

Group Size Variability in Primates

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ABSTRACT. The effects of mean troop size, diet, territoriality, and habitat upon temporal variability of group size in primates were investigated using variance functions relating mean group size and temporal variability. Two different types of variability were described: (1) within group variability where a single troop was followed over a given period of time; and (2) between group variability where the author(s) did not distinguish one troop from the other. In the second category, CV (SD/mean) as an index of temporal group size variability proved to be dependent on mean group size among the Cercopithecidae. Large groups are more unstable in size than small ones. In the Cebidae, variability was independent of mean group size and therefore large groups are as variable through time as small ones. Ecological factors showed no effects on the observed level of between group variability. Within group variability was found to be smaller than the level of between group variability in all species tested. The results are related to social organization and to the degree of feeding interference observed within and between troops. Future practical applications for our results are considered.

Key Words: Group size; Variability; Social organization; Feeding interference.

INTRODUCTION

Studies on group size in primates have focussed mainly on factors influencing the mean or average group size in certain species. In their pioneer work relating ecology and primate social organization, CLUTTON-BROCK and HARVEY (1977) investigated the effects of ecological factors on interspecific differences in mean group size. Factors such as diet, habitat, and territoriality, among others, were found to be important determinants of average group size. The influence on mean group size of predation risk (ALEXANDER, 1974), competition for food sources between groups (WRANGHAM, 1980, 1983), and demography has also been investigated (i.e. VAN SCHAIK & VAN HOOFF, 1983; DE RUITER, 1986; STACEY, 1986; CROCKETT & EISENBERG, 1987).

A topic which has received much less attention is the temporal variability of group size. The size of primate groupings is known to vary through time, either on a daily or a seasonal basis. On practical grounds, changes in group size observed over a certain period of time can be assigned to two types of variability. Temporal changes in the size of a specific troop may be labelled as within group variability. When changes in the size of many troops are recorded during a time interval, the label between group variability is more appropriate since different groups may be sampled during the time period. Group size variability in general has been related to the stability of social groups (POIRIER, 1969; DAWSON, 1977), the availability of food resources (DITTUS, 1977; FEDIGAN & BAXTER, 1984; ALTMANN et al., 1985; CALDECOTT, 1986; MELNICK & PEARL, 1987), and to competition for food sources between groups (WRANGHAM, 1980; VAN SCHAIK & VAN NOORDWIJK, 1986; DITTUS, 1987). Nevertheless, interspecific differences in group size variability remain to be investigated.

So far only a few studies have quantified the temporal variability of group size across species. Levels of between group variability have been investigated by COHEN (1972), VAN SCHAIK (1983), and MELNICK and PEARL (1987). COHEN provided the first interpretation of the distribution of group sizes observed over a certain period of time in primates. He described the dynamics of group size as a BIDE process (for Birth-Immigration-Death-Emigration). Note that in groups with slowly changing membership such as occur in many primate species, the parameters given by the BIDE family of stochastic models are likely to represent true demographic variables. However, estimates of the parameters of a BIDE model can provide useful insights only when ecological and behavioural factors are invoked to explain the dynamics of group size (PULLIAM & CARACO, 1984). In a recent review comparing demographic data from different species, VAN SCHAIK regressed variance in group size on mean group size among territorial and non-territorial species in order to test the hypothesis that diurnal variability is smaller among territorial troops. The study showed no differences in the level of variability observed among the two types of groupings. However, the results were based on a small sample size and derived from a rather naive statistical technique (i.e. the number of points lying above or below the regression line). Another important objection is that different studies of the same species were included as independent points, which leads to an overestimate of the number of independent points (CLUTTON-BROCK & HARVEY, 1977). Hence, the scaling of variability is questionable in this study. Recently, MELNICK and PEARL (1987) have provided estimates of group size variability in a number of Cercopithecids in order to investigate differences in mean group size across species. Nevertheless, there is still no theory which could suggest how much variability to expect in the size of primate groupings. The purpose of this paper is thus to investigate the scaling of temporal variability in primate groupings and the effects of factors such as diet, habitat, and territoriality, on the level of variability observed in different species.

