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RESEARCH ARTICLE

Assessing the Effects of Cognitive Experiments on the Welfare of Captive Chimpanzees (*Pan troglodytes*) by Direct Comparison of Activity Budget Between Wild and Captive Chimpanzees

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We investigated the effects of cognitive experiments by direct comparison of activity budgets between wild and captive chimpanzees. One goal of captive management is to ensure that the activity budgets of captive animals are as similar as possible to those of their wild counterparts. However, such similarity has rarely been achieved. We compared the activity budget among three groups of chimpanzees: wild chimpanzees in Bossou (Guinea, $n = 10$), and captive chimpanzees who participated in cognitive experiments (experimental chimpanzees, $n = 6$) or did not participate in the experiments (nonexperimental chimpanzees, $n = 6$) at the Primate Research Institute (Japan). The experimental chimpanzees voluntarily participated in computer-controlled cognitive tasks and small pieces of fruits were provided as rewards. The data from captivity were obtained on the experimental days (weekdays) and nonexperimental days (weekends). In both study sites, we followed each chimpanzee from about 7 a.m. until the time when chimpanzees started to rest in the evening. The behaviors were recorded every 1 min. The results showed that on weekdays, feeding time and resting time of the experimental chimpanzees were almost the same as those of wild chimpanzees. However, for the nonexperimental chimpanzees, feeding time was significantly shorter and resting time was longer than those of the wild chimpanzees. In contrast, no difference was found in feeding time or resting time of the two groups of captive chimpanzees on weekends. The results suggested that the cognitive experiments worked as an efficient method for food-based enrichment. Am. J. Primatol. 73:1231–1238, 2011.

Key words: cognitive experiments; activity budgets; chimpanzees; welfare; wild-captive comparison

INTRODUCTION

One goal of environmental enrichment is to encourage captive animals to express natural behaviors which are seen in the wild [Bloomsmith, 1988; Hosey et al., 2009; Pruetz & McGrew, 2001]. This is because there is usually an assumption that behavioral differences between wild and captive animals denote deficiencies in the captive environments [Duncan & Fraser, 1997]. For example, chimpanzees in the wild spend considerable time foraging and processing food items. In contrast, chimpanzees in captivity get processed food easily from humans and eat it without effort. In order to compensate for these differences, there have been some attempts to increase feeding time by food-based enrichment [Baker, 1997; Bloomsmith, 1988]. However, it is difficult to increase the feeding time in captive environments to the level of that of wild chimpanzees because of limitation of the amount of food and human labor. Therefore, developing an efficient way of increasing feeding time in captive animals to approximate that in the wild counterparts.

Cognitive experiments are now conducted in many zoos as well as research facilities around the world, and their potential positive effects on the welfare of subject animals have been suggested [for review; Ross, 2010]. For example, since animals can get food rewards during the cognitive experiments, the daily cognitive experiments might work as a method for efficient food-based enrichment. Therefore, also considering a growing interest in animal welfare [Morimura et al., 2010], it is

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important to assess its effects from the point of view of food-based enrichment. Nevertheless, no systematic assessment has been conducted on this topic.

This study directly compared behaviors between wild and captive chimpanzees to assess the effects of cognitive experiments. In order to assess the success of environmental enrichment, most enrichment research has focused on changes in animals' activity budgets [Young, 2003], although direct comparisons of activity budget between wild and captive animals have rarely been conducted [Kerridge, 2005; Veasey et al., 1996]. However, without actually comparing the behaviors between wild and captive individuals, it is not clear how and which aspects of captive animals' life we should change [Hosey et al., 2009]. Thus, such comparison of behaviors is important for validating the research and management of captive animals [Höhn et al., 2000; Kerridge, 2005].

Chimpanzee behaviors in the wild have been studied for a long time at several field sites. The activity budgets of chimpanzees have been published and found to vary across field sites. For example, the chimpanzees spent around 56% of the day feeding in Gombe [Wrangham, 1977], 43 % in Tai [Doran, 1997] and 30% in Mahale [Matsumoto-Oda, 2002; Pruetz & McGrew, 2001]. Even at the same research site, the activity budgets differed in different report. In Bossou, feeding time was about 40% in Yamakoshi [1998], 25.6% in Takemoto [2004], and 22.5 % in Hockings et al. [2009]. Therefore, using the data that were collected using different methodologies can cause problems in analyzing the data and interpreting the results.

Hence, the purpose of this study was to examine whether cognitive experiments work as an efficient food-based enrichment method by directly comparing the activity budgets of captive chimpanzees with their wild counterparts.

