# SHORT COMMUNICATION

## PRE-FEEDING AGONISM AND SEASONALITY IN CAPTIVE GROUPS OF CHIMPANZEES (PAN TROGLODYTES)

### S M Howell, M Matevia, J Fritz[†], L Nash and S Maki

Primate Foundation of Arizona, PO Box 20027, Mesa, AZ 85277, USA

[†] Contact for correspondence and requests for reprints

Abstract                                                    *Animal Welfare 1993, 2:* 153-163

*Captive chimpanzees fed at regular, predictable intervals are known to exhibit higher rates of aggression immediately prior to, and during feeding. Presumably, anticipation of food creates tensions leading to increased agonistic interactions prior to feeding. This study was conducted to determine if seasonal variabilities might contribute to pre-feeding agonism. A quantitative examination was made looking at events affected by seasonal (summer versus autumn) changes. Seasonal fruit diversity and the amount of available space during feeding bouts in socially housed, captive chimpanzees were tested for an effect on pre-feeding agonism. Groups were observed for a five-week period during both seasons. Each social group was observed five times per season for 30 minutes, beginning 30 minutes prior to the morning feeding. All occurrences of agonistic behaviours were recorded. Average frequencies of agonistic behaviours were calculated for each group and compared across season using a Wilcoxon matched-pairs test to determine the effect of seasonal fluctuations in fruit diversity. There were no significant differences in the number of agonistic behaviours exhibited during summer versus autumn seasons. A strong negative correlation was found for agonistic behaviours in both seasons: as space decreased, agonism increased in both summer and autumn. In addition, males scored significantly higher in the summer versus the autumn for submissive behaviours when space decreased. The provision of a variety of seasonal fruits did not result in increased pre-feeding agonism in captive chimpanzees. In fact, cage size had a greater effect on levels of agonism than did the provision of seasonal fruits.*

Keywords: *agonism, animal welfare, chimpanzees, dietary diversity, feeding enrichment, social density*

## Introduction

Chimpanzees in the wild are social primates, living in fluid fission-fusion communities (Halperin 1979). Providing for their well-being in captivity mandates housing animals socially whenever possible (Fritz 1989). However, Nieuwenhuijsen and deWaal (1982) noted that more aggression is observed among social groups in captive settings, eg large outdoor areas, when compared to typical levels of aggression exhibited among chimpanzees in the wild (Goodall 1965, Reynolds & Reynolds 1965, Nishida 1970, Bygott 1974, Wrangham 1977). Managers of captive chimpanzees should make every effort to identify the variables which contribute to these elevated levels of aggression.

Observation of groups of captive chimpanzees housed in a large outdoor compound, revealed that aggressive incidents were highest in the intervals immediately prior to and during established feeding times, when competition was likely to occur, or when close proximity was also a factor (Wilson & Wilson 1968, Reynolds & Luscombe 1969, deWaal & Hoekstra 1980). A similar situation occurred in the wild when groups of free-ranging chimpanzees were provisioned to facilitate habituation and observation (Wrangham 1977, Goodall 1986). They found provisioning had to be managed to prevent increased aggression. It should be noted that such provisioning in the wild is no longer done.

In captive animals, anticipation of food distributed at established feeding times creates tensions leading to increased aggression levels (Wilson & Wilson 1968, Reynolds & Luscombe 1969, Fritz & Fritz 1979). Fights erupt as anticipation for food increases (Reynolds & Luscombe 1969).

Since wild chimpanzees spend most foraging time searching for and eating fruit, (*Budongo:* Reynolds & Reynolds 1965, *Kasakati Basin:* Izawa & Itani 1966, *Gombe:* Goodall 1968, *Rio Muni:* Jones & Sabater Pi 1971, *Ipassa, Gabon:* Hladik 1977, *Kibale Forest:* Ghiglieri 1984), fruit is plausibly a preferred food resource (Ghiglieri 1984). Wild chimpanzees also seem to prefer to exploit rare food types (Ghiglieri 1984 p86). Diversity is a consistent and apparently preferred feature in the diets of wild chimpanzees (Wrangham 1977, Uehara 1990). The importance of dietary diversity to captive primates has been widely acknowledged, but direct quantitative evidence of its effect upon their behaviour is lacking (McGrew 1981). Given that rare fruit species are most likely preferred by wild chimpanzees, seasonal provision of rare fruit types may result in increased agonism in captive chimpanzees (Ghiglieri 1984). Excitement in anticipation of rare foods might lead to increased pre-feeding aggression. When fruit diversity is increased during the summer months, the incidence of aggression should be greater compared to times when fruit diversity is decreased during the autumn.