THE SCALING OF VARIABILITY IN GROUP SIZE

The coefficient of variation ($CV = \text{standard deviation} * 100/\text{mean}$) is commonly used as an index of variability. Given the strong positive relation between standard deviation (SD) and the mean, CV allows a comparison of data with different mean values (VAN VALEN, 1978). However, this index may also be correlated with the mean. An allometric equation of the form: $\log_{10}SD = \text{Slope} * \log_{10}\text{mean} + \log_{10}\text{intercept}$ was used by CABANA and BELL (in press) to control for such possible correlations. The slope indicates whether the ratio SD/mean increases (slope > 1) or decreases (slope < 1), or is independent of the mean (slope = 1). This formulation is essentially similar to the mean-variance allometric equation used to investigate the effect of density on aggregations in animals (i.e. TAYLOR et al., 1980).

Two problems often occur with allometric analyses. The first is the choice of a technique to determine the relationship between two variables. Two methods are commonly used to achieve this goal: the familiar least-squares technique and the reduced major axis technique (HARVEY & MACE, 1982). The choice of the reduced major axis technique usually follows because no control is exercised on the independent variable. However, the two methods lead to similar results when the correlation between the two variables is high (i.e. CLUTTON-BROCK & HARVEY, 1980). Nevertheless, the reduced major axis technique is not without practical and theoretical problems. Some of these problems are reviewed by WOLPOFF (1985).

Three reasons motivated the use of the least-squares regression technique in this study.

First, an assumption underlying the use of the reduced major axis technique is that the dispersion (or variance) of both the y and x variables be equal. However, in our regression of variance on mean group size, it is clear that the dispersion of means (the x variable) is smaller than the dispersion of variances (the y variable). Second, deviations (log observed SD minus log expected SD) from a reduced major axis depend implicitly on the independent variable (see CABANA & BELL, in press). An advantage of the least-squares technique is that the residuals or deviations from the regression line for each species constitute an index of variability independent of the mean. We have used this index of variability (hereafter referred to

Table 1. Between troop size variability.