METHODS

Study Sites and Study Subjects

The subjects were 10 wild chimpanzees and 12 captive chimpanzees. The field site of the wild chimpanzees was Bossou village (N 7.39, W 8.30), in Guinea Republic, West Africa [Matsuzawa et al., 2011]. This village is located near the boundary of Cote d'Ivore and Liberia. Ten out of the 13 chimpanzees in Bossou were the subjects of this study (Table I; Fig. 1). The home range of the Bossou chimpanzee group was 15–20 km^2. It was comprised of primary, regenerated, and secondary forests on hills and in villages, and included old and new cultivated fields of villagers. We chose Bossou for the study field for wild chimpanzees since the social composition of the Bossou chimpanzees was similar to that of subject chimpanzees in the captivity and they were well habituated to humans because of the research activity conducted there since 1976

TABLE I. List of the Subjects (a) Bossou Chimpanzees and (b) PRI Chimpanzees

	Name	Sex	Age	Mother	Group
(a) Bossou chimpanzees					
Juvenile	Joya	F	5	Jire	
Adolescent	Peley	M	11	Pama	
	Jeje	M	12	Jire	
	Fanle	F	12	Fana	
Adult	Yolo	M	18	Yo	
	Foaf	M	29	Fana	
	Jire	F	33<[a]	NA	
	Fana	F	33<[a]	NA	
	Velu	F	33<[a]	NA	
	Yo	F	33<[a]	NA	
(b) PRI chimpanzees					
Adolescent	Pal	F	9	Pan	Exp
	Cleo	F	9	Chloe	Exp
	Ayumu	M	9	Ai	Exp
Adult	Pan	F	25	Puchi	Exp
	Popo	F	27	Puchi	Non-Exp
	Chloe	F	28	NA	Exp
	Ai	F	31	NA	Exp
	Mari	F	31	NA	Non-Exp
	Akira	M	31	NA	Non-Exp
	Reiko	F	43	NA	Non-Exp
	Puchi	F	43	NA	Non-Exp
	Gon	M	43	NA	Non-Exp

Four adult chimpanzees in Bossou (Jire, Fana, Velu, and Yo) were already adult in 1976. Six chimpanzees in PRI (Pal, Cleo, Ayumu, Pan, Chloe, and Ai) were the experimental chimpanzees.
[a]These four females were already adult in 1976.

Fig. 1. An example of processing food. A chimpanzee in Bossou tried to eat fruits of oil palm (*Elaeis guineensis*). They need to choose ripe one and remove it from substrate before eating. (Photo taken by A. Shah & F. Rogers).

[Sugiyama & Koman, 1979]. Since 1988, intensive studies on tool use have been performed in the ''outdoor laboratory'' in the core area of the Bossou group [Biro et al., 2003; Matsuzawa, 1994]. The laboratory was open occasionally from October 11, 2009 to October 21, 2009 during this study period, and on these days, oil palm nuts and stones were

provided by the other researcher [Carvalho et al., 2009]. The chimpanzees stayed at the laboratory for less than 1 hr.

The study site of the captive chimpanzees was the Primate Research Institute (PRI), in Aichi prefecture, Japan (N23.06, E136.57). The subject chimpanzees were 12 chimpanzees (three males and nine females) aged between 9 and 43 years (Table I). We gave the name ''experimental chimpanzee'' to the chimpanzees who participated in the experiments ($n = 6$) and ''nonexperimental chimpanzee'' to the other chimpanzees ($n = 6$). Cognitive experiments have been conducted on the chimpanzees at the PRI since 1978 [Hayashi & Matsuzawa, 2003; Hayashi & Takeshita, 2009; Matsuzawa, 2003; Matsuzawa et al., 2006]. For these cognitive experiments, the experimenters called the chimpanzees in the outside enclosures and led them to the experimental rooms through corridors. An example of a cognitive experiment is shown in Figure 2. The chimpanzees participated in the experiments voluntarily and it was completely up to the chimpanzees whether he or she would come to the experimental rooms [Matsuzawa, 2006]. We never observed that the chimpanzees refused to participate in the experiment during this period of study, and regarded that they voluntarily participated in the experiments from their behaviors. For example, before experimenters arrived, chimpanzees already sat down in front of the door of the corridor leading to the experimental rooms, sometimes checking human activities through windows. Also, when the experimenters came to call the subjects, they rushed to the door of the corridor and sometimes exhibited grunts similar to food grunts and pant-hoots [Goodall, 1986]. The experiments were usually carried out six days per week from Monday to Saturday. The maximum number of the cognitive experiments per day was five and each experiment continued from 5 to 60 min. The first experiment started at around 9:00, and then the second at 10:00, the third at 13:30, the fourth at 14:30, and the last at 15:00. The number of experiments varied across the subjects and days. During the cognitive experiments, small pieces of apples were provided approximately every 10 sec as a reward. The experimenters occasionally gave the chimpanzees small amounts of other seasonal fruits too. The total amount of food per day was the same between experimental and nonexperimental chimpanzees, but the time for eating and processing foods could be prolonged via the experiments.

