TEMPORARY FISSIONS IN A GROUP OF LION-TAILED MACAQUES *Macaca silenus* IN THE WESTERN GHATS, INDIA

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ABSTRACT

Group living primates sometimes split into smaller subgroups for varying periods and merge again. Intragroup competition for food appears to be one of the main reasons for such temporary splits. We here report 11 instances of temporary fissions in a group of Lion-tailed Macaques *Macaca silenus* in the Western Ghats of India. More group splits occurred in the dry season than in the wet season. The frequency of fissions was higher in the mornings than in the afternoons. The subgroup that initiated the group fission was always smaller than the main subgroup, defined as the subgroup with the alpha male. The average duration of the splits was 133.6 minutes. The second subgroup travelled greater distances during fission events than the main subgroup. We infer that *M. silenus*, especially larger groups, form fission-fusion social groups, especially when resources are scarce.

Keywords: *Macaca silenus*, temporary group fission, season, day time, Western Ghats

INTRODUCTION

Most primate species live in groups and experience associated costs and benefits (Markham & Gesquiere, 2017). In many group-living animal species, some individuals stray from the main group for periods ranging from a few hours to several days and then join the group again. If this is a frequently repeated phenomenon, such a social system is called a fission-fusion society (Kummer, 1971). Fission-fusion can be found in many species of primates, including Golden Snub-Nosed Monkeys *Rhinopithecus roxellana* (Milne-Edwards) (Qi et al., 2014), Hamadryas Baboons *Papio hamadryas* (Linnaeus) (Henriquez et al., 2021), Spider Monkeys *Ateles geoffroyi* (Kuhl) (Pinacho-Guendulain & Ramos-Fernández, 2017; Hartwell et al., 2018) and Black-and-White Ruffed Lemurs *Varecia variegata* (Kerr) (Holmes et al., 2016).

In general, the fission-fusion social organization has been explained as a response to environmental constraints, constrained by social relationships and the trade-off between the benefits and costs of association. Group living offers several advantages, such as decreased risk of predation, increased foraging efficiency, and ease of finding mates. However, living with other individuals in a group also leads to within-group competition for food resources, with larger groups predicted to experience higher costs (Janson, 1988). For example, larger groups in Mountain Gorillas *Gorilla beringei beringei* (Matschie) tend to have larger home ranges and core areas but show less core area fidelity, indicating that they experience greater within-group feeding competition (Seiler & Robbins, 2020). When a group does not have sufficient food resources to meet the requirements of all of its members, it is likely to split into smaller subgroups that forage in different places (Sueur & Maire, 2014). Fission may also become permanent, resulting in the formation of separate groups. In recent years, many authors have discussed the dynamics of fission-fusion social groups (Aureli et al., 2008) and analyzed the context and consequences of fission-fusion grouping, considering proximate factors favouring temporary fission, collective decision-making by individuals initiating the split, and the relationships among individuals that split into groups. For example, Sueur et al. (2010) demonstrated that in Rhesus Macaques *Macaca mulatta* (Zimmermann), which have a nepotistic social structure, fission tended to be structured along kinship lines. In contrast, in the more non-kin tolerant Tonkean Macaques *M. tonkeana*

(Meyer), sub-grouping was structured by patterns of affiliation, which did not map perfectly onto kinship. Using group size, nutritional needs, and changes in social network after a temporary fission, Sueur & Maire (2014) modelled group fission and demonstrated that irreversible group fission should occur in fewer days if the nutritional needs were great and the network of social relationships was weak among group members. Species differ in their probability of having more than one subgroup at a given time. Using Shannon's entropy for quantification of temporal variation in subgroup composition, Ramos-Fernandez et al. (2018) demonstrated that the composition of Gelada *Theropithecus gelada* (Rüppell) subgroups was more stable than those of Chimpanzees *Pan troglodytes* (Blumenbach) and Spider Monkeys *Ateles geoffroyi* (Kuhl). However, more field studies are required on fission-fusion systems for models to be developed based on the field data.

