reservoir, a region that has experienced low-level activity in the past.

We conclude that the recent activity in the vicinity of the Idukki Reservoir is unusual, considering the long gap since the initial filling and the onset of activity. However, the activity occurred in regions in the vicinity of the reservoir, which have been previously activated. The current spurt of earthquakes could be related to the changes in the hydrologic equilibrium, caused by the monsoonal recharge of the region. It may be recalled that all such periods of increased rainfall may not necessarily lead to increase in micro-seismicity. Earthquakes occur where the faults are critically close to failure, and the small change in pore water pressure conditions induced by the combined effect of the reservoir and the monsoonal recharge of the area provides the trigger for failure. The hydrologic conditions of the Idukki Reservoir appear to be conducive to sustain some low-level seismic activity and there is a need to strengthen the seismic monitoring in this region. This would enable us to know the precise location of active zones, migration of seismic activity and also understand the temporal and spatial correlation with the reservoir filling and seasonal recharge. As one of the oldest reservoirs that continues to generate low-level seismic activity, the seismicity associated with the Idukki Reservoir is worth monitoring also from the point of understanding the long-term behaviour of seismogenic reservoirs.

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Social relationships among lion-tailed macaque (*Macaca silenus*) males in differently structured social units

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There is a need to study male–male relationships since models on the evolution of social relationships among primates have mainly focused on females. In this study aspects of the social relationships among lion-tailed macaque males in differently structured social units have been studied. The units include three heterosexual groups with (i) one adult, one subadult, and eight juvenile males; (ii) two adult males, one of which was castrated and (iii) two adult males and a subadult male compared under two different conditions, viz. in a small indoor and a much larger outdoor enclosure. The studies used focal animal sampling and covered minimally three months each. In the first study, over 40% agonistic interactions occurred between adult and subadult males. The interactions with juvenile males were largely of affiliative nature. The castrated male received lower aggression than the normal subadult male. The males showed more aggressive behaviour in the outdoor than in the indoor enclosure. In the latter condition, however, the males showed more disturbed behaviour. Observations from field studies, earlier attempts at establishing captive all-male groups, and the present study point to a high degree of social intolerance among adult lion-tailed macaque males. Therefore, the establishment of all-male groups in the zoos does not appear to be possible.

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However, due to the fact that the males, especially the related males, show largely affiliative behaviours, it is possible to maintain all-male groups, preferably of individuals from the same groups, up to subadulthood.

Keywords: Agonistic and affiliative interactions, lion-tailed macaques, male–male relationships, social tolerance.

TWO models explain the evolution of social relationships among primates. The socio-ecological model[1–3] illustrates the role of ecological factors such as food distribution, predator density, arboreal/terrestrial habitats, etc. producing variations in the frequency and nature of social interactions across and within species. The second model considers that most traits in primates are rather conservative and the interaction patterns within a species or taxa remain relatively invariant due to internal and external constraints[4]. Both the models and the resulting theories are largely based on the behaviour of primate females. The behaviour of males has largely been seen to be guided by reproductive competition and male behaviour varying as female patterns vary. It is only recently that increasing attention has been paid to the males and they are being seen as active agents that can influence the whole pattern of social interactions in a species[5]. At a more applied level, an understanding of the behaviour of males assumes an even greater significance when an endangered species needs to be maintained and managed as a reserve. Due to several constraints such as space and the total number of individuals that an institution managing a captive group can hold, the demographic structure of groups in captivity is almost always different from that in the natural habitats of the species. Since birth ratios are assumed to be 1 : 1, and since more than one adult female is kept, and even recommended to be kept, in a group, it results in several reproductively potential males as 'surplus males'. These males have to be housed either individually, in all-male groups, or in other ways, for example, a castrated male in a heterosexual group.

