Feeding Captive Siamangs: A Nutrition Analysis and Some Proposals to Enhance Feeding in a More Natural Manner

Mathias Orgeldinger
Seumestraße 13, D-90478 Nürnberg, Germany

INTRODUCTION

Feeding of captive siamangs (*Hylobates syndactylus*) as part of the daily routine normally works without problems. It is usually based on experience, but there is little or no representative information on the quantity and quality of food or on the way in which it should be presented to the animals in order to ensure an optimal simulation of natural conditions. The aim of this study is to fill this gap by providing an empirical description of zoo experience and by comparing these findings with published data from wild siamangs.

1. FOOD COMPOSITION AND DAILY CONSUMPTION

1.1. Method

The process of food provision and intake was analysed at the zoological gardens of Berlin, Erfurt and Zürich (one visit each), Budapest, Dresden and Duisburg (two visits each) and Frankfurt (four visits). Each visit had a duration of 3-7 consecutive days. Neither the amount or diversity of provisions nor the mode of food preparation was changed for the purpose of this study. The weight of every food type provided (e.g. apple, banana, carrot) was determined with a digital scale and compared with the uneaten items found in the cage the next day. In order to estimate the loss by drying or vermin, small amounts of each food type were placed outside the cage and weighed simultaneously. These control data were used to calculate the original fresh weight of the remaining food items. A total of 2,450 weight data were collected during 65 days. Food intake was measured for pairs and groups, respectively, including a total of 26 siamangs (15 adults, 3 subadults, 4 juveniles, 4 infants). The results of siamang weight estimation by age (Orgeldinger, 1994a) were used to calculate the biomass of the different pairs and groups. Data sets of the same zoo were pooled in order to get independent samples of seven different housing conditions. Food type components (water, protein, fat and available carbohydrate) are listed in nutrition tables as constituents per 100-gram edible portion - (Souci et at., 1986). Nutrition values of some items have not been analysed by Souci et at. (e.g. some skins of fruits, mealworms, leaves of deciduous trees). The amount of these food types was very small. In such cases, nutrition values of supposedly similar items or data reviewed in Berger et at. (1986) were used, if available.

The following list shows all food types which were offered during this study; they are arranged in twelve food categories (following Soucietat., 1986). 1: milk and dairy products (cream cheese, dried milk, milk, yoghurt). 2: eggs. 3: meat, poultry and insects (chicken, mealworms, migratory locusts, minced meat). 4: cereals and cereal products (barley, biscuit, bread, concentrated feed, crisp bread, maize, porridge oats, rice, wheat bran, wheat grits, wheat seedlings). 5: roots and tubers (beetroot, carrot, celeriac, kohlrabi, potato, radish, swede). 6: leaves and stems (broccoli, brussels sprout, cabbage, cabbage lettuce, kale, cauliflower , chicory, chive, cress, fennel, foliage of different deciduous trees, garlic, leek, onion, parsley, spinach, watercress). 7: vegetable fruits (bean, cucumber, sweet peppers, tomato, zucchini), 8: legumes and oil

seeds (linseed, soybean flour, sunflower seeds). 9: fruits with cores and stone fruits (apple, cherry; peach, pear, quince). 10: berries (grapes, raisins). 11: exotic fruits (avocado pear, banana, Chinese gooseberry, fig, grape- fruit, lemon, lychee, melon, orange, pineapple, tangerine, water melon). 12: nuts (peanuts, almonds). Provisions of food categories 1,2 and 4 were usually mixed, and enriched with vitamins and minerals, offered as 'monkey bread'.

1.2. Results

At each zoo, a mean of 26 (range: 19-37) different food types were offered to the animals. Daily food provision ranged from 1.17 kg to 1.71 kg per siamang (mean: 1.50 kg, SD = 0.2, N = 7 housing conditions). Figure 1 [not reproduced] shows the provided amount of food (kg) and the corresponding intake by siamangs expressed in % by weight of the total food offered (N = 7). A mean of 82.5% (range: 70.6-92.2) of the daily food provision was actually consumed (Fig. 1, sum of food intake values). Four categories (i.e. fruits with cores and stone fruits, exotic fruits, roots and tubers, leaves and stems) make up 65.4%, whereas the eight remaining categories represent only 17.1 % by weight (Fig. 1). Food intake as a percentage of the provided food is shown in Figure 2 [not reproduced]. Siamangs eat particularly high proportions of such items as succulent berries and various fruits. In contrast, relatively high proportions of the dry items (oil seeds, cereals, nuts) or of items with a high fibre content (leaves and stems) remain in the cage (Fig. 2), even if they are offered rarely (see Fig. 1).