The Lion-tailed Macaque *M. silenus* (Linnaeus) is endemic to the rainforests of the Western Ghats of India, and has been categorized as Endangered (Singh et al., 2020) by the IUCN Red List. *Macaca silenus* has a modal group size of about 18 in large forest complexes, though the group size varies significantly in forest fragments (Singh et al., 2002). Most groups have only one adult male with several adult females and immature individuals (Kumar, 1987). They are primarily frugivorous, but faunal components account for about 19% of their total diet (Kumara et al., 2000). Here, we report systematic observations of temporary group splits in a group of *M. silenus* in Nelliyampathy Forest Reserve and add to the growing literature on fission-fusion behaviour in group-living species. In Nelliyampathy Forest Reserve, the wet season has the highest resource abundance, and the dry season is a period of relative scarcity for *M. silenus* (Erinjery et al., 2015). *Macaca silenus* groups increase their home range and daily path length during the dry season when compared with the wet season. Since meeting their nutritional needs appears to be more challenging in the dry season, we predicted that *M. silenus* would fission more frequently during the dry season than the wet season.

MATERIALS AND METHODS

The study was conducted on a single group of *M. silenus* from December 2010 to October 2012 in the Nelliampathy Reserve Forest, which is located at $10^{0}25'$–$10^{0}30'$N and $76^{0}35'$–$76^{0}45'$E, Western Ghats, Kerala, India (Fig. 1). Nelliyampathy Reserve Forest is inhabited by at least five large groups (>25 individuals) of *M. silenus*. Nilgiri Langurs *Semnopithecus johnii* (J. Fischer) and Bonnet Macaques *M. radiata* (É. Geoffroy) are sympatric with *M. silenus* in the area. In the Anamalai Tiger Reserve, an area adjoining Nelliyampathy with similar forest types, *M. radiata* and *M. silenus* were observed competing for flowers of *Cullenia exarillata* (A. Robyns) for about two months in the rainforest habitat of *M. silenus*, but during the rest of the year, *M. radiata* ranged only in the adjoining dry forests (Sushma & Singh, 2006); *S. johnii*, being primarily folivorous, had very little food niche overlap with macaques, but spatially overlapped with *M. silenu*s. June to November is considered the wet season in this region, and December to May is the dry season. *Artocarpus heterophyllus* (Lamarck) and *C. exarillata* in the wet season, and *Ficus amplissima* (Smith) in the dry season, accounted for about 74% of the diet of *M. silenus* (Erinjery et al., 2015). For the present study, we observed *M. silenus* for a total of 845 hours, comprising 430 hours in the wet season and 415 hours in the dry season. The study group was followed from 08:00 h to 17:00 h, which was the main activity period of these macaques in this region. The study group comprised 38 animals, including three adult males (10 years+), 21 adult females (5 years+), two sub-adult males (5–10 years), nine juveniles (1–4 years) and three infants (<1 year) (age classifications based on Kumar, 1987). We collected data on group fissions *ad libitum* during a long-term study on the ecology and behaviour of the group. In the present study, we considered the group to have split if the distance between the two nearest individuals in the subgroups was at least 110 metres, which is the maximum group spread in *M. silenus* as reported by Kumara et al. (2014). In an earlier study (Sakthivelou & Kumar, 1998), a group was considered to be split if the two subgroups were at a minimum distance of 100 m which was almost the same as in the present study. We also recorded the season, time of the day, number of individuals in each subgroup, and duration of the temporary fissions.

DATA ANALYSIS

We used an independent-sample t-test to compare the number of animals in the two subgroups caused by temporary group fissions, with Subgroup 1 identified as the group that contained the alpha male. We ran a chi-square test to determine the association between the number of group splits and hourly time slots. We calculated Pearson product-moment correlation (Pearson's r) to determine the relationship between the number of individuals in the subgroup and the distance