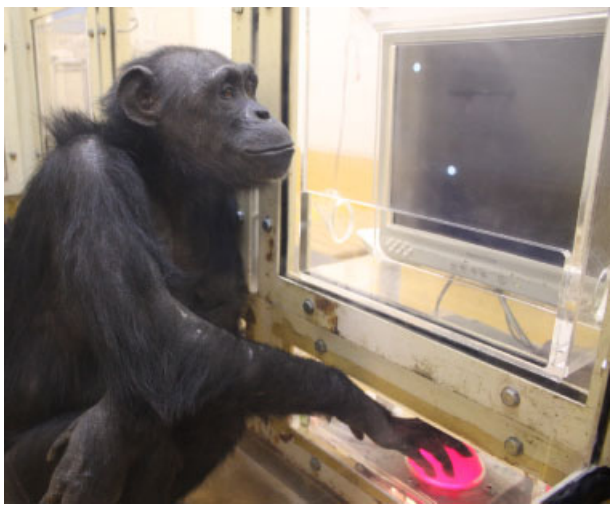

Fig. 2. An example of cognitive experiments in which the chimpanzees participated. A chimpanzee manipulated a trackball to get a reward. (Photo taken by T. Kaneko).

These 12 subject chimpanzees lived in an outdoor enclosure with the other conspecific (13 in total and divided into two groups). The outdoor enclosure was separated into two compartments: one was a 700-m^2 outdoor compound with 15-m-high climbing frames, a small stream and numerous trees, and the other was a 250-m^2 outdoor compound with climbing frames and two small streams [Matsuzawa, 2006; Ochiai & Matsuzawa, 1997]. The chimpanzees were fed seasonal fruits and vegetables, and monkey pellets three times a day. A few branches were provided after lunch both on weekdays and weekends.

In addition to cognitive experiments, there were some differences in husbandry of chimpanzees between on weekdays and weekends. On weekdays, the caregivers gave the chimpanzees additional foods such as sugar cane a few times per day. Also, there was a difference of use of space, as each group of chimpanzees alternately used the larger outdoor compartment every other day on weekdays. In contrast, on weekends when there were less keepers worked around than on weekdays, the chimpanzees could use only smaller outdoor compartments for safety reasons. However, the important thing is that only the existence of cognitive experiments was different between experimental and nonexperimental chimpanzees. The care and use of the chimpanzees complied with the Guide for the Care and Use of Laboratory Primates 2nd Edition [2002] of this institute, and the legal requirements of the country, and adhered to the ASP Principles for the Ethical Treatment of Non Human Primates.

Data Collection

The observations were made in Bossou from September to October 2009. The total observation time was 134.7 hr (13.28 ± 6.0 hr/ind.). The first author (Y. Y.) followed the chimpanzees by using the focal animal sampling method and recorded the behaviors every 1 min [Martin & Bateson, 2007]. The local guides and Y. Y. usually started from the base

camp at around 6:30 and came back after the chimpanzees started to make a nest for rest in the evening (around 18:30). The order of the focal subjects was decided randomly. The time when the chimpanzees were found varied depending on the observation day. If we lost the subject chimpanzee, we changed the focal subject. The observations that continued more than 90 min were included in the analysis. In order to check for possible bias in the time of day, we divided the data into three time periods (7:00–11:00, 11:00–15:00, 15:00–18:30). We compared the individual sum of observation time in each time period and found no differences among them (Analysis of variance, df = 2, $F = 2.05$, n.s).

The observations were made in the PRI from December 2009 to February 2010. The total observation time was 227.05 hr (20.6 ± 0.19 hr/ind.). The data collection method was basically the same as that in Bossou. The data for each subject were obtained both on the days when the cognitive experiments were conducted (weekdays) and the days when no experiments was conducted (weekends). There was no difference in the mean temperature between on weekdays and weekends (measured in Nagoya; N35.10, E 136.57). As mentioned in the previous section, chimpanzees could use only smaller outdoor compartments on weekends. Therefore, we observed the behaviors only on the days when the subjects used smaller outdoor compartments both on weekdays and weekends.

