

Folia Primatologica

International Journal of Primatology
 Internationale Zeitschrift für Primatologie
 Journal international de Primatologie

Index Vol. 28, No. 4, 1977

<i>Boskoff, K.J.</i> (Durham, N.C.): Aspects of Reproduction in Ruffed Lemurs (<i>Lemur variegatus</i>)	241
<i>Hobson, B.M.; Hearn, J.P.; Lunn, S.F., and Flockhart, J.H.</i> (Edinburgh): Urinary Excretion of Biologically Active Chorionic Gonadotrophin by the Pregnant Marmoset (<i>Callithrix jacchus jacchus</i>)	251
<i>Goodall, J.</i> (Tanzania): Infant Killing and Cannibalism in Free-Living Chimpanzees	259
<i>Riss, D.C. and Busse, C.D.</i> (Stanford, Calif.): Fifty-Day Observation of a Free-Ranging Adult Male Chimpanzee	283
<i>Nadler, R.D. and Tilford, B.L.</i> (Atlanta, Ga.): Agonistic Interactions of Captive Female Orang-Utans with Infants	298
<i>Nass, G.G.</i> (Madison, Wisc.): Intra-Group Variations in the Dental Eruption Sequence of <i>Macaca fuscata fuscata</i>	306
Book Review	315
Addendum	315
Author Index	316
Index Vol. 28	after · nach · après 316



S. Karger · Basel · München · Paris · London · New York · Sydney

**Fifty-Day Observation of a Free-Ranging
Adult Male Chimpanzee**

David C. Riss and Curt D. Busse

Department of Psychiatry and Program in Human Biology, Stanford University,
Stanford, Calif.

Key Words. *Pan troglodytes schweinfurthii* - Gombe National Park - Feeding behavior -
Agonistic behavior

Abstract. An adult male chimpanzee living in Gombe National Park, Tanzania, was observed for 50 consecutive days during the 1974 dry season, for a total of 563 h. This individual, Figan, was the alpha male of a community of 42 chimpanzees. The composition and size of temporary associations within the community was influenced largely by the presence of one estrus female and by characteristics of the food resources. Figan's daily time budget varied little for travel and grooming, but there were major changes in time spent feeding and inactive over the 50 days. Predatory behavior occurred periodically and meat was eaten on five occasions. Agonistic and sexual behaviors are discussed relative to Figan's high social status. A cooperative relationship was maintained between Figan and his older brother.

Concentrated observation of selected individuals over successive days is reported in several field studies of nonhuman primates, including orangutans [GALDIKAS-BRINDAMOUR, in press] and olive baboons [COLLINS, in preparation]. At Gombe National Park focal chimpanzees are typically observed all day: i.e., from the time that they unnest in the morning until they construct a nest in the evening. Multiple-day observations of focal chimpanzees at Gombe are reported by WRANGHAM [1975] and TUTIN [1975]. One individual was observed continuously for 25 days [PIERCE, in press]. Chimpanzee parties living in the Mahali Mountains have been observed for continuous days by NISHIDA and his colleagues [NISHIDA, 1968; in press].

We observed an adult male chimpanzee at Gombe for 50 consecutive days during the summer of 1974. The objectives of our concentrated study were to observe infrequent events such as predatory behavior and intercommunity interactions, and to obtain a data base for the analysis of optimal behavioral sampling procedures [KRAEMER et al., 1977]. In addition, the study permitted a unique observation of a chimpanzee community from the perspective of one of its members. This paper describes the behavior and intraspecific associations of one chimpanzee during a short period of time. A study of a different focal animal or at a different time might yield vastly different results. Consequently, this paper focuses on social and environmental factors that may have influenced individual behavior.

Study Population and Procedures

VAN LAWICK-GOODALL [1968, 1973, 1975] and others have described in detail the habitat and population structure of the Gombe chimpanzees (*Pan troglodytes schweinfurthii*). The chimpanzee population consists of several heterosexual 'communities' [VAN LAWICK-GOODALL, 1968] or 'unit-groups' [NISHIDA, 1968] of approximately 10-80 individuals with core areas [GOODALL et al., in press] of 5—20 km². The individuals within each community form temporary associations (parties), whose size and composition change frequently as individuals split off to forage or join other parties. At the time of the present study, the Kasakela community was comprised of 9 adult males, 2 cycling females, and 13 non-sexually cycling females and their 18 dependent offspring. This community has been studied by GOODALL and her numerous associates since 1961, and has been provisioned with bananas since 1962 to facilitate habituation and observation of the animals.

The focal animal of our study, Figan, was approximately 22 years old at the time of the study. He was first recognized by GOODALL in 1961, and since 1963 he has been fully habituated to human observers. During this period Figan rose steadily in dominance, becoming the alpha male of the community in 1973 [RISS and GOODALL, 1977]. Two siblings were alive at the time of the study: a brother Faben (approx. 26 years old) and a sister Fifi (approx. 16 years old).

Tanzanian field assistants accompanied us during 563 daylight observation hours from 30 June through 18 August, 1974. Observations began when Figan left his nest in the morning and ended after he had constructed a new nest in the evening. There were 44 full days of observation and 6 partial days when we lost Figan for a total of 32 h. Figan showed no apparent signs of uneasiness throughout the observation, and we assume that his behavior was minimally affected by our constant presence.