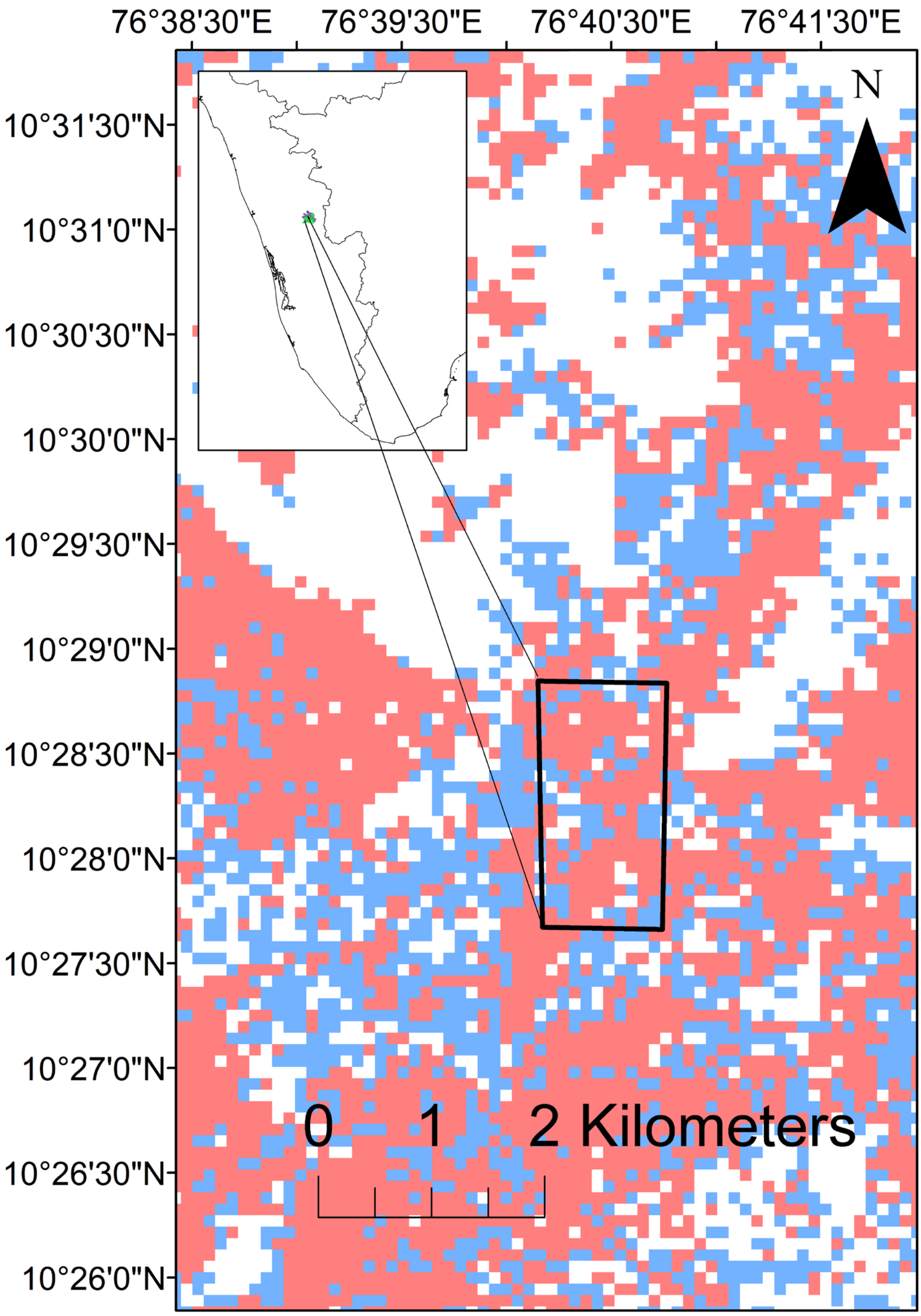

Fig. 1. Map showing the location of the study site in the Nelliyampathy hills with forest and shade plantation cover indicated (Inset: Map of South India). Red pixels indicate forest cover; blue pixels indicate shade plantation cover; white pixels indicate other land cover types.

travelled. All statistical analyses were carried out in SPSS ver. 10.

RESULTS

We recorded a total of 11 temporary group splits (Table 1). In ten of these instances, the group split into two subgroups and it split into three in one instance. The number of individuals in subgroups varied among fission events. The subgroup with the alpha male (Subgroup 1) always had more individuals (mean 24.55 ± 5.57) than Subgroups 2 (mean 12.36 ± 4.34) (independent samples t-test: t=5.92, p<0.01) and 3 (12 individuals). In each instance, it was Subgroup 2 (and, where relevant, Subgroup 3) that moved away from Subgroup 1. Group fission occurred more frequently in the dry season (N=10, 91%) than in the wet season (N=1, 9%). During the dry season, the group had five sleeping sites, and nine of the ten fissions occurred on days when the group slept at one particular sleeping site during that night. All instances of group fission occurred between 08:00 h and 14:00 h (Fig. 2). Significantly more instances of splits occurred between 10:00 h and 12:00 h (42.86 %, a*), and 08:00 h and 10:00 h (39.29 %, b), than between 12:00 h and 14:00 h (17.86%, c) (Marascuilo's procedure for multiple proportions : χ^2= 16.44, df=2, p<0.05; *Post-hoc tests; p-value was kept based on Bonferroni correction: a-b: χ^2= 0.26, p=0.87; a-c: χ^2= 15.96, p<0.017; b-c: χ^2= 11.92, p<0.017). The mean fission duration of each group was 133.6 ± 71.5 minutes. During the splits, the average distance covered by Subgroup 1 was 498±181 m and by Subgroup 2 was 693±239 m (Fig. 3). In Subgroup 1 and Subgroup 2, the number of individuals in the subgroup and the distance travelled were not correlated (Pearson's r: r=0.28, N=11, p=0.28; r=0.12, N=11, p=0.74). Either one or two adult males other than the alpha male were present in Subgroup 2 during five of the six splits where we could identify all animals. Females with infants less than one year old always remained in Subgroup 1. Most of the splits occurred when the animals were feeding on fruits of *C. exarillata* and *Toona ciliata* (M. Roem). The group members generally maintained lower inter-individual distances in the wet season than in the dry season (Fig. 4).

