

The effect of group size on time budgets and social behaviour in wild long-tailed macaques (*Macaca fascicularis*)

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Summary. A comparison of data on ranging, activity budgets and frequencies of social behaviour gathered over a range of group sizes for an omnivorous, forest-living monkey, the long-tailed macaque (*Macaca fascicularis*), showed that the length of the day journey, the time spent travelling and searching for dispersed food items, as well as social tension, show a monotonic increase with group size. A behavioural mechanism behind these patterns is the “puhing forward” effect: foraging animals tend to move away when approached by others, presumably because they reduce the availability of dispersed food items in patches they have searched. By avoiding being overtaken animals are not forced to search in depleted patches. An alternative mechanism, the limited capacity of fruit trees, does not operate in the present case. It is concluded that theories postulating feeding advantages to be the primary factor favouring group living do not apply in this case.

Introduction

Several theoretical studies suggest that the avoidance of predation must have been an important selective force in the selection of group living in mobile animals (Hamilton 1971; Pulliam 1973; Treisman 1975; Taylor 1977). Empirical studies tend to support the idea that larger groups are better at detecting predators than small ones (birds: Hoogland and Sherman 1976; Bertram 1978; ground squirrels: Hoogland 1981; forest primates: van Schaik et al. 1983). This is in agreement with Alexander's (1974) speculation that predation pressure alone has been responsible for the evolution of primate sociality, i.e. with respect to all other basic requirements of an individual, group

living is disadvantageous. Recent reviews of the social evolution of primates, however, deny the importance of predation pressure, either explicitly (Wrangham 1979, 1980; see also Krebs and Davies 1981), or implicitly (e.g. Raemaekers and Chivers 1980). The question thus is whether primate groups are held together entirely by the external factor of predation risk, by internal factors favouring living in groups arising from cooperatively locating, harvesting or defending food, or by a combination of both. There has as yet been no systematic empirical investigation of this question.

In this paper we concentrate on the procurement of food as the most important factor besides predation risk to determine an individual's fitness, thus ignoring the avoidance of disease and the availability of mating partners. Alexander (1974) suggested that the high level of (near-)physical contact caused by sociality is conducive for the spreading of contagious diseases, whereas Freeland (1976) suggested that the opposite holds true for vector-borne diseases. The availability of mating partners will usually not be related to group size.

With respect to the procurement of food there are two main possibilities. The first is that feeding in a group enhances an individual's feeding success, because animals in a group are better at exploiting and detecting food with a patchy and unpredictable distribution (Horn 1968; Ward and Zahavi 1973), can cooperatively defend their food sources or home range (Schoener 1971; Wrangham 1980), can exploit their area more efficiently by optimising return times to patches depleted by earlier visits (Cody 1971), or have to spend less time watching out for predators, which leaves more time for feeding (Pulliam 1973). Most primatologists subscribe to the view that feeding in a group offers some advantages to the individuals involved (e.g. Eisenberg et al. 1972; Clutton-Brock 1974;

Wrangham 1980). The second possibility is that feeding efficiency will decrease monotonically with group size due to competition among group members (Alexander 1974). These possibilities are of course not mutually exclusive; it is, on the contrary, likely that both processes operate simultaneously: the question is whether the proposed advantages for feeding are sufficient to outweigh the inevitable feeding competition in the range of sizes encountered among natural groups.

Here we present the results of an investigation into the relation between group size, time budgets and frequencies of social behaviour in wild long-tailed macaques (*Macaca fascicularis*) and conclude that Alexander's prediction that competition for food should show a monotonic increase with group size is confirmed in this species.

Materials and methods

Species and study area. We studied five groups of long-tailed macaques inhabiting the forest surrounding the Ketambe Research Station, which is located at about 350 m altitude in the upper Alas Valley (Aceh Province, northern Sumatra, Indonesia; 3°41'N, 97°39'E). In this area, long-tailed macaques are highly arboreal, living in non-territorial multi-male groups of 10 to 45 individuals. In Fig. 1 the approximate home range boundaries of the study groups in 1980/81 are indicated. Group A split off from T some time in 1978 or 1979, whereas group G split off from T around January 1981. Group A used an area that consisted to a large extent of young forest, rather low (up to 25 m) and poor in species, growing in a former river bed. Rijksen (1978) provides a general description of the study area. From his data and our own counts of two study groups it is estimated that the population's yearly rate of increase was about 6% over the past 10 years. The composition of the study groups is presented in Table 1.

Apart from the present study the natural history of long-tailed macaques has been studied by Kurland (1973) and Wheatley (1980) in East Kalimantan (Borneo) and by Aldrich-Blake (1980) in West Malaysia. Although in many areas groups generally split into several foraging parties, in our study groups it was nearly always possible to recognize a main part of the

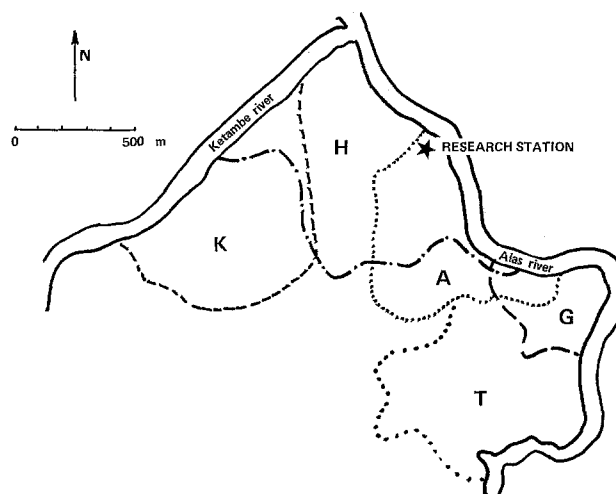


Fig. 1. Map of the Ketambe study area with the approximate boundaries of the home ranges of the study groups, as of 1980/81

group, although the monkeys could be dispersed over more than 100 m.

