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Competition and group size in Thomas's langurs (*Presbytis thomasi*): the folivore paradox revisited

Abstract Among primates, group size is highly variable. The standard ecological model assumes that better predation avoidance as group size increases favours living in larger groups, whereas increased travel costs and reduced net food intake due to within-group competition for resources set the upper limit. Folivorous primates, however, tend to defy this generalisation in that some live in small groups despite low costs of feeding competition. To resolve this 'folivore paradox', it has been suggested that folivore group size is limited by social factors such as male harassment or infanticide, or that females can disperse more easily and thus maintain group size near optimum levels. In this paper, we examine the effects of group size on home range size, day-journey length, activity budget and diet in wild Thomas's langurs (*Presbytis thomasi*), which live in one-male multi-female groups with a limited life cycle. We examined only data from the stable middle tenure phase when factors such as the strength of the breeding male or the way in which groups were formed did not influence ranging and activities. During this phase, group size affected day-journey length and home range size, and had a minor effect on diet, but did not influence time spent feeding or resting, allogrooming or birth rates. Hence the upper limit to group size during the middle tenure phase in Thomas's langurs is not set by feeding competition. The folivore paradox is not due to frequent female dispersal in Thomas's langurs. The timing of female dispersal is not as expected if it serves to keep group sizes near the ecological optimum, and groups seem to be below this optimum. Instead, female reproductive success is presumably maximised in small to mid-sized groups because larger groups show a clear trend to experience higher risk of take-over, often accompanied by infanticide. Because females can redistribute themselves among nearby groups when groups reorganise each time a new male starts up a new group, females can keep the group small. Thus, a social factor, risk of infanticide, seems to provide the selective advantage to small group size in Thomas's langurs.

Keywords Food competition · Group size · Day-journey length · Home range size · Thomas's langur · Activity budget · Diet · Relative ranging costs

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Introduction

One of the main tasks of socioecology is to explain variation in group size, within and between animal species. This variation can be appreciable. In primates, for example, group sizes vary by two orders of magnitude across species, and up to about fivefold within some species (Clutton-Brock and Harvey 1977; Dunbar 1988). Socioecological theory assumes that ecological factors are largely responsible for this variation: better predation avoidance as group size increases favours living in larger groups, whereas increased travel costs and reduced net food intake due to within-group competition for resources set the upper limit to viable group size (Dunbar 1988, 1992; Janson 1992). Janson and Goldsmith (1995) provided broad support for this idea, showing that species or populations with larger mean group sizes are less affected by within-group competition (cf. Wrangham et al. 1993), and tend to be species experiencing a high risk of predation.

Several folivorous primates, however, defy this generalisation, living in small groups even though costs of feeding competition are low (Janson and Goldsmith 1995) or absent (Isbell 1991). Since they do experience significant predation risk (e.g. Steenbeek et al. 1999), the socioecological model predicts that fitness is maximised

in larger groups where the increased competition is balanced by improved survival. To resolve this 'folivore paradox', it has been suggested that the upper limit to group size is set not by ecological but rather by social factors, such as male harassment or infanticide (Treves and Chapman 1996; C.M. Crockett and C.H. Janson, unpublished data). An alternative suggestion would be that folivore females can easily disperse or transfer between groups, and group size can therefore be maintained near its optimum (Janson and Goldsmith 1995). In most non-folivores, by contrast, groups are larger than optimal because females cannot easily join other groups and can only found new groups by fissioning (Sterck et al. 1997).

The Thomas's langur (*Presbytis thomasi*) is a folivore-frugivore with an enlarged sacculated stomach that enables it to digest leaves and seeds. We studied it in a Sumatran rainforest, where groups inhabit widely overlapping home ranges, and contain a single adult male and one to six adult females and their offspring. Both males and females disperse from their natal groups, and female secondary transfer to a new male is also common (Sterck 1997; Steenbeek 1999a). After their primary transfer from the natal group, females change breeding males on average every 4.5 years (Steenbeek 2000). Infanticide by males occurs (Steenbeek 1996, 2000; Sterck 1997; Steenbeek et al. 1999). Groups can be reconstituted whenever the single adult male is replaced (Sterck 1997; Steenbeek 2000; Steenbeek et al. 2000). Thus, groups go through a typical life cycle. In this cycle, four tenure phases can be recognised (Steenbeek 2000; Steenbeek et al. 2000). (1) The early phase when females join a new adult male and thus form a new group, defined as the period in which none of the females has an infant. (2) The stable middle phase when females have offspring. (3) The late phase, defined as the final year of a male's tenure, when his strength declines and all females over 3 years of age gradually leave him. After all the females have left the breeding male, the late tenure phase has ended and (4) an all-male band remains (all-male band phase). These new all-male bands consist of the former breeding male and his sons. Groups usually start gradually, when females join over a period of time, and also end gradually when they leave the group one or more at a time (around 80% of the cases). However, groups can also begin and end suddenly, as in the case of a male take-over or the death of the breeding male (Steenbeek et al. 2000).