On each day, Y. Y. followed a focal individual from 7:00 until around 17:00, when the chimpanzees started to rest. The general behaviors were recorded every 1 min. The behaviors observed before the experiments were also recorded ad-lib. The order of the focal subjects was decided randomly. We used PDA (Clie, sony PEG-TG50) for collecting data in captivity. The software used was ''PBRS zoo cafeteria'' developed by N. Morimura and Y. Ueno [Morimura & Ueno, 2004]. The behaviors were divided into four categories: Feed, Rest, Move, and Others. Feed included three types of behaviors: Eat, Explore, and Experiment. Eat was ''Put foodstuff into mouth, bite and chew, wadge and swallow it,'' Explore was ''Search foodstuff and remove foodstuff from the substrate, feeder and process it,'' and Experiment was ''Work at a cognitive task. Chimpanzees manipulate a touch panel, track ball, buttons or blocks to solve the task provided and get rewards sporadically depending on the reinforcement schedule.'' Rest was ''Remain immobile while sitting or lying.'' Move was ''Quadrapedal walking with knuckles on the ground or with open palm on the ropes, bipedal walking and brachiation'' [Nishida et al., 1999].

Data Analysis

For comparing the activity budgets among the three groups of chimpanzees, we used the independent *t*-test. We used the paired *t*-test to compare the activity budget of captive chimpanzees between on weekdays and weekends. To compare the feeding rate per hour (diurnal feeding rhythm) between the different groups of chimpanzees, we used two-way ANOVA to determine whether there was significant interaction between time of day and group. For the data analysis, we used the statistical software SPSS 13.0. The level of significance was set at $P < 0.05$, two-tailed and adjusted with Bonferroni correction for multiple tests.

RESULTS

Comparison of the Activity Budget Between Wild and Captive Chimpanzees

The activity budgets of each group of chimpanzees are shown in Figure 3. On weekdays, the feeding time and resting time of the experimental chimpanzees and wild chimpanzees were almost the same (Independent *t*-test: Feeding $t = 0.051$, df = 14, $P = 0.960$; Resting $t = 0.869$, df = 14, $P = 0.399$), whereas for the nonexperimental chimpanzees, feeding time was significantly shorter and resting time was significantly longer than those of wild chimpanzees (Feeding $t = -6.026$ —This t value was calculated by assuming that variances were not equal. —, df = 14, $P < 0.001$; Resting $t = 2.796$, df = 14, $P = 0.014$;). In contrast, on weekends, for the both groups of captive chimpanzees, feeding time was shorter and resting time was longer than those

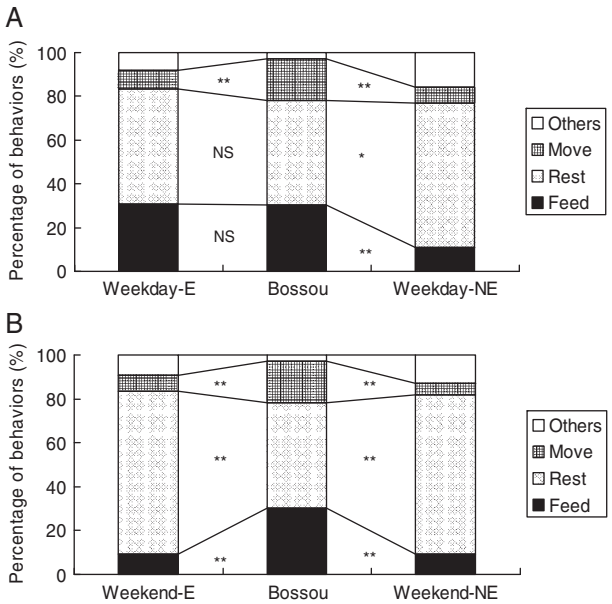

Fig. 3. Comparison of activity budgets of the three groups of chimpanzees. (**A**) Comparison of activity budgets of experimental (E) and nonexperimental (NE) chimpanzees on weekdays and Bossou chimpanzees. (**B**) Comparison of activity budgets of experimental (E) and nonexperimental (NE) chimpanzees on weekends and Bossou chimpanzees. The level of significance was set at $P = 0.017$ corrected with the Bonferroni method, $^{**}P < 0.01$, $^{*}P < 0.017$.

