Brief Report

Folia Primatol 1993;61:31–34

Colin A. Chapman[a]
Frances J. White[b]
Richard W. Wrangham[a]

[a] Peabody Museum, Harvard University, Cambridge, Mass.;
[b] Department of Biological Anthropology and Anatomy, Duke University, Durham, N.C., USA

Defining Subgroup Size in Fission-Fusion Societies

Key Words
Spider monkeys
Chimpanzees
Party size
Association patterns
Fission-fusion societies
Social organization

Introduction

Several mammalian species possess a pattern of social organization characterized by flexibility in both the size and composition of groups within a community (e.g. *Panthera leo* [1]; *Tursiops truncatus* [2]; *Pan troglodytes* [3]; *Macropus giganteus* [4]; *Pan paniscus* [5]; *Ateles geoffroyi* [6]). Generally, this type of social organization is referred to as a fission-fusion society [7], although the use of this term fails to distinguish fission and fusion between subgroups that are relatively predictable (e.g. hamadryas, long-tailed macaques) from that in which subgroups are unpredictable (e.g. chimpanzees, lions). In the latter category of societies, each individual has the option of associating with subgroups of different sizes. This natural variation in subgroup size within communities provides the basis for testing general ecological models of animal group size, since changes in subgroup size can be related to variation in ecological conditions. For primates, studies of fission-fusion societies have also been used to examine the generality of ecological models of group size by the comparison of subgroup sizes among species and among different geographically isolated communities of the same species [3, 8, 9]. However, the comparative approach when applied to fission-fusion societies is somewhat limited by variation in the existing definitions of 'subgroups' and controversy over the operationalization of these definitions for the field.

Difficulties in quantifying subgroup size arise from 3 basic issues. The first concerns the problem of counting animals that are dispersed throughout a habitat where visibility is limited. Under these conditions, the further

Received:
November 23, 1992
Accepted:
October 26, 1993

Colin A. Chapman
Department of Zoology
University of Florida
Gainesville, FL 32611 (USA)

0015–5713/93/
0611–0031$5.00/0

the animal is from the observer or the denser the vegetation, the higher the probability that it will not be included in a count of subgroup size. Thus, reported differences in subgroup size between studies may simply reflect habitat differences in visibility or the spread of the subgroup. Secondly, comparisons of subgroup size are often made between studies that differ in duration. It is probable that, as an investigation proceeds, the study animals become more habituated, easier to see and thus more likely to be included in a count of subgroup size. The third issue concerns the method by which animals are located. If subgroups are found by different methods, variation in subgroup size between studies may simply reflect differences in the methods used.

The objective of this work is to demonstrate these problems, and to discuss possibilities for improving the compatibility of data. We present data on subgroup dynamics of 3 fission-fusion societies: spider monkeys *(Ateles geoffroyi)* in Santa Rosa National Park, Costa Rica; pygmy chimpanzees *(Pan paniscus)* in Lomako, Zaire, and common chimpanzees *(P. troglodytes)* in Kibale Forest Reserve, Uganda. These populations have somewhat similar fission-fusion social organizations and have been studied over a number of years. Information on the methods used in these investigations, on the duration of the study and on habitats is provided elsewhere [5, 6, 10].

Results and Discussion

Two studies provide evidence for a change in recorded subgroup size with an increase in habituation. For the spider monkeys of Santa Rosa, recorded subgroup size increased steadily from 1983 to 1987 (subgroup sizes: 1983 = 3.52; 1984 = 4.16; 1985 = 5.26; 1986 = 4.26; 1987 = 6.28). At Lomako, the trend was slightly different, but party size did change with habituation. The first response of Lomako pygmy chimpanzees to observers was crypsis, followed by mobbing, and finally what appeared to be more natural behaviour was observed. When first studied from 1974 to 1979, 83% of observed subgroups contained 1–4 individuals [11]. From 1980 to 1982, modal subgroup size was similar (2–5 individuals), but accounted for fewer sightings (36%), and average subgroup size was 7.6 animals [12]. This change corresponded to a time when observers were mobbed by males and resulted in a male bias in the sightings [5]. With more habituation from 1983 to 1985, mobbing ceased, subgroups averaged 5.4 individuals, and the male bias in composition disappeared [5]. Perceived subgroup size now appears to be stable, as indicated by the observations of subgroup size in 1985–1986, which averaged 5.8 animals.

To test whether the observation method influenced recorded subgroup size, we documented subgroup size and the method of finding common chimpanzee subgroups for two communities in Kibale Forest Reserve, Uganda. Parties located from vocalizations (normally pant-hoots) were over twice as large as those found by checking fruit trees (community 1: mean size of subgroups found by calls = 5.1, n = 31; mean size of subgroups found in fruiting trees = 2.4, n = 64; community 2: mean size of subgroups found by calls = 6.8, n = 64; mean size of subgroups found in fruiting trees = 2.5, n = 27 [10]). We believe that this occurred because larger subgroups made louder calls and were therefore located more easily than smaller subgroups.