Figure 3 [not reproduced] shows the relative contribution of each food category to the total energy and water intake, respectively. Water content is highly correlated with the fresh weight of each food category (see Fig. 1), in contrast to the energy value. About 20% of the energy budget, for instance, is covered by cereals and cereal products (Fig. 3), although they represent only 5% by weight of diet intake (Fig. 1). Figure 4 [not reproduced] shows the relative contribution of each food category to the total intake of proteins, fat and carbohydrates, respectively. Although all categories listed in Figure 4a [not reproduced] represent only 6% of the food consumed by captive siamangs, the contribution of these categories (nuts, meat, eggs and dairy products) to the protein and fat budget of the animals is important. Furthermore, captive siamangs take about 20% of both their protein and fat budget from cereals and cereal products including commercial concentrated feed (Fig. 4b [not reproduced]). On the other hand, more than half of the carbohydrate budget comes from core fruits, stone fruits or exotic fruits (Fig. 4b).

Daily food intake per kg live weight of siamangs ranged from 95 g to 165 g (mean: 130 g, SD = 24, N = 7 housing conditions). Other parameters of daily intake per kg live weight are: energy 331 KJ (range: 262-410), water 107 g (76-136), protein 2.6 g (2.0-4.6), fat 1.0 g (0.7-1.5), available carbohydrate 14.3 g (11.0-19.3). These values were first calculated using 26 siamangs of all age classes, including lactating females. The reproductive status, locomotor activity and size of the animals, however, influence their energy consumption to some degree. The younger the animal, for example, the higher is its energy intake per kg body weight. Therefore data of four siamang pairs living in three zoos with similar housing conditions were pooled in order to determine the daily intake rates (per kg live weight) for adults only: diet weight 127 g, energy 322 KJ , water 105 g, protein 2.3 g, fat 1.0 g and available carbohydrate 14.0 g. Mean body weights of captive adult siamangs are 12.8 kg for males and 10.5 kg for females (Orgeldinger, 1994a). Using a mean body weight of 11.65 kg and assuming a food composition similar to that in Figure 1, the daily food consumption of an adult siamang is 1.48 kg. This diet provides it with 3,751 KJ energy, 1.2 litres water, 26.8 g protein, 11.7 g fat and 163 g available carbohydrate.

1.3. Discussion

The goal of this part of the study is an empirical description of the quantity and quality of food consumption in zoo siamangs. The results are less accurate than values determined in a metabolic experiment. They are, nevertheless, of practical use to zoos wishing to supplement the diet of their siamangs. In spite of two decades of research in wild siamangs, it would be extremely difficult to carry out a detailed analysis of nutrients or a consistent description of food categories for this species in the wild. A gibbon group has access to perhaps 500 species of trees and climbers (Chivers and Raemaekers, 1986). Even if the apes select only a small proportion of these for intensive feeding (e.g. 34 identified plant species at Kuala Lompat; Chivers, 1974), the exact observation of food composition remains problematical. The results of six studies in West Malaysia and Sumatra, based on feeding time rates, indicated a highly variable diet: 32% to 61% fruits, 18% to 67% leaves and flowers, and 1% to 21% insects (see review in Orgeldinger, 1994b). Among the factors which may be responsible for this variability, I would like to mention population-specific, geographic and seasonal variation as well as different observation methods.

