Group Size and Stability: Why Do Gibbons and Spider Monkeys Differ?

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ABSTRACT. Gibbons and spider monkeys have similar diets, body size, and locomotor patterns. They are therefore expected to be subject to similar socioecological rules. However their grouping patterns differ. Gibbons live in small stable groups, whereas spider monkey form unstable sub-groups that vary from small to large during different seasons. If similar principles apply to the two species, food abundance should vary more for spider monkeys than for gibbons; food density should be similar for the two species when spider monkey sub-groups are the same size as gibbon groups; and the highest level of food abundance should be higher for spider monkeys than for gibbons. These predictions are upheld for a comparison of particular populations of *Hylobates muelleri* and *Ateles geoffroyi*.

Key Words: Social organization; Food abundance; Gibbon; Spider monkey; Foraging group size.

INTRODUCTION

Understanding why animal species differ in their social organization is a question that has engendered much field research and theoretical debate (TERBORGH, 1983; VAN SCHAIK, 1983; RUBENSTEIN & WRANGHAM, 1986). Progress is often made using interspecific comparisons with a large number of field studies, but because research protocols vary, this method makes it difficult to provide quantitative analyses of ecological differences.

In this study, we contrast the ecology and social organizations of gibbons (*Hylobates*, represented here by *H. muelleri*) and spider monkeys (*Ateles*, represented here by *A. geoffroyi*) based on findings from two field studies which employed comparable methodologies. Although the nearest common ancestor of these two genera was likely to have existed in the early Oligocene (35 million years ago) (GINGERICH, 1980), they have striking similarities in their diets, morphologies, locomotor styles, body sizes, and life histories. Both are large-bodied, slow-maturing primates, with brain volumes that are indistinguishable in relation to body weight (SCHULTZ, 1941, Fig. 1). Both are almost exclusively arboreal, use suspensory posture, and locomotion, and are heavily reliant on ripe fruits, particularly figs. They have similar mean group sizes and individual home ranges (Table 1). Based on these similarities, it might be expected that the two species would have similar patterns of social organization. Yet most gibbons groups are territorial monogamous pairs travelling together with their pre-adult offspring (LEIGHTON, 1987; see HAIMOFF et al., 1986 for the exception). Spider monkeys, by contrast, invariably have a fission-fusion type of social organization involving the formation of subgroups which change size (range 1–35) and compositions frequently (ROBINSON & JANSON, 1987). In this paper we present data to test an ecologically based hypothesis to explain the species differences in social organization.

Seasonal variation in spider monkey subgroup size is apparently determined by variation

Table 1. Comparison of life history and behavioural parameters for gibbons (*Hylobates muelleri*) and spider monkeys (*Ateles geoffroyi*).

	Hylobates muelleri[1]		*Ateles geoffroyi*[2]
Life History			
Body size (kg)	5.0		6.0[3]
Gestation (Month)	7[3]		7[3]
Interbirth interval (Month)	36[3]		32 – 36[3]
Age at maturity (Year)	8[3]		7 – 8[3]
Neonate weight (g)	411[3]		426[3]
Neonate brain (g)	52.6[3]		64[3]
Diet			
Fruit (%)	62		71
Figs (%)	24		31
Leaves (%)	32		13
Flowers (%)	4		14
Insects (%)	2		2
Feeding bout length (min)			
Fruit			
Male	16.9	Both sexes	14.0
Female	16.5		
Leaf			
Male	8.6	Both sexes	14.2
Female	10.9		
Ranging/grouping			
Home range (ha)			
Group	36	Community	170
Individual	36	Individual	53
Day range (m)	850		?
Population density (/km²)	9.4		<28
Mean group size	3.4		4.9

1) From Leighton (1987), unless otherwise stated; 2) from Chapman and Chapman (1990b), unless otherwise stated; 3) derived from Harvey et al. (1987) and calculated as the average for the genus excluding *H. syndactylus*. Male and female values are averaged.

in ecological constrains, because whenever food resources are abundant and uniformly distributed, spider monkeys congregate in large subgroups (Chapman, 1990). At these times the costs of travelling between patches are low, time spent travelling is greater, and the energy spent in travelling is easily recovered (Chapman, 1990). When food resources are relatively scarce and located in patches which are far apart, by contrast, spider monkeys are found in small subgroups. Because they are small, these subgroups deplete patches relatively slowly. By localizing their activity around one or a few patches, the spider monkeys minimize travel costs.