Genus	Species	Mean ¹⁾	V ²⁾	N ³⁾	Time ⁴⁾	Ecology ⁵⁾	References
Cebidae							
<i>Alouatta</i>	<i>caraya</i>	7.9	-0.087	17	—	NTFOA	POPE, 1969
<i>Alouatta</i>	<i>palliata</i>	18.5	0.013	44	60	NTFOA	CARPENTER, 1962
<i>Alouatta</i>	<i>seniculus</i>	5.3	-0.030	23	455	NTFOA	IZAWA, 1978
<i>Ateles</i>	<i>belzebuth</i>	2.2	-0.37	13	455	NTFRA	IZAWA, 1978
<i>Ateles</i>	<i>geoffroyi</i>	4.5	0.16	329	365	NTFRA	CHAPMAN, pers. comm.
<i>Callicebus</i>	<i>torquatus</i>	3.0	0.25	8	455	TEFRA	IZAWA, 1978
<i>Pithecia</i>	<i>monachus</i>	3.0	0.072	5	455	NTFRA	IZAWA, 1978
Cercopithecidae							
<i>Cercocebus</i>	<i>albigena</i>	16.6	-0.023	5	115	NTFRA	CHALMERS, 1968
<i>Cercopithecus</i>	<i>aethiops</i>	17.3	-0.15	6	—	TEFRT	STRUHSAKER, 1976
<i>Cercopithecus</i>	<i>l'hoesti</i>	17.4	0.035	25	—	TEFRA	BUTYNSKI, unpub.
<i>Colobus</i>	<i>guereza</i>	8.9	-0.044	13	—	TEFOA	MARLER, 1969
<i>Erythrocebus</i>	<i>patas</i>	35.5	-0.12	10	—	NTFRT	CHISM & OLSON, unpub.
<i>Macaca</i>	<i>assamensis</i>	21.8	0.11	9	—	NTFRT	FOODEN, 1971
<i>Macaca</i>	<i>fascicularis</i>	32.2	-0.10	14	365	NTFRT	VAN SCHAİK, 1983
<i>Macaca</i>	<i>fuscata</i>	28.8	-0.052	7	—	TEFRT	MARUHASHI, 1982
<i>Macaca</i>	<i>nemestrina</i>	44.7	0.19	6	600	NTFRT	CALDECOTT, 1986
<i>Macaca</i>	<i>radiata</i>	25.4	-0.26	9	180	NTFRT	KOYAMA & SHEKAR, 1981
<i>Papio</i>	<i>anubis</i>	47.8	0.038	6	90	NTFRT	ALDRICH-BLAKE et al., 1971
<i>Papio</i>	<i>cynocephalus</i>	56.0	0.12	20	—	NTFRT	ALTMANN & ALTMANN, 1970
<i>Papio</i>	<i>ursinus</i>	79.0	-0.039	7	—	TEFRT	HAMILTON et al., 1976
<i>Presbytis</i>	<i>entellus</i>	15.3	0.11	20	—	TEFOT	SUGIYAMA & PARTHASARATHY, 1979
<i>Presbytis</i>	<i>geei</i>	10.0	-0.014	12	—	TEFOA	MUKHERJEE & SAHA, 1974
<i>Presbytis</i>	<i>melalophos</i>	5.5	-0.0010	10	—	TEFOA	KOYAMA, 1977
<i>Presbytis</i>	<i>phayrei</i>	11.4	0.11	36	240	—FOA	MUKHERJEE, 1982
<i>Presbytis</i>	<i>pileatus</i>	11.6	-0.12	6	—	TEFOA	ANWARUL ISLAM & HUSAIN, 1982
<i>Presbytis</i>	<i>potenziani</i>	12.2	-0.019	74	—	TEFOA	WATANABE, 1981
<i>Presbytis</i>	<i>obscurus</i>	5.5	0.028	22	—	TEFOA	KOYAMA, 1976
<i>Simias</i>	<i>concolor</i>	17.5	0.14	166	—	—A	WATANABE, 1981
<i>Theropithecus</i>	<i>gelada</i>	9.6	0.088	31	—	NTFOT	KAWAI, 1979
Pongidae							
<i>Pan</i>	<i>paniscus</i>	7.8	-0.25	19	800	NTFRT	BADRAN & BADRAN, 1984
<i>Pan</i>	<i>trogodytes</i>	5.2	0.35	267	—	NTFRT	TUTIN et al., 1983
<i>Pongo</i>	<i>pygmaeus</i>	1.8	-0.094	191	—	NTFRA	MACKINNON, 1974

1) Mean group size; 2) the index of variability, which is obtained for each species by computing: $V = \log \text{observed SD} - \log \text{expected SD}$ (the values represent deviations from a regression line); 3) the sample size; 4) the duration of the study period in days; 5) FR: frugivores; FO: folivores; TE: territorial; NT: non-territorial; T: terrestrial; A: arboreal.

Table 2. Within troop size variability.

Genus	Species	Mean ¹⁾	Obs. CV ²⁾	Obs.—exp. CV ³⁾	References
Cebidae					
<i>Cebus</i>	<i>albifrons</i>	8.5	5.9	-40.7	TERBORGH, 1983
<i>Cebus</i>	<i>apella</i>	13.2	17.5	-30.5	TERBORGH, 1983
Cercopithecidae					
<i>Colobus</i>	<i>badius</i>	20.2	6.9	-37.0	STRUHSAKER, 1975
<i>Macaca</i>	<i>sinica</i>	16.1	22.1	-19.6	DITTUS, 1977
<i>Macaca</i>	<i>sylvanus</i>	43.5	7.7	-44.6	MÉNARD et al., 1985
<i>Papio</i>	<i>cynocephalus</i>	177.3	14.1	-58.2	ALTMANN & ALTMANN, 1970
<i>Presbytis</i>	<i>entellus</i>	19.6	21.7	-21.9	WINKLER et al., 1984
Pongidae					
<i>Gorilla</i>	<i>gorilla</i>	27.0	6.9	-860.7	SCHALLER, 1963
<i>Pan</i>	<i>trogodytes</i>	27.5	30.8	-868.6	SUZUKI, 1979

1) Mean group size; 2) the observed coefficient of variation; 3) the difference between observed and expected CV.

as the index V). Third, the least-squares technique seems well suited for the investigation of group size variability in animals since one is interested in the question: Can large groups be expected to be more unstable in size than small ones because of their large sizes? By its predictive power, a least-squares technique can provide an answer to such a question (WOLPOFF, 1985).