It is evidently hard to get nutrition or even consistent food category - information from research in natural habitats. While, in the past, H. syndactylus has been labeled as a folivore species, the correct description is that of a 'fig seeker' (Chivers and Raemaekers, 1986). Anatomical research seems to support this classification. Using the 'coefficient of gut differentiation', which is the ratio of surface area of stomach plus caecum plus colon to surface area of small intestine, the siamang seems to be more of a frugivore (Chivers and Hladik, 1984). 'The colon is relatively bulky ... and some bacterial fermentation is likely to occur, just as it does in humans, but there is therefore some doubt as to how much use the gibbons can make of fibre' (Chivers and Raemaekers, 1986).

The results of the present study suggest that fruits of different forms are mainly offered (Fig.l) and that siamangs seem on the whole to prefer these succulent food items, whereas leaves and stems are ignored to a greater extent (Fig. 2). Nevertheless, fibre must be an important component of siamang food for the prevention of looseness of stools (M. Roberts, cited in Chivers and Raemaekers, 1986). It also appears that the composition of zoo diets usually simulates the diversity as well as the significance of fruits in the natural diet to a sufficient extent. Food items differing extremely from the natural diet in consistency (dry provisions) or in origin (e.g. meat, eggs, milk) were offered only in small amounts to ensure the protein and fat budget of the zoo-living apes.

Information about animal matter in the natural siamang diet is rare. Perhaps the apes occasionally plunder eggs from nests (Bünning, 1947). Daily feeding times devoted to insects vary widely, as we have already seen. Because the observation of feeding time leads to an over-representation of assumed insect intake (Chivers and Raemaekers, 1986), the calculation of animal diet in the wild is very difficult. Nevertheless, Chivers and Raemaekers (1986) estimate that the apes could ingest from 2 g to 38 g of insects each day. It is therefore desirable that zoos try to ensure this intake of invertebrates (e.g.living mealworms, locusts etc.) as far as possible. In fact, about 3.5% of animal matter (meat, eggs and milk products, see Fig. 1) is enough to ensure a sufficient intake of essential amino-acids, but this cannot maintain or increase the apes' ability to capture living insects. As suggested below, zoo diet should not merely provide the basal nutrients but also enhance the possibility of a natural manner of feeding.

The regular provision of water or tea, for example, is the rule in most but not all the zoos I have visited in recent years. The present study reveals that zoo diet itself ensures an amount of about 1.2 litres of water per day per adult siamang. Beyond this, the apes are free to lick water from the ground of their cage after cleaning. One can assume that this quantity of water

is sufficient for the health of the apes. Nevertheless, changes in the weather and in the health of the animals make it necessary to provide fluid daily. Moreover, a dish with water allows the animals to drink in the typical 'gibbon manner', by dipping the hand into the fluid and sucking or licking it from the hair on the back of the hand or from the fingers, as wild siamangs have been described using water holes in trees (Chivers, 1974).

Nordin (1981) kept a 4.3-year-old female siamang in a metabolic cage where the animal could feed from five different food types ad libitum. After two weeks of adaptation a few metabolic parameters were measured during the third week. The juvenile ape preferred bananas to papayas, monkey pellets, cucumbers and 'kangkongs' (Ipomoea reptans) (order of dry matter intake; Nordin, 1981). The finding was that the daily gross energy intake per kg of live weight was 830 KJ , i.e. more than double the energy value which can be deduced from the present study. The difference between the two results exemplifies the dilemma of such research in a concrete manner. On one hand, the findings of this zoo study are generalizations because of the different siamangs, age classes and feeding conditions involved. On the other hand, however, Nordin's study presents data of a single juvenile kept in isolation for three weeks; with that method, social influences on feeding time and activity level were totally neglected.

Another way of interpreting consumption rates leads to Hladik's finding that 'primate species tend to consume food daily to the order of 15% of their body weight', leading to a predicted daily intake for wild siamangs of I.575 kg food (Chivers and Raemaekers, 1986). Beyond that, the two authors deduced daily food intake by using feeding time rates and consumption rates for different food categories, resulting in estimates of 1.25 kg to 1.7 kg per day. Bearing in mind that captive siamangs have a lower level of activity and zoo diet has a higher nutrient quality, the estimate obtained in the present study {1.48 kg/day/adult) seems to be comparable and plausible.