of wild chimpanzees (Exp vs. Bossou: Feeding $t = -5.166$, df = 14, $P < 0.001$; Resting $t = 4.872$, df = 14, $P < 0.001$; Non-Exp vs. Bossou: Feeding $t = -5.042$, df = 14, $P < 0.001$; Resting $t = 3.812$, df = 14, $P < 0.01$). However, the moving times of both groups of captive chimpanzees on weekdays and weekends were significantly shorter than that of wild chimpanzees (Exp vs. Bossou: Weekday Moving $t = -4.386$, df = 14, $P < 0.01$; Weekend Moving $t = -4.719$, df = 14, $P < 0.01$; Non-Exp vs Bossou: Weekday Moving $t = -4.163$, df = 14, $P < 0.001$; Weekend Moving $t = -5.792$, df = 14, $P < 0.001$). For all the above analyses, Bonferroni corrections were included.

Comparison of the Activity Budget Between Experimental and Nonexperimental Chimpanzees

There was no difference between the activity budgets of the two groups of captive chimpanzees on weekends (Independent t-test: Feeding $t = 0.046$, df = 10, $P = 0.964$; Resting $t = 0.317$, df = 10, $P = 0.758$; Move $t = 0.969$, df = 10, $P = 0.356$). On weekdays, the feeding time of experimental chimpanzees was significantly longer than that of nonexperimental chimpanzees ($t = 7.296$, df = 10, $P < 0.001$). The resting time of experimental chimpanzees tended to be shorter than that of nonexperimental chimpanzees on weekdays ($t = -2.149$, df = 10, $P = 0.057$), whereas the moving time was not significantly different ($t = 0.359$, df = 10, $P = 0.727$). For all the above analyses, Bonferroni corrections were included.

Comparison of the Activity Budget Between Weekdays and Weekends

For the experimental chimpanzees, feeding time on weekdays was longer than that on weekends (Paired t-test: $t = 14.05$, df = 5, $P < 0.001$). Resting time on weekdays was significantly shorter than that on weekend ($t = -6.066$, df = 5, $P < 0.01$). Moving time was not significantly different between weekdays and weekends ($t = 0.833$, df = 5, $P = 0.443$). For the nonexperimental chimpanzees, none of the behavioral patterns was significantly different between on weekdays and weekends (Feeding $t = 1.110$, df = 5, $P = 0.317$; Resting $t = -1.758$, df = 5, $P = 0.139$; Moving $t = 1.461$, df = 5, $P = 0.204$). For all the above analyses, Bonferroni corrections were included.

Diurnal Feeding Rhythm

Diurnal feeding rhythms are shown in Figure 4. We compared the behavioral rhythm of the experimental chimpanzees on weekdays with those of nonexperimental chimpanzees and the wild chimpanzees in Bossou. There were significant interactions between time of day and observational day (weekday or weekend) with both the nonexperimental (time: $F = 6.944$, df = 9, $P < 0.01$, partial $\eta^2 = 0.385$; group: $F = 49.681$, df = 1, $P < 0.01$, partial $\eta^2 = 0.332$; time*group: $F = 4.801$, df = 9, $P < 0.01$, partial $\eta^2 = 0.302$) and wild (time: $F = 2.016$, df = 9, $P < 0.05$, partial $\eta^2 = 0.123$; group: $F = 0.003$, df = 1, $P = 0.956$, partial $\eta^2 = 0.000$; time*group: $F = 2.836$, df = 9, $P < 0.01$, partial $\eta^2 = 0.165$) chimpanzees. However, there was no interaction between time of day and group when comparing the feeding rhythm of experimental chimpanzees and nonexperimental chimpanzees on weekends (time: $F = 20.657$, df = 9, $P < 0.01$, partial $\eta^2 = 0.650$; group: $F = 0.032$, df = 1, $P = 0.859$, partial $\eta^2 = 0.000$; time*group: $F = 0.734$, df = 9, $P = 0.677$, partial $\eta^2 = 0.062$).