Methods. If differences between groups in time budgets and frequencies of social behaviour are to reflect differences in group size, the effects of other variables have to be minimized. Other sources of variation between groups are differences 1) in productivity between home ranges, 2) between months and years, 3) in the social situation of a group, 4) in habituation of the groups, 5) in forest structure and hence visibility of the monkeys, and 6) between different observers. The first three of these influence the time budgets and behaviour frequencies while the last three influence the accuracy with which these parameters can be measured. The data were collected by two pairs of observers. As to activity data it was found that within-pair reliability was very high but that between-pair reliability was rather poor. Hence, the activity data are presented separately. Sample sizes will be indicated in the relevant tables or figures.

We have tried to minimize the effect of habitat quality by 1) comparing groups that inhabited adjacent ranges in the same continuous forest area, 2) comparing the same groups over two periods in which group size was different, 3) compar-

Table 1. The composition of the study groups ('young' are those less than 1 year of age, juveniles are up to 5 years of age, subadult males are 5–8 years of age, adult females are older than 5 years, adult males are older than 8 years)

Group	Date	Adult ♂	Adult ♀	Subadult ♂	Juvenile	Young	Group size
A	March 1980	2	4	2	1	1	10
A	April 1981	3	4	1	2	2	12
G	May 1981	2	4	1	4	1	12
K77	May 1977	4	7	5	6	2	24
H77	May 1977	5	9	1	9	5	29
K	February 1980	5	9	2	10	5	31
K	May 1981	7	8	0	12	4	31
H	January 1980	5	9	1	12	5	32
H	May 1981	7	10	1	13	2	33
T	May 1981	5	11	4	11	3	34

^a Value was taken as 33, because there were 33 in the group for the greater part of the time

ing two groups that had recently formed from the fission of a large group and lived in greatly overlapping home ranges, and 4) comparing the same group on different days when different numbers of group members were present.

Individual activities. Samples of individual activities were made by scanning the surroundings every fifth minute for exactly 1 min. For each animal detected in the scan (cf. Altmann 1974) we recorded its age-sex category, its activity, its height and its nearest neighbour (if within 5 m). This technique requires instantaneous recognition of an animal's activity, and individual activities are therefore defined differently from those of the group as a whole (see below) as follows:

Immobile: animal sits, lies or stands; Locomotion: walking, jumping or climbing; Forage: handling and eating dispersed food items (often insects); Eat: eating from clumped food sources, mainly fruit; Groom: both groomer and groomee scored as grooming; Social, other: playing, copulating, involved in agonistic interaction; Cling: (infants only) clinging to the mother.

The total of activity records ('cling' excluded) of all age-sex categories of a group was used to compare different groups.

Group activities. For each 5-min period the main activities of the whole group were recorded. The score for each 5-min bout could consist of 1, 2 or 3 activities, weighed equally. Because indirect cues could also be used, group activities enabled us to keep a record of what the group as a whole was doing without seeing many monkeys. Group activities were defined as follows:

Rest: group is stationary; individuals immobile, grooming, playing or eating from their cheek pouches; Travel: group is moving in a certain direction; Search: group is searching for dispersed food items; includes walking, standing and looking around for food items, as well as handling and eating them; Feed: group is eating from clumped food sources (usually fruit); includes walking, handling and eating the food.

Presence of adults. After each hour we noted which of the known adult group members had actually been present in the group. Animals trailing far behind the main body of the group, although using approximately the same route, were not recorded as present. All adult and subadult males of the five groups were known, but females were only known in the later stages, for groups A, K and H only. As it was impossible to keep records on the presence of immatures, in most comparisons between groups we had to use the total group size (as established independently).

Social behaviour. Grooming interactions were recorded whenever encountered. All agonistic interactions accompanied by vocalisations were recorded. In groups A, K and H all interactions were recorded separately, for which both time (about 15 s, see de Waal et al. 1976) and space were used to separate interactions. In groups G and T only the number of minutes with screams, grunts or both of these vocalisations were recorded.

Foraging protocols. Focal animal sampling (Altmann 1974) was applied by RdB and IdT to obtain continuous observations of searching animals and the influence of approaches by others on their foraging behaviour. Activities were defined as in the scan samples of individual activities. Foraging protocols were made during the morning hours when the occasion arose and usually ended because the focal animal walked out of sight. Recording was performed by means of a tape recorder in which a running commentary was given of all behaviour transitions. The event 'an individual approaches' was scored the very sec-

ond another individual entered the 5 m sphere around the focal animal, regardless of whether the approach was caused by the focal or the other animal. The data were collected in group H only, since this group was often fairly low in the canopy and best habituated to observers.

Censuses. The composition of the study groups was known exactly. From February to April of 1980 till 1983 other groups in the surroundings were censused. Groups were recognized from position and characteristic individuals and counted in the late afternoon when they came to the river to sleep. Estimates of group size and composition were used only when they had not changed after several repeated counts. Full details of methods and data will be published elsewhere (van Schaik, unpublished data).