The second problem is the choice of taxonomic level at which to perform the analysis. A common problem arising in comparative studies is whether it is reasonable to consider values for different species as independent points (CLUTTON-BROCK & HARVEY, 1984). Congeneric species usually show similar patterns of behaviour. This may be related to independent adaptation to similar environments (convergence) or to phylogenetic constraints (homology). Genera in which relevant ecological and behavioural variables are similar between species are usually represented by only one point, which represents an average for different species (CLUTTON-BROCK & HARVEY, 1980, 1984). However, the rationale behind such a choice is not clear. There is no indication that the mean is an unbiased estimate of these distributions, which are based on only a few species. Moreover, the utilization of dichotomous traits (e.g. frugivores vs folivores) to characterize the ecological niche of a species overestimates the apparent similarity between species. For example, two species could well be classified as frugivores even though the amount of fruit introduced in their diet was different. In this study, six genera were represented by more than one species (see Tables 1 & 2). However, relevant ecological and behavioural factors such as diet and territoriality are known to vary within five of these genera (CLUTTON-BROCK & HARVEY, 1980). Consequently, each species has been represented by a single point.

METHODS

DATA COLLECTION

The following variables were collected from the literature for those species where data on group size variability were available: (1) *Group size*: Average number of individuals found together in a specific group (within group data set) or in different troops of unspecified composition (between group data set) over a certain period of time. The standard deviation was

computed using available counts or was given by the author(s). In some species group organization is a complex phenomenon. For example, one can distinguish at least two levels of complexity in chimpanzee troops: a community level and a party level (see WRANGHAM, 1986). Parties of chimpanzees are formed and dissolved easily within the community level. The most detailed data were usually reported at the community level. For this reason and in order to reflect the most characteristic features of some primate societies, group sizes were taken at the community level when such a distinction was made. (2) *Diet*: The type of food actually eaten by the species. Species were characterized as either frugivores (FR) or folivores (FO) depending on whether they were eating mainly fruit or foliage, respectively. We agree that this dichotomy is particularly crude, especially for those species that are not well studied. (3) *Territoriality*: The distinction between territorial (TE) and non-territorial (NT) spacing systems was made using the nature of intergroup encounters (conflicts of avoidance) and the amount of overlap between home ranges as criteria [this following MITANI & RODMAN'S (1979) characterization]. When such data were not available, the distinction was inferred where possible from other information in the paper. (4) *Mode of locomotion*: A distinction was made between arboreal (A) and terrestrial (T) species based on the location of diurnal activity.

As mentioned previously, temporal variability in group size was based on two types of measure. The first type of measure corresponds to a within group variability. In this type of measure a single given troop was followed through time. The temporal variability of group size therefore refers to this single troop. The second type of measure is a between group variability. In this type of measure more than one troop was followed through time and no attempts were made by the author(s) to distinguish one troop from the other. Hence some troops may have been included in the data set more than once. As a consequence this type of measure incorporates some elements of the aforementioned within group variability. It proved impossible to quantify the amount of variability introduced in the data set by inaccurate estimates of group size by human observers since this information was rarely presented. It is therefore assumed that this possible source of error was randomly distributed across species and along the mean group size continuum.

Only available estimates based on the largest data base (number of counts or number of troops) were selected. We have tried to maximize the number of species selected for the analyses while avoiding the inclusion of different studies of the same species. For statistical purposes, we opted for the above procedure in order to avoid the overestimation of the number of independent points.

