)^	(2)^	(1)^^	(2)^^	(1)*	(2)*
BUL	1.60	0.90	0.52	0.20	0.03	0.01	0.02	0.05	0	0.02
Mean	0.58	0.63	0.22	0.10	0.01	0.03	0.03	0.08	0.01	0.11
*RM alone; **BC alone; ^RM when RM and BC together; ^^BC when RM and BC together										
(1) Appro	ached (e.	g. Approa	ached by H	FAC); (2)	Approach	es (e.g. Ar	proaches	FAC)	-	

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Female groom males

RM and BC when alone were groomed by the females in 4.58 and 2.60 per cent of intervals respectively (Table 5). However, when there were two males present in the group, RM and BC received grooming from females only in 0.38 and 0.73 per cent of intervals respectively. However, the migratory male was groomed by the females more than twice as compared with resident male. Grooming of RM remained low (in 0.8 per cent intervals) even after BC left the group, and RM was the only adult male.

Male proximity to females

The proximity to females by males was high when either RM or BC were lone adult males, occurring in 2.12 and 1.45 per cent of intervals respectively (Table 6). It came down to only in 0.43 per cent intervals, added for both of the males, during their togetherness. The frequency with which the migratory male made proximity to females was again about twice as much as the frequency for the resident male. This frequency remained low occurring in 0.69 per cent intervals when RM was alone again.

Female	RM alone	BC alone	RM*	BC*	RM alone
FAC	4.40	4.60	0.90	2.30	2.90
BRE	3.30	4.10	0	0.20	0
NIP	9.70	0	0.20	0	0.30
BUL	0.90	1.70	0.40	0.40	0
Mean	4.58	2.60	0.38	0.73	0.80
*WI DM					

Table 5: The occurrence of female groom males in percent intervals.

*When RM and BC were together in the group

Table 6: The occurrence of male proximity to females in percent intervals.

	FAC	BRE	NIP	BUL	Mean			
RM alone	4.20	0.20	2.10	2.00	2.12			
BC alone	1.64	1.30	1.50	1.35	1.45			
RM*	0.08	0.17	0.23	0.10	0.12			
BC*	0.38	0.18	0.13	0.41	0.28			
RM alone	2.45	0	0.25	0.07	0.69			
*When RM an	*When RM and BC were together in the group							

Sexual present and sexual mounts

A pattern similar to other social interactions can also be seen in the case of sexual present by females to males (Table 7). Sexual present occurred in 1.40 and 0.55 per cent of intervals for RM and BC respectively when they were the single adult males in the group. This occurrence came down to only in 0.155 per cent intervals added for two males when both were present. This is inspite of the fact that the conception in the case of female BUL occurred when the two males were together in the group. However, the females sexually presented to the migratory male about 9 times as often as compared to the resident male. This frequency also remained low when RM was the lone male once again. A similar pattern was also observed in the case of sexual mounts by males (Table 7). The frequency was higher when there was a single male as compared to when two males were present in the group.

Table 7: The occurrence of sexual presents by female and mounts by males in percent intervals.

Female	(1)*	(2)*	(1)**	(2)**	(1)^	(2)^	(1)^^	(2)^^	(1)*	(2)*
FAC	2.10	1.90	0.10	0.50	0.03	0.05	0.30	0.30	0.70	1.00
BRE	0.20	0	0.70	0.80	0	0.01	0.10	0.10	0	0
NIP	1.90	2.10	0	0	0.01	0.01	0.05	0.06	0.05	0.05
BUL	1.40	2.20	1.40	0.50	0.02	0	0.10	0.10	0.05	0.02
Mean	Mean 1.40 1.55 0.55 0.45 0.02 0.02 0.14 0.14 0.20 0.26									
*RMalone; **BC alone; ^RM when RM and BC together; ^^BC when RM and BC together										

Distance between males and females

Records were maintained on the distance between each adult male and adult female at regular intervals. The estimated distance was noted in terms of meters. However, for the analysis purpose, we have converted the actual distance into five categories including less than 2 meters, 2 to 4 meters, 4 to 8 meters, 8 to 15 meters and more than 15 meters (Table 8). Further, in this data table, a male's distance has been taken as an average distance from all adult females.