Observations were made at an average distance of 10-15 m from Figan. His activity and the identity of all other party members (within 100 m from Figan) were recorded at 5-min intervals. We recorded all agonistic and sexual interactions with party members and any points of interest, such as predatory behavior. The field assistants contributed to the collection of data on feeding and ranging behavior.

Time Budgets

KRAEMER et al.[1977] analyzed subsets of the time budgets data to determine optimal procedures for sampling behavior from the 50 days. A comparison of five successive 10-day intervals reveals little variation in time spent traveling and allo-grooming, and substantial variation in time spent feeding and inactive (fig. 1). Feeding and inactive times are inversely related, indicating that inactive time may be sacrificed when more time is spent feeding. WRANGHAM [1975] suggested that feeding activities might interfere with reproductive activities; however, the large percentage of time Figan spent inactive during this dry season

does not support this hypothesis. The general activity values were very similar to those obtained by WRANGHAM [1975] during a long-term study of Gombe male chimpanzees. WRANGHAM found no significant seasonal variation in these behavioral categories, although considerable variation was evident. Strong daily variation in activities was found during the present study, particularly for feeding.

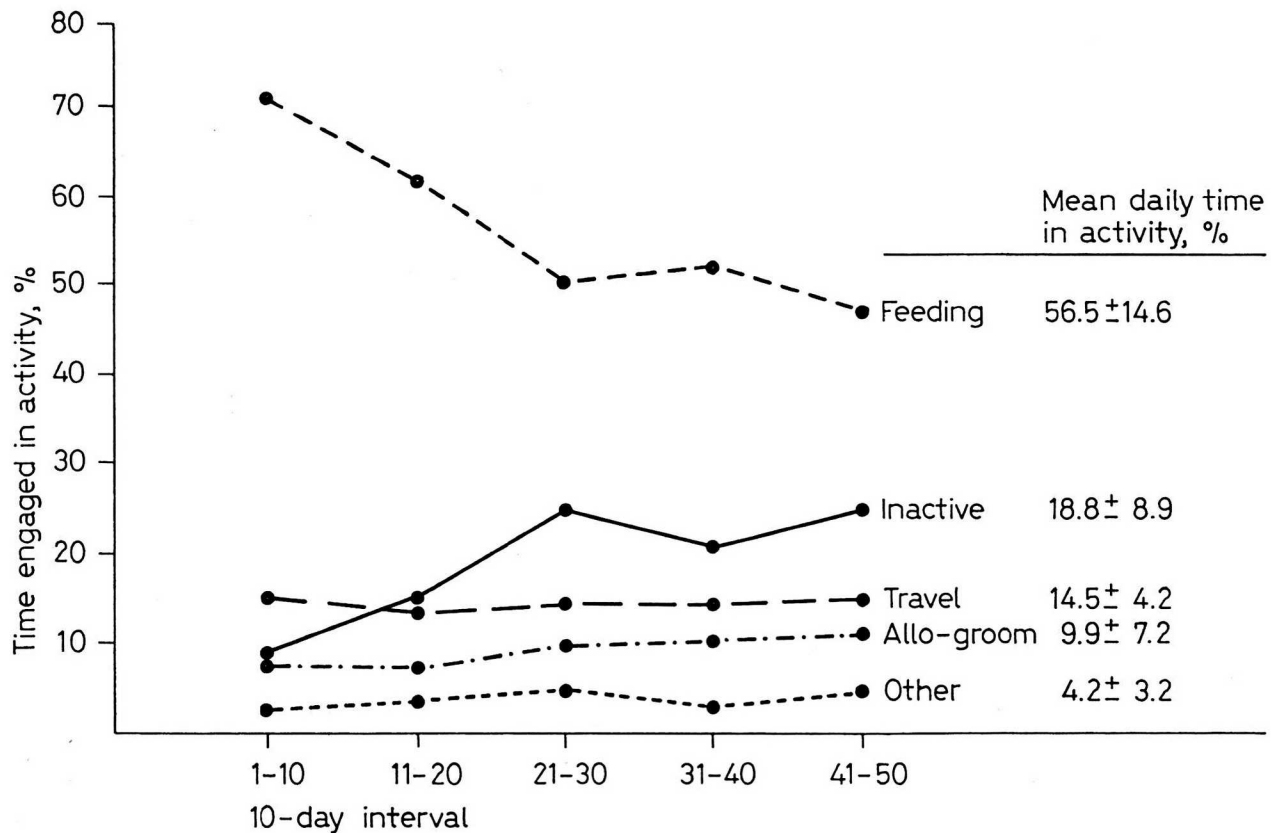


Fig. 1. Percentage of time spent in different activities is broken down into five 10-day periods. Mean daily time spent in activity (in percentage) is also given.