Data sets. Data set I (MvN, CvS) contains a set of 239 complete days (for various analyses sample sizes are smaller) with data on group activity, ranging, presence of adults and social behaviour of the groups A, K and H (January 1980 – May 1981) and of groups K and H (January – August 1977). Data in 1980/81 were collected with alternating observers. In addition CvS collected individual activity records in A, K and H (March – June 1981) on separate days from group activities, mostly half days only.

Data set II (RdB, IdT) contains a set of 24 complete plus 24 half days with individual and group activities, ranging, presence of adult males and the number of minutes with agonistic vocalisations of group G and T. These groups had greatly overlapping ranges, the small group G being formed by fissioning from T (Fig. 1).

Statistical procedures. Apart from day journey lengths, the variables were not normally distributed (Fisher's test on normality using skewness and kurtosis, performed on daily percentages of group activities and frequencies of agonistic behaviour). Hence, for both individual and group activities non-parametric tests were employed and daily (or half-day) totals used as single observations. The results of individual activities are, however, presented as overall totals because these provide the best estimates of time budgets due to the great variation in daily totals. Statistical tests on the direct totals are not allowed because subsequent scans of individual activity appeared to be not statistically independent, as assessed from alternative data.

For the two-group comparisons of data set II it was possible to arrange the follow days of both groups in pairs on which Wilcoxon's matched-pairs signed-rank test (Siegel 1956) was performed. The days of a pair were at most two weeks apart, which eliminates the problem of a temporal trend (apparent in all data). The use of half-day data as an additional comparison is justified because the differences between the groups on all afternoons were in the same direction as the differences found on complete days.

For the multi-group comparisons of data set I the median values and the 95% confidence limits to the median (Colquhoun 1971) were calculated. Where a large range of group sizes was available trends with group size were assessed using Jonckheere's (1954) non-parametric test, which tests the null-hypothesis of no difference between k samples against the alternative that the samples are arranged in increasing (or decreasing) order. Where group sizes are distributed in a few, widely scattered clusters, with per cluster a few groups of about equal size, it was deemed most appropriate to use the Kruskal-Wallis one-way analysis of variance, which tests the same null-hypothesis as Jonckheere's test but against the general alternative that the k samples are not drawn from the same population.

To investigate the effect of an approaching individual on

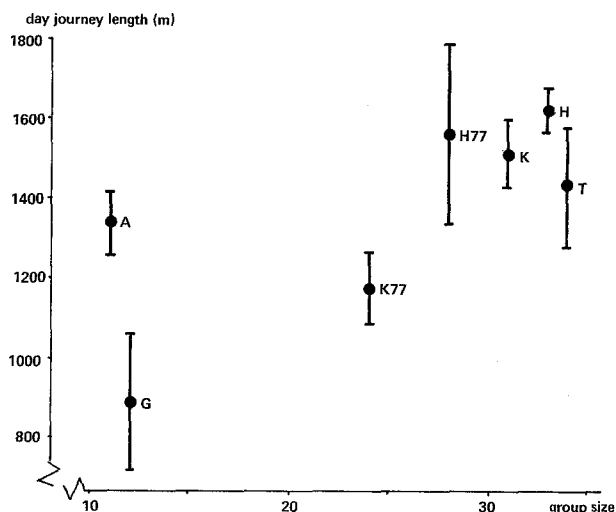


Fig. 2. Mean day journey length as a function of group size. Indicated are the 95% confidence limits for the mean. Sample sizes (days): A: 30; K77: 38; H77: 9; K: 54; H: 108; G: 12; T: 12

the activities of a focal animal in the foraging protocols, the difference in seconds of locomotion between the 10-s period before and the same period after the approach was subjected to the Wilcoxon matched-pairs signed-rank test. If within the 20-s period around an approach another approach occurred, both observations were deleted. If there were series of overlapping 10-s periods, we used only the first approach.

Results

Day journey lengths

Figure 2 shows that there was a clear and approximately linear increase in day journey length (DJL) with group size. A rough regression analysis, considering each group's average to be only one single observation, illustrates this: $DJL (m) = 873 + 19.7 \times \text{group size}$ ($n=7$, $r=0.75$, $P \approx 0.05$). Within groups the presence score of adults correlated positively with DJL in group H ($r=0.31$, $n=46$ days, $P < 0.05$) and in group K ($r=0.13$, $n=12$, N.S.). In the small group A, however, the relationship was negative ($r = -0.37$, $n=19$, N.S.), which suggests that subgroups in small groups travel further, probably in order to reunite before the night. If it is assumed that the adult presence score provides an estimate of total presence of group members, we can calculate the actual daily group size and thus combine data of different groups. This yields: $DJL = 1120 + 20.7 \times \text{actual daily group size}$ for the three groups ($r=0.420$, $n=77$, $P < 0.001$). The scatter diagram (not shown here) suggests that the relationship is linear in this case as well. Thus the data clearly indicate that DJL shows a monotonic increase with group size.