DISCUSSION

This study obtained the first evidence that cognitive experiments work as an efficient food-based enrichment for chimpanzees. The feeding time and resting time of the experimental chimpanzees on weekdays were not significantly different from those of wild chimpanzees in Bossou, whereas those of the nonexperimental chimpanzees on weekdays were significantly different. This is also the first report of a captive chimpanzee group achieving the same feeding time as wild chimpanzees. Although the apparatus is artificial, the subject chimpanzees can make an effort to get foods before eating, as wild chimpanzees do. This can be a good alternative enrichment method in a captive environment, where resources (space, food, etc.) are limited compared with those in wild habitats. Also, the fact that chimpanzees participated in the experiment voluntarily is an essential factor to conclude that the cognitive experiments worked as a tool for

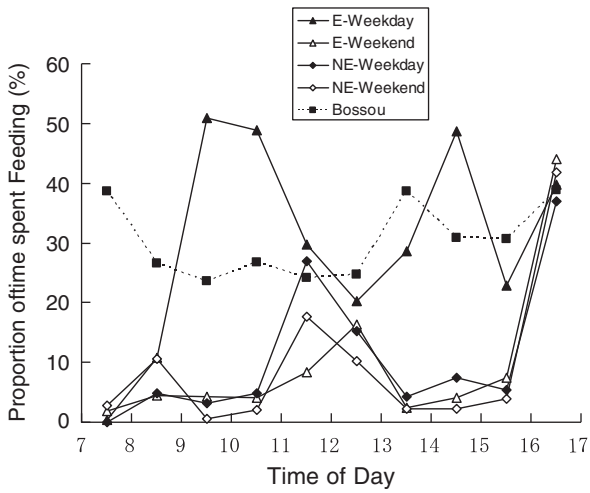

Fig. 4. Diurnal feeding rhythm at two field sites. Diurnal feeding rhythms of Wild (Bossou), experimental (E), and nonexperimental (NE) chimpanzees are shown.

enrichment. They waited for the coming of the experimenters and exhibited behaviors similar to those in various positive contexts (such as before meals and social encounters with conspecifics) when the experimenters called them. These behaviors indicated that they were not forced to engage in the tasks, but rather they were motivated to participate. Some previous studies also reported animals' motivation to use a computer apparatus for getting food. Washburn and Rumbaugh [1992] showed that when they attached a computer apparatus to the cage of the singly housed rhesus macaques, they used it 40% of a 24-hr day. Tarou et al. [2004] also reported that group-living orangutans used a computer-based enrichment feeder voluntarily for 3–5 weeks. Thus, the automated techniques of cognitive experiments might also be useful in the daily lives of captive chimpanzees on weekends, when the activity budgets of these captive chimpanzees were different from those in the wild.

Our results for the Bossou activity budgets were within the range of those in previous studies on activity budget in Bossou chimpanzees [Hockings et al., 2009; Takemoto, 2004; Yamakoshi, 1998]. Feeding rhythm was also similar to that in a previous report [Yamakoshi, 1998]. Compared with the data from Gombe and Tai, Bossou chimpanzees seemed to spend more time in resting and less time in feeding as Mahale chimpanzees [Doran, 1997; Matsumoto-Oda, 2002; Pruetz & McGrew, 2001; Wrangham, 1977]. The difference might be derived from differences of the regime of data collection, subjects, diet, and/or the level of chimpanzees' habituation to humans. Also, there might be effects of seasonality on the activity budgets [Doran, 1997; Goodall, 1986; Matsumoto-Oda, 2002]. Hockings et al. [in preparation] reported that during fruit scarcity, chimpanzees in Bossou spent less time feeding. We collected data in September to October, when wild fruit is relatively scarce compared with that in the dry season. Thus, in order to establish individual welfare measurements, we need to collect more data systematically from more individuals across different seasons and field sites possibly by cooperating with researchers working at the different field sites.

Changes in activity budgets have often been used as a method to assess the effects of environmental enrichment, but direct comparisons of activity budgets between wild and captive individuals have rarely been carried out hitherto [Höhn et al., 2000; Kerridge, 2005]. Direct comparison of wild and captive behaviors and research on wild animals from the view of animal welfare are important because they can provide objective information for welfare assessment. Furthermore, such comparison can facilitate environmental enrichment since it can suggest what is lacking in the captive environment. For example, this study pointed out the importance of providing enrichment on the weekends when there are fewer human workers at the PRI.