Range

Chimpanzee ranging patterns are influenced by various factors, including the distribution of foods, the number of estrus females, foraging group size, other chimpanzee communities, and the camp provisioning area. WRANGHAM and SMUTS [in preparation] will give much needed insight into the importance of these factors. Figan traveled an average of 4.4 km per day, compared to the mean daily range of 4.9 km found by WRANGHAM in his study of adult males. Figan utilized a small part of his usual core range during the 50 days. Camp had a major influence on Figan's ranging behavior: several times Figan traveled directly to camp from as far as two valleys upon terminating feeding. He visited camp on 41 of the 50 days of the follow for a median visit length of 20 min. 7.2% of all daylight hours were spent in camp.

GOODALL et al. [in press] describe chimpanzee intercommunity interactions at Gombe. Large chimpanzee parties sometimes travel ('patrol') deep into neighboring community territories and attack any chimpanzees that are encountered. During the past few years 5-6 individuals from neighboring communities have died as a result of vicious attacks by the Kasakela chimpanzees. During the present study Figan rarely traveled to the periphery of his range. Only two boundary patrols occurred during this time period, and no neighboring chimpanzees were encountered.

Feeding Behavior

Detailed descriptions of chimpanzee feeding behavior are given by VAN LAWICK-GOODALL [1968], SUZUKI [1969] and WRANGHAM [1977]. Figan's mean daily percentage of time spent feeding was $56.6 \pm 13.4\%$. Fruit consumption comprised 52.0% of the feeding time, and leaves (27.0%) and seeds (16.4%) were also eaten extensively. Animal foods consisted of invertebrates, mostly ants, and vertebrates, including five red colobus monkeys, one bushbuck, and one guinea fowl. Soil was eaten from termite mounds and fishing huts. Figan ate from at least 33 of the 77 plant species that have been consistently eaten by these chimpanzees since detailed records began in 1971 [WRANGHAM, 1975]. Included are two exotic foods, bananas, introduced in 1961, and palm fruits from *Elaeis guineensis*, introduced to the park prior to 1943. The median daily number of foods eaten during 44 full days of observation was 9, with a range of 5-12. *E. guineensis* fruits were top-ranked in terms of feeding time (17.1%), and the top ten ranked foods comprised 80.8% of Figan's overall feeding time.

A comparison of the five consecutive 10-day intervals reveals major changes in the percentage of time Figan spent feeding and the types of food he ate (table I). These changes in the feeding time budget are related to differences in the processing times of foods eaten. Foods requiring long processing times included the seeds of *Diphlorhynchus condylocarpon* and the fruits of *Elaeis guineensis*, *Monanthotaxis poggei* and *Harungana madagascariensis*. These foods were eaten extensively during the first two 10-day intervals, and contributed to the high percentage of time (67.5%) that Figan spent feeding. Foods having short processing times included the leaves of *Parinari curatellifolia* and *Asystasia ganetica*, and, to a lesser degree, fruits of *Ficus* sp. and *Pseudospondias microcarpa*. These foods were eaten primarily during the last 30 days when Figan only spent 49.8% of his time feeding. These observations indicate that variability between foods in processing rates was a major factor influencing changes in the feeding time budget over the 50 days.

Despite seasonality in rainfall and humidity patterns at Gombe, there is no direct evidence of significant seasonal variation in absolute food abundance. The failure of *Parinari curatellifolia* to fruit in the dry season of 1972 was an indication of depressed overall food availability compared with the 1973 dry season when this fruit was abundant [WRANGHAM, 1975]. However, despite the failure of *P. curatellifolia* to fruit during the present study in the 1974 dry season, Figan had no apparent difficulty finding foods. Changes in the abundance of specific foods were quite marked in many cases (table I), and it was possible to trace the

Table I. Percentage of time spent feeding on different types and on different species of food, along with the percentage of total time spent feeding, is divided into five 10-day blocks. Species are divided into those requiring a long time versus a short time to process.

Plant species	Part eaten ¹	Percentage feeding time: 10-day periods					Total 1-50
		1-10	11-20	21-30	31-40	41-50	
Those foods requiring long processing times							
<i>Elaeis guineensis</i>	F	8.8	9.3	18.3	31.9	21.9	17.1
<i>Diphlorhynchus condylocarpon</i>	S	25.4	13.5	10.3	6.3	0.0	12.1
<i>Harungana madagascariensis</i>	F	17.7	23.6	5.6	0.0	0.0	10.3
<i>Monanthotaxis poggei</i>	F	11.4	10.9	3.3	0.0	0.1	5.7
<i>Dalbergia</i> sp.	L	0.0	0.0	0.0	0.0	27.1	5.1
Subtotal		63.3	57.3	37.5	38.2	49.1	50.3
Those foods requiring short processing times							
<i>Parinari curatellifolia</i>	L	2.7	9.5	12.7	9.3	8.0	8.1
<i>Ficus</i> sp.	F	2.1	3.8	8.4	19.3	3.7	6.9
<i>Pseudospondias microcarpa</i>	F	1.2	1.2	13.5	6.6	12.0	6.4
<i>Asystasia gangetica</i>	L	1.5	3.0	7.7	9.3	4.4	4.8
Subtotal		7.5	17.5	42.3	48.5	28.1	26.2
Other foods		30.6	25.2	20.7	17.2	22.1	24.5
Total		100.4	100.0	100.5	99.9	99.3	100.0
Percent total time spent feeding		70.3	64.6	49.6	53.3	46.5	56.5

¹ L = leaf; F = fruit; S = seeds.

incorporation of several new foods into the diet. At no time did Figan appear to be searching for food, but typically returned to foods eaten on the same or previous days. Paths of travel between food sources soon became very familiar to the observers.