Group activities

Figure 3 shows the median percentages of the group activities of the five groups of data set I. The percentage of time spent travelling and time spent searching both increased significantly with group size (Jonckheere's test, $\tau=0.255$, $z=3.89$, $P < 0.001$, and $\tau=0.250$, $z=3.80$, $P < 0.001$, resp.), while time spent feeding and time spent resting decreased significantly with group size ($\tau=0.329$, $z=5.01$, $P < 0.001$ and $\tau=0.129$, $z=1.96$, $P=0.05$, resp.). As judged from the trend apparent in other groups, group A was somewhat deviant, feeding more and resting less than expected. It had a home range consisting in part of secondary forest and heavily used some species with either very small fruit (*Villebrunea rubescens*; an *Urticaceae* liana) or fruit that required a long handling time (*Macaranga* spp.; *Glochidion* sp.) these fruits were eaten less frequently by other groups even though they were also available. It is likely that social factors forced group A to use its area more intensively than other groups (e.g. Mitani and Rodman's 1979, D index was 2.37 for A, vs 2.00 for K and 2.04 for H) and hence to take more fruit (8.96 species of fruit on average per day for A, versus 6.43 for K and 6.25 for H; Kruskal-Wallis test, $P < 0.01$).

In the two-group comparison of data set II the differences in resting (significant), travelling (significant for half-days) and searching are in the same direction (Fig. 4), but the small group G spent somewhat less time feeding than group T (N.S.). Differences in time spent feeding reflect differences in intake only when feeding rates are similar. Despite serious efforts only a single small sample could be obtained in which feeding rates were collected in the same tree at the same day. The results suggest higher feeding rates for individuals of the larger group T (0.51 vs 0.22 and 0.08 fruits per second for individual adult females of T and G, respectively, and 0.54 and 0.50 vs. 0.43 and 0.15 fruits per second for adult males).

Hence, the data show that travel and search clearly increase with group size and that rest decreases. Feeding time, however, shows different trends in the two data sets. The decrease with group size in data set I does not necessarily imply that fruit intake is lower in larger groups because of the possible compensation through higher feeding rates in those groups. It is clear, however, that time budgets are most favourable in smaller groups, because the most costly activities (travel, search) show an unambiguous, monotonic increase with group size.

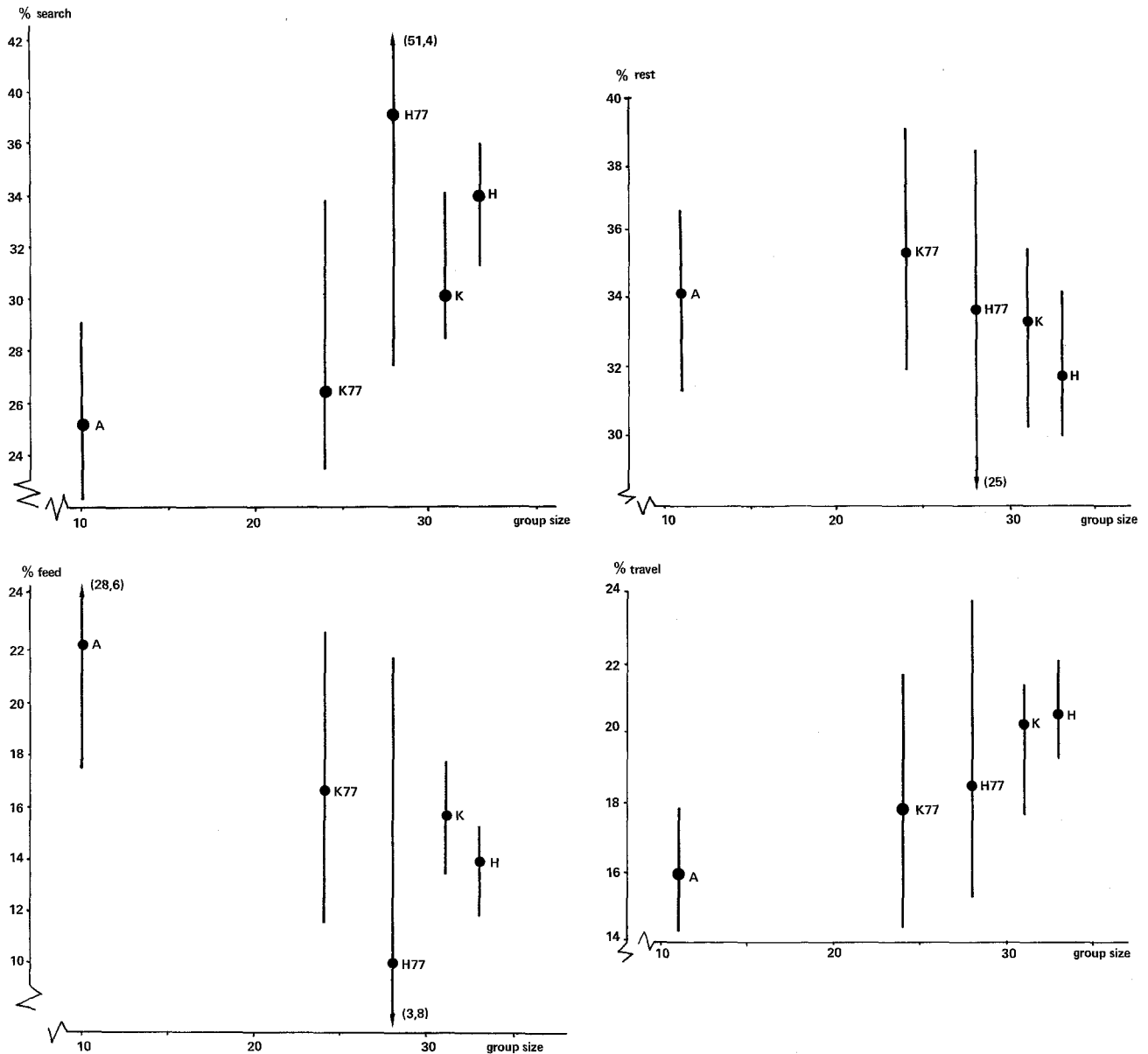


Fig. 3. Median percentage of time spent in each type of group activity in relation to group size (data set I). Indicated are the 95% confidence limits for the median. Sample sizes (days): A: 25; K77: 23; H77: 6; K: 44; H: 108