The effect of habitat visibility on counts of subgroup size is difficult to assess because visibility through the vegetation may covary with ecological variables thought to influence subgroup size, such as food abundance. In

Kibale, we quantified the differences in the subgroup size of common chimpanzees recorded before and after the animals had left a fruiting tree. In a large fruiting tree, visibility is often good. However, when animals descend to the ground, visibility can be obscured by ground vegetation. One hour after subgroups had left a large fruiting tree, recorded subgroup size decreased by an average of 2.1 individuals (n = 57). This result could reflect a decrease in recorded subgroup size resulting from lower visibility on the ground, the tendency for subgroups to divide after leaving a fruiting tree or a combination of these two effects. In contrast to chimpanzees, when spider monkeys leave a large fruiting tree, visibility does not necessarily decline. One hour after leaving a large fruiting tree, recorded subgroup size for spider monkeys decreased by only 0.4 individuals (n = 197). This suggests that, for chimpanzees, the observed decrease in subgroup size subsequent to leaving a fruiting tree is at least partially an effect of changes in visibility.

A similar trend was observed in the study of pygmy chimpanzees of Lomako. Here, as visibility increased from the ground to the middle and upper canopies, size at first sighting also increased (ground 3.73, n = 30; mid-canopy 5.4, n = 34; upper canopy 7.09, n = 44). At Gombe, where visibility is greater and habituation improved (allowing the observer to move around to identify animals in denser vegetation), the average within day subgroup size on the ground (3.7 ± 2.2, n = 21) was similar to when subgroups were 0–2 m off the ground (3.2 ± 3.2, n = 13) or when they were more than 2 m from the ground (3.6 ± 2.4, n = 21). This suggests that the trend observed in Lomako may be the result of differences in visibility and habituation.

Studies of animals with fission-fusion social organizations might consider a number of different techniques to improve the compatibility of the data they collect. Good descriptions are needed for the types of habitats used by the study animals, the visibility in these habitats, the degree of habituation and how the subgroups were located. To address specific questions, researchers might define subgroup size in specific contexts (e.g. foraging subgroups, socializing subgroups). Where individual recognition of animals is possible, researchers might also consider defining the subgroup over a longer period. Typically, subgroup size is determined during a single scan, often following a period of behavioural observation. Alternatively, the identity of all animals seen could be recorded during successive scans made over a long period of time, such as 1 h. This method would be less likely to omit animals from the subgroup that were present all along but were temporarily out of the observers' field of view, thus decreasing the significance of visibility and habituation problems. Subsequently, subgroup size could be considered to have changed following an observed departure of a splinter subgroup or if an individual or number of individuals had not been seen in a set number of scans.

Acknowledgments

We thank L.J. Chapman, A. Clark, G.I. Basuta, A. Johns and L. Gardner for helpful comments on this work.

References

1 Schaller GB: The Serengeti Lion: A Study of Predator-Prey Relations. Chicago, University of Chicago Press, 1972.

2 Wursig B: Occurrence and group organization of Atlantic bottlenose porpoises *(Tursiops truncatus)* in an Argentine bay. Biol Bull 1979;154: 348–359.

3 Wrangham RW: Ecology and social relationships in two species of chimpanzees; in Rubenstein DI, Wrangham RW (eds): Ecological Aspects of Social Evolution. Princeton, Princeton University Press, 1986, pp 352–378.

4 Jarman PJ: Group size and activity in eastern grey kangaroos. Anim Behav 1987;35:1044–1050.

5 White FJ: Party composition and dynamics in *Pan paniscus*. Int J Primatol 1988;9:179–193.

6 Chapman CA: Association patterns of spider monkeys: The influence of ecology and sex on social organization. Behav Ecol Sociobiol 1990;26: 409–414.

7 Kummer H: Primate Societies. Chicago, Aldine, 1971.

8 Nishida T, Hiraiwa-Hasegawa M: Chimpanzees and bonobos: Cooperative relationships among males; in Smuts B, et al (eds): Primate Societies. Chicago, University of Chicago Press, 1987, pp 165–180.

9 White FJ, Wrangham RW: Feeding competition and patch size in the chimpanzee species *Pan paniscus* and *Pan troglodytes*. Behaviour 1988;105:148–164.

10 Wrangham RW, Clark AP, Isabirye-Basuta G: Female relationships and social organization of Kibale Forest chimpanzees; in Nishida T, et al (eds): Human Origins. Tokyo, University of Tokyo, 1992, pp 81–98.

11 Badrian NL, Badrian A, Susman RL: Preliminary observations on the feeding behaviour of *Pan paniscus* in the Lomako Forest of Central Zaire. Primates 1981;22:173–181.

12 Badrian NL, Badrian A: Group composition and social structure of *Pan paniscus* in the Lomako Forest; in Susman RL (ed): The Pygmy Chimpanzee. New York, Plenum Press, 1984, pp 325–346.