The fluid nature of chimpanzee social organization permits an ideal study of the influence of foods on foraging group size. While we made no direct measurements of relevant ecological variables, it was evident that chimpanzee party size was related in part to certain characteristics of the food supplies. There was little variation in the mean size of parties feeding on 9 of the top 11 ranked foods. Mean party sizes ranged from 2.2 to 4.4 except when feeding on *Dalbergia* sp. (7.4) and meat (7.2) (table II). *Dalbergia* sp. leaf buds were the only major food which appeared to have been discovered accidentally; Figan had not visited the site of its localized distribution (200 m radius) for 35 days prior to its discovery. Figan fed on these buds for 53% of his daylight hours during the 2 1/2 days following discovery, after which the site

was abandoned; possibly this food had been depleted. The extensive feeding upon *Dalbergia* sp. in the presence of alternative foods indicates that this was a highly preferred food. Meat was another highly preferred food, and like *Dalbergia* sp. it attracted large chimpanzee parties, was only eaten on a few days, and had a highly localized spatial distribution once it became available. In addition, the length of feeding bouts for *Dalbergia* sp. and meat was extraordinarily high in relation to the other foods (table II). The strong preference for these foods and their highly localized spatial and temporal distributions appeared to be major factors attracting the large chimpanzee parties.

Chimpanzee predatory behavior and carnivory is widely reported [e. g., VAN LAWICK-GOODALL, 1968; NISHIDA, 1968; TELEKI, 1973; WRANGHAM, 1975]. Red colobus monkeys are the main prey of Gombe chimpanzees [WRANGHAM, 1975; BUSSE, in press], and they were encountered during 12 of the 50 days. There were 7 predation attempts resulting in 5 kills, or 1.1 kills per 100 observation hours. BUSSE [in press] found a red colobus kill rate of 0.95 per 100 observation hours for the 39 kills observed in a recent 2-year period. Figan participated in all of the 7 colobus hunts and made 3 kills. In addition, a mother-infant colobus pair was killed by a group consisting of Figan, Faben, Gigi, and Goblin. The actual captures were not observed, but moments afterwards Gigi was seen eating the infant, and Faben and Goblin were seen holding the mother which later was killed and abandoned [VAN ZINNICQ BERGMANN-RISS and RISS, in preparation].

Table II. Mean party size and bout length during feeding on top 11 ranked foods. The mean party size is based on 1/2-hour observation periods.

Food species	Feeding time, %	Mean party size	Number of days eaten	Number of bouts	Median bout length, min
<i>Elaeis guineensis</i>	17.1	2.2	42	92	31
<i>Diphlorhynchus condylocarpon</i>	12.1	3.5	28	62	31
<i>Harungana madagascariensis</i>	10.3	4.3	19	51	31
<i>Parinari curatellifolia</i>	8.1	4.4	34	53	25
<i>Ficus</i> sp.	6.9	4.3	27	34	31
<i>Pseudospondias microcarpa</i>	6.4	2.7	32	58	17
<i>Monanthe poggei</i>	5.7	3.3	17	52	13
<i>Dalbergia</i> sp.	5.1	7.4	3	7	161
<i>Asystasia gangetica</i>	4.8	3.5	37	67	12
<i>Piliostigma thoningii</i>	4.3	2.9	11	15	58
Meat	3.1	7.2	5	5	120

In addition to the 5 colobus kills Figan ate meat once after stealing part of a bushbuck kill from a male baboon [MORRIS and GOODALL, 1977]. Baboons were encountered during 32 of the 50 days and were only hunted once by Figan, unsuccessfully.

Agonistic Behavior

The contexts and components of chimpanzee displays and attacks have been discussed by VAN LAWICK-GOODALL [1968], HAMBURG [1971] and BYGOTT [1974]. TUTIN [1975] found that the alpha status does confer benefit in terms of copulatory success, but for the non-alpha adult males there is no significant correlation between dominance rank and copulatory reproductive success. Factors influencing dominance may include age, size, physical fitness, dominance status of the mother, and personality [BYGOTT, 1974]. The most important factor may be the formation of cooperative coalitions with other individuals.