Steenbeek (1999a) showed that group size is a good predictor for home range size during the stable middle tenure phase. However, during the early and late phases of a male's tenure, home range size was not determined by group size, but mostly by the way groups were formed (gradually or suddenly), and by the time since group formation. When groups formed suddenly, home range size increased rapidly and then remained approximately constant. In contrast, when groups formed gradually, they started in a small range that continued to increase to reach a stable size within 2 years. During the last year of a breeding male's tenure, his declining strength led to a strong avoidance of extra-group males (Steenbeek 1999b), resulting in a smaller home range and sometimes even a new home range location (Steenbeek 1999a). This pattern suggests that if ecological costs to grouping exist, they should become apparent during the stable middle phase (lasting 60 months on average), when social effects on ranging are minimal and the number of females is highest.

In Thomas's langurs, dominance hierarchies are weakly expressed (inside food patches) or not apparent at all (outside food patches; Sterck and Steenbeek 1997), indicating that most of the competition for resources, if any occurs, is through scramble (van Schaik and van Noordwijk 1988). We hypothesise that, when examined during the stable middle tenure phase, scramble competition for food among Thomas's langurs increases with group size. Individuals in larger groups are expected to compensate for the reduced mean intake by increasing their effort [day-journey length (DJL) and time spent feeding]. When full travel compensation becomes impossible, we expect animals to suffer reduced intake of preferred food and to include more non-preferred food in their diet (see Fig. 2 in Sterck et al. 1997). Furthermore, we expect larger groups to occupy larger ranges or ranges with higher food production. If individuals in larger groups suffer from food competition, we expect a negative impact on female reproduction.

Our results indicate that during the stable middle tenure phase, costs to grouping can be demonstrated and that relative ranging costs are appreciable. However, because group size is small, the overall impact of competition is limited, with dietary switching marginal and no effect on birth rate. On the other hand, groups with a larger number of adult females seem to face a higher risk of an aggressive male take-over. The results suggest that the lower limit of group size is set by predation avoidance, whereas the upper limit is set by infanticide avoidance.

Methods

Study area and subjects

This study was conducted at the Ketambe Research Station (3°41′ N, 97°39′ E), Gunung Leuser National Park, in northern Sumatra, Indonesia. The study area, approximately 200 ha, mainly consists of undisturbed primary rainforest, as described by Rijksen (1978) and van Schaik and Mirmanto (1985).

The study subjects were wild Thomas's langurs. Data on home range size and DJL were collected for 14 mixed-sex groups under the responsibility of C.P.v.S. (November 1987–1988), E.H.M. Sterck (1989–1991), R.S. (1992–1995) and A.H. Korstjens (1996). Details of group composition are described elsewhere (Steenbeek 1999a). Data on activities and diet were collected for 12 mixed-sex groups from 1993 to 1996. All mixed-sex groups had a different breeding male. Because females transferred between males, females may be represented in more than one group.

Phenological data collection

To monitor food availability, 19 plots were checked monthly on the 10th until the 13th. These plots were randomly spaced through

the area and measured 25×25 m, including all trees with a diameter of at least 10 cm at breast height, and lianas in those trees. For each food patch (a tree or a liana) the presence of fruits, young leaves and flowers was recorded, and percentages of food patches carrying these organs were calculated. In these calculations, we first distinguished between food patches with items known to be regularly included in the langur diet, and other patches, in order to test if the overall productivity of the forest could be used to estimate the food available to Thomas's langurs. This was indeed the case: the percentage of total food patches with fruit (or young leaves) showed a very strong positive correlation with the percentage of food patches with fruit (or young leaves) consumed by Thomas's langurs (phenological data, $n=33$ months; fruit: $r=0.986$, $P<0.001$; young leaves: $r=0.997$, $P<0.001$). Hence, we used the total productivity of the forest in our analyses.

Data collection: activities and diet

Groups were mostly followed from dawn (when the monkeys left the sleeping tree) until dusk (when they entered the sleeping tree). A total of 1,762 focal hours were collected by ten different observers under the responsibility of R.S., from March 1993 until November 1995. Observations were only made after observers had been trained to reach inter-observer reliability indices over 90% with R.S. Data on individuals were collected with the focal-animal method (instantaneous sampling; Martin and Bateson 1986). Every minute, on the minute, the activity of the focal animal was noted. Activity categories used in this study were feeding, resting and allogrooming. If individuals were feeding, the food item was recorded: fruit, leaves, leaf matter (pith, stems), flowers, snails, and other (all categories below 1% of the diet for most individuals, e.g. insects, bark, earth). In this study, we only used the categories fruit and young leaves.

Focal sampling with a maximum duration of 15 min was evenly distributed over the day, and individuals were sampled in a pre-determined sequence. If the next focal individual could not be found, the observer was allowed to move on to the subsequent animal. We attempted to collect focal samples of 15 min, before switching to the next animal, but an animal could move out of sight before the 15 min had elapsed. Such focal records were kept and used, unless it had lasted less than 3 min. A group was followed for a number of days until the sum of these 15-min focal samples had reached at least 400 min per adult female. Because adult males could temporarily leave the group, a male was continuously observed for at least 2 consecutive days until a minimum of 600 focal min was attained. Thus, one focal period of one group consisted of at least 600 min for the adult male and at least 400 min for every adult female. We collected several focal periods for most groups. Table 1 shows the number of focal periods which are used in the analysis.

Data collection and preparation: home range size and DJL

As explained above, groups were mostly followed from dawn until dusk. When groups were only followed for part of the day, the number of hours was divided by an average 12-h day. Thus, 3 contact hours with a group counted as 0.25 days.