The feeding routines carried out at the Primate Foundation of Arizona (PFA) provided an opportunity to focus on the relationship of dietary diversity to pre-feeding agonism. A degree of seasonal variation in dietary diversity is both necessarily and preferentially built into feeding routines at PFA. Management at PFA provides as much affordable dietary diversity as possible and purchasing seasonal fruit and vegetables in season is cost effective. Citrus fruit, eg oranges which are a locally grown crop, is the most readily available and inexpensive fruit during the autumn. However, a greater variety of fruit is in season during the summer. Thus, a higher diversity of fruit is provided during this period, and a comparatively lower diversity of fruit is provided during the autumn (Figure 1). Free-ranging chimpanzees are also primarily frugivorous, and consume the largest portion of their daily fruit intake during an early morning feeding (Hladik 1977, Wrangham 1977, Ghiglieri 1984, Goodall 1986). Therefore, at PFA, feeding times are arranged to reflect this diurnal feeding rhythm. Fruit is provided during the early morning feeding, followed at midday by vegetables and monkey chow in the late afternoon.
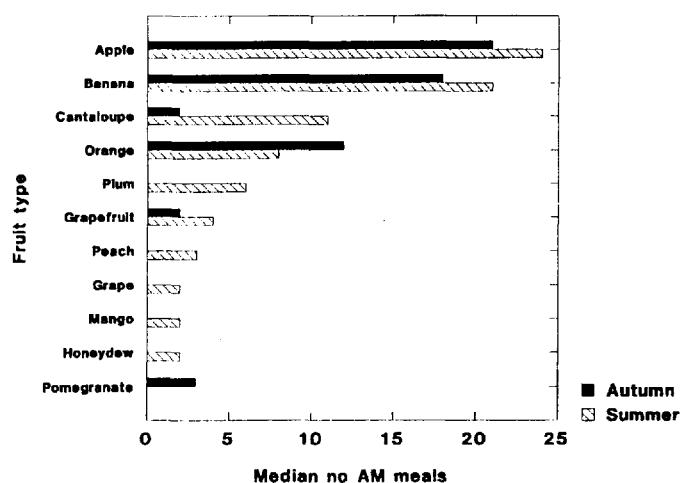
Figure 1    Median number of morning meals at which each food item was provided. Meals never included fewer than two fruit types.

This study took advantage of standard practices already in effect at PFA: an established feeding routine that is based on seasonal fruit diversity and the availability of different group sizes housed in similar sized cages. It was predicted that agonistic behaviours would be significantly greater during the summer season when a greater variety of fruit was provided. In the wild, male chimpanzees of all age classes exhibit more aggression than females (Goodall 1986). Since wild male chimpanzees also travel further each day and range more widely than females, it is likely that less space or social crowding will have a greater effect on males in captivity. Prior research on captive and wild chimpanzees indicates social density may have an effect on levels of aggression and males are likely to be more aggressive than females (Nieuwenhuijsen & deWaal 1982, Goodall 1986). Therefore sex and group size differences were also considered in this analysis.

## Methods

### Subjects and sampling
Focal subjects were 28 captive chimpanzees *(Pan troglodytes)* housed in five social groups comprised of two to eight animals per group. There were 14 male and 14 female subjects ranging from 3.6 to 20.5 years of age (see Table 1). All subjects were housed in well established social groups. Prior to the study, all groups had been together for at least one year. However there was one change in housing during the experiment. For management reasons, one young juvenile female was removed from her group (group 4) to an adjacent enclosure between the summer and autumn seasons. Her data were not included in this analysis. The indoor housing system provided floor space ranging from 38.65m² to 49.31m² per social group and all enclosures had a vertical height of 2.79 meters. The space provided per subject varied between 4.83m³ and 19.32m³ (Table 1).