2. FEEDING TIME

2.1 Method

Thirty-four siamangs (27 adults, 2 subadults, 5 juveniles) from 14 pairs or groups were observed in ten zoos (Antwerp, Berlin, Branfere, Budapest, Dresden, Duisburg, Erfurt, Frankfurt, Krefeld and Zürich). Feeding time was scanned every minute {in some cases every two minutes) for a total of 275 hours. Each pair and group was observed for 20 hours, except for one pair (10 hours), and two groups {15 and 30 hours respectively). Observations were carried out simultaneously for each member of a pair or group. Data collection was equally distributed over the day from 7 a.m. to 5 (6) p.m., with the same amount of scans for each hour of the animals' activity time. The observation period usually covered at least one week per group to ensure a random distribution of scan sampling. The data sets of each individual were calculated separately. Time when food was offered to the animals varied between zoos and even between groups in the same zoo, but in all cases at least one feeding took place before 12 a.m. In four cases food was provided once, in eight cases twice and in two cases three times a day. The greatest amount of daily provision, however, was offered between 8 a.m and 1 p.m. in 12 out of 14 pairs/groups. With only a few exceptions food was always available throughout the whole day (remember the consumption rate of 82.5%).

2.2. Results

On average captive siamangs spend 14.1% (SD = 5.8, range: 6.2-33.3, N = 34) of daily activity in feeding. Juveniles and subadults seem to spend a little more time feeding (mean: 16.3%, SD = 4.4, range: 9.8-21.8, N = 7) than their parents {mean: 13.7%, SD = 8.0, range: 6.2-33.3, N = 9), but the difference is not significant. Similarly, adult females {mean: 14.8%, SD = 7.4,

range: 6.2-33.3, N = 14) spend insignificantly more time in feeding than adult males (mean: 12.1 %, SD = 3.8, range: 6.5-18.9, N = 13). Mean distribution of daily feeding time (= 100%) of adults (N = 27) and juveniles (V = 5) is shown in Figure 5 [not reproduced].

Drinking behaviour, including licking of water drops, amounted to 0.27% (SD = 0.71, range: 0-3.5, N = 34) of daily activity, but this value is, influenced by two individuals exhibiting extreme amounts of licking behaviour .If we exclude these two samples, mean water intake rate is only 0.1% of daily activity (SD = 0.18, range: 0-0.8, N = 32).

2.3. Discussion

Wild siamangs spend 40% to 55% of their daily activity budget feeding and an additional 12% to 26% ranging, i.e. probably in search of food resources (see review in Orgeldinger, 1994b). In contrast, captive siamangs spend only about 14% of the day feeding, without any need for ranging and searching. As a result, these captive apes increase their social activities to a remarkable degree (Orgeldinger, 1994b), as has been reported for other captive primates such as baboons (Rowell, 1972). Nevertheless, zoo-living adults spend 29% of their daily activity in watching (without a special social or territorial function) and 13% in non-social resting behaviour (Orgeldinger, 1994b). Clearly, captive siamangs spend much more time in 'inactivity' than wild ones. Possibly they could be stimulated to be more active by using environmental enrichment methods (see section 3, below). This could reduce boredom in the animals and also make them more attractive from the point of view of zoo visitors.

Daily feeding activities of captive adult siamangs increase steadily throughout the day (with a slight decrease around midday) and peak at about 4 p.m. (Fig. 5). Except in the early morning,juveniles show a similar daily feeding activity, but this result may not be significant in view of the low sample size for juveniles (Fig. 5). As a whole, captive siamangs spend most time feeding in the afternoon. Considering that most zoos offer the main feed in the morning, this finding seems paradoxical. Certainly the low feeding rate in the early morning is traceable to the fact that the animals disdain food which has been left out overnight. Clearly, the dispersal of food items throughout the enclosure increases with time up to the point of feeding by the keepers, and the longer the food is displayed the more time is needed to select the items. Furthermore, the apes seem to feed more quickly during the first 15 minutes after new food is offered than later when their interest in food has decreased. Nevertheless, captive siamangs do most of their feeding in the afternoon, irrespective of the , amount of available fresh provisions.

