Social Aspects of Sleep Cluster Formation and Sleep Behaviour in a Mixed Group of Longtailed Macaques (Macaca fascicularis)

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Gygax, L. and Tobler, I. (2001) Social Aspects of Sleep Cluster Formation and Sleep Behaviour in a Mixed Group of Longtailed Macaques (Macaca fascicularis). Available on http://www.proximate-biology.ch/downl/manu.html: Aspects of behavioural sleep were investigated in a group of longtailed macaques (Macaca fascicularis) with emphasising the influence of social rank. Observations were performed on a social group consisting of 8 males and 16 females, living in a primate research compound. Behaviour was scored during the first two hours after lights off. Animals typically slept in clusters. The composition of thewe sleeping clusters was remarkably stable from night to night, but kin was not a good predictor of sleep cluster composition. Neither for females nor males did social rank determine the choice of cluster size. Behaviour during the sleep period ranged from small movements to extensive social interactions. Higher ranking females had a larger amount of movements. The movements in females of high rank tended to be induced more often by conspecifics moving within the same sleep cluster than in females of lower rank. However, the higher ranking females chosen for observation were in larger clusters than the lower ranking ones and females encountered in bigger clusters in general showed a higher proportion of movements elicited by an individual in the same sleeping cluster. Thus, activities during sleep was a consequence of cluster size rather than rank.

The function of sleep is still unknown. Its complexity suggests that sleep has been shaped by natural selection. Thus, chronical sleep disruption is likely to decrease individual fitness, especially if sleep has a restorative and energy saving function. On the other hand, sound sleep may be dangerous if predation rate is high (Bert et al., 1975; Balzamo et al., 1977).

Little is known about the effect of social status or daily experience on sleep in monkeys. Bonnet monkeys raised by their mothers showed less sleep fragmentation than those raised together with peers under laboratory conditions (Reite and Short, 1986; Kaemingk and Reite, 1987). In a semi-natural setting, lower ranking females showed more movements at night than higher ranking ones (Kummer, 1956, reanalysed in this study). In the field the focus has been on choice of sleeping sites (Hamilton, 1982; Ansorge et al., 1992; Caine et al., 1992; Zhang, 1995), though Goodall (1962) and Riss and Goodall (1976) mention some social aspects in chimpanzees.

Here, we present the first attempt to combine the information on cluster formation, presleep social interactions, social patterns (rank)

and behavioural sleep into a comprehensive picture of the transition from wakefullness to the initial two hours of sleep in a group of long-tailed macaques (Macaca fascicularis).

Methods

The social rank of the adult individuals (8 males, 16 females) was determined based on the regular observation of submissive bareteeth-display (de Waal et al., 1976). The rank relationship resulted in a linear hierarchy between the individuals and was stable in the course of this study. The group was kept in an outdoor enclosure $(1000 \ m^2)$ connected to a well furnished stall $(80 \ m^2)$.

All observations took place in the stall using a night-vision-scope (Wild Big 2; red light in stall < 2 lux, light of neon tubes from 06.30–20.00 h, 100–700 lux, natural daylight from 06.45–18.20 h at the start, and from 05.15–18.55 at the end of the study). Animals were habituated to the red light and the presence of the observer at night for 2 weeks.

The composition of sleeping clusters was determined after all monkeys had remained in a specific cluster for at least 5 min (this was at $20.35 \text{ h} \pm 6 \text{ min}$, SD; mean of 12 nights).

The number of movements and the type of behaviour was protocolled for one hour starting at $20:46 \text{ h} \pm 10 \text{ min}$ on 9 nights for several females sitting in two to three clusters. In total, 12 females were observed for a median of 2.5 (range 1–5) nights. The choice of animals covered a broad rank spectrum and was restricted to females because males either sat together in one sleeping cluster or in clusters separated by a large distance. Movements determined per minute were classified as "shortly delayed" if they started during or immediately after a movement of another animal in the same sleeping cluster or as "independent" when no external stimulus was apparent.

In addition, one female was observed for 2 h before and after lights off on 6 nights to assess the influence of pre-sleep experiences on sleep.

Statistical Analyses

To assess the monotonous effect of social rank on movements the Page test was used (comparison between k individuals within n single nights), after significance in a Friedman test (Bortz et al., 1990). In case of missing values (not all females were observed on every night), the Page test was modified by estimating the distribution of the test statistic with a bootstrap method (1000 bootstraps, Manly, 1997). Ranks were randomly assigned (from one up to the total number of observations within a row) to the locations where values were available. From these randomly generated data the Page test statistic was computed (1000 times). The resulting distribution was compared with the Page test statistic resulting from the data (L). When comparisons were computed within a cluster, only 2 females were available per night, and therefore a Wilcoxon test was applied (T = test statistic).