Individual activities

As to individual activities, the differences between the two groups of data set II are all in the same direction as those in group activities (significant for immobile + groom and for social on complete days; also significant for locomotion on half-days). In data set I the differences between the three groups are extremely small, which relates to a sudden increase in day journey length of group A in April 1981 following the change in leadership. The mean length of half-day journeys during the 2 months in which the data on individual activities

were collected was highest for the smallest group (727, 650 and 689 m, for A, K and H resp.), contrasting strongly with the data over the whole period (Fig. 2). Despite the high proportion of locomotion, group A still seemed to spend somewhat less time obtaining food and more time immobile plus grooming (none of the differences significant, however; Kruskal-Wallis test).

Presence of adults

The presence scores of adult group members clearly decrease with group size (Fig. 5).

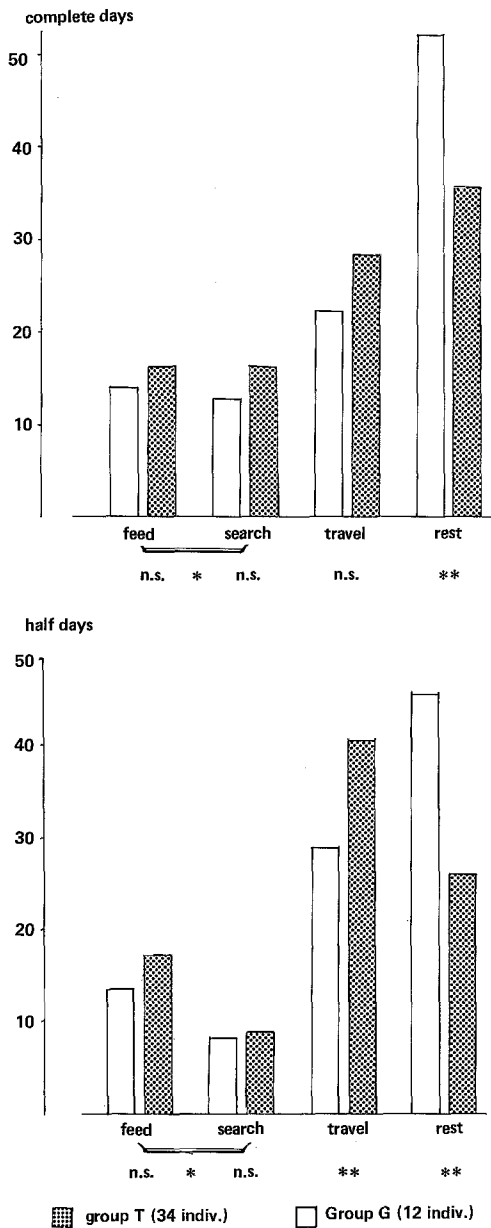


Fig. 4. Median percentage of time spent in each type of group activity for group G and T, for both complete days and half days (data set II). Asterisks indicate the outcome of Wilcoxon's matched-pairs signed-ranks test on pairs of complete or pairs of half days (* $P < 0.05$, ** $P < 0.01$). Sample sizes: G: 12; T: 12 for complete days; G: 14, T: 10, half-days

Agonistic interactions

No clear trend can be discerned in the five groups of data set I as to the total daily number of agonistic interactions per group member. Because not all group members are present in the group each day, however, it is better to calculate the daily total of agonistic interactions per member of the group actually present. If it is assumed that the percentage of adults present can be extrapolated to the