**Table 1**    Composition of social groups[a] and space per subject[b].

| Group composition[a] | Sex | Group 1 | Group 2 | Group 3 | Group 4 | Group 5 |
|---|---|---|---|---|---|---|
| *Juveniles* | F | 0 | 0 | 0 | 3 | 0 |
|  | M | 0 | 0 | 0 | 3 | 0 |
| *Adolescents* | F | 3 | 0 | 2 | 1 | 0 |
|  | M | 2 | 0 | 6 | 0 | 0 |
| *Adults* | F | 0 | 3 | 0 | 0 | 2 |
|  | M | 0 | 3 | 0 | 0 | 0 |
| *Total in group* |  | 5 | 6 | 8 | 7 | 2 |
| *Space per subject (m³)[b]* |  | 9.86 | 6.44 | 4.83 | 6.16-7.73[c] | 19.32 |

[a] As defined by age classes: juvenile = 4 to 7 years, adolescent = 7 to 9 years, adult = 9 years and older

[b] Total enclosure size divided by total number of subjects in the social group

[c] Space per subject after and before removal of juvenile female

**Table 2**    Behaviour definitions.

| Behaviour | Definition |
|---|---|
| *Attack* | Individual makes physical contact with another, which could cause bodily injury. The behaviour patterns include: biting, dragging, hitting, grappling, kicking, scratching, slamming, slapping, and stamping on. The attacking animal has erected hair. |
| *Threat* | Individual shows a non-contact behaviour pattern which signals that a physical attack may be imminent. The behaviour pattern includes: arm raising, head tipping, screaming, throwing, and soft barking. |
| *Escape* | Individual tries to or succeeds in breaking contact or moving away from an attacking or threatening animal. |
| *Submit* | Individual yields or gives up a place or object in response to a threat, attack, or an approach of a higher status animal (Wilson & Wilson 1968). The behaviour patterns also include bobbing, crouching, embracing, grooming, kissing, mounting, pant shrieking, presenting, and squeak calling. |

Observations were conducted at PFA during five-week periods in the summer and autumn of 1989. Summer observations were collected between June 19 and July 28 1989, and autumn observations were collected between October 31 and December 6 1989. Five observations were collected for each social group during each season. During the summer season, observations were conducted at 0630h, half an hour before the 0700h morning feeding. During the autumn season, observations were conducted at 0700h, half an hour prior to the 0730h feeding. The change in feeding time was an accommodation for shorter daylight hours. All occurrences of target behaviour patterns exhibited by each subject were recorded continuously across a 30 minute period. The following agonistic behaviours were recorded: attack, threat, escape and submit (see Table 2). In both seasons, each behavioural measure was positively correlated with each other behavioural measure (Spearman correlation coefficients ranged from 0.354 to 0.973). The frequencies of target behaviours were also summed to provide frequencies of aggression (attack + threat), submission (escape + submit) and agonism (attack + threat + escape + submit).

*Feeding*

Monday through Friday across each seasonal observation period, records were kept of fruit type (Table 3) and fruit mass (number of pieces provided per fruit type). This provided an estimate of fruit diversity. All subjects within a social group received the same portions (number of pieces and types) of food each day. Smaller fruit, eg apple, banana, orange were fed whole to increase feeding time, although larger fruit, eg honeydew melon were sectioned to fit into the feeding container. Animals housed in social groups were fed individually. Each animals' food portion was placed in an individual feeding container, and animals were watched to ensure they removed each piece of food from it (Fritz & Fritz 1979).

**Table 3**      **Fruit type provided during summer and/or autumn seasons.**

| Fruit type | Scientific name |
|---|---|
| *Apple* | *Malus sylvestris* |
| *Banana* | *Musa paradisiaca* |
| *Cantaloupe melon* | *Cucumis melo cantalupensis* |
| *Grape* | *Vitis spp* |
| *Grapefruit* | *Citrus paradisi* |
| *Honeydew melon* | *Cucumis melo* |
| *Mango* | *Mangifera indica* |
| *Orange* | *Citrus sinensis* |
| *Peach* | *Prunus persica* |
| *Plum* | *Prunus spp* |
| *Pomegranate* | *Punica granatum* |

During both seasons, subjects were provided with apple and banana at each AM meal. These were considered dietary staples. Rare fruit, ie grape, honeydew melon, mango, peach and plum came in season for a short period of time (one day to one week) during the year. These were provided whenever available. Although a few were available throughout the autumn, they were abundant during the summer season (see Figure 1).