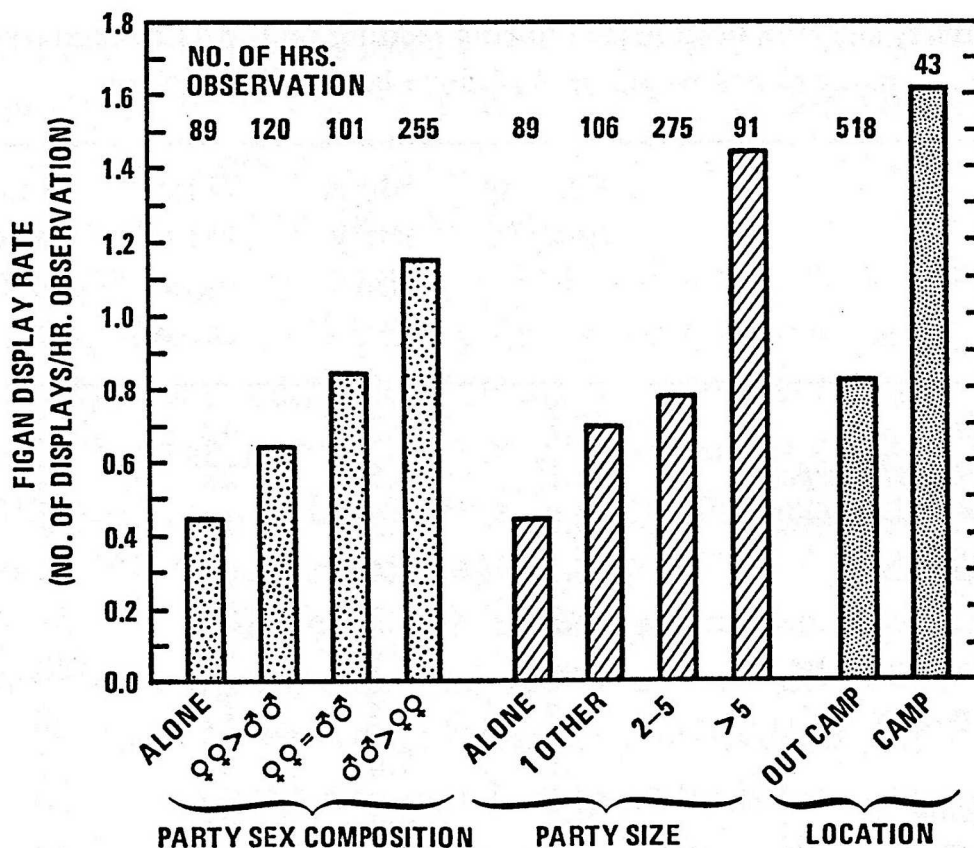


Fig. 2. Different factors influence Figan's display rate. Influences include: (a) party sex composition; (b) party size; and (c) location.

Figan's high social status was manifested by high levels of aggression towards others and submission from others (table III). Figan performed 501 displays during the study; a median of 8 displays per day and an average of 0.9 displays per hour. His display rate varied in direct relation to party size and the number of other adult males present (fig. 2). In addition, the display rate was 3 times higher in the camp area than it was outside the camp area (fig. 2). The difference is in part related to the larger mean party size and the occurrence of 35% of all reunions in the camp area. BAUER [1975] found a pulse-like increase in the frequency of aggressive behavior during reunions.

Attacks constitute 2% of all agonistic interactions; the attack rates and attack/display ratios vary widely between individuals [BYGOTT, 1974]. During this study Figan attacked males 6 times and females 6 times. 6 of the 12 attacks occurred at vertebrate kill sites when meat was being eaten. None of the attacks resulted in any serious injuries.

Table III. Display and submission rates from the 50-day Figan observation.

	Evered	Faben	Median of adult males (n = 6 others)	Fifi	Gigi	Median of adult females (n = 15 others)
Number of hours of as- sociation with Figan ¹	21	327	66	73	210	16
Association percentage of Figan's total following time	4	59	12	13	37	3
Figan displays per hour of association	3.2	0.9	1.5	1.3	0.9	1.3
Percentage of total Figan displays that are directed at other	30.0	0.7	14.3	5.4	7.7	6.7
Total displays by other in Figan's presence	1	204	11	1	4	0
Total mutual displays	0	160	7	0	2	0
Number of pant-grunts to Figan	40	1	17	0	11	2
Number of bobs to Figan	28	0	5	0	0	0
¹ n _{total} = 563 h.						

Associations

Chimpanzee social organization is described in detail by VAN LAWICK-GOODALL [1975] and WRANGHAM [1975]. Males live in a closed community; i.e., they apparently do not transfer between communities. Unfortunately, there have been no long-term systematic studies of Gombe female chimpanzees, and it is not certain how females relate within and between male communities. Some females have transferred between communities [PUSEY, in press], and most females have smaller ranges than males.

NISHIDA [in press] found that the strongest social bonds in the Mahali Mountain chimpanzees were between adult males and the weakest social bonds were between adult females. Although our study population consists of more mature females than mature males, the mean percentage of association with Figan was twice as high for males than it was for females (19 vs 8%, respectively; table IV). A majority of the females had very low percentages of association with Figan. Some females were encountered in very localized areas of his range, while others were seen throughout the range. One female, Passion, who has long been a stable member of the Kasakela community and a daily visitor to camp, associated with Figan for only 0.3% of the study, lowest of all chimpanzees, including several unhabituated females not generally considered to be community members. Unfortunately, the long history of banana feeding at Gombe has obscured attempts to assess the status of females as community members.