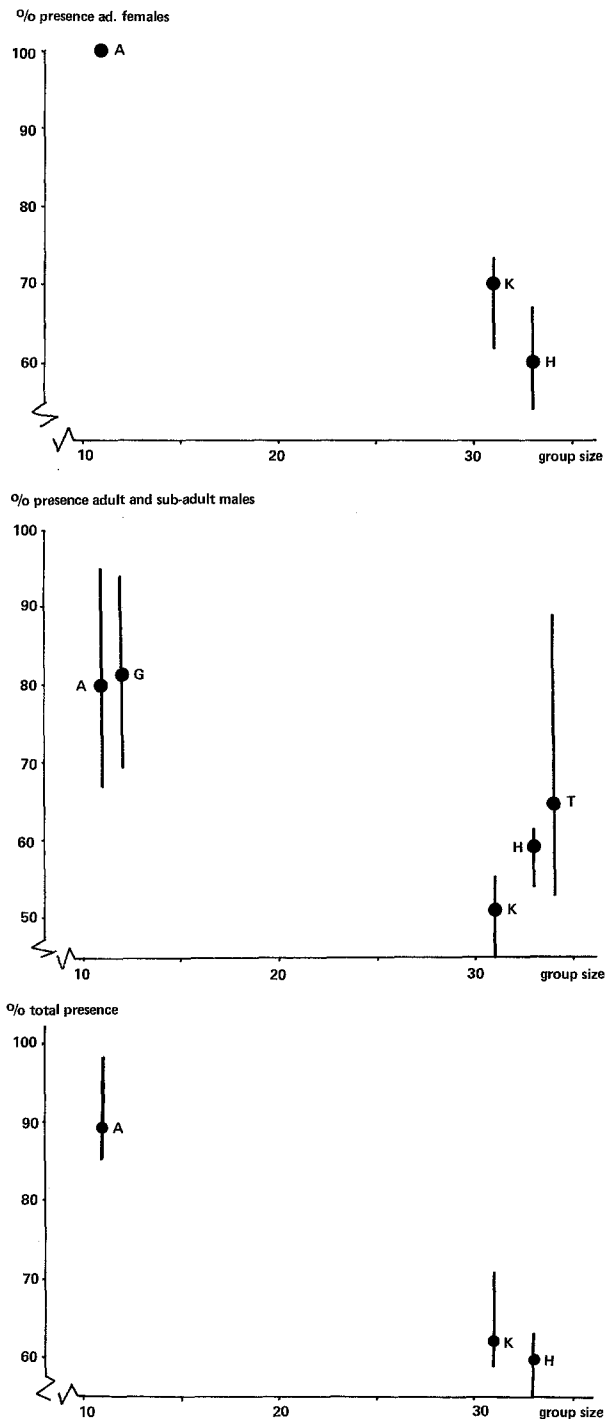


Fig. 5. The median percentage of the daily maximum number of hourly presence scores of adults (and the 95% confidence limits) as a function of group size. Sample sizes (days) for males: A: 19, K: 26, H: 63, G: 7, T: 7. For females and total adults sample sizes are: A: 19, K: 12, H: 46

total number of animals present the average daily number of agonistic interactions per group member present is 2.29 for the small group A and 3.78 and 3.77 for the large groups K and H (taking the average over the whole period for agonistic

interactions, presence percentage and group size). This difference can be tested by taking those days for which all these variables were available and is significant (Kruskal-Wallis test, $H=30.20$, $df=2$, $P<0.001$; $n=19$, 8 and 45 for A, K and H respectively).

In data set II the number of minutes with screams and/or grunts was considered to be an indication of the total number of agonistic interactions with vocalisations. This number, divided by the number of group members, has a median of 0.41 in the small group G ($n=24$ mornings) and of 0.58 in the large group T ($n=21$, Mann-Whitney U -test, $U=197$, N.S.). The more severe interactions were considered to be characterized by the number of minutes with both screams and grunts. The median per group member was 0 in G and 0.07 in T (Mann-Whitney, $U=147.5$, $P<0.02$). If the actual percentage of animals present in the group had been taken into account (Fig. 5), these differences would have been even larger.

The combined data sets support the conclusion that animals present in larger groups are more often involved in agonistic interactions.

Grooming

From a comparison of the three groups in 1980/81 of data set I it appeared that both the total number of grooming bouts observed per day and the total number of observed grooming-pair minutes were highest in the smallest group A (Kruskal-Wallis test, $P<0.05$ in both cases). If the lower presence percentage in the larger groups is taken into account, this amounts to an enormous difference in the time spent grooming between large and small groups. In the smaller sample of individual activities no such difference was apparent.

Data set II reveals the expected differences also in the individual activity scores: the percentage of grooming was higher in the small group G than in T (Wilcoxon's matched-pairs test, $T=16$, $n=13$ pairs, $P<0.05$ for half-days; and N.S. but in same direction for complete days).

Neighbours

The percentage of individual activity records in which a neighbour was scored provides some indication of group cohesion. Differences between groups appear to be negligible. There are, however, consistent differences between activities: animals that forage are most often without a neighbour in all cases. These results suggest that individuals attempt to surround themselves with neighbours to the same extent in groups of all sizes but that