	< 2	2-4	4-8	8-15	> 15
RM alone	4.10	3.30	11.80	19.20	61.60
BC alone	2.80	8.30	8.30	30.60	50.00
RM*	0.90	1.50	11.80	22.00	63.70
BC*	1.20	1.90	9.90	13.60	73.20
RM alone	1.70	4.20	15.40	17.10	61.50
*When RM an	d BC were toget	her in the grou	ip	1	

Table 8: Males' distance (in meters) from females in percent intervals.

The values in table 8 present per cent occurrence of a distance between a male and females. The values have been highlighted for the first two categories, that is up to 2 and 2 to 4 meters. We believe that the per cent occurrence for longer distances could be due to chance. A pattern similar to other social interactions can be seen here with only one difference. The per cent occurrences of lesser distance between males and females were higher when there was a single adult male, be it RM or BC. The per cent of short distance was significantly reduced between either of the males and females when the two males were present in the group. However, unlike in other aspects of sociality where the values remained low after BC left the group, the short distance per cent quickly started to rise between RM and females after BC left the group.

When RM and BC were the two adult males in the group, two females, BRE and NIP were already pregnant. Another female, BUL, became pregnant within the first month of their joint presence. This being the case, it might appear that since three of the four adult females in the group were pregnant, this fact alone might account for the reduced interaction between males and females. If that is the case, then at least the social interactions among the adult females themselves should not be influenced. We, therefore, further analyzed the data on female-female interactions in relation to the various events of male migration.

Female-female interactions

The data on female-female interactions are presented in Table 9. In most cases, the relationship of female-female interactions to the events of male migration was more or less the same as it was in the case of male-female interactions.

Activity	RM alone	BC alone	RM+BC	RM alone
Approach	0.77	0.53	0.38	0.50
Present for groom	0.60	0.80	0.27	0.60
Proximity	3.93	5.96	2.92	1.41
Social grooming	6.80	3.80	6.60	6.50

Table 9: The female-female interaction in percent intervals.

Approaches among females: The per cent occurrence of approaches among female was high when either of the males was the sole adult male in the group; it became considerably low when two males were present; and it became high again after BC left the group.

Present for groom: The per cent occurrence of present for groom by the females to each other was high when either RM or BC was in the group; it became significantly low when both males were present; and it again started to rise when RM was the sole adult male in the group.

Proximity among females: The per cent occurrence of proximity among females was high when a single male was present; it considerably reduced at the time of the presence of two males; and it remained low even when RM was the only male in the group.

Social grooming among females was however not influenced by the male migratory events.

The data were also analyzed on the total occurrence of aggression related behavior in the group under the events of male migration (Table 10). As was the case with male-female interactions, and female-female interactions, the per cent occurrence of attack/chase on one hand, and fear grimace on the other hand, was high when there was the presence of a single adult male; it became low when two adult males were present in the group; and remained low even after BC left the group.

	RM alone	BC alone	RM+BC	RM alone
Chase/Attack	0.81	0.64	0.18	0.33
Fear grimace	2.60	0.79	0.41	0.44

Table 10: Total occurrence of aggression in percent intervals.

Discussion

WILSON et al. (1975) and BUSH et al. (1977) postulated that the rapid rates of chromosomal evolution and speciation among mammals were determined by the social subdivisions, the resulting inbreeding and reduced effective population size. However, MELNIK et al. (1984), working on natural populations of rhesus monkeys in Pakistan, refuted this explanation. They suggested that the rapidity of the speciation process and chromosomal evolution among social mammals might be found in the combined effects of social structure and ecological or geographic isolation. They observed that reproduction takes place within social groups by males coming from an array of social groups, extending far beyond the immediate neighborhood. They also observed male-limited natal group emigration, relatively short nonnatal group male tenure, and a seemingly random distribution of male migration. The study of male migration, therefore, is interesting not only from the point of view of understanding dispersal but also for its effect on the genetic structure and sociobiology of a population.

The information presented in this paper is interesting the several reasons:

Male migration has been known in lion-tailed macaques but this is the first case of a systematic recording of data with relation to pre-migratory, migratory and post-migratory events. The fact that we have often observed solitary adult liontailed macaque males and also the number of adult males varying in a group, as well as recorded the whole process of migration of a male, suggests that frequent inter-troop male migration is a regular feature of lion-tailed macaque societies.