For the analysis of the relation between cluster size and movements a Jonkheere test was used (Bortz et al., 1990, S = test statistic). Since the present data set was limited, it was assumed that the observations were independent of individuals and nights.

Results

Sleeping clusters

The abrupt onset of darkness seemed to startle the animals. Dark onset was immediately followed by vocalisations lasteing 15–60 min. By then the animals had settled in sleeping clusters, usually on the highest beams, where they sat in close body contact. Most individuals remained in the initial sleeping cluster for the first two hours of the night.

The 8-11 clusters encountered per night consisted of 3.3 ± 2.2 individuals (range 1 to 8). Though the same animals were often found in the same locations, the exact composition of the sleeping clusters was quite variable. Kin did not seem to be crucial in the choice of

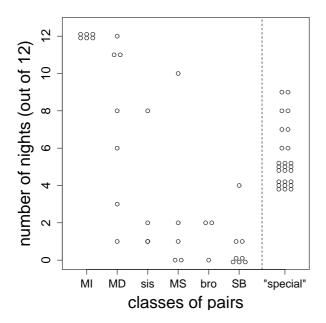


Figure 1: Number of nights (total number = 12) during which pairs of monkeys with a specific relationship were found in the same sleeping cluster. MI: Mother-infants (< 3 years of age), MD: Mother-daughter, sis: sisters, MS: Mother-son, bro: brothers, SB: Sister-brother, "special": other pairs which were often encountered together (see text).

partners for a sleeping cluster. Only the 6 infants (up to 3 years) invariably stayed with their mothers. This closeness loosened between mothers and elder daughters, between sisters, mothers and sons (except for the α -male) and even more between brothers, and brother and sisters (Fig. 1). In addition to these 32 pairs which were based on close kin, 26 other pairs were defined. These stayed for at least 4 of the 12 nights in the same sleeping cluster, indicating that the composition may be based on "special" relationships (Fig. 1).

Ten of these "special" pairs were formed by females, 10 by males and 6 were mixed. Only four of the pairs composed of females were formed within the same matriline, but among more distant kin. Eight of the pairs formed by males included the two youngest males (almost four years of age) and the remaining two were formed by the second ranking and the lowest ranking male, and by the fourth rank-

ing and the second of the two lowest ranking males (adult males ranking from 1 - 8).

Movement activity

After settling down, the monkeys no longer reacted to vocalisations though they seemed to be easily aroused by movements within the same sleeping cluster. Behaviours after settling down were diverse, ranging from small movements of single body parts to extensive social interactions, such as friendly encounters with raising of eyebrows and grooming or aggressive interactions.

The total amount of movements ("independent" plus "shortly delayed") was significantly reduced with decreasing rank from an average of 12.8/hour in the four highest ranking females to 10.8/h in the four lowest ranking ones (Fig. 2, p < 0.01). The contribution of "independent" movements to the total tended to increase from an average of 54~% to 75~% in high ranking females compared to low ranking ones, respectively (Fig. 2, lower panel left; p = 0.08).

This result could be confounded by the fact that, when all females are compared, they were either in the same or in different clusters. Thus the analysis was restricted to the comparison of females within the same cluster. Again, the higher ranking females had a lower proportion of "independent" movements than lower ranking females (Wilcoxon test, n=9, T=6, p=0.055).

Our reanalysis of 4 Hamadryas females showed that in this species, the lower ranking females moved more often than those with higher rank (data from Kummer, 1956, Page test, $n=8,\,k=4,\,L=227,\,p<0.01$).

The proportion of "independent" movements declined significantly with increasing cluster size (Fig. 2 bottom right, p < 0.01). In the sample of females for which movements were observed, higher ranking females were found in bigger clusters (bootstrapped Page test, n = 9, k = 12, L = 458, p < 0.01), though in general there was no significant dif-