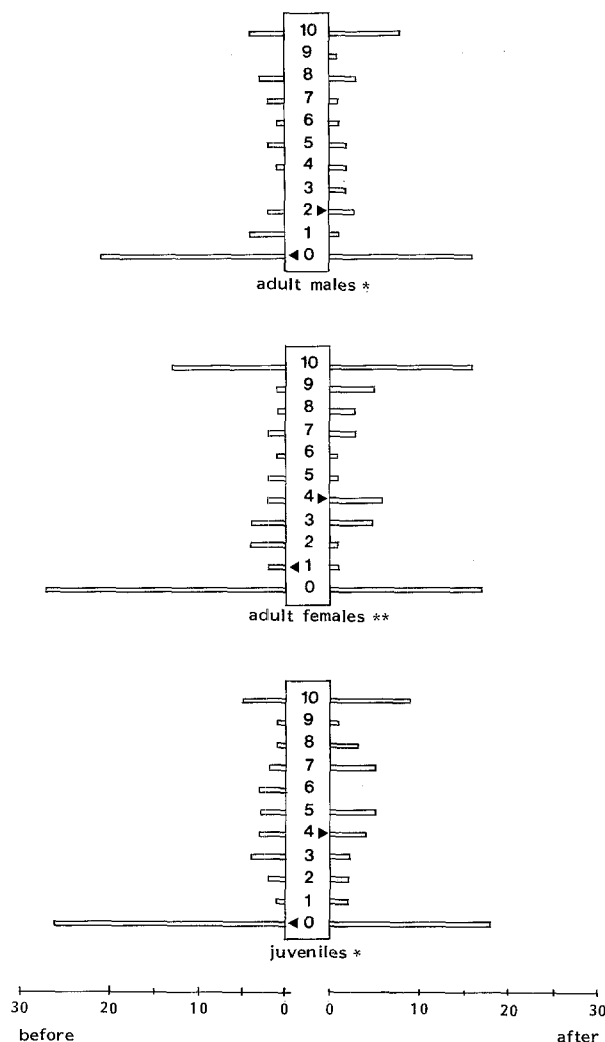


Fig. 6. The observed distribution of the number of seconds locomotion during the 10 s before and the 10 s after the event "another individual approaches" in the foraging protocols. Arrows indicate median values (Wilcoxon's matched-pairs signed-rank test, * $P<0.05$, ** $P<0.01$). Sample sizes (events): males: 40, females: 59, juveniles: 51.

they tend to avoid the close proximity of others during foraging (searching for dispersed food items).

Foraging and neighbours

The avoidance of neighbours during searching may indicate that an individual's foraging success will be lower when it has to search in patches already covered by others. This implies that foraging efficiency decreases when other individuals are allowed to join at the foraging site or when the searching individual is getting behind, which would happen if it allows others to overtake. Thus, if food depletion is an important factor we expect animals to leave when others encroach on their

Table 2. Young per female as a function of member of females per group, based on yearly census counts made of groups of wild long-tailed macaques (*Macaca fascicularis*)

Year	Number of groups	Slope	<i>r</i>	Average young/female
1980	10	-0.0160	-0.418	0.57
1981	14	-0.0242	-0.635 ^a	0.26
1982	18	-0.0101	-0.295	0.70
1983	14	+0.0102	+0.164	0.22

^a $P < 0.02$, two-tailed

foraging sites. The null-hypothesis, by contrast, is that an individual spends just as much time in locomotion after the moment that another individual approaches as it does before. To test this hypothesis several hours of detailed protocols of searching individuals were collected. The results clearly show the effect of moving away from approaching neighbours (Fig. 6). The effect of social rank of the approaching individual is small: focal animals moved as much or more after the approach of a higher ranking individual in 89% of the (46) cases, while this happened in 77% of the (43) cases where the approaching individual ranked lower ($\chi^2 = 2.44$, N.S.).

This 'pushing forward' effect can be interpreted as the behavioural expression of competition through local depression of food availability and is the most likely mechanism underlying the longer day journeys of larger groups.

Birth rates per female

Censuses were made when the young born the preceding year were on average about 5 months old. Table 2 summarizes the aspects relevant to the present study. In 3 out of 4 years the slope of the regression of the number of infants per adult female on the number of females in the group is negative, in 1 year significantly so. This suggests that females in larger groups give birth to fewer infants or that early infant mortality is considerably higher in larger groups. Assuming that most early mortality is caused by inadequate maternal nutrition rather than by predation, this indicates that adult females in larger groups are in poorer physical condition than those in smaller groups.

Discussion

The results of this study clearly show that among long-tailed macaques an increase in group size leads to less favourable time budgets: animals in larger groups have to expend more energy to ob-

tain food. Likewise, social tension increases with group size, whereas tension-reducing interactions such as grooming decrease in frequency. All this suggests that in this case there is a monotonic increase in competition among group members with increasing group size overshadowing any possible feeding advantage to living in groups. Hence, the data do not contradict Alexander's (1974) hypothesis that in primates living in groups is maintained entirely by the safety against predation afforded by it.

The stronger competition for food in larger groups leads to a reduction in the rates at which females give birth. This decrease in female birth rate with group size is apparent in the majority of primate species (review in van Schaik, in press) and suggests that primate groups are often larger than is optimal from the reproductive point of view. This is not to imply, however, that fitness is highest in the smallest groups, because predation risk may well decrease with group size (e.g. Pulliam 1973). Indirect demographic evidence (van Schaik, in press) suggests that it does, but direct proof is still lacking. If survival is found to increase with group size there will be an optimum group size in which average fitness is maximal. This optimum size, however, is of course unstable as groups will quickly outgrow it, after which fissioning is likely. In the present study population, two such cases have been observed and others can be inferred. Fissioning must have occurred when the original groups numbered over 40 individuals, about the size at which time budgets will seriously run out of hand (see Fig. 3). An alternative to permanent fissioning is subgroup formation and this too is more common in larger groups (Fig. 5). Animals leaving the group on their own or in a small subgroup free themselves to a large extent of competition and social interference but at the cost of increased predation risk (cf. van Schaik et al. 1983). Because the negative effects of competition will affect low-ranking individuals more severely, these animals are expected to leave the group more often and to be the ones that form a small break-away group (cf. Chepko-Sade and Sade 1979).