The lion-tailed macaque (*Macaca silenus*) is a representative case in which the knowledge about male behaviour is critical concerning the management of males. It is an endangered species (C2a(i)) inhabiting the tropical rainforests of the Western Ghats in southern India[6]. Its habitat is becoming largely fragmented[7], and at present, there appears to be no viable population[8]. Recognizing its threatened status in the 1980s, the lion-tailed macaque was brought under the Species Survival Plan (SSP) of North America and European Endangered Species Breeding Programmes (EEP). As expected, these programmes also have to deal with 'surplus males' on a large scale[9,10]. Several management attempts have been made[10–12], but the know-how of dealing with these males is still limited due to lack of knowledge about the potential of lion-tailed macaques to develop intra-sexual social relationships. In natural habitats, lion-tailed macaques usually live in a group of several adult females, immatures and usually one or few adult males[13]. Adult males often migrate between groups and also can be seen as solitary individuals[14]. However, in the groups inhabiting forest fragments most of which are smaller than 2–3 sq. km, the adult males have a constraint on their dispersal and the groups end up with more than one adult male[15]. Since habitat fragmentation is of recent origin, and the detailed studies on behaviour are limited, we do not know how these males deal with each other. The data available so far from the wild habitats on male–male relationships indicate that the adult males of a group maintain long distances among them and rarely interact with each other. Whenever such interactions occur, they are largely of agonistic nature[7]. However, in the wild habitats, even if a group inhabits a small forest fragment, there is sufficient space for the individuals to maintain long distances within a group. Under captivity, no enclosure can match the size of the home range of a wild group, and therefore, the animals are forced to remain in relative proximity. Whether the males of a species have the potential to deal with such a situation is hard to study from the wild habitats. Captive groups however provide a variety of social set-ups providing an opportunity to obtain knowledge about male behaviour under different social situations, which may become useful to deal with males in natural habitats. We ask the question: how would males behave when (i) housed with several females and males of various age classes; (ii) housed in a heterosexual group with a normal and a castrated male and (iii) housed with others in a small indoor enclosure and a relatively large outdoor enclosure? In this communication, we report results of the study of the behaviour of male lion-tailed macaques in such differently structured social units.

This communication is based on the data on male–male interactions extracted from three independently carried out studies in Cologne, Szeged and Rostock zoos under EEP.

Let us consider male–male interactions in a mixed-ages group. This study was carried out on a group of lion-tailed macaques comprising one adult male (165 months – age class I), one subadult male (57 months – age class II), three juvenile males (34–41 months – age class III), two juvenile males (23–24 months – age class IV), three male infants (> 9 months – age class V) with three adult and seven immature females at Cologne Zoo, Germany. All non-adult individuals were the offspring of the adult male. Males were the focus of observation and were observed for a period of 122 h. Focal animal sampling was employed to gather data on agonistic and affiliative social interactions. One indoor and two outdoor enclosures were connected by a tunnel amounting to a total ground space of about 240 sq. m with the height varying between 2.5 and 6.5 m. The study was carried out by Vorwerk[16] during October–December 2007.

Let us next consider male–male interactions between a castrated and a normal male. This study was carried out on a group of lion-tailed macaques at Rostock Zoo, Germany. The group comprised of two adult males, one of which was castrated, one subadult male and three adult females. For the purpose of the present study, we have used data only on the interactions among two adult males and one subadult male of the study group. Data on agonistic and affiliative interactions between the dominant male (Guru) and castrated adult male (Bastian), and between dominant male and subadult male (Kay) were recorded using focal animal sampling. The indoor enclosure was 50 sq. m and the outdoor enclosure was 1240 sq. m. The study was carried out by Zimmermann[17] during May–August 2004.

For male–male interactions in a small indoor and a larger outdoor enclosure, the study was carried out on a group comprising two adult males, one adult female, one subadult male and one juvenile in Szeged Zoo, Hungary. During the first phase (January–March 2001), the animals were observed in a small indoor enclosure mainly maintained for emergency purposes. During the second phase (June–October 2001), the group was released and observed on an island. Each animal during each phase was observed for a period of 10 h amounting to a total of 100 h of observation carried out through focal animal sampling. Besides interactive behaviours, the occurrence of 'disturbed behaviour'[18] was also recorded. The indoor enclosure measured 1.5 × 2.0 m, with a height of 3 m. The outdoor enclosure had a ground space of about 250 m. The study was carried out by Cseh[19].

The results of the present study bring out information on the development of male–male relationships in heterosexual groups and the role of space in the regulation of male–male interactions.

In the case of male–male interactions in a mixed-ages group, the subadult male showed the highest frequency of agonistic behaviour per hour followed by the adult male (Table 1). The adult male was the recipient of highest frequency of agonism by other males. Over 40% of the total agonistic interactions occurred between the adult male and the subadult male, in which the subadult male showed higher aggression toward the adult male than the adult male did toward the subadult male. Agonistic behaviour by the younger males directed towards adult and subadult males, and vice versa, occurred only with quite low frequencies. The highest frequency per hour of affiliative behaviours was received by the adult male, mainly from the subadult male (Table 2). The adult male, on the other hand, was the lowest donor of affiliative behaviours. The affiliative behaviours received by the subadult male came largely from the younger males. In the group at Rostock Zoo, the dominant male (Guru) directed most of its aggression towards the subadult male (Kay; Figure 1), as was the case in Cologne Zoo. Another adult but castrated male (Bastian) received lower aggression and more affiliative behaviours from the adult male ($\chi^2 = 11.28$, d$f = 1$, $P < 0.01$).