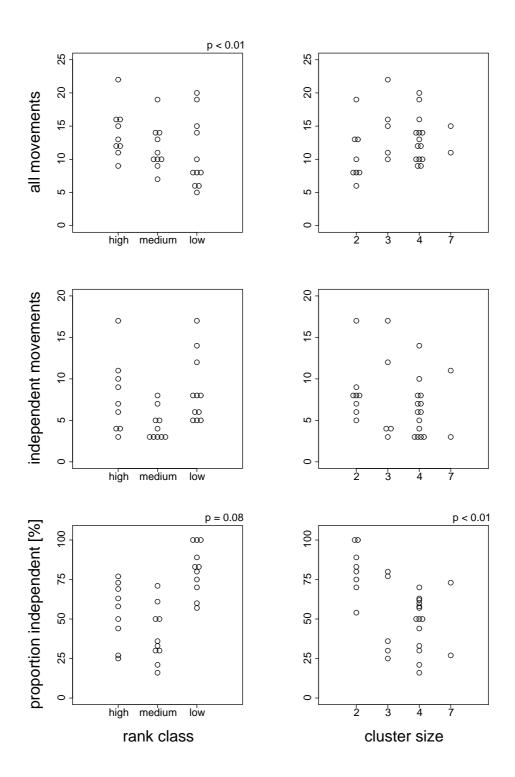


Figure 2: Influence of rank class and of size of sleeping cluster on the total number of movements, "independent" movements and proportion of "independent" movements during behavioural sleep. Rank classes are arbitrary subdivisions of the female monkeys into three classes of equal size according to the social rank of the females (12 females in total). Cluster size = number of animals within a cluster. P values based on bootstrapped Page test (top left panel: n = 9, k = 12, L = 462; bottom left panel: n = 9, k = 12, L = 444), and Jonkheere trend test (bottom right panel: n = 29, k = 4, k = 5, data from each female and night treated as if they were independent).

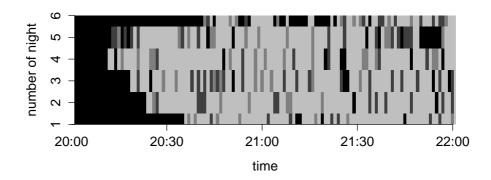


Figure 3: Activity of a single female during 6 nights (1-4 and 5-6 are consecutive) after lights were turned off (20:00 h). Progressively darker shading of gray indicates an increasing intensity of movements.

ference in cluster size between animals of different ranks (Friedman: females, n=12, k=16, F (15,165)=2.6, p=1.00; males n=12, k=8, F (7,77)=2.25, p=0.96).

The single female observed for 2 h before and after lights off, was alone with her infant on 4 of the six nights. A large inter-night variability of sleep latency and movement activity was evident (Fig. 3) but no effect of the social experiences preceding sleep (data not shown) was found.

Discussion

It is remarkable that kin and rank seem to be secondary factors determining sleep cluster formation both, in males and females, and that animals with widely different ranks can be often found in the same sleeping cluster. This could indicate that,xs during the night, where sleep is the preferred behaviour, the importance of rank and even of kin is diminished compared to daytime hours, when the monkeys are predominantly active.

It is unresolved why the specific individuals observed in a cluster sleep together, since the "special" relationships were very diverse. More detailed observations are necessary to establish the contribution of "personal" history and coincidence on the mechanisms of cluster formation (Riss and Goodall, 1976).

One of the main results was that the higher

ranking females in this mixed group of monkeys moved more often during sleep and tended to have a lower proportion of "independent" movements than the lower ranking ones. This finding could be related to the more stressful social position of high ranking females in multi-male multi-female groups (Cavigelli, 1999). Another contributing factor may be related to the increasing proportion of "shortly delayed" movements i. e. movements induced by conspecifics, in larger sleeping clusters. Interestingly, such clusters were more often chosen by these higher ranking females.

This increase does not seem to be of biological relevance for sleep, as it can be assumed that higher ranking females do have the possibility to choose a cluster of suitable size. The result could be a coincidental effect resulting from the choice of the females which were selected for observation. This notion is supported by small inter-rank differences compared to large intra-rank variability (Fig. 2) and the relatively small average number of movements (11-13) which is in the range of the amount reported in other Cercopithecines by Kummer (3.5 to 12 in 1956). Also values between 22 to 30 (Reite and Short, 1986) and > 50 (Kaemingk and Reite, 1987) have been reported. Moreover, there seems to be a large night to night variability in the amount of movement activity during sleep (Figs 2, 3) which could not be predicted by the experiences before settling down to sleep.

Contrary to our results, the observations of Papio hamadryas (Kummer, 1956) showed an increasing number of movements with decreasing rank of the females, though his methods were similar to ours. The hamadryas group consisted of only one harem group and data on sleeping cluster formation is unavail-Interactions between individuals are more restricted in hamadryas, occurring primarily within (small) one-male units compared to the larger groups of the multi-male multifemale social structure of the macaques. It is possible that under the latter conditions the dependence of sleep on social factors is more complex.

In conclusion, it seems that factors other than rank and kin play a role in sleep cluster formation and composition, and that, despite the differences in the amount of movements of certain rank classes and cluster sizes, they are in the normal range and are not detrimental.

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