In most of the social interactions between males and females and among females, there was a significant drop in frequency when two adult males were present in the group. It should be noted that such a change cannot be attributed to the presence of a migratory male because the frequency of social interactions was high when BC was the lone adult male in the group for a few days. In large forest complexes where there is space available for dispersal, a group of lion-tailed macaques usually has a single adult male. The changed social interaction patterns indicate that unless otherwise forced by the circumstances (such as inhabiting an isolated forest fragment with no room for dispersal), one adult male per group appears to be a rule in lion-tailed macaque societies.

Xenophobia is a characteristic of most of the non-human primate societies. However, a distinction must be made between the reactions of the resident adult male(s) and rest of the group members to the sight of a new adult male. When BC entered our study group, an immediate fight occurred between BC and RM and RM was chased out of his group. Even when RM was again back in the group, the group females preferred the migratory male to the resident male. Proximity to, and grooming of, the migratory male by adult females was higher than that of the resident male. SOLTIS et al. (1997a) reported that in Japanese macaques, females choose males by maintaining proximity to some males and avoiding others, thereby increasing mating opportunity with preferred males and the time spent in proximity with them. SOLTIS et al. (1997b) also demonstrated that male attractivity significantly predicted actual male reproductive success, and female mate choice was a more powerful predictor of overall mating. In our study, the adult females made most of their sexual presents to the migratory male.

The costs of becoming a migratory male are enormous, even sometimes resulting in death (RAJPUROHIT and SOMMER, 1993). Though BC was mostly seen as a solitary male, he did enter the larger group PT-1 which contained several adult males. He was observed to mate with females in that group. He then entered our study group PT-1, and after 8 months of stay, he again became a solitary male. Migration, therefore, must have strong associated benefits to counter risk and costs. It would be worthwhile to determine whether certain males have some unique characteristics which develop in them a tendency to become a migratory individual more often than usual.

Apart from the theoretical aspects, the study of the process of male migration has far reaching implications for the management of lion-tailed macaques in their natural habitats as well as in captivity.

Habitat management: The lion-tailed macaques in most of their habitats now inhabit forest fragments. Some of the fragments, each harboring only one group of lion-tailed macaques, have been isolated for several decades. Since the migration of adult males appears to be a regular phenomenon in this species, the populations in these fragments can be managed through minimal habitat management. Most of the forest fragments are located in private tea estates and it is not possible to link these fragments through large forest corridors. Our own surveys in Anaimalai Hills, where most forest fragments are now found, indicate that narrow corridors through streams and valleys still could be established between the fragments by planting selected fruit bearing tree species. Such narrow strips may not be enough for dispersal of large number of individuals, but could be sufficient to facilitate male migration between isolated groups.

Animal management: The data also teach us a lesson about animal management. If establishment of corridors is not at all possible (as it is the case in many fragments such as Pannimed in Anaimalai Hills) among far flung areas, adult males could be comfortably exchanged between the groups. Unlike many other macaque societies, the female lion-tailed macaques appear to be least xenophobic about new males. No aggression of dangerous proportions may be expected if the males are so exchanged for the maintenance of genetic diversity in the natural populations. Similar strategies could also be tried on captive populations of lion-tailed macaques.

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References

ALBERTS, S.C. and ALTMANN, J.: Balancing costs and opportunities: dispersal in male baboons. Amer. Natural. (1995) 145: 279-306.

BORRIES, C.: Male dispersal and mating season influxes in Hanuman langurs living in multimale groups. In: KAPPELER, P.M. (ed.): Primate Males. Cambridge: Cambridge University Press (2000): 146-158.

BUSH, G.L., CASE, S.M., WILSON, A.C. and PATTON, J.L.: Rapid speciation and chromosomal evolution in mammals. Proc. Nat. Acad. Sci. USA (1977) 72: 3942-3946.

DITTUS, W.P.J.: The social regulation of population density and age-sex distribution in the toque monkey. Behav. (1977) 63: 281-321.

DOBSON, F.S.: Competition for mates and predominant juvenile male dispersal in mammals. Anim. Behav. (1982) 30: 1183-11292.

DRICKAMER, L.C. and VESSEY, S.H. : Group changing in free ranging male rhesus monkeys. Primates (1973) 14: 359-368.