For male–male interactions in indoor and outdoor enclosures, data shown in Figure 2 reveal that males showed more disturbed behaviour in the indoor enclosure than on the island ($\chi^2 = 18.61$, d$f = 1$, $P < 0.01$). A higher frequency of overt agonistic interactions occurred on the

Table 1. Frequency of agonistic behaviour per hour among males of five age-classes in Cologne Zoo

	Receiver/age-class					
Actor/age-class	I	II	III	IV	V	Total
I	–	0.56	0.17	0.10	0.22	1.05
II	0.93	–	0.19	0.25	0.10	1.47
III	0.24	0.12	0.07	0.03	0.04	0.50
IV	0.31	0.04	0.03	0.06	0.03	0.47
V	0.11	0.01	0.01	0.01	0.08	0.21
Total	1.59	0.73	0.47	0.45	0.47	3.70

Table 2. Frequency of affiliative behaviour per hour among males of five age-classes in Cologne Zoo

	Receiver/age-class					
Actor/age-class	I	II	III	IV	V	Total
I	–	0.33	0	0.13	0.03	0.49
II	2.02	–	0.34	0.19	0.08	2.63
III	0.60	0.84	0.34	0.18	0.12	2.08
IV	0.38	0.39	0.12	0.23	0.10	1.22
V	0.39	0.14	0.11	0.17	0.24	1.05
Total	3.39	1.70	0.91	0.90	0.57	7.47

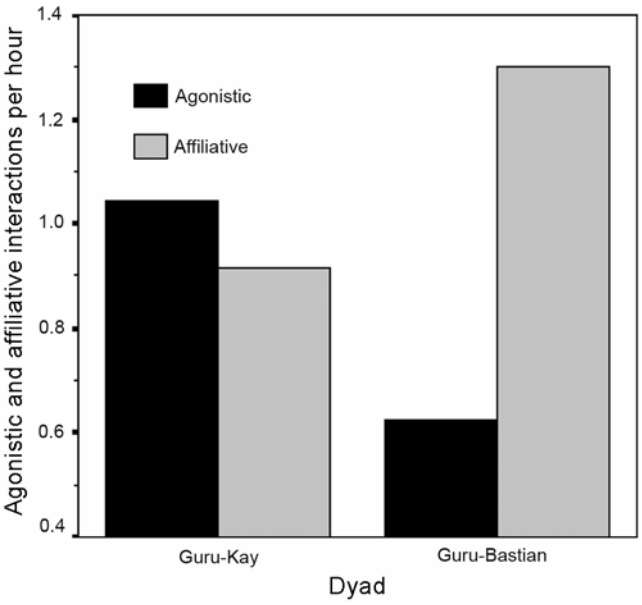

Figure 1. Frequency per hour of agonistic and affiliative interactions in dyads of lion-tailed macaque males.

island than in the indoor enclosure ($\chi^2 = 4.64$, d$f = 1$, $P < 0.05$). More matings occurred on the island than indoors ($\chi^2 = 6.0$, d$f = 1$, $P < 0.05$). Grooming between males was observed only once indoors and never on the island.

The main results of the present study can be summarized as follows: (i) The agonistic interactions between the adult male and his male offspring were quite low when the offspring were younger than 45 months. These interactions became high when one of the male offspring reached subadulthood. The subadult male was more agonistic towards the adult male than vice versa. (ii) The dominant adult male was more aggressive toward the 'normal' subadult male than toward an adult but castrated male. (iii) In the small enclosure, males showed a high degree of disturbed (self-directed) behaviours, but did not indulge much in agonistic interactions. Once transferred to an island with a relatively large space available, inter-male aggression increased. This was also accompanied by an increase in the frequency of matings with a female in estrous. These results allow several important inferences. As observed in the wild habitats, most of the intrasexual male interactions in the present study were of agonistic nature. However, such interactions should be viewed in a developmental perspective as the adult male showed little agonism toward juvenile males, and the hostile relationships developed only when a juvenile became subadult and when it might be perceived as a competitor for reproduction. In the wild habitats, the adult males can minimize overt agonistic interactions by maintaining large inter-individual distances[7]. Under the extremely reduced spatial conditions in captivity, the males might be coping with the situation by indulging in a higher frequency of disturbed behaviours with low frequency of agonistic interactions. Once large space is available, non-physical agonistic interactions increase and the frequency of disturbed behaviour decreases. Males up to the age of 45 months or so in the Cologne Zoo group maintained quite a high degree of affiliative (groom, contact, play) interactions and indulged in agonistic behaviours with a rather low frequency. These observations point to the fact that it is possible to maintain all males in a group up to a certain age, more so, if they are brothers or half-brothers.