The daily travel route was plotted on a map, with a mark for every half hour. All maps were digitised as follows: half-hour locations were digitised for all maps, while for some maps, extra locations were digitised when groups had travelled in an extreme curve between two half-hour locations. These extra locations were only used for the calculation of DJL. Maps were digitised with a maximum of 3% variation between digitised locations. These digitised locations were analysed with the program RANGES V (Kenward and Hodder 1996). We calculated concave polygons with selected edges of 0.1. Range overlap was calculated from overlapping range outlines. Further details on data preparation and the calculation of home range size are described elsewhere (Steenbeek 1999a).

When data had been combined to meet the minimal requirements for calculating range size (Steenbeek 1999a), most ranges included data from periods with variation in diet. Therefore, we could only analyse seasonal effects on DJL, but not on range size, while groups are expected to range in larger areas when they eat relatively more fruit and less young leaves. To detect an influence of season on relative home range size, we recalculated range size for periods with the lowest and highest values of the percentage of fruit in the diet. The difference between the lowest and highest had to be at least 20%, and half-hour locations had to be collected within 1 month. In this way, we were able to compare the fruiting season with the non-fruiting season for six groups. Note that when the langur diet contains a high percentage of fruit, it contains a low percentage of young leaves and vice versa.

The 'middle-tenure' range

To study the effects of group size and habitat quality, we needed to control for seasonal influences on the size of the home range and DJL. This was done as follows: we prepared one large 'middle-tenure' home range for each group by combining ranges from all seasons. Thus, the 'middle-tenure range' illustrates the total area used by a stable middle-tenure group. We had sufficient data to create these middle-tenure home ranges for fourteen groups (Table 1). Group size was defined as the total number of independent individuals. Because it varied over time, mean group size for the middle-tenure home range was time-weighted. From the focal periods, we calculated average middle-tenure values for DJL, activities, and the percentage of young leaves in the diet (which is strongly negatively correlated with the percentage of fruit).

Table 1 Middle-tenure values of the study groups (see text for details). Not all focal periods contain data on males and females

Group	Aveage home range size[a] (ha)	Average day-journey length[a] (m)	Group size[b]	Number of focal periods[c]
B1	38.8 (77)	1,066 (19)	8 (7–8)	–
B2	48.9 (213)	1,193 (163)	7 (7–8)	12
J1	53.4 (136)	1,264 (139)	9 (7–9)	10
J2	22.9 (42)	1,078 (50)	5 (5)	4
M1	31.8 (145)	1,228 (151)	7 (4–7)	2
M2	23.8 (94)	948 (89)	6 (6)	8
M3	27.3 (67)	1,049 (77)	6 (5–7)	5
K1	31.0 (84)	1,189 (89)	11 (11–12)	6
K2	29.7 (50)	1,094 (43)	7 (7)	5
R	21.6 (20)	1,170 (12)	7 (7)	–
L	14.1 (49)	1,143 (41)	7 (7)	5
RL	18.4 (44)	903 (34)	5 (4–5)	4
N	7.1 (41)	754 (33)	3 (3)	6
A	15.2 (89)	869 (67)	5.5 (5–7)	5

[a] Number of observation days in parentheses
[b] Range in parentheses
[c] Not all focal periods contain data on activities and diets of bath sexes

Home range quality

The study area contains several terraces and mountain slopes of varying age and soil fertility. Van Schaik and Mirmanto (1985) found that these geomorphologic units showed systematic differences in productivity, as estimated by fruit production (number of fruit sources with fruit per 100 m of trail) and leaf litter production (tonnes ha^{-1} year^{-1}). The quality of each of the 14 middle-tenure home ranges was estimated by taking the area within each geomorphologic unit to calculate a weighted mean productivity of fruit and litter per hectare.

Data preparation: activities, diet and food availability

Activity and diet measures were calculated for each focal period. Activity variables were corrected for active daylength. Active daylength was defined as the time between leaving a sleeping tree in the morning and entering a sleeping tree in the evening. Because active daylength varied between 661 and 797 min between focal periods, time spent on an activity was controlled for active daylength by calculating minutes per day rather than percentages of time. For each focal period of each group, we took the variables of the adult breeding male and the average values of all adult females, resulting in one value for the male and one value for the females. The diet variable was percentage of time spent feeding.

We calculated the availability of food items at the time of a focal period as follows: for each observation period (which is spread over the number of days needed to collect a focal period of one group), the date of the median of the sum of all focal minutes served as a main point. Because the main points of langur observations often did not coincide with the main point of the phenological data (the 11th of each month), we made the following correction: Each month was divided into ten parts of 3 days. The phenological data points from 2 months were then weighed according to the main point of the langur observation. For example, when the main point of a focal period fell on the 14th, the availability of a food item of the first month was multiplied by 0.9 and added to 0.1×the availability of the food item of the second month. This yielded a more accurate figure for food availability during each observation period.