However, Veasey et al. [1996] proposed several theoretical and methodological problems of direct comparison of the behaviors. Methodological problems include comparison of data that were collected by different observers and the effects of observers on the behaviors of animals. Owing to the habituation of the wild chimpanzees and the collection of data by the same researcher in the two field sites, this study avoided some of those methodological problems, but some theoretical problems still remain. The critical problem is whether the change in the activity budgets really reflected an improvement of welfare or not [Fraser, 2008]. For example, behaviors in the wild include behaviors for coping with a severe climate and for predator avoidance, which could have detrimental effects on animal welfare [Duncan & Fraser, 1997]. Also, some behaviors such as tool-use of chimpanzees occur only in particular environments [Whiten et al., 1999]. Hence, there is ambiguity about which types of behaviors are important for animal welfare and which are not [Duncan & Fraser, 1997]. In addition, some animals are already adapted to a captive environment genetically or empirically [Carlstead, 1996]. For such animals, wild activity budgets might not match with their behavioral needs if we check the effects from different aspects. Therefore, we need to specify important features of natural behaviors for animal welfare by investigating the effects of natural behaviors on other welfare measures such as reproduction, stress, and mortality, using multiple methodologies both in wild and captivity.

Thus, in order to strengthen the finding of this study we should also investigate the effects of cognitive experiments from other points of view. For example, we need to consider the changes in aberrant behaviors which were reported to be reduced through environmental enrichment in some previous reports [Baker, 1997; Bloomsmith, 1988]. Also, we should consider the stress of chimpanzees, as previous studies showed that task errors and increased task difficulty might elicit arousal in subject chimpanzees [Itakura, 1993; Leavens et al., 2001; Yamanashi & Matsuzawa, 2010]. However, if we are careful to provide an appropriate level of challenge, it is possible that cognitive experiments might work as good opportunities to express chimpanzees' cognitive abilities, namely, might provide cognitive enrichment [Meehan & Mench, 2007; Morimura, 2006]. The potential positive and negative effects of cognitively challenging aspects on their welfare are important points for future research. Furthermore, the level of control would also be an interesting point to be investigated. Control is thought to be psychologically and physiologically important to animals [Bassett & Buchanan-Smith, 2007]. Even though the chimpanzees could decide whether they would participate in the experiments or not, they could not control the timing of the

experiments. As a result, the feeding rhythm of the experimental chimpanzees on weekdays was still different from that of wild chimpanzees in Bossou. If captive animals had more choice and control in foraging, the feeding rhythm might also be more similar to that in the wild. In that case, there might be better effects on subject welfare. Future studies should address these issues to clarify the detailed effects of cognitive experiments.

In conclusion, cognitive experiments worked as an efficient food-based enrichment for captive chimpanzees as long as we make sure that the subjects participate in the experiments voluntarily. Also, wild-captive comparison was a valid method to assess the status of animal welfare, but we need to study more about natural behaviors of wild animals to understand those observed effects on the welfare of captive animals.

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REFERENCES

Baker KC. 1997. Straw and forage material ameliorate abnormal behaviors in adult chimpanzees. Zoo Biology 16:225–236.

Bassett L, Buchanan-Smith HM. 2007. Effects of predictability on the welfare of captive animals. Applied Animal Behaviour Science 102:223–245.

Biro D, Inoue-Nakamura N, Tonooka R, Yamakoshi G, Sousa C, Matsuzawa T. 2003. Cultural innovation and transmission of tool use in wild chimpanzees: evidence from field experiments. Animal Cognition. 6:213–223.

Bloomsmith MA. 1988. Successful feeding enrichment for captive chimpanzees. American Journal of Primatology 16:155–164.

Carlstead K. 1996. Effects of captivity on the behavior of wild mammals. In: Kleiman DG, Allen ME, Thompson KV, Lumpkin S, editors. Wild mammals in captivity: principles and techniques. Chicago, IL: University of Chicago Press. p 317–333.

Carvalho S, Biro D, McGrew W, Matsuzawa T. 2009. Tool-composite use and reuse in wild chimpanzees (*Pan troglodytes*): archaeologically invisible steps in the technological evolution of early hominins? Animal Cognition 12:103–114.

Doran D. 1997. Influence of seasonality on activity patterns, feeding behavior, ranging, and grouping patterns in Taï chimpanzees. International Journal of Primatology 18:183–206.

Duncan IJH, Fraser D. 1997. Understanding animal welfare. In: Appleby M, Hughes BO editors. Animal welfare. Wallingford: CAB International. p 19–31.

Fraser D. 2008. Understanding animal welfare: the science in its cultural context. West Sussex: Wiley-Blackwell.

Goodall J. 1986. The chimpanzees of Gombe: patterns of behaviour. Cambridge, MA: Harvard University Press.

Hayashi M, Matsuzawa T. 2003. Cognitive development in object manipulation by infant chimpanzees. Animal Cognition 6:225–233.

Hayashi M, Takeshita H. 2009. Stacking of irregularly shaped blocks in chimpanzees (*Pan troglodytes*) and young humans (*Homo sapiens*). Animal Cognition 12:49–58.