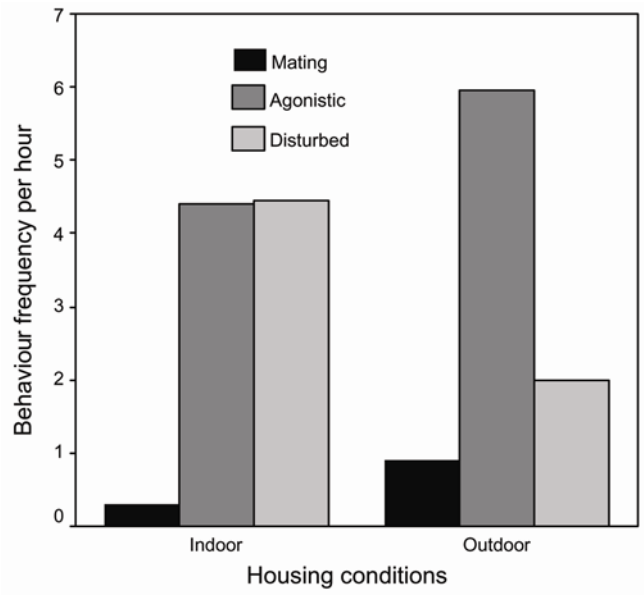

Figure 2. Frequency per hour of agonistic, disturbed and mating behaviour in indoor and outdoor enclosures in lion-tailed macaque males.

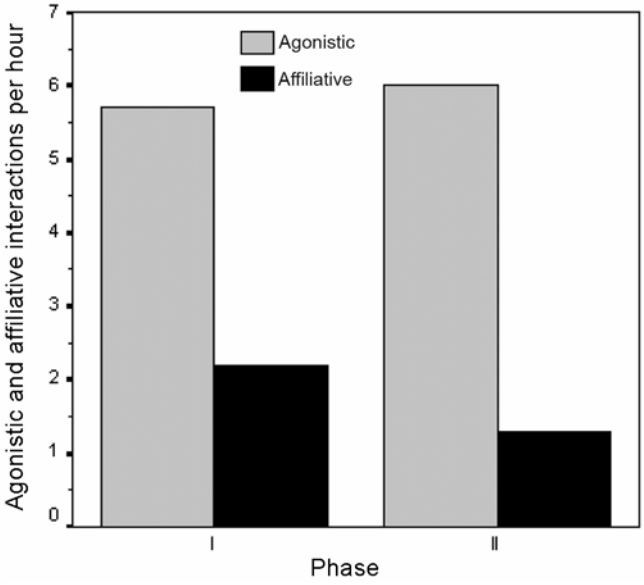

Figure 3. Frequency per hour of agonistic and affiliative interactions among lion-tailed macaque males during two phases (see text) of the study.

In their attempt to establish an all-male group of lion-tailed macaques coming from different groups, Stahl *et al.*[12] concluded that it was possible to have such a group since the individuals continued to have some socio-positive interactions with each even after several weeks of their simultaneous release. However, a reanalysis of their data revealed that though the frequency of agonistic behaviour from phase-I (7–24 days after introduction) to phase-II (49–66 days after introduction) did not significantly increase (Figure 3), there was a significant reduction in the proportion of affiliative to agonistic interactions during phase-II ($\chi^2 = 15.87$, d$f = 1$, $P < 0.01$). It may also be mentioned that at the time of the study by Stahl *et al.*[12], all males in the group were not yet fully adults. Although no recorded data are available on this group beyond the study by Stahl *et al.*[12], the all-male group was dissolved later due to increasing intolerance among the males (Werner Kaumanns – personal commun.). All other attempts at establishing all-male groups of lion-tailed macaques in North America also failed[10]. These observations and the field data point to the low levels of social tolerance among adult lion-tailed macaques. On the other hand, it has been possible to

establish an all-male group successfully in the white crowned managbey[20]. In wild bonnet macaques, the males maintained closer proximity, more affiliative and less agonistic interactions than the wild lion-tailed macaques[7], pointing to the possibility of establishing all-male groups in other macaques that have higher levels of social tolerance.

Although it is difficult to make a generalized statement due to a small sample size, our results clearly point the following: (i) The studies from captive groups confirm the findings from the wild groups of lion-tailed macaques indicating low levels of tolerance among adult males. (ii) Establishment of all-male groups in lion-tailed macaques may be attempted up to the subadult stage, especially among related males coming from the same groups. (iii) Due to the high levels of intolerance among males, it does not appear to be possible to establish all adult male groups in lion-tailed macaques. (iv) Data from the wild and the present study point to the need of establishing links between forest fragments to facilitate at least male dispersal so that the natural demographic structure in the wild groups is not disturbed.

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