In the summer, subjects received an average of between 3.28 and 3.80 different types of fruit per meal. During the autumn, they received an average of between 2.12 and 2.68 different types of fruit per meal. The greater variety of fruit types provided during the summer season also resulted in a greater number of pieces of fruit fed at a single meal. During the summer, subjects in each social group received an average of between 7.23 and 7.98 pieces of fruit per meal, but in the autumn subjects received an average of between 5.06 and 6.70 pieces of fruit per meal. However, the daily calorific intake was comparable during summer and autumn seasons since additional vegetables were provided at PM meals during the autumn when fruit was less abundant.

## Analysis
### Feeding diversity
Based on the number of items offered per subject, a Shannon index of diversity measure (Subcommittee on Conservation of Natural Populations 1981 p25) was used to calculate the daily diversity of fruit offered to each social group. This score considers both the number of different fruit types provided and the number of pieces provided per fruit type. It was also used to represent the diversity of food each subject received.

To test the association between seasonal dietary diversity and agonistic behaviour, the diversity index was calculated by three different methods. A Spearman rank-order coefficient was then calculated across groups ($n = 5$) to determine which of the three indices showed the highest correlation with the average per capita frequency of behaviours (both seasons combined). The diversity measures tested were as follows:

1. *Previous day*: the diversity of fruit offered per social group at the morning meal, one day prior to each observation;

2. *Previous week*: the mean daily diversity of fruit offered to each social group between test periods, for each group, usually across a five to seven day period;

3. *Seasonal*: the mean daily diversity of fruit offered to each social group, across both five-week test periods.

### Behaviour
For each behavioural variable, each subject's frequency per observation was divided by the total number of individuals in the group to arrive at an individual per capita score. To estimate a central tendency for each group for each observation, a median was calculated across subjects' per capita scores. Then to arrive at seasonal central tendency for each group for each season, an average was computed across median per capita scores. Although an average is provided herein, the median per capita score was also

computed. Mean and median per capita scores were similar.

Seasonal averages were also calculated based on median per capita scores for male and for female subjects. For each target behaviour, a total frequency per observation for each male subject was divided by the total number of male subjects in the group to arrive at a male per capita score. Likewise, female subjects' frequencies per observation were divided by the total number of females in the group to arrive at a female per capita score. For each social group, median values were calculated across male per capita scores and across female per capita scores to establish a central tendency for male per capita scores and for female per capita scores for each observation. Last, an average was taken across median scores for male per capita scores and for female per capita scores to arrive at a central tendency for males and a central tendency for females within each group for each season.

A Wilcoxon matched-pairs test was used to compare summer average per capita scores to autumn average per capita scores for each behavioural variable. That test was also used to compare average male per capita scores across seasons and to compare average female per capita scores across seasons.

In addition, average group per capita scores, average male per capita scores, and average female per capita scores were also compared to the total space provided per animal per social group ($n = 5$ male group per capita scores; $n = 4$ female group per capita scores). A Spearman rank order correlation coefficient was used to measure the relationship between enclosure size and behavioural frequencies (Martin & Bateson 1986).

## Results

**Table 4** Correlation between agonistic behaviours and dietary diversity across all groups and both seasons[a].

| Dependent variable | Diversity method used | | |
| --- | --- | --- | --- |
| | Previous day | Previous week | Seasonal |
| Attack | 0.058 | 0.058 | 0.407 |
| Threat | 0.188 | -0.072 | 0.039 |
| Escape | -0.069 | -0.147 | 0.409 |
| Submit | 0.037 | 0.003 | 0.269 |

[a] Spearman's rank order correlation coefficients between the average per capita frequency of each behaviour for each group, in both seasons ($n = 10$, one per capita group score per season), with the diversity of food each subject in the group received in both seasons. Note: all subjects in each social group received the same number of pieces and types of fruit at each feeding.

## Shannon diversity measures

The autumn season was characterized by a lower seasonal Shannon index of diversity range than was the summer season (autumn season diversity = 0.94 to 1.03; summer season diversity = 0.76 to 0.96). Although correlations were non-significant, overall, the seasonal diversity index was more closely associated with the behaviour scores than diversity indices calculated from the previous day or previous week ($n = 10$, one per capita group score per season) (Table 4).