STATISTICAL ANALYSIS

Due to constraints on sample size, the following section deals only with data on between group variability. The allometric equation described earlier was fitted for each family by least-squares regression technique (SOKAL & ROHLF, 1981). Such a regression model can test whether SD is positively correlated with the mean. If this is so, variability has to be estimated in relative terms (CV). The analysis is performed by testing the departure of the slope from 0 with a *t*-test. The regression model can also test the independence of CV from the mean. In other words, it can test whether CV tends to be higher or smaller in larger troops. A *t*-test is used to test for departure of the slope from 1. Slopes significantly higher or lower than 1 indicate respectively that the CV increases or decreases as the mean increases.

Where the slope is equal to 1, the intercept of the regression line is proportional to the overall CV for that particular family. Hence, an analysis of covariance on two such variance functions would tell us if their elevation is different. However, the relevance of this analysis is restricted when one of the slopes is different from 1. Among the Cercopithecidae, the regression slope has proven to be different from 1. The analysis of between-family differences in the level of variability is also complicated by the minimal overlap of mean group size between families (i.e. Cercopithecids are characterized by very large groups; Table 1). It therefore proved impossible to carry an analysis of between-family differences in group size variability.

Mean-standard deviation relations may be biased with the number of replicate samples taken (N : number of counts or number of troops included in each variance estimate). We investigated the effect of sample size and also of the length of time interval used (t : amount of time in days during which troop sizes were reported) on the estimation of group size variability with multiple regression models. The significance of the increase in predictive power (r^2) associated with the introduction of these factors in the regression model was tested with F -tests (DRAPER & SMITH, 1972).

The effect of ecological factors was investigated with the Mann-Whitney non-parametric test. The analysis was performed with the different values of the index V . Analyses were confined to families which included species falling into different ecological and behavioural categories. Comparisons are only possible with families whose members did show a variation in the relevant ecological and behavioural categories.

Under the hypothesis of an equilibrium distribution of group size, between group variability would be equal to within group variability. All troops would undergo the same changes in group size across time and could be considered as identical replicates. This null hypothesis allows one to compare the level of variability observed within a troop to the one observed between troops. The expected value of within variability for a given species can be easily obtained from the family regression equations described earlier. The expected CV is computed using the observed mean group size (within type of measure) and the expected SD is obtained from the regression equation. Under the null hypothesis, the difference between observed and expected CV should be 0.

RESULTS

A list of the species included in the between group variability data set along with the following parameters: N , t , Mean, and V is given in Table 1. Table 2 gives mean group size and CV

Table 3. Regression fit of the log SD—log mean relations.

Family	N	Slope (SE)	$p = 0?$	$p = 1?$	Int.	R^2
Cebidae	7	1.07 (0.28)	**	>0.05	-0.40	0.74
Cercopithecidae	22	1.23 (0.11)	***	*	-0.66	0.93
Pongidae	3	2.96 (0.95)	>0.05	>0.05	-1.86	0.91

Least-squares regression fit of the relation between log SD and log mean in the Cercopithecidae, the Cebidae, and the Pongidae. The sample size (N), the intercept (Int.), and the percentage of explained variance (r^2) are given for each regression line. The departure of each slope from 0 and 1 was investigated with a t -test. The level of significance is shown for each test (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$). See text for the goodness of fit of these regressions.

for the within group data set. As mentioned earlier the following results concerned the between group variability data set. There was a highly significant, positive relationship between log SD and log mean in the Cercopithecidae and the Cebidae (Table 3). Among the Cercopithecidae the slope was significantly greater than 1. Therefore, temporal variability as measured by CV is not independent from the mean and tends to increase with increasing values of the mean. The index V is free from these scaling problems as mentioned earlier. Among the Cebidae, the slope was not different from 1. In this family we could not find differences in variability between troops of different sizes. The inclusion of more species in the regression line may shed some light on the generality of this conclusion. Although the slope of the relation between log SD and log mean was not significantly different from 0 in the Pongidae, its high value suggests that group size variability is greater in *Pan* sp. than in *Pongo pygmaeus*.