DISCUSSION

Temporary fissions in the study group occurred mostly in the dry season and during the hours before noon. The average duration of the split was a little more than two hours. A smaller subgroup usually travelled away from and moved a longer distance than the subgroup with the alpha male. Although temporary group splits have been observed by many researchers working on wild *M. silenus*, prior to this study, there has been only one published report of systematic recording of group fissions (Sakthivelou & Kumar, 1998) which showed that group splits occurred more in fragmented habitats than in contiguous forests, probably due to the scarcity of resources and higher predation pressure

Table 1. Number of individuals in each of the subgroups during each fission event

Event No.	Subgroup 1	Subgroup 2	Subgroup 3
1	26	12	
2	25	13	
3	19	19	
4	34	4	
5	30	8	
6	14	12	12
7	27	11	
8	19	19	
9	27	11	
10	26	12	
11	23	15	
Mean	24.5	12.4	-
SD	5.6	4.3	-

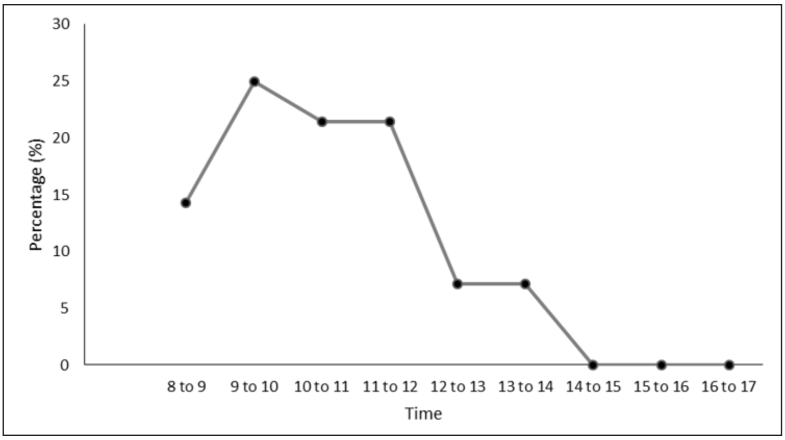

Fig. 2. The percentage of temporal temporary group fission events.

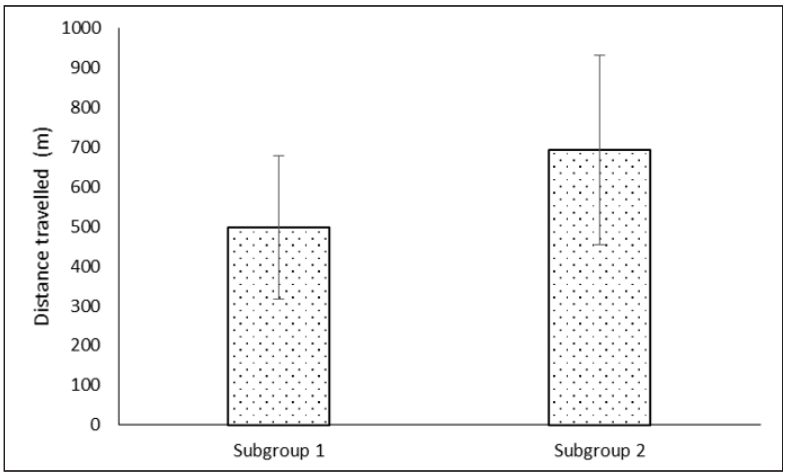

Fig. 3. Distance (in metres) travelled by different subgroups during temporary group fission.