Data analysis

All analyses were carried out with SPSS. The following variables correlate significantly and cannot, therefore, be used in the same ANOVA: time spent feeding and time spent resting, and the percentage of fruit and the percentage of young leaves in the diet (Table 2; cf. Steenbeek 1999a). Taking these correlations into account, a general factorial ANOVA was carried out to analyse diet, home range size and DJL, with the following factors: (1) group identity (numbered 1 through 12) and (2) sex (male or female; only included in the analyses of diet and DJL; see below); and the following covariates: (1) for all analyses, group size (only independent individuals were included), (2) for the analysis of DJL, the percentage of fruit or leaves in the diet, or time spent feeding or resting, and (3) for the analysis of diet, the availability of the food item considered. The factor sex was included in the analyses of diet to investigate whether there is a sex difference in diet, and in the analysis of DJL in combination with time spent feeding and resting because males and females differ in time spent on these activities (R. Steenbeek, unpublished data).

We started an analysis by including all possible two-way interactions between factors and covariates. We then repeated the analyses with all factors and covariates, but including only the significant interaction effects. Only the latter analysis is presented in Table 3. For covariates that showed a significant interaction with any of the factors, no overall regression coefficient is given. Multiple tests were corrected with a modified Bonferroni procedure (Hochberg 1988).

Table 2 ANOVA validation: significant correlations

Correlated varables	Sex	n	r
Percent fruit vs percent young leaves in diet	Males	58	−0.854***
	Females	46	−0.826***
Percent time spent feeding vs resting	Males	57	−0.840***
	Females	45	−0.901***

***$P<0.01$, corrected for six tests

Properties of the general factorial ANOVA

When a large dataset is available, as in this study, we can analyse effects on DJL and home range size with a general factorial ANOVA. The factor group identity is necessary because different groups had a different number of measurements (focal periods) and including all these ensured high variation. Unfortunately, when the effect of group identity is included, the covariate group size will only measure the effect of group size variation within the same group over time. During the middle tenure phase of Thomas's langurs, this variation was small, namely 1–3 individuals, whereas the same variable between groups varied from 3 to 12 individuals. When group identity turns out to be the main explanatory variable, this means there are differences between groups, which could reflect the effects of group size, but also of other factors, such as home range quality. Because we used only data from the stable middle tenure phase, variables such as male strength are assumed not to play a major role. Correlation analyses on grand averages during the middle tenure phase were used to analyse the influence of differences between groups, i.e. group size and home range quality. When correlations were significant, a regression analysis is presented, to better describe the effects.

Results

Our aim was to examine the effects of group size on DJL, home range, activities and diet. However, some factors may confound the effect of group size on these variables. First, temporal variation in food abundance is likely to affect diet, and therefore activities and ranging. Second, home range quality is expected to affect ranging, activities and diet. Hence, we first examined the results of general factorial ANOVAs to estimate these confounding effects. This analysis would also reveal any effects of group size variation within groups. We subsequently examined the relationship between group size and ranging, reproduction, and the risk of an aggressive male take-over.

Confounding factors and within-group effects

Temporal variation in food availability

On average, the Thomas's langur diet contains 83% leaves and fruit. Therefore, only these two food items were included in the general factorial ANOVA of the effect of food abundance on diet (Table 3). For both fruit and young leaves, the effect of group identity was significant, indicating that aspects of group identity, possibly including size, are responsible for variation among groups.

Table 3 Food availability and diet: statistical results of the general factorial ANOVA. For covariates that showed a significant interaction with any of the factors, no overall regression coefficient is given [*Group* group identity, *SS* sum of squares, *MS* mean sum of squares, *B* regression coefficient, *β* standardised regression coefficient, SE(*B*) standard error of B]

Source of variation	SS	df	MS	F	B	β	SE(B)	t
Diet: Percentage fruit								
Within+residual	25,229.1	83	304.0					
Regression (covariate)	10,068.6	1	10,068.6	33.12***				
Sex	72.6	1	72.6	0.24				
Group	9,244.9	11	840.4	2.76**				
Group size	182.3	1	182.3	0.60				
Group×group size	7,920.1	8	990.0	3.26**				
Covariate: availability of fruit					2.95	0.47	0.51	5.755***
Diet: Percentage young leaves								
Within+residual	26,915.1	80	336.4					
Regression (covariate)	2,139.0	1	2,139.0	6.36*				
Sex	320.9	1	320.9	0.95				
Group	11,661.5	11	1,060.1	3.15**				
Availability of young leaves	475.6	1	475.6	1.41				
Group×availability of young leaves	11,947.8	11	1,086.2	3.23**				
Covariate: group size					7.30	0.74	2.90	2.521*

*P<0.05; **P<0.01; ***P<0.001

The percentage of fruit in the diet was positively related to the availability of fruit in the forest, whereas the percentage of young leaves in the diet was not affected by the availability of young leaves. This result indicates that Thomas's langurs prefer to eat fruit when it is abundant, and that competition for food, if it occurs, should be expressed in a reduced percentage of fruit in the diet. The percentage of fruit in the diet was affected by the interaction between group identity and group size. This interaction effect arose because one group consumed less fruit as its size increased. Closer examination of four groups with a sufficient number of data points and variation in group size (one to two individuals) showed that females consumed more leaves and less fruit when group size increased, but males did not. This within-group effect, while not as strong as predicted, is in accordance with the scramble competition hypothesis.

The other significant effect shown in Table 3 was that the percentage of young leaves in the diet was affected by the interaction between the availability of young leaves in the forest and the identity of the group. This arose because some groups ate more young leaves when there were more available but others did not.

Overall, these results suggest that we need to control for the effect of varying food availability when examining the effects of group size. This was done by taking long-term averages for each group.