Chivers and Raemaekers (1986) reported the variation of feeding by adult males in each hour of the day. (In Figure 6 [not reproduced] these data are compared with the findings of the present study.) It appears that free-ranging males show most feeding between 7 and 8 a.m., and remain on approximately the same level in the following hours, while captive males show their feeding peak in the late afternoon. How can we explain this difference? As Oates (1987) pointed out, in general 'primates wake up with empty stomachs', and their first feeding bout is concentrated on highly digestible and high- energy food such as Jipe fruits or young leaves, in order to out-balance the overnight energy loss. Captive primates, however, living usually in temperature-controlled enclosures and having access to high-quality zoo food, do not seem to be forced to early morning feeding in the same way. Perhaps more important, according to my own experience of about 2,500 hours of observation, food competition in captive siamangs is usually insignificant. Therefore, the individuals are free to feed at any time of day, and they actually do so when external stimuli, locomotion and some social activities decrease, that is in the late afternoon hours.

3. METHODS OF FEEDING

The quality of husbandry efforts should not be judged solely by the number of surviving offspring. In order to save a species from extinction, it should have the opportunity to reproduce while retaining all its motor and social abilities. Therefore, housing conditions should simulate natural habitats as far as possible. The diversity, quantity and quality of zoo foods seem to fit the demands of siamangs. Much effort remains to be directed, however, at increasing individual feeding times and at encouraging siamangs to use their specific motor abilities, such as 'terminal branch feeding'.

First, feeding by keepers should occur at least twice, better three or more times a day to ensure fresh food and to stimulate the apes repeatedly. Feeding time in the wild is more or less equally distributed throughout the day (Fig. 6 [not reproduced]), and the simulation of this condition can be promoted by offering smaller amounts of food at more frequent intervals. Second, except for infants, food items need not be prepared or cut -juveniles, subadults and adults are able to handle whole apples, carrots and potatoes very well and therefore it is not necessary to cut them into small pieces. Fruits with non-poisonous skins, such as bananas, should also be provided whole. As an extreme example, juvenile siamangs are able to get to eat even small coconuts: by throwing and kicking them the shell was broken accidentally, Besides, whole food items do not dry out so quickly, and provide more intensive occupation for the animals. Clearly, it is easier for an individual to monopolise a favourite food, but, in my experience, the opposite occurred. Passive food sharing is common in captive siamangs, but even active food sharing was observed in one pair and one family group. In both situations whole apples were offered by the keepers and the adult male bit pieces out of the apple or a larger piece of it and offered them to the female and juvenile respectively (Orgeldinger, 1994b). So larger food items possibly influence food sharing behaviour, as is reported in bonobos, too (White, 1992), In short, offering whole fruits may influence both feeding and social behaviour in a positive way.

Offering branches with leaves is another method of both increasing feeding time and demanding motor abilities from the apes. Because of the siamang's mainly frugivore status, it does not appear to be necessary to offer frozen or dried leaves in the winter as in mainly folivorous colobine monkeys (Walter and Perschke, 1994). In summer, on the other hand, fresh twigs and branches are easily available in the zoo or elsewhere, and could be offered without great expenditure of work. Krefeld Zoo, for example, is quite successful in feeding long willow branches. These branches, or even small trees, were fixed at the back of the cage (and had the incidental effect of making the enclosure more natural-looking). On the first two days intensive leaf-plucking behaviour could be observed, and later on the apes sometimes peeled the bark or manipulated the branches in other ways. In any case, a change in their manner of feeding was ensured for at least some days.

Usually food was offered on the floor or on platforms not higher than one metre. As a result, adult siamangs spent a mean of 41.1% of daily feeding time on the ground (SD = 27.4, (0-89.8), N = 27) while in all daily activity they used the floor in a mean of only 27.7% (SD = 25.0, (0.8- 78.6), N = 27) In other words, the proportion of feeding on the ground was distinctly higher than expected. In contrast to terrestrial primates, wild gibbons never pick up food items from the ground. Their characteristic feeding posture is hanging below, or sometimes sitting or standing on, a branch. Even if their health in captivity does not appear to be compromised by the traditional mode of feeding, some efforts should be directed at stimulating these arboreal apes to display their locomotor abilities. With this goal, the author conducted several tests during which siamang food was presented in a net hanging from the top of the cage.