Two interesting features of troop size variability are the absence of an effect of time and of sample size (see Table 1). These two factors were introduced in the aforementioned regression models to investigate a possible increase in predictive power. Multiple regression analyses showed that the two variables did not explain significantly any variation in log SD independent of log mean (Sample size and slope of the multiple regression model for each variable; Time: Cercopithecidae, $N = 6$, slope = 0.0006, NS; Cebidae, $N = 6$, slope = 0.002, NS; Sample size: Cercopithecidae, $N = 22$, slope = 0.001, NS; Cebidae, $N = 7$, slope = 0.018, NS). Such an analysis cannot be performed with the Pongidae due to constraints on sample size. Variability as measured by the index V is not biased with these statistics. Hence, errors introduced in the system by the different values of sample size and time were randomly distributed along the mean group size continuum. This result means that no correction for these factors is necessary for a comparison of studies in which these factors are different.

Ecological factors did not affect the level of between group variability observed in primate troops. The Mann-Whitney non-parametric analyses revealed no differences in the value of the index V between territorial and non-territorial species [$U(15, 12) = 98$, $p > 0.2$, two-tailed test], between terrestrial and arboreal species [$U(14, 12) = 92$, $p > 0.2$, two-tailed test], or between frugivorous and folivorous species [$U(16, 12) = 96$, $p > 0.2$, two-tailed test]. Between group variability among territorial troops has been found to be similar to that among non-territorial ones. This supports the results of VAN SCHAIK (1983) based on a smaller data set. However, it is still impossible to claim that territorial troops may often be too large for an effective range defense (WRANGHAM, 1980) because this idea is formulated in terms of within troop variability. Unfortunately, it was impossible to document the level of within group variability among these troops.

Table 2 compares the level of variability observed within and between troops. Under the null hypothesis of an equilibrium distribution of group size across time, the two levels of variability should be equal. The table gives the difference between the level of variability observed within a troop and the one expected from the family regression. Among the Cercopithecidae, within group variability was smaller than between group variability (mean value of observed minus expected CV = -36.25, SE = 7.21, $N = 5$, $p < 0.001$). Among the Pongidae and the Cebidae, within group variability was also qualitatively much lower than between group variability. The significant effect of the factor "type of measurement" on the observed level of variability has some practical importance. One should be careful in comparing data culled from studies in which the measurements are not of the same type.

DISCUSSION

BETWEEN GROUP VARIABILITY

The positive relation between variability and mean group size in the Cercopithecidae has two corollaries. First, it implies that corrections for mean effects are necessary prior to comparing species living in groups of different sizes. Second, it suggests that along the mean group size continuum the pattern of temporal variability is not constant. Among the Cebidae and the Pongidae, between group variability is independent of mean troop size in the rather limited range of group sizes available. Between group variability thus seems to scale in different ways within the primate order. As pointed out earlier, factors such as diet, habitat, and territoriality are known to influence mean group size. However, these factors which can explain why a species is living in a group of 10 as opposed to a group of 30, seem to affect in a similar way the temporal variability of these groups. Ecological and behavioural factors thus appear to have no direct effects upon temporal group size variability. The next section considers some possible factors which may influence between group variability in primates.