## Seasonal diversity and behaviour

The Wilcoxon matched-pairs tests revealed no significant differences between summer and autumn group average per capita behaviour frequencies. There was also no significant difference between summer and autumn male per capita behaviour scores or between summer and autumn female per capita behaviour scores.

## Enclosure size and behavioural frequencies

Spearman rank order correlation tests revealed negative correlations between space per animal and group average per capita behaviour frequencies. Less space per animal was generally associated with increased frequencies of agonistic behaviours during both summer and autumn seasons (Table 5). In addition, for male average per capita frequencies, there was a significant negative correlation between levels of submissive behaviours and enclosure size during the summer season, when fruit diversity was increased ($r_s = -1.000$).

## Discussion

The impact of dietary diversity on social interactions in captive primates has not been specifically addressed in previous feeding enrichment studies. The present study suggests that pre-feeding agonism is not strongly correlated with the provision of a higher diversity of fruit at their morning meal. Increased fruit diversity provided during the summer months was not correlated with increased pre-feeding agonism when all subjects were considered together. Agonistic event totals did not differ significantly between summer and autumn seasons, but since the sample size (number of groups) was small and group size and composition could not be experimentally altered, this result must be treated with caution. Additionally, the summer season, which was necessarily confounded with fruit diversity, had no effect on agonism. To separate these two variables, one would need to experimentally vary fruit diversity within a season or decrease diversity in summer and increase it in autumn. This was not possible in the present study because purchasing large quantities of out-of-season fruit was cost prohibitive and the fruit was rarely available. Nieuwenhuijsen and deWaal (1982) found that when chimpanzees were moved from a large outdoor enclosure to a smaller indoor enclosure during the winter, levels of aggression increased as compared to the summer months. However, in the Nieuwenhuijsen and deWaal study, increased levels of agonistic behaviours may be attributed to housing changes (outdoor to indoor) and space reduction rather than the

seasonal differences in food availability. The negative correlation between space provided per subject and levels of agonism found in the present study supports these findings.

**Table 5** Spearman correlation coefficients $(r_s)$ comparing space per animal per social group and average per capita frequencies of behavioural variables.

| Dependent variable | Spearman correlation coefficient $(r_s)$ | |
|---|---|---|
| | Summer | Autumn |
| *Attack:* | | |
| *All subjects* | -0.707 | 0.000 |
| *Female subjects* | 0.000 | 0.000 |
| *Male subjects* | -0.775 | -0.738 |
| | | |
| *Threat:* | | |
| *All subjects* | -0.791 | -0.894 |
| *Female subjects* | -0.354 | 0.000 |
| *Male subjects* | -0.600 | 0.000 |
| *Total aggression:* | | |
| *All subjects* | -0.718 | -0.894 |
| *Female subjects* | -0.354 | 0.000 |
| *Male subjects* | -0.600 | 0.000 |
| *Escape:* | | |
| *All subjects* | -0.707 | -0.354 |
| *Female subjects* | 0.000 | 0.000 |
| *Male subjects* | -0.775 | -0.800 |
| | | |
| *Submit:* | | |
| *All subjects* | -0.564 | -0.900 |
| *Female subjects* | -0.158 | -0.894 |
| *Male subjects* | -1.000* | 0.258 |
| *Total submissive:* | | |
| *All Subjects* | -0.500 | -0.975 |
| *Female Subjects* | -0.158 | -0.975 |
| *Male Subjects* | -1.000* | -0.800 |
| *Total agonism:* | | |
| *All Subjects* | -0.800 | -0.900 |
| *Female Subjects* | -0.158 | -0.872 |
| *Male Subjects* | -0.872 | -0.200 |

* $P = 0.05$ (two-tailed test)

Significant correlations between available space and levels of submissive behaviours during summer months at PFA, when fruit diversity was increased, suggest that results may be affected by the interaction of fruit diversity with available space for male subjects. Correlations in Table 4 suggest sex, space, and seasonal fruit diversity may interact to affect levels of pre-feeding agonism. To more adequately test for this effect, subject sample sizes should be increased and fruit diversity should be varied independently of the annual calendar or season.

### Animal welfare implications

Enriching the environments of groups of captive chimpanzees by providing a variety of attractive foods (fruit) does not seem to increase tension or lead to increased pre-feeding agonism. Managers should be encouraged to provide a varied diet reflecting the food preferences exhibited by chimpanzees in the wild. Results indicate enclosure size can also impact animal welfare as decreased space resulted in increased agonism regardless of season.