Figan spent 84% of his time in groups and 16% of his time alone. The mean party size was 4 individuals (excluding subadolescents); the mean party size in the camp area was 5 individuals. HALPERIN [in press] found that Figan in 1971-1973 showed the lowest *lone male* score of any of the other 8 males he analyzed. The highest concentration of his sample points were in the all male division (almost 50%). BYGOTT [1974] suggested that in these all male parties Figan could demonstrate his prowess as a high-ranking male. NISHIDA [in press] found that higher-ranking males were more often found in larger sub-groups than were lower-ranking males. VAN LAWICK-GOODALL [1968] has emphasized the strong individuality of Gombe chimpanzees, based in part upon age, sex, kinship relationships, dominance position, personality, and other characteristics. HALPERIN [in press] has shown that individuals within the same age/sex class may show distinct differences in their grouping patterns. Here we will describe Figan's relationships with three other community members who appeared to have strongly influenced his behavior during our study. These individuals included his brother Faben, the estrus female Gigi, and the second highest-ranking male Evered.

Faben

RISS and GOODALL [1977] described the long cooperative relationship between Figan and Faben, and found that Figan's acquisition of the alpha rank in 1973 would probably not have been possible without Faben's support. During our study, Figan associated with Faben more frequently than with any other chimpanzee (59% of his time). The brothers displayed

together frequently (table III) and twice attacked the second highest-ranking male Evered. The cooperative relationship between Figan and Faben appears to be a major factor in maintaining their high social status. 4 of the 5 alpha males studied at Gombe since 1961 have had a supportive relationship with a known or suspected male sibling. The one exception retained the alpha rank for the shortest time, 20 months. The supportive relationship between male sibling chimpanzees is another possible case of kin-selected cooperation [also see, for example, WATTS and STOKES, 1971].

Table IV. The percentage of 563 total h of observation in which adult male and adult female chimpanzees were in association with Figan.

	Percent association with Figan	Number of days seen with Figan
<i>Males</i>		
Faben (brother)	59	42
Goblin (adolescent)	35	40
Humphrey	16	27
Sherry	14	36
Mike	13	22
Jomeo	11	27
Satan	11	25
Hugo	10	26
Evered	4	10
\bar{X}	19.2	28.3
<i>Females</i>		
Gigi (cycling)	37	34
Patti (cycling)	28	37
Fifi (sister)	13	25
Athena	12	28
Miff	8	21
Gilka	8	23
Winkle	6	22
Nope	4	19
Sparrow	4	14
7 other females	1-3	2-16
\bar{X}	8.1	17.5

BYGOTT [1974] found that the most frequent and harmonious chimpanzee associations appear to be between known relatives, or individuals with stable dominance/subordinate relationships (i.e., a high-ranking male in his prime, with an older or disabled subordinate).

Faben was overtly submissive to Figan only once. Their reunions following separations were less aggressive than Figan's reunions with other adult males. Figan did attack Faben twice, however: once during competition for access to a burlap bag, and once immediately after Faben had copulated with Gigi. Of all the females, Figan's sister Fifi had the lowest rates of aggressive and submissive interactions with Figan. She was never observed being submissive to Figan. Fifi's associations percentage with Figan was the highest of all anestrus females but lower than that of the two estrus females, Gigi and Patti. Figan's cooperative relationship with Faben contrasts with his more neutral relationship with Fifi: chimpanzee sex differences in daily range size, aggressiveness, and reproductive strategies appear to inhibit the formation of supportive relationships between brothers and sisters.

Also of interest was the frequent exchange of tonal grunts between these brothers, suggesting a special form of communication not evident between Figan and the other adult males. Figan groomed with Faben more than with any other adult male, but this seemed to be a consequence of their high association percentage and not a special feature of their relationship. Grooming time relative to association time was lower for Faben than for most other males.

Gigi

Gigi was the only sexually cycling female during our study except for the adolescent female Patti, who was observed in estrus only for the first few days of the observation. Gigi has been sexually receptive since 1965 without conceiving an infant, and is presumed to be sterile. Gigi is a very large, masculine-appearing female, and is one of two females that have been seen to catch a red colobus monkey. Gigi displayed 4 times in Figan's presence, more than any other female.

TUTIN [1975] found that when Figan became the alpha male he utilized his position to successfully monopolize a number of females when they reached the later half of their maximal sexual tumescent cycle phase. Figan and Gigi associated together 78% of the time during the 17 days when she was in estrus, and only 16% of the 33 days when she was anestrus (fig. 3). This difference is significant ($p < 0.005$). TUTIN noted that Figan as alpha male was not involved in any consortships, but was involved in a number of "possessive incidents", defined by TUTIN as the pattern of behavior shown by males in the maintenance of proximity to the female and in interruptions of copulation by other males. She found that Figan actively interrupted copulations and copulation attempts during all five possessive incidents in which he was involved. We observed frequent attempts by Figan to maintain proximity to Gigi approximately midway through her estrus cycle. For example, Figan sat idly once for over 3 h while Gigi consumed a red colobus monkey. Another time he sat for 50 min, grunting frequently while looking towards Gigi who was eating insects; upon finishing, she followed Figan to a tree only 50 m away to begin feeding. Figan did not attempt to consort Gigi. Figan had the highest observed number of copulations with Gigi (23), although some copulations between Gigi and the other males invariably were not observed. Faben had the second highest number of copulations (8). Overt competition was observed only once when Figan attacked

Faben. Figan's presence may have partially inhibited other males from attempting to copulate with Gigi.