DJL and home range in relation to diet

The influence of diet on DJL was also analysed with a general factorial ANOVA (Table 4). DJL was mostly affected by the identity of the group, which could be a group size effect. DJL was also affected by the interaction between group identity and the percentage of young leaves in the diet: three groups travelled less far when they consumed relatively more young leaves, but two groups showed the opposite pattern. These results show that diet had no major or general influence on DJL, and we can therefore ignore it as a possible confounder of group size effects on DJL.

The effect of diet on home range was examined by comparing groups over longer periods. For six groups, we could calculate the home range size for a period when the diet contained a small percentage of fruit and for a period when the diet contained a large percentage of fruit (the difference between a small and large percentage of fruit varied from 26.6 to 62.3% with an average of 41.1%, n=6). Five groups showed a decrease in home range size when the percentage of fruit was lower, and one group an increase (paired *t*-test, t=1.66, P=0.157). Hence, groups tended to use a larger part of their middle-tenure home range when fruit was abundant. To examine the effect of group size, it is safest to take long-term averages to control for the effects of fluctuations in diet.

The percentage of fruit or young leaves in the diet did not influence activities when tested with a general factorial ANOVA (not shown). Thus, we can ignore the possibility that diet confounds the effect of group size on activities.

Home range quality

The general factorial ANOVA of home range size (Table 4) shows that home range size was mostly determined by the identity of the group, and to a small extent by the interaction between group identity and group size (i.e. three groups used a larger home range as their group size increased, whereas two groups showed the opposite effect). Thus, within-group changes in group size did not have a consistent influence on range size, but groups dif-

Table 4 Day-journey length (DJL; m) and home range size (ha): statistical results for the general factorial ANOVA [*Group* group identity, *SS* sum of squares, *MS* mean sum of squares, *B* regression coefficient; β standardised regression coefficient, SE(*B*) standard error of B]

Source of variation	SS	df	MS	F	B	β	SE(B)	t
DJL and percentage of young leaves								
Within+residual	1,301,626.4	79	16,476.3					
Regression (covariate)	16,396.7	1	16,396.7	1.00				
Group	883,184.0	11	80,289.5	4.87***				
Percentage of young leaves	29,341.6	1	29,341.6	1.78				
Group×percentage of young leaves	45,7231.1	11	41,566.5	2.52**				
Covariate: group size					−24.52	−0.25	24.58	−0.998
DJL and percentage of fruit								
Within+residual	1,869,148.9	90	20,768.3					
Regression (covariates)	69,061.0	2	39,530.5	1.90				
Group	1,355,005.8	11	123,182.3	5.93***				
Covariate: group size					−31.54	−0.32	24.98	−1.263
Covariate: percentage of fruit					1.06	0.12	0.72	1.488
DJL and time spent feeding								
Within+residual	1,692,941.8	83	20,396.9					
Regression (covariates)	37,111.4	2	18,555.7	0.91				
Group	1,050,428.9	11	95,493.5	4.68***				
Sex	2,751.3	1	2,751.3	0.13				
Covariate: group size					−32.11	−0.34	25.60	−1.254
Covariate: time spent feeding					0.10	0.02	0.36	0.275
DJL and time spent resting								
Within+residual	1,679,841.4	83	20,239.1					
Regression (covariates)	50,211.7	2	25,105.9	1.24				
Group	1,069,137.3	11	97,194.3	4.80***				
Sex	1,636.1	1	1,636.1	0.08				
Covariate: group size					−37.23	−0.40	25.54	−1.457
Covariate: time spent resting					0.28	0.08	0.33	0.851
Home range size								
Within+residual	170.2	20	8.5					
Group	917.2	6	152.9	17.96***				
Group size	1.2	1	1.2	0.15				
Group×group size	166.9	4	41.7	4.9**				

**P<0.01; ***P<0.001

fered in home range size. The possible effect of home range quality was tested with a correlation analysis on grand middle-tenure averages for each group. Home range quality did not affect ranging: it was not significantly correlated with home range size, DJL or group size (Table 5). Note, however, that the correlations between the average productivity per hectare and the size of the range are positive and not negative, as would be expected if lower productivity necessitates ranging in a larger area. Home range quality also did not affect activities or diet (Table 5). Hence, there is no need to control for home range quality when examining the effect of group size on ranging variables, and the effect of group identity most likely reflects that of group size.

Conclusion

The results showed that changes in group size within groups did not influence DJL, home range size or activi-

ties, and had only marginal effects on diet. They also indicated that temporal variation in food abundance was the only confounding factor for the analysis of group size effects. Its effect is easily eliminated by using middle-tenure averages that cover all seasons for each group. We could therefore embark on the analysis of group size effects by analysing groups of different sizes.

Effects of group size

Effects of group size on ranging and activities

Among groups, we found a significant positive relationship between group size and home range size (Fig. 1a; $n=14$; regression: $B=60.167$, $F=17.566$, $P<0.01$, $r=0.643$), and between group size and DJL (Fig. 1b; $n=14$; regression: $B=4.353$, $F=8.454$, $P<0.05$, $r=0.771$). Group size did not affect diet: a correlation analysis on grand middle-tenure averages showed no significant results (Table 6).