The first test was made with a family group at Krefeld Zoo in June 1991. The net, with mesh of about 4 cm diameter, was filled with lucerne, lettuce, cabbage, broccoli, fennel and sweet peppers. In the beginning, all group members were irritated and exhibited brachiating and fearful observation alternately. Although the adult male was more interested than the juvenile female, it was finally the adult female who, after about three minutes, carefully approached the net and smelt it. Four minutes later she picked a food item out of the net and ate it. Five minutes after that, the adult male followed the example of his mate, who by then had already twenty times plucked plant parts. In the minutes that followed, both adults used the net simultaneously. The juvenile, on the other hand, obtained food items from its parents (by passive food sharing) or got items that had fallen out of the net. Thirty-one minutes after the beginning of the experiment, the juvenile had learnt to take food out of the net, too. On the following day the experiment was repeated. All group members used the net immediately in the expected manner. Usually, the apes hung by one hand from the bars above the net, using both feet to hold it steady while plucking the food items out of it (see photo below). Aggressive food competition did not occur.

Siamangs in 'natural feeding posture' at Krefeld Zoo. (Photo: Mathias Orgeldinger)

The second test was undertaken with an adult pair of siamangs at Budapest Zoo in October 1991, during a period of four days. Two nets were installed. On the first day the male collected food items from the net after three minutes, while the female needed 1.5 hours to learn to use it. On the following days, both adults used this new food supply frequently. At most only 10% of the provided food remained in the net. In contrast to the situation at Krefeld, however, the male sometimes tried to monopolise a net by showing agonistic behaviour towards his mate. On other occasions, peaceful feeding from the same net was observed as well (see photo, front cover).

A third test was carried out with a family group kept at Frankfurt Zoo (November 1991). Its success was limited, however. Two nets were installed on three consecutive days. Five minutes after the beginning of the experiment, the juvenile female Vera succeeded in using this new feeding mode. Both parents followed her example about 40 minutes later. During the following test period, Vera used the nets frequently, whereas her parents mostly ate food items which had fallen down. The adults showed r little interest in the new way of feeding. The juvenile, however, played with the two nets and defended them against her parents.

It became apparent during these tests that the net should not hold more than 2-3 kg of food, to make it easier for the animals to pluck a food item out of it. Sometimes, several siamangs were hanging on the net simultaneously; the material should therefore be strong enough to carry these weights. Furthermore, the net should be filled predominantly with roots, tubers, leaves, stems and some vegetable fruits instead of succulent fruits, because the latter decay more quickly, especially if the net is exposed to sunshine. Another point of interest is the size of the food items. Most vegetables and leaves can be used uncut, but items of harder consistency should be cut to the size of about the diameter of the mesh. Otherwise the apes will use their teeth to break out pieces of the food items and by doing so may quickly damage the net. To sum up, although the animals should 'work' for their food to some extent, it should not be too difficult for them.

The three tests demonstrated that the individual responses may differ widely, irrespective of age and sex. The unfamiliar mode of food presentation led to some agonistic food competition at Budapest Zoo, although the same pair would sit peacefully in front of their familiar food plate. Similarly, the juvenile female at Frankfurt tried to monopolise the nets as objects of play for her exclusive use. In none of these cases did food competition lead to serious aggression, however; this is, in any case, extremely rare within siamang groups. Obviously, this method of food presentation slightly increases the keepers' work; but this seems acceptable if we keep in mind that the net should stimulate the apes repeatedly and therefore is to be used only a few times per month.

In conclusion, feeding by net represents a closer simulation of natural conditions for captive gibbons. Food cannot be collected without effort, but must be plucked item by item, resulting in an increase of feeding time. It is not displayed on the floor but in a mobile net which can be attached to various locations at the top of the cage. In addition, food is better protected from mice and from contamination by faeces.