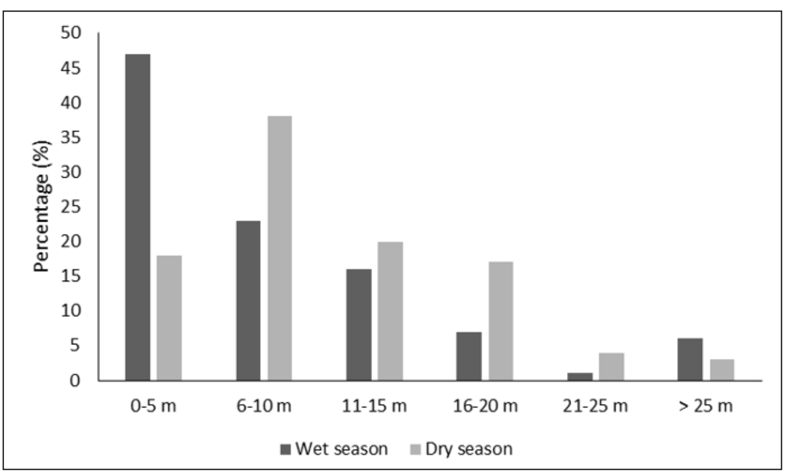

Fig. 4. Percentage of inter-individual distances in each distance class in the wet and dry seasons.

in fragmented habitats than in continuous forests. In the present study, we observed that group splits in *M. silenus* occurred mainly in resource-scarce dry months.

As intragroup competition for food is one of the major factors explaining temporary group fissions (van Schaik & van Hooff, 1983; Koenig, 2002), more splits are expected to occur when food resources are scarce. In the Yunnan Snub-nosed Monkey *R. bieti* (Milne-Edwards), group fission events were highly seasonal, occurring during only two months of the year, and appeared to be triggered by the presence of bamboo shoots, a seasonally important food item in their diets (Ren et al., 2012). In the rainforest habitats of *M. silenus* in the Western Ghats, food resources are far more abundant during the wet season than in the dry season (Singh et al., 2011; Roy et al., 2013; Erinjery et al., 2015). Low dry-season food availability may explain why more than 90% of the group splits observed during this study happened during the dry season. Most of the splits also occurred when the monkeys were feeding on fruits of *C. exarillata* and *T. ciliata* which are two of the most important foods for the wild *M. silenus*. The larger inter-individual distances also indicated more exploration for food during the dry season than in the wet season. Since most fissions occurred from a single sleeping site (see Erinjery et al., 2015 for information about sleeping sites, the frequency of use of each sleeping site, home range size, etc.), it appears that resource distribution around that sleeping site was the important factor for the split. A previous study (Erinjery et al., 2015) showed that macaques used this sleeping site more than other sleeping sites between September and January, and they spent more time around this sleeping site (while ranging; although they used multiple sleeping sites for sleeping during this period) between February and that May. *Macaca silenus* were more likely to feed on *C. exarillata* and *T. ciliata* when they used this sleeping site than when they used other sleeping sites, likely because of a higher abundance of *Cullenia* and *Toona* near this sleeping site (Erinjery et al., 2015). The higher rate of group fission before noon than after noon in the present study can be explained by the fact that in *M. silenus*, more feeding and foraging occurred during the morning hours than during the remainder of the day. In the earlier study on group splits in *M. silenus* (Sakthivelou & Kumar, 1998), most fissions also occurred during the morning hours.

In each case of group split, females with dependent infants remained in the larger Subgroup 1 with the alpha male, suggesting that the group split involves some amount of risk for infant-carrying females, which may become more vulnerable in the smaller subgroup. For example, predation risk might be higher in the smaller than in the larger subgroup. Also, the costs due to travelling, access to high-quality resources etc., may influence the behaviour of females carrying infants. The average distance covered by Subgroup 2 was more than that covered by Subgroup 1. However, regardless of the number of individuals in Subgroup 2, they covered approximately the same area (from visual observation) and travelled the same distance when separated from the main group, indicating that they foraged in a restricted area during the split. Although we do not have data on resource abundance and quality in the areas visited by the subgroups during fissions, previous studies show that subgroup size during fission is correlated with availability, abundance and quality of food in other primates (Asensio et al., 2009; Di Fiore et al., 2011).

Since temporary group fission was observed only 11 times during the relatively long-term field study, the frequency appears to be quite low. Furthermore, the present study area was in a relatively large patch of contiguous forest. Kumar (1987) also observed a low frequency of group splits in a similar continuous forest. On the other hand, in a group inhabiting a forest fragment interspersed with coffee plantations, the frequency of temporary fissions was very high (Sakthivelou & Kumar, 1998) probably due to the scarcity of food in such forests. Since the number and identities of individuals during the temporary fissions kept changing, it may be concluded that these splits were not a precursor to permanent group fission but instead represented a pervasive foraging strategy.

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