We analysed the influence of group size on activities for males and females separately because males spent less time feeding and allogrooming, and more time resting than females (R. Steenbeek, unpublished data). For both males and females, there were no significant relationships between ranging and activity budgets: neither group size, home range size nor DJL were significantly correlated with time spent feeding, resting or allogrooming (Table 6; Fig. 2). Note that the correlations between group size and time spent allogrooming are positive and not negative or humped, as would be expected if time to socialise became limited above a given group size.

Effects of group size on reproduction

The question that arises next is whether the increased ranging effort in larger groups compromises energy budgets to the point that birth rates are affected. Figure 3 shows the relationship between group size and average reproductive rates (including all data from the middle and late tenure phases). Although the sample size of seven groups may be too small to draw a definite conclusion, the number of infants born per female year did not show the expected decrease in larger groups ($n=7$, $r=0.210$, $P=0.651$). The number of surviving infants per female year even tended to increase with group size ($n=7$, $r=0.726$, $P=0.065$), suggesting improved infant survival in larger groups.

Group size and the risk of an aggressive male take-over

The number of reproductive females may influence the risk of an aggressive male take-over. Two aggressive
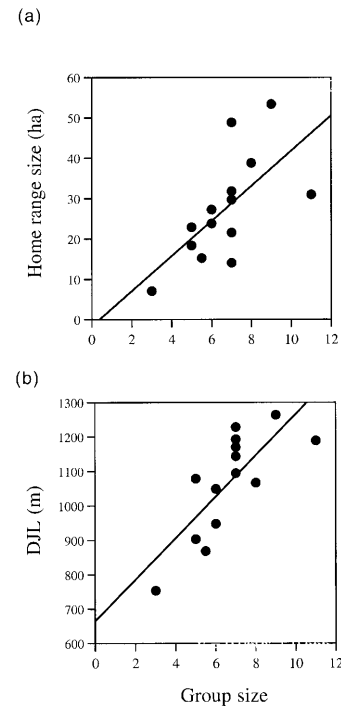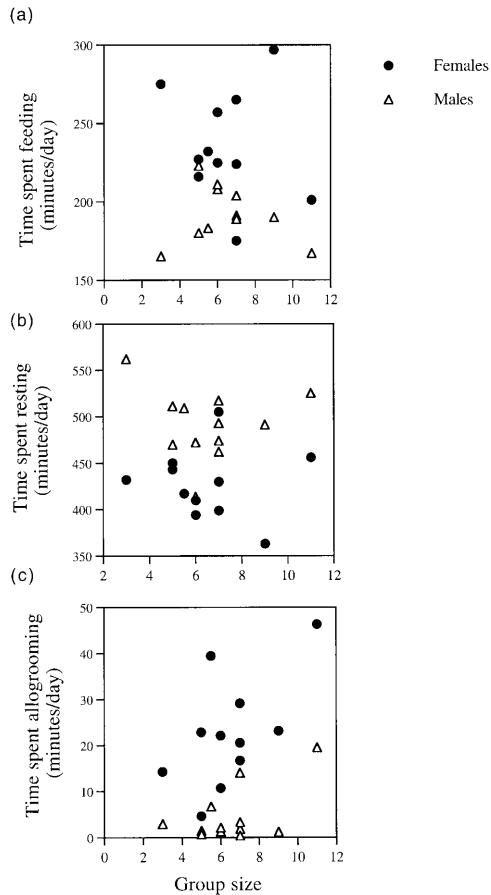

Fig. 1 The relationship between group size and home range size (**a**) and day-journey length (DJL) (**b**). There is a significant positive relationship between group size and home range size ($P<0.01$) and DJL ($P<0.05$)

Table 5 Correlations with home range quality. Activities were calculated as minutes per day. Correlations were not significant. (*Fruit per hectare* the total productivity of fruit per range, divided by the home range size; *Leaves per hectare* total leaf litter production per range, divided by the home range size)

Middle tenure average	Fruit per hectare	Leaves per hectare
Home range size	0.481	0.340
DJL	0.123	0.094
Group size	−0.009	−0.054
Males		
Time spent feeding	−0.010	−0.121
Time spent resting	−0.218	−0.241
Time spent grooming	−0.039	−0.057
Diet: percentage of young leaves	−0.033	−0.094
Females		
Time spent feeding	0.325	0.134
Time spent resting	−0.356	−0.115
Time spent grooming	−0.157	−0.151
Diet: percentage of young leaves	−0.038	0.181

Table 6 Correlations among activities, diet, group size and ranging variables. No correlations were statistically significant

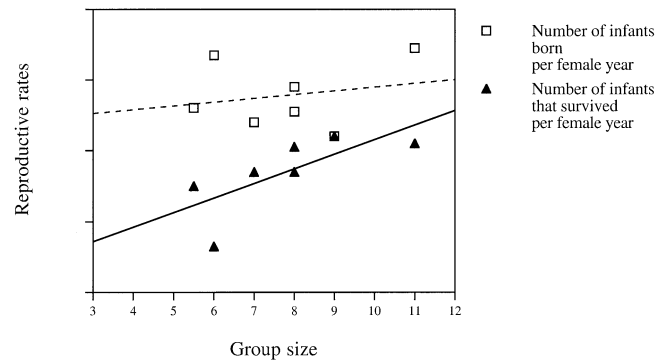| Activity (min day^{-1}) and diet	Sample size (groups)	Group size	Home range size	DJL	Diet (percentage of young leaves in the diet)
Males					
Time spent feeding	12	−0.127	0.127	0.042	−0.232
Time spent resting	12	−0.093	−0.168	−0.050	0.020
Time spent allogrooming	12	0.566	0.278	0.231	0.105
Diet: percentage of young leaves	11	0.449	−0.024	0.308	
Females					
Time spent feeding	11	−0.162	0.311	−0.074	−0.260
Time spent resting	11	−0.055	−0.525	−0.099	0.521
Time spent allogrooming	11	0.592	0.065	0.295	−0.094
Diet: percentage of young leaves	8	0.304	0.014	0.421	