ACKNOWLEDGEMENTS

I am grateful to the officials of the following zoos for permission to work and live in the zoo, and to the keepers for their help and patience: director F. Daman, B. van Dyck, B. van Puijenbroek {Antwerp); director Dr H.-G. Klos, T. Klutznick, R. Opitz, Dr P. Rahn (Berlin); director K. Regardin, F . Bout tin, L. Desideri, C. Fournier, B. Svendsen (Branfere); director Dr J . Szijj, Dr I. Bogsch, E. Fonad, Z. Graf, L. Torok, I. Vedakovics (Budapest); director Dr H. Lucker, E.i}n8.usch, W. Ludwig, Dr H. Schneider {Dresden); directorDrW. Gewalt,J. Fengler, M. Fischer,J. Hammes,DrB. Neurohr, Dr F. Ostenrath, E. Schramke (Duisburg); director Dr N. Neuschulz, K. Hellwig, H. Hubner, C. Walter, M. Scheuner {Erfurt); director Dr R. Faust, W. Brudziak, Dr R. Dmoch, H. Fischer, C. Knott, K. Krummholz, Dr B. Matern, Dr C. Scherpner, E. Wolf, J. Zirkel (Frankfurt); director Dr W. Encke, G. Eberle, W. Golinowska, B. Karbe, H. Krull, M. Pramschiefer, K. Reymer, D. Schuler, Dr P. Vogt (Krefeld); director H. Steiner, H.-J. Dietrich, M. Hiltbrant (Studen- Biel); director Dr A. Rubel, R. Erni, Dr C.R. Schmidt, J. Stahli (Zurich). Furthermore, I would like to extend my gratitude to the supervisor of my doctoral thesis, Dr Rosl Kirchshofer, for her support and guidance during the last five years. Thanks also to my wife Jutta for encouraging this undertaking, to Dr Thomas Geissmann for correcting the manuscript and providing suggestions, and to Nicholas Gould for editing and publishing the article.

REFERENCES

Berger, G., et al. (1986): Zootierhaltung (Band 1). Verlag Harri Deutsch, Frankfurt/Main.

Bünning, E. (1947): In den Wäldern Nordsumatras. Ferd Dümmlers Verlag, Bonn.

Chivers, D.J. (1974): The siamang in Malaya: a field study ora primate in tropical rain forest. Contrib. to Primatology Vol. 4. S. Karger, Basel.

Chivers, D.J., and Hladik, C.M. (1984): Diet and gut morphology in primates. In: Chivers, D.J ., et al. (eds.): Food Acquisition and Processing in Primates, pp. 213-230. Plenum Press, New York. Chivers, D.J., and Raemaekers, J.J. (1986): Natural and synthetic diets of Malayan gibbons. In: Else, J.G., and Lee, P.C. (eds.): Primate Ecology and Conservation, pp, 39-56. Cambridge University Press.

Nordin, M. (1981): Voluntary food intake and digestion in Malaysian primates with special reference to the intake of energy and protein. Malaysian Applied Biology 10, pp. 163-175.

Gates, J .F. (1987): Food distribution and foraging behaviour. In: Smuts, B.B. et al. (eds.): Primate Societies, pp. 197-209. Univ. of Chicago Press.

Orgeldinger, M. (1994a): Monitoring body weight in captive primates, with special reference to siamangs. I.Z.N. Vol. 41/1 (No.250), pp. 17-26.

Orgeldinger, M. (1994b): Ethologische Untersuchung zur Paarbeziehung beim Siamang (Hylobates syndactylus) und deren Beeinflussung durch Jungtiere. Doctoral thesis, University of Heidelberg. Rowell, T.E. (1972): The Social Behaviour of Monkeys. Penguin Books, London.

Souci, S. W., et al. (1986): Food Composition and Nutrition Tables 1986/ 37. Wissenschaftliche Verlagsgesellschaft mbH, Stuttgart.

Walter , K., and Perschke, M. (1994): The use of leaves in feeding colobine monkeys. I.Z.N. Vol. 41/3 (No.252), pp. 10-12. [Originally published in German in Arbeitsplatz Zoo Vol. 2, No.1 (1991), pp. 28-35.

White, F. J. (1992): Meat and fruit sharing in Pan paniscus. Manuscript, 14th Congress of the International Primatological Society, Strasbourg, France, August 16-21.