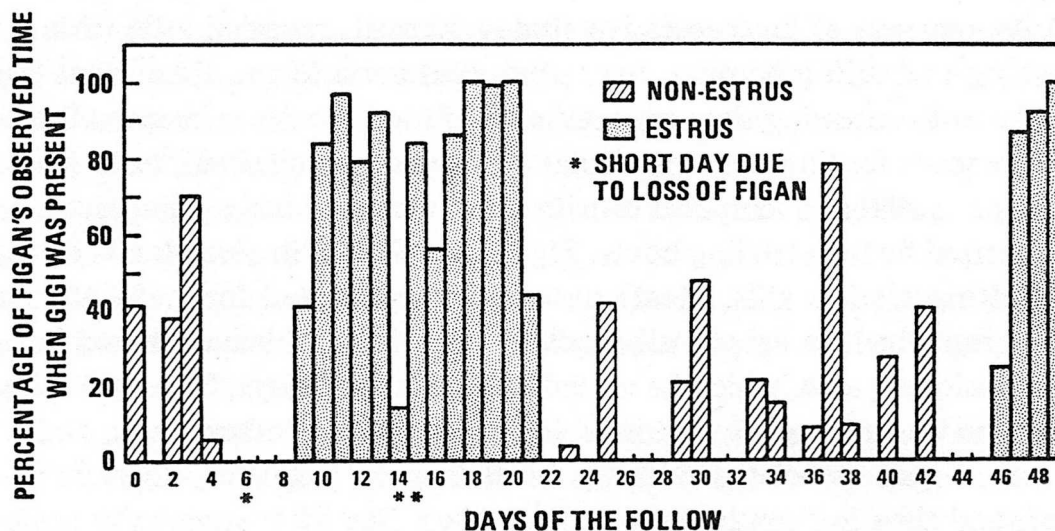


Fig.3. The percentage of Figan's observed time in association with the cycling female Gigi for each of the 50 days when Gigi was (a) in estrus versus (b) when she was anestrus.

Evered

Figan and Evered were of nearly equal status during a 9-month period following Humphrey's fall from the alpha rank in September, 1972. Both high-ranking males displayed in each other's presence and were not submissive to each other. During June of 1973 Figan and Faben attacked Evered several times, establishing Figan as the alpha male [RISS and GOODALL, 1977]. Evered has remained dominant to the other males but during the present study he was the most submissive male to Figan as measured by rates of pant-grunt vocalizations and bobbing gestures (table III). The next most submissive male to Figan was Humphrey, now the third highest ranking male. BYGOTT [1974] found that males who did not appear to have a clear-cut agonistic relationship spent less time together. This certainly did not hold true for the relationship between Figan and Evered, in which a very definite and predictable dominance/subordinate relationship existed, yet the two males had the lowest rate of association together than did any other adult male with Figan. It appeared in fact that Evered may have actively avoided associating with Figan, often not visiting the camp area for periods of weeks in duration. BYGOTT[1974] also found that agonistic interactions were usually more frequent between males of different rank than between males of similar rank. Our data showed that the next two highest ranking males to Figan had the highest rate of agonistic interactions with Figan. Figan's display rate was higher in the presence of Evered (3.2 displays per hour) than in the presence of other adult males (1.5 displays per hour). When Evered was present, Figan directed 30% of his displays at Evered, the highest percentage of directed displays. Figan displayed at every reunion with Evered. In addition, Figan participated in a group attack upon

Evered. The antagonism between these top-ranking males was further indicated by the virtual absence of allo-grooming. Figan and Evered have only been seen to groom each other for 30 sec in a 12-year period.

Summary

This paper describes the behavior and activity patterns of the alpha male, Figan, of a community of 42 chimpanzees living in Gombe National Park during 50 consecutive days in 1974. A comparison of five successive 10-day intervals revealed little variation in time spent traveling and allo-grooming, but substantial variation in time spent feeding and inactive. Different processing time requirements of food species influenced the percentage of time Figan spent feeding. One particular plant species and meat, both resources with highly localized spatial and temporal distributions, attracted large chimpanzee parties and were characterized by long feeding bouts. Figan participated in seven hunts on red colobus monkeys, and made three kills. Meat consumption accounted for 3.1% of Figan's total feeding time, ranking 11th among all foods. Figan's ranging behavior was influenced by the camp provisioning area, which he visited on 41 of the 50 days. Figan's display rate was highest when he was among large groups, in the presence of other males, and in the provisioning area. Figan associated with his brother more frequently than with any other chimpanzee, and they frequently displayed together. The most submissive male to Figan was the second highest-ranking male of the community. Figan's sister had the lowest rates of aggressive/submissive interactions with Figan among the females. Figan and the sexually cycling female Gigi associated together much more frequently when she was in estrus (78%) than when she was anestrus (16% of the time).

Acknowledgments

We are very grateful to J.GOODALL, D. HAMBURG, H. KRAEMER, R. WRANGHAM, B. HILL and E. RISS for their helpful comments and encouragement. We would like to thank Tanzanian National Parks for permission to study at Gombe; the Grant Foundation of New York and the L.S.B. Leakey Foundation of Los Angeles for financial support; the Program in Human Biology and the Department of Psychiatry of Stanford University for use of facilities; and the many Tanzanians who helped us immensely.