In this study the "pushing forward" effect during searching for dispersed food items was suggested as accounting for the observed increase in time spent searching and travelling and hence in day journey length. Waser (1977) found that larger groups of mangabeys (*Cercocebus albigena*) had longer day journeys. He ascribed this to the limited capacity of fruit trees, which results in smaller individual meal sizes per visit. To compensate for this the monkeys have to visit more fruit trees each

day, thus making longer day journeys. It is difficult to distinguish between these two mechanisms by observing day journeys and time budgets only: they both lead to more travel and it might either be argued that animals travelling more in order to visit more fruit trees accidentally search more on their way or that animals travelling more in order to search more encounter more fruit trees. If, however, it is found that larger groups of long-tailed macaques do not visit more fruit trees than smaller ones, this would refute the patch size argument in the present case. Because some species grow in groves the number of trees visited per day could not be calculated. However, since the majority of fruit species are rare and scattered, visiting more trees will inevitably lead to using more species. There was no relationship between the average number of fruit species eaten per day and group size for the combined groups of data sets I and II ($r = -0.14$, $n = 7$, N.S.), contrary to the increase predicted by Waser's argument. The best explanation for the increased day journey length in larger groups of long-tailed macaques is therefore the 'pushing forward' effect resulting from the active avoidance of conspecifics by foraging individuals because the availability of dispersed food (mainly insects) is reduced after a visit by a searching monkey.

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References

- Aldrich-Blake FPG (1980) Long-tailed macaques. In: Chivers DJ (ed) *Malayan forest primates*. Plenum Press, New York, pp 147–165
- Alexander RD (1974) The evolution of social behavior. *Annu Rev Ecol Syst* 5:325–383
- Altman J (1974) Observational study of behavior: sampling methods. *Behaviour* 49:227–267
- Bertram BCR (1978) Living in groups: predators and prey. In: Krebs JR, Davies NB (eds) *Behavioural ecology*. Blackwell, Oxford, pp 64–96
- Chepko-Sade BD, Sade DS (1979) Patterns of group splitting within matrilineal kinship groups: a study of social group structure in *Macaca mulatta*. *Behav Ecol Sociobiol* 5:67–86
- Clutton-Brock TH (1974) Primate social organization and ecology. *Nature* 250:539–542
- Cody ML (1971) Finch flocks in the Mohave desert. *Theor Popul Biol* 2:142–158
- Colquhoun D (1971) *Lectures on biostatistics*. Clarendon Press, Oxford
- Eisenberg JF, Muckenhirn NA, Rudran R (1972) The relation between ecology and social structure in Primates. *Science* 176:863–874
- Freeland WJ (1976) Pathogens and the evolution of primate sociality. *Biotropica* 8:12–24
- Hamilton WD (1971) Geometry for the selfish herd. *J Theor Biol* 31:295–311
- Hoogland JL (1981) The evolution of coloniality in white-tailed and black-tailed prairie dogs (*Sciuridae: Cynomys leucurus* and *C. ludovicianus*). *Ecology* 62:252–272
- Hoogland JL, Sherman PW (1976) Advantages and disadvantages of bank swallow (*Riparia riparia*) coloniality. *Ecol Monogr* 46:33–58
- Horn HS (1968) The adaptive significance of colonial nesting in the Brewer's blackbird. *Ecology* 49:682–694
- Jonckheere AR (1954) A distribution-free k-sample test against ordered alternatives. *Biometrika* 41:133–145
- Krebs JR, Davies NB (1981) *An introduction to behavioural ecology*. Blackwell, Oxford
- Kurland JA (1973) A natural history of kra macaques (*Macaca fascicularis* Raffles 1821) at the Kutai Reserve, Kalimantan Timur, Indonesia. *Primates* 14:245–262
- Mitani JC, Rodman PS (1979) Territoriality: the relation of ranging pattern and home range size to defendability, with an analysis of territoriality among primate species. *Behav Ecol Sociobiol* 5:241–251
- Pulliam HR (1973) On the advantages of flocking. *J Theor Biol* 38:419–422
- Raemaekers JJ, Chivers DJ (1980) Socio-ecology of Malayan forest primates. In: Chivers DJ (ed) *Malayan forest primates*. Plenum Press, New York, pp 279–316
- Rijksen HD (1978) A field study of Sumatran Orang-Utans (*Pongo pygmaeus abeli* Lesson 1827). Veenman, Wageningen
- Schaik CP van (in press) Why are diurnal primates living in groups? *Behaviour*
- Schaik CP van, Noordwijk MA van, Warsono B, Sutriono E (1983) Party size and early detection of predators in Sumatran forest primates. *Primates* 24:211–221
- Schoener TW (1971) Theory of feeding strategies. *Annu Rev Ecol Syst* 2:369–404
- Siegel S (1956) *Non-parametric statistics for the social sciences*. McGraw-Hill, New York
- Taylor RJ (1977) Value of clumping to prey and the evolutionary response of ambush predators. *Am Nat* 110:13–29
- Treisman M (1975) Predation and the evolution of gregariousness I: models for concealment and evasion. *Anim Behav* 23:779–800
- Waal FBM de, Hooff JARAM van, Netto WJ (1976) An ethological analysis of types of agonistic interactions in a captive group of Java-monkeys (*Macaca fascicularis*). *Primates* 17:257–290
- Ward P, Zahavi A (1973) The importance of certain assemblages of birds as 'information-centres' for food-finding. *Ibis* 115:517–534
- Waser P (1977) Feeding, ranging and group size in the mangabey, *Cercocebus albigena*. In: Clutton-Brock TH (ed) *Primate ecology*. Academic Press, London, pp 183–222
- Wheatley BP (1980) Feeding and ranging of East Bornean *Macaca fascicularis*. In: Lindburg DG (ed) *The macaques*. Van Nostrand Reinhold, New York, pp 215–246
- Wrangham RW (1979) On the evolution of ape social systems. *Soc Sci Inf* 18:335–368
- Wrangham RW (1980) An ecological model of female-bonded primate groups. *Behaviour* 75:262–300