Table 7 The relationship between adult female group size and male take-overs

Female group size	Early tenure phase				Middle+late tenure phase			
	Number of groups	Number of group years	Number of take-overs	Take-over per group year	Number of groups	Number of group years	Number of take-overs	Take-over per group year
1	0	–	–	–	1	2.17	0	0.00
2	0	–	–	–	2	3.25	0	0.00
3	2	1.25	0	0.00	6	25.9	0	0.00
4	4	2.04	1	0.49	6	11.58	1	0.09
5	2	1.17	0	0.00	2	3.95	1	0.26
6	2	1.75	1	0.57	0	–	–	–
Total		6.21	2	0.32		50.5	2	0.04

(a)

(b)

(c)

Fig. 2 The relationship between group size and time spent feeding (**a**), time spent resting (**b**), and time spent allogrooming (**c**). There are no significant relationships between group size and activity budgets

Fig. 3 The relationship between group size and reproductive rates. The number of surviving infants per female year (and not the number of infants born per female year) tends to increase with group size ($P<0.10$)
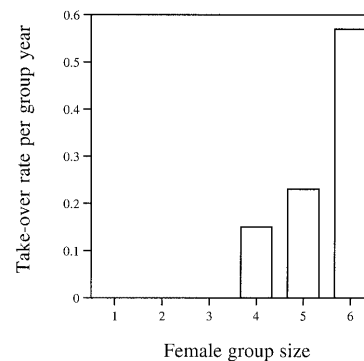
Fig. 4 The relationship between adult female group size and aggressive take-overs. Groups with more adult females seem to face a higher risk of being aggressively taken over

take-overs took place during this study, and two took place in 1998 (S.A. Wich, personal observation). Table 7 shows the relationship between the number of reproductive females and the risk of an aggressive take-over. Aggressive take-overs occur more often during the early than during the middle tenure phase. Two take-overs occurred during the early tenure phase, and two during the middle tenure phase in groups with small group sizes but a relatively large number of adult females. Both middle-tenure groups had one infant. In one group, the small in-

fant soon died (Steenbeek 1999a) and in the other group, the large male infant left with the ousted male (S.A. Wich, personal communication).

Does take-over risk increase with female group size? All observed take-overs were of groups with four, five or six females, and none were of groups with one to three females. The size of group R had increased with two adult female immigrants only 3 months before the take-over. Because the sample size is rather small, we cannot draw a definite conclusion, but when the tenure phases

are taken together (Fig. 4), the tendency is for groups with more adult females to face a higher risk of being aggressively taken over.

Discussion

Group size and food competition

Larger groups of Thomas's langurs at Ketambe had larger middle-tenure ranges and travelled farther, which is indicative of scramble competition for food. To compare the costs of increased group size with those found in other taxa, one can express the increase with group size relative to the day-journey expected for a hypothetical group of 1 (the relative ranging cost, RRC, of Janson and Goldsmith 1995). For the Thomas's langurs, the RRC is 0.083, higher than the average for folivores in Janson and Goldsmith's sample, but still lower than expected for a group of frugivores with similar mean group size.

Although scramble competition can be demonstrated, its effects are relatively small in the Thomas's langurs because most of the larger groups compensated for the increased travel costs by eating more of the same foods. If access to the preferred food (fruit) was compromised in larger groups, we should see dietary switching towards more vegetable matter. While this may happen on a seasonal basis, the data indicated only a slight trend towards a higher incidence of such switches in larger groups. Another indication of the low intensity of scramble competition was that group size had a very weak effect on activity budgets. Large groups did not spend less time resting and allogrooming, or more time feeding. Thus, these patterns indicate that time was not a limiting factor for groups at the group sizes found at Ketambe. Consistent with these ecological findings, group size did not negatively affect birth rate, which would have been expected if females in larger groups were suffering from food competition (van Schaik and van Noordwijk 1988). Hence, Thomas's langur groups are not large enough for the effects of scramble competition to seriously affect diet, energy budgets or female reproductive performance.

These effects of group size were unlikely to be artefacts. Effects of food availability and diet on ranging and activity levels were controlled for by averaging over longer periods including all seasons. Several other correlates of group identity did not confound the effects of group size. Home range quality did not play a role. Differences in male strength were controlled by using only data from the stable middle tenure phase. However, ranges of different groups inevitably contain different food species, which may influence how strongly groups react to changes in food availability.