References

- BAUER, H.R.: Behavioral changes about the time of reunion in parties of chimpanzees in Gombe National Park; in *Contemporary primatology*. Proc. Sth Int. Congr. Primatology, Nagoya 1974 (Karger, Basel 1975).
- BUSSE, C.D.: Chimpanzee predations as a possible factor in the evolution of red colobus monkey social organization. *Evolution* (in press).

- BYGOTT, J.D.: Agonistic behavior and dominance in wild chimpanzees; PhD thesis, University of Cambridge (1974).
- COLLINS, D.A.: Sexual consortship among olive baboons of the Gombe National Park; PhD thesis, University of Edinburgh (in preparation).
- GALDIKAS-BRINDAMOUR, B.: Orang-utan adaptation at Tanjung Puting Reserve: mating and ecology; in HAMBURG, McCOWN and GOODALL Perspectives on human evolution. IV. The behavior of the great apes (Staples Press/Benjamin, Menlo Park, in press).
- GOODALL, J.; BANDURA, A.; BUSSE, C.D.; MATAMA, H.; MPONGO, E.; PIERCE, A.; RISS, D.C., and ZINNICQ BERGMANN, E. VAN: Intercommunity interactions in the chimpanzee population of the Gombe National Park; in HAMBURG, McCOWN and GOODALL Perspectives on human evolution. [V. The behavior of the great apes (Staples Press/Benjamin, Menlo Park, in press).
- HALPERIN, S.D.: Temporary association patterns in free-ranging chimpanzees: an assessment of individual grouping preferences; in HAMBURG, McCOWN and GOODALL Perspectives on human evolution. IV. The behavior of the great apes (Staples Press/Benjamin, Menlo Park, in press).
- HAMBURG, D.A.: Aggressive behavior of chimpanzees and baboons in their natural habitat. *J. Psychiat. Res.* 8: 385-398 (1971).
- KRAEMER, H.C.; ALEXANDER, B.; Busse, C.D.; CLARK, C., and Riss, D.C.: Empirical choice of sampling procedures for optimal research design in the longitudinal study of primate behavior. *Primates* 18: 4 (1977).
- LAWICK-GOODALL, J. VAN: The behavior of free-living chimpanzees in the Gombe Stream Reserve. *Anim. Behav. Monogr.* J: 161-311 (1968).
- LAWICK-GOODALL, J. VAN: The behavior of chimpanzees in their natural habitat. *Am. J. Psychiat.* 130: 1-12 (1973).
- LAWICK-GOODALL, J. VAN: Chimpanzees of Gombe National Park: 13 years of research; in EIBL-EIBESFELDT *Hominisation und Verhalten* (Fischer, Stuttgart 1975).
- MORRIS, K. and GOODALL, J.: Competition for meat between chimpanzees and baboons of the Gombe National Park. *Folia primatol.* 28: 109-121 (1977).
- NISHIDA, T.: The social group of wild chimpanzees in the Mahali Mountains. *Primates* 9: 167-227 (1968).

- NISHIDA, T.: The social structure of chimpanzees in the Mahali Mountains; in HAMBURG, McCOWN and GOODALL Perspectives on human evolution. IV. The behavior of the great apes (Staples Press/Benjamin, Menlo Park, in press).
- PIERCE, A.: The behavior of a small community of chimpanzees at Gombe National Park; in Proc. 7th Int. Congr. Primatology, Cambridge, England, 1976 (Academic Press, New York, in press).
- PUSEY, A.: Intercommunity transfer of chimpanzees in Gombe National Park; in HAMBURG, McCOWN and GOODALL Perspectives on human evolution. IV. The behavior of the great apes (Staples Press/Benjamin, Menlo Park, in press).
- RISS, D.C. and GOODALL, J.: The recent rise to the alpha-rank in a population of free-living chimpanzees. *Folia primatol.* 27: 134-151 (1977).
- SUZUKI, A.: An ecological study of chimpanzees in a savanna woodland. *Primates* 10: 103-148 (1969).
- TELEKI, G.: The predatory behavior of wild chimpanzees (Bucknell University Press, Lewisberg 1973).
- TUTIN, C.E.G.: Sexual behavior and mating patterns in a community of wild chimpanzees (*Pan troglodytes schweinfurthii*); PhD thesis, University of Edinburgh (1975).
- WATTS, C.R. and STOKES, A.W.: The social order of turkeys. *Scient. Am.* 224: 112-118 (1971).
- WRANGHAM, R.W.: Behavioral ecology of chimpanzees in Gombe National Park, Tanzania; PhD thesis, University of Cambridge (1975).
- WRANGHAM, R.W.: Feeding behavior of chimpanzees in Gombe National Park, Tanzania; in CLUTTON-BROCK Feeding behavior of primates (Academic Press, London 1977).
- ZINNICQ BERGMANN-RISS, E. VAN and RISS, D.C.: Development of predatory skills in a free-ranging adolescent chimpanzee (in preparation).

David C. Riss, Office of Student Affairs, M105, Stanford School of Medicine, Stanford University, Stanford, CA 94305 (USA)

|