GREEN, S. and MINKOWSKI, K.: The lion-tailed macaque and its south Indian rainforest habitat. In: BOURNE, G.H. and RAINIER, PRINCE CHARLES (eds.): Primate Conservation. New York: Academic Press (1977): 283-337.

HENZI, S.P. and LUCAS, J.W. : Observations on the inter-troop movement of adult vervet monkeys (*Cercopithecus aethiops*). Folia Primatol. (1980) 33: 220-235.

HRDY, S.B.: Male-male competition and infanticide among the langurs (*Presbytis entellus*) of Abu, Rajasthan. Folia Primatol. (1974) 22: 19-58.

ITANI, I.: A preliminary essay on the relationship between social organization and social avoidance in nonhuman primates. In: POIRIER, F.E. (ed.): Primate Socialization. New York: Random House (1972): 165-171.

KARANTH, K.U.: Conservation prospects for lion-tailed macaque in Karnataka, India. Zoo Biol. (1992) 11: 33-41.

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KOFORD, C.B. : Population changes in rhesus monkeys: Cayo Santiago, 1960-64. Tulane Studies Zool. (1966) 13: 1-7.

KUMAR, A.: The Ecology and Population Dynamics of the Lion-Tailed Monkeys (*Macca silenus*) in South India. Ph.D. Thesis (1987). Cambridge: Cambridge University.

MELNICK, D.J., PEARL, M.C. and RICHARD, A.F.: Male migration and inbreeding avoidance in wild rhesus monkeys. Amer. J. Primatol. (1984) 7: 229-243.

MOORE, J. and ALI, R.: Are dispersal and inbreeding avoidance related? Anim. Behav. (1984) 32: 94-112.

PUSEY, A.E. and PACKER, C.: Dispersal and philopatry in primate societies. In: SMUTS, B.B., CHENEY, D.L., SEYFARTH, R.M. WRANGHAM, R.W. and STRUH-SAKER, T.T. (eds.): Primate Societies. Chicago: University of Chicago Press (1987): 252-266.

RAJPUROHIT, L.S. and SOMMER, V.: Juvenile male emigration from natal onemale troops in Hanuman langurs. In: PEREIRA, M.E. and FAIRBANKS, Y.A. (eds.): Juvenile Primates: Life History, Development and Behavior. New York: Oxford University Press (1993): 86-103.

RUDRAN, R.: Adult male replacement in one-male troops of purple faced langurs (*Presbytis senex*) and its effect on the population structure. Folia Primatol. (1973) 19: 166-192.

SHIELDS, W.M.: Dispersal and mating systems: Investigating their causal connections. In: CHEPKO-SADE, B.D. and HALPIN, Z.T. (eds.): Mammalian Dispersal Patterns: The Effects of Social Structure on Population Genetics. Chicago: University of Chicago Press (1987): 3-24.

SOLTIS, J., MITSUNGA, F., SHIMIZU, K., YANAGIHARA, Y. and NOZAKI, M.: Sexual selection in Japanese macaques I: female mate choice or male sexual coercion? Anim. Behav. (1997a) 54: 725-736.

SOLTIS, J., MITSUNGA, F., SHIMIZU, K., NOZAKI, M., YANAGIHARA, Y., DO-MINGO-ROURA, X. and TAKENANA, O.: Sexual selection in Japanese macaques II: female mate choice and male-male competition. Anim. Behav. (1997b) 54: 734-746.

SPRAGUE, D.S.: Life history and male intertroop mobility among Japanese macaques (*Macaca fuscata*). Int. J. Primatol. (1992) 13: 437-454.

SUGIYAMA, Y.: Life history of male Japanese monkeys. In: HINDE, R.A., SHAW, E. and BEER, C. (eds.): Advances in the Study of Behavior, Volume 7. New York: Academic Press (1976): 255-284.

SUSSMAN, R.W.: Male life history and intergroup mobility among ringtailed lemurs (*Lemur catta*). Int. J. Primatol. (1992) 13: 395-413.

WILSON, A.C., BUSH, G.L., CASE, S.M. and KING, M.C.: Social structuring of mammalian populations and the rate of chromosomal evolution. Proc. Nat. Acad. Sci. USA (1975) 72: 5061-5065.

Authors'address: Biopsychology Laboratory, University of Mysore, Mysore – 570 006. India. Email: mewa@vsnl.com