Watts (1998) reported very similar results for long-term range use in the highly folivorous mountain gorilla (*Gorilla gorilla beringei*). Mean annual group size was significantly positively correlated with mean annual home range size, but only between, and not within, groups. He suggested that scramble competition for food

only affects very large groups. On the other hand, the more frugivorous long-tailed macaques (*Macaca fascicularis*) inhabiting the same site as the Thomas's langurs of this study live in larger groups, and both group size and dominance rank clearly affect DJL, activity budgets, food choice and sometimes net food intake (van Schaik and van Noordwijk 1988). Most importantly, females in larger groups, especially the lower-ranking ones, suffer dramatic reductions in their lifetime reproductive success (van Noordwijk and van Schaik 1999).

While our findings explain the absence of a negative correlation between birth rate and group size, the suggestive trend toward improved infant survival in larger groups (Fig. 3) requires a separate explanation. For this study, most of the data used to calculate birth rates come from middle tenure phases, when the average group contains three to four adult females and three dependent offspring of various ages. The positive correlation between per capita production of surviving offspring and group size is most likely a result of better protection against predators or infanticidal attacks in larger groups. Predation protection is most likely because all independent individuals react vocally to the presence of predators. Protection against infanticidal attacks by extra-group males (see Steenbeek 2000) is not likely to be higher in larger groups, because non-breeding mature males in age-graded groups are not vigilant for the extra-group males that attack infants (Steenbeek et al. 2000). Hence, females benefit from being in larger groups by improved infant survival, most likely due to improved protection against predators.

Infanticide risk and the folivore paradox

The conclusion for Thomas's langurs is that there is demonstrable scramble competition, but that groups are too small for individual performance to be affected by it (especially when compared to groups of many other, more frugivorous primates). However, since infant survival probably increases in larger groups due to improved predator detection, mean group sizes closer to (or larger than) the upper limit of observed group sizes would be optimal, balancing the opposing pressures of predation avoidance and feeding competition. Thus, the 'folivore paradox' also applies to Thomas's langurs.

If feeding competition does not limit group size in Thomas's langurs, what does? Two possibilities were mentioned in the Introduction. First, females may be able to move more freely, and thus group size can remain closer to optimum for folivores (implying that the larger group sizes of frugivores are above optimum, and females in the larger groups are stuck due to dispersal limitations). Second, females may prefer to live in smaller groups because the risk of infanticide strongly increases with group size.

In Thomas's langurs, females can move more freely between groups than in most other frugivore species, where female philopatry is rather strict and females can

only leave their groups by forming new splinter groups. Hence, group sizes are set by female dispersal decisions. However, the results suggest that mean female group size is not on or at least near the optimum size, but instead less than expected if only the balance of predation avoidance and feeding competition determine fitness as a function of group size. Moreover, female dispersal is not a simple and direct function of group size. Most females leave during the last half-year of tenure, and time their departure to minimise losing their infant to infanticide (Steenbeek 1999a). Thus, while female dispersal is common in this species, it does not serve to reduce scramble competition, but is, rather, related to the inability of the current male to protect the female and her infant from attacks (Steenbeek 2000; Steenbeek et al. 2000). Hence, female dispersal is not the solution to the folivore paradox, at least for Thomas's langurs.

As to the second possibility, we found a suggestive trend for increased risk of violent group take-over with increasing group size. Increased take-over risk in larger groups has also been found for gelada baboons, *Theropithecus gelada* (Dunbar 1984), and red howler monkeys, *Alouatta seniculus* (Crockett and Janson 2000). Since these take-overs are often accompanied by infanticide, females may avoid groups that are attractive take-over targets. This suggests that when females join males that are starting up new groups or males that have done so fairly recently, they base their joining decisions at least in part on group size considerations. Maximum group size depends mainly on the number of maturing offspring, and hence on male tenure length. Male tenure is never long enough for groups to reach the size where competition reduction could be an appreciable advantage to dispersing females.

To illustrate the critical role of female joining decisions, consider alternative possibilities. Females could form pairs or, alternatively, form much larger groups around unusually strong males. Bonded monogamy may not be attractive to the females. Although they would most likely achieve a reduction of infanticide risk by making male tenure much longer, they would probably lose in increased predation risk. Patterns in vigilance (Steenbeek et al. 1999) and the group size effect on infant survival suggest that Thomas's langur females benefit from gregariousness in terms of predation reduction.

The other alternative, larger groups around very strong males, may not be a good option because they may be too attractive for take-over attempts by other males. These larger groups might possibly become permanent multi-male groups. Among primates in general, infanticide risk is reduced in multi-male groups (Janson and van Schaik 2000), but in two other folivores, red howlers and hanuman langurs (*Semnopithecus entellus*), it is not (Borries and Koenig 2000; Crockett and Janson 2000), raising the possibility that something about folivore ecology prevents the reduction of infanticide risk when multiple males are present and mate. Unfortunately, at this stage, there are not enough quantitative estimates of vital parameters to demonstrate that female

Thomas's langurs maximise fitness by forming small to mid-sized single-male groups rather than pairs or much larger groups that contain multiple adult males, although the patterns are suggestive.

This explanation for the folivore paradox may also remove another puzzle about folivores. Despite low costs of feeding competition (Isbell 1991; Janson and Goldsmith 1995; this study), folivores, paradoxically, often experience a strong decline in inferred birth rate with group size (van Schaik 1983). However, if larger groups are more at risk of take-over by outside males followed by infanticide, infants per female may decline with group size even if birth rates are actually constant (or even increase somewhat due to more frequent infanticide in larger groups) (cf. Crockett and Janson 2000).

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