### Acknowledgements

### References

Bygott J D 1974 Agonistic behaviour and dominance in wild chimpanzees. *PhD Thesis* University of Cambridge

deWaal F B M and Hoekstra J A 1980 Contexts and predictability of aggression in chimpanzees. *Animal Behaviour 28:* 929-937

Fritz J 1989 Resocialization of captive chimpanzees: an amelioration procedure. *American Journal of Primatology Supplement 1:* 79-86

Fritz P and Fritz J 1979 Resocialization of captive chimpanzees: ten years of experience at the Primate Foundation of Arizona. *Journal of Medical Primatology 8:* 202-221

Ghiglieri M P 1984 *The Chimpanzees of Kibale Forest: A Field Study of Ecology and Social Structure.* Columbia University Press: New York

Goodall J van Lawick 1965 Chimpanzees of the Gombe Stream Reserve. In DeVore I (ed) *Primate Behavior: Field Studies of Monkeys and Apes.* Holt, Reinhart and Winston: New York

Goodall J 1968 Behaviour of free-living chimpanzees of the Gombe Stream Reserve. *Animal Behaviour Monographs 1:* 161-311

Goodall J 1986 *The Chimpanzees of Gombe: Patterns of Behavior.* Belknap Press: Cambridge, Massachusetts

Halperin S D 1979 Temporary association patterns in free ranging chimpanzees: an assessment of individual grouping preferences. In Hamburg D A and McCown E R (eds) *The Great Apes* Benjamin/Cummings Publishing Company: Menlo Park

Hladik C M 1977 Chimpanzees of Gabon and chimpanzees of Gombe: some comparative data on the diet. In Clutton-Brock T H (ed) *Primate Ecology: Studies of Feeding and Ranging Behavior in Lemurs, Monkeys and Apes.* Academic Press: New York

Izawa K and Itani J 1966 Chimpanzees in Kasakati Basin, Tanganyika: (1) ecological study in the rainy season, 1963 - 1964. *Kyoto University African Studies 1:* 73-156

Jones C and Sabater Pi J 1971 Comparative ecology of *Gorilla gorilla* and *Pan troglodytes* in Rio Muni, West Africa. *Bibliotheca Primatologica 13:* 1-96

Martin P and Bateson P 1986 *Measuring Behaviour: An Introductory Guide.* Press Syndicate of the University of Cambridge: New York

McGrew W C 1981 Social and cognitive capabilities of nonhuman primates: lessons from the wild to captivity. *International Journal for the Study of Animal Problems 2(3):* 138-149

Nieuwenhuijsen K and deWaal F B M 1982 Effects of spatial crowding on social behavior in a captive chimpanzee colony. *Zoo Biology 1:* 5-28

Nishida T 1970 Social behavior and relationship among wild chimpanzees of the Mahali Mountains. *Primates 11:* 47-87

Reynolds V and Luscombe G P 1969 *Social Behavior of Chimpanzees in an Open Environment.* 6571st Aeromedical Research Laboratory, Aerospace Medical Division, United States Air Force

Reynolds V and Reynolds F 1965 Chimpanzees of the Budongo Forest. In DeVore I (ed) *Primate Behavior: Field Studies of Monkeys and Apes.* Holt, Reinhart and Winston: New York

Subcommittee on Conservation of Natural Populations 1981 In *Techniques for the Study of Primate Population Ecology.* National Academy Press: Washington DC

Uehara S 1990 A preliminary report on age differences in plant-feeding behaviors among adult and adolescent males. In Nishida T (ed) *The Chimpanzees of the Mahali Mountains: Sexual and Life History Strategies.* University of Tokyo Press: Tokyo

Wilson W L and Wilson C C 1968 Aggressive interactions of captive chimpanzees living in a semi-free-ranging environment. *Technical Report No. 68-9.* Aeromedical Research Laboratory, Holloman Air Force Base, New Mexico

Wrangham R W 1977 Feeding behaviour of chimpanzees in Gombe National Park, Tanzania. In Clutton-Block T H (ed) *Primate Ecology: Studies of Feeding and Ranging Behavior in Lemurs, Monkeys and Apes.* Academic Press: New York