This note tests whether similar factors may have constrained the evolution of gibbon group size. If so, we expect that: (1) when spider monkeys subgroups are the same size as gibbon groups, the size and density of food resources should be similar for the two spicies; (2) spider monkey food resources should show greater temporal variability in abundance than gibbon food resources; and (3) the highest level of food abundance should be greater for spider monkeys than gibbons.

METHODS

A spider monkey community living in Santa Rosa National Park, Costa Rica was studied by CAC for 36 months between 1983 and 1989. To obtain information on the association patterns and range use of individuals, behaviour was monitored during three-week sam-

pling periods. Subgroups containing specific recognizable individuals were located in the morning, and behavioural data were collected using focal animal sampling. At the end of each period the density and distribution of the food resources eaten during the preceding three weeks were determined. The location, size, and phenological status of all food trees with a DBH (Diameter at Breast Height) greater than 10 cm were determined in three 4-ha grids. Each grid consisted of 400 cells, each cell 10 × 10 m in size. Corners of the cells were marked with steel posts. The density of the spider monkey's food resources was calculated every month based on these data. For more information see CHAPMAN (1989, 1990) and CHAPMAN and CHAPMAN (1990a).

A population of gibbons inhabiting the Kutai Nature Reserve, East Kalimantan, Indonesia was studied by DR for 23 months from October 1977 to September 1979. One group consisting of an adult male, an adult female, and an infant was studied intensively for 15 months, beginning in June 1978. Their behaviour was monitored monthly during two 10 – 12 day periods which were split by a five to ten day block of ecological sampling. When possible behavioural observations entailed full day follows (8 days/month on average). Temporal changes in gibbon fruit patch density were quantified using monthly monitoring of trees greater than 10 cm DBH, lianas, and strangler figs located in 19 vegetation plots. Eight of these plots belonged to a sample of 30 plots (50 × 50 m) located randomly throughout the study area in October 1977. Between January and May 1978, 11 25 × 50 m plots were added to increase sampling within the study group's home range. In November 1978, the larger plots were reduced to quarter hectare size. For more information see LEIGHTON (1987) and LEIGHTON and LEIGHTON (1983).

RESULTS AND DISCUSSION

The average size of the trees used by spider monkeys and gibbons was very similar [spider monkeys, 43.1 cm DBH; gibbons, 40.7 cm DBH (excluding *Eusideroxylon zwageri* a dominant upper canopy tree that mast fruited in 1978, but was not a significant fruit food source], and 42.6 cm DBH (including *E. zwageri*). Following prediction (1), therefore, we expect that when spider monkey subgroups were similar in size to gibbon groups, the density of food resources used by the two species was similar.

Gibbons live in stable groups, in which changes in composition usually arise only from births, deaths, and emigration of maturing offspring. The average size of gibbon groups in the study area was 3.4 animals and the yearly average abundance of food resources was 6.5 patches/ha of ripe fruit and 6.8 patches/ha of ripe and unripe fruit (excluding *E. zwageri*). During the months that the average spider monkey subgroup size was less than four animals (range 3.9 – 2.3, mean 3.5, $N=8$ sample periods), they used food resources (including fruits and flowers) occurring at a mean density of 6.2 patches/ha. Spider monkey food resources therefore occurred at similar density to those of gibbons when spider monkey subgroup size was comparable to that of gibbons.

Prediction (2) is that there is greater fluctuation in food abundance for spider monkeys than for gibbons. Since patch size was similar for the two species, patch density is expected to vary more for spider monkeys. Gibbons indeed had relatively stable levels of food availability (range 2.3 to 16.5 ripe fruit patches/ha, CV 55.3%; range 2.5 to 16.8 ripe and unripe fruit patches/ha, CV 52.4%) compared to spider monkeys (range 0.6 to 24.6 patches/ha, CV 85.6%). Prediction (3) is also supported. Thus, peak food density was greater for spider monkeys (24.6 patches/ha) than for gibbons (16.5 patches/ha).