A positive allometry could be the result of two phenomena, not mutually exclusive. The first phenomenon is related to social organization. A positive allometry suggests that large groups are more unstable in size than small groups. There are some indications that species living in large groups share a similar type of social organization, which is characterized by the instability of group size across time. Unstable groups have often been referred to as fission-fusion groups. A typical feature of these groups is the repeated splitting and joining of subgroups which are organized on a higher community level. Since group size variability had never been investigated in a consistent way, a fission-fusion type of social organization was considered to be rare in primates. Any change in the size of a group was thus related to a BIDE process (RICHARD, 1985). However, recent studies have suggested that this type of social organization may be present in a number of species. Among the Cercopithecidae included in the data set, the following species are thought to possess a fission-fusion type of social structure: *Cercopithecus aethiops* (CHAPMAN, pers. comm.), *Macaca fascicularis* (VAN SCHAİK & VAN NOORDWIJK, 1986), *Macaca nemestrina* (CALDECOTT, 1986), and *Papio ursinus* (ANDERSON, 1981). Subgroupings have also been observed in *Macaca fuscata*, a frugivorous species living in large groups (MARUHASHI, 1982). Note that all these species are living in large groups. This observation is consistent with the above hypothesis. Among the Pongidae, *Pan* sp. are thought to possess a fission-fusion type of social organization (WRANGHAM, 1986) and accordingly are living in large, unstable groups. Note that species thought to live in fission-fusion groups are mostly terrestrial and frugivores. Among the Cebidae, *Ateles* sp. are thought to live in fission-fusion societies (FEDIGAN & BAXTER, 1984). Of the two species, only *Ateles geoffroyi* shows a relatively important variability. Hence the picture is not clear and much research is clearly needed in this case. However, the relative homogeneity of the Cebidae in terms of ecology [i.e. all species are arboreal, most of them are frugivores and living in small groups of 3–5 individuals (CLUTTON-BROCK & HARVEY, 1977)] as opposed to the Cercopithecidae, is probably responsible for the absence of effects of mean group size on group size variability.

An important benefit of fission-fusion societies is that it allows individuals to respond to changes in the availability and distribution of their food resources (CALDECOTT, 1986; WRANGHAM, 1986). This is consistent with the fact that species living in large, unstable groups are mainly terrestrial and frugivores. Frugivorous and terrestrial species travel longer

and further than arboreal and folivorous species (CLUTTON-BROCK & HARVEY, 1977). This indicates that their food resources are probably widely dispersed and unpredictably distributed. This would in turn favour the evolution of fission-fusion societies (VAN SCHAIK & VAN NOORDWIJK, 1986).

Second, a greater between variability in group size would be expected if the processes underlying group formation are different between troops. For example, birth and immigration rates could be much lower in certain troops than in others. Consequently, troops of a given area would not undergo the same changes in size across time and this would lead to a greater between group size variability. Such inter-group differences could conceivably be the result of two phenomena. The first one is related to the size of a troop. It is well-known that individuals living in large groups experience more feeding interference than those living in small groups. Food competition has been related to birth rate in many species. Within a species, a negative relation is found between group size and birth rate (VAN SCHAIK, 1983). The second one is related to inter-group relationships. CORDS and ROWELL (1986), in a recent review of troop fission in some primate species, reported that fission has been observed in groups where hierarchical relationships are marked. The end result of these fissions is often the splitting into groups of unequal size. The smallest group is usually confined into a less profitable area which probably affects some parameters such as birth and death rates. Hence these parameters could be different between troops of a given area. Since studies of feeding interference within a group and inter-group relationships are still relatively few, the relation between these factors and mean group size is unclear. Hence, the extent to which these phenomena can account for the allometry of group size variability remains to be investigated.

WITHIN GROUP VARIABILITY

It should be noted that such phenomena could probably explain why the variability of group size within a given troop is smaller than the level of between group variability. The low level of within group variability in many species indicates that some troops are always larger or smaller than some others. Hence, an equilibrium of group size wherein each troop would undergo the same changes in size through time does not seem to be common in these species. Factors such as dominance between troops and feeding interference within troops are probably at the heart of this observation, since they can lead to disparities in terms of demographic processes among troops of a given area.

FUTURE APPLICATIONS

We would like now to indicate some future practical applications for our results. Predicted log mean-log SD relationships can be viewed as null hypothesis in interspecific comparisons of observed troop size variability. The general picture drawn in this paper could also help to identify species-specific differences in troop size variability. Furthermore, it could help to test directly some hypotheses relating variability and the importance of some ultimate factors on the evolution of group living in primates (i.e. WRANGHAM's hypothesis, 1980; see above). Our results could be extended to the characterization of primate groupings. The distinction between the types of primate groupings is usually based on troop closure or lack of permeability (CARPENTER, 1962). As these factors are possibly related to observed troop size variability, our estimates of variability could be used as quantitative tools in this classification.

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