Our data thus conform to predictions. They therefore suggest that the reason why

gibbons form small, stable groups rather than adopting a fission-fusion organization similar to spider monkeys, is that their environments do not exhibit sufficient variability in food abundance and peak levels of food abundance are lower. We do not know if other factors that might influence group formation, such as predator pressure or interspecific competition, differ for spider monkeys and gibbons, or if these factors play a role in the determination of these species groups sizes. What our results suggest is that the ecological variables of food patch size and distribution are critical for both species as contributing factors affecting group size.

In the process of conducting these analyses we discovered a number of apparent differences between the species, e.g. while gibbon and spider monkey food patch densities are similar, in any given month, gibbons eat a greater variety of food types than spider monkeys and the diet of gibbons appears to change more rapidly. A study explicitly designed to compare these species and their habitats would allow us to ask more elaborate questions, such as what factors are contributing to differences in patterns of territorial defence.

REFERENCES

CHAPMAN, C. A., 1989. Patterns of foraging and range use by three species of neotropical primates. *Primates*, 29: 177–194.

————, 1990. Association patterns of spider monkeys: the influence of ecology and sex on social organization. *Behav. Ecol. Sociobiol.*, 26: 409–414.

———— & L. J. CHAPMAN, 1990a. Density and growth rate of some tropical dry forest trees: comparisons between successional forest types. *Bull. Torr. Bot. Club*, 117: 226–231.

———— & ————, 1990b. Reproductive biology of captive and free-ranging spider monkeys. *Zoo Biol.*, 9: 1–10.

GINGERICH, P. D., 1980. Eocene adapidae, paleobiogeography, and the origin of South American Platyrrhini. In: *Evolutionary Biology of the New World Monkeys and Continental Drift*, R. L. CIOCHON & A. B. CHIARELLI (eds.), Plenum Press, New York, pp. 123–138.

HAIMOFF, E. H., X-J. YANG, S-J. HE, & N. CHEN, 1986. Census and survey of wild black-crested gibbons (*Hylobates concolor concolor*) in Yunnan Province, People's Republic of China. *Folia Primatol.*, 46: 205–214.

HARVEY, P. H., R. D. MARTIN, & T. H. CLUTTON-BROCK, 1987. Life histories in comparative perspective. In: *Primate Societies*, B. B. SMUTS, D. L. CHENEY, R. M. SEYFARTH, R. W. WRANGHAM, & T. T. STRUHSAKER (eds.), Univ. of Chicago Press, Chicago, pp. 181–196.

LEIGHTON, D. R., 1987. Gibbons: Territoriality and monogamy. In: *Primate Societies*, B. B. SMUTS, D. L. CHENEY, R. M. SEYFARTH, R. W. WRANGHAM, & T. T. STRUHSAKER (eds.), Univ. of Chicago Press, Chicago, pp. 135–145.

LEIGHTON, M. & D. R. LEIGHTON, 1983. Vertebrate responses to fruiting seasonality within a Bornean rain forest. In: *Tropical Rain Forest: Ecology and Management*, S. L. SUTTON, T. C. WHITMORE, & A. C. CHADWICK (eds.), Blackwell, Oxford, pp. 181–196.

ROBINSON, J. G. & C. H. JANSON, 1987. Capuchins, squirrel monkeys, and atelines: socioecological convergence with Old World primates. In: *Primate Societies*, B. B. SMUTS, D. L. CHENEY, R. M. SEYFARTH, R. W. WRANGHAM, & T. T. STRUHSAKER (eds.), Univ. of Chicago Press, Chicago, pp. 69–82.

RUBENSTEIN, D. I. & R. W. WRANGHAM, 1986. *Ecological Aspects of Social Evolution*. Univ. of Princeton Press, Princeton.

SCHULTZ, A. H., 1941. The relative size of the cranial capacity in primates. *Amer. J. Phys. Anthropol.*, 28: 273 – 287.
TERBORGH, J., 1983. *Five New World Primates*. Princeton Univ. Press, Princeton.
VAN SCHAIK, C. P., 1983. Why are diurnal primates living in groups? *Behaviour*, 87: 120 – 144.
WRANGHAM, R. W., 1987. Evolution of social structure. In: *Primate Societies*, B. B. SMUTS, D. L. CHENEY, R. M. SEYFARTH, R. W. WRANGHAM, & T. T. STRUHSAKER (eds.), Univ. of Chicago Press, Chicago, pp. 282 – 296.

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