Hockings KJ, Anderson JR, Matsuzawa T. 2009. Use of wild and cultivated foods by chimpanzees at Bossou, Republic of Guinea: feeding dynamics in a human-influenced environment. American Journal of Primatology 71:636–646.

Höhn M, Kronschnabl M, Ganslo̧er U. 2000. Similarities and differences in activities and agonistic behavior of male Eastern grey kangaroos (*Macropus giganteus*) in captivity and the wild. Zoo Biology 19:529–539.

Hosey G, Melfi V, Pankhurst S. 2009. Zoo animals: behavior, management and welfare. Oxford: Oxford University Press.

Itakura S. 1993. Emotional behavior during the learning of a contingency task in a chimpanzee. Perceptual and Motor Skills 76:563–566.

Kerridge FJ. 2005. Environmental enrichment to address behavioral differences between wild and captive black-and-white ruffed lemurs (*Varecia variegata*). American Journal of Primatology 66:71–84.

Leavens DA, Aureli F, Hopkins WD, Hyatt WD. 2001. Effects of cognitive challenge on self-directed behaviors by chimpanzees (*Pan troglodytes*). American Journal of Primatology 55:1–14.

Martin P, Bateson P. 2007. Measuring behaviour, 3rd ed. Cambridge: Cambridge University Press.

Matsumoto-Oda A. 2002. Behavioral seasonality in mahale chimpanzees. Primates 43:103–117.

Matsuzawa T. 1994. Field experiments on use of stone tools by chimpanzees in the wild. In: Wrangham R, McGrew W, de Waal F, Heltne P, editors. Chimpanzee cultures. Cambridge: Harvard University Press. p 351–370.

Matsuzawa T. 2003. The Ai project: historical and ecological contexts. Animal Cognition 6:199–211.

Matsuzawa T. 2006. Sociocognitive development in chimpanzees: a synthesis of laboratory work and fieldwork. In: Matsuzawa T, Tomonaga M, Tanaka M, editors. Cognitive development in chimpanzees. Tokyo: Springer. p 3–33.

Matsuzawa T, Tomonaga M, Tanaka M, editors. 2006. Cognitive development in chimpanzees. Tokyo: Springer.

Matsuzawa T, Humle T, Sugiyama Y, editors. 2011. Chimpanzees of Bossou and Nimba. Tokyo: Springer.

Meehan CL, Mench JA. 2007. The challenge of challenge: CAN problem solving opportunities enhance animal welfare? Applied Animal Behaviour Science 102:246–261.

Morimura N. 2006. Cognitive enrichment in chimpanzees: an approach of welfare entailing an animal's entire resources. In: Matsuzawa T, Tomonaga M, Tanaka M, editors. Cognitive development in chimpanzees. Tokyo: Springer. p 368–391.

Morimura N, Ueno Y. 2004. The new methodology for behavioral management using PDA devices: Management of zoo animals and assessment of enrichment (The spring conference of Japanese Society of livestock management and Japanese Society for Applied Animal behaviour in 2004). Animal Behaviour and Management 40: 28–29 (in Japanese).

Morimura N, Idani G., Matsuzawa T. 2010. The first chimpanzee sanctuary in Japan: an attempt to care for the ''surplus'' of biomedical research. American Journal of Primatology 73:226–232.

Nishida T, Kano T, Goodall J, McGrew WC, Nakamura M. 1999. Ethogram and ethnography of Mahale chimpanzees. Anthropological Science 107:141–188.

Ochiai T, Matsuzawa T. 1997. Planting trees in an outdoor compound of chimpanzees for an enriched environment. Proceedings of the Third International Conference on Environmental Enrichment, Orlando, Florida. p 355–364.

Pruetz JDE, McGrew WC. 2001. What does a chimpanzee need? Using natural behavior to guide the care and management of captive populations. In: Brent L, editor. Care and management of captive chimpanzees. San Antonio: American Society of Primatologists. p 16–37.

Ross SR. 2010. How cognitive studies help shape our obligation for ethical care of chimpanzees. In: Lonsdorf EV, Ross SR, Matsuzawa T, editors. The mind of the chimpanzees: ecological and experimental perspectives. Chicago: The University of Chicago Press. p 309–319.

Sugiyama Y, Koman J. 1979. Social structure and dynamics of wild chimpanzees at Bossou, Guinea. Primates 20:323–339.

Takemoto H. 2004. Seasonal change in terrestriality of chimpanzees in relation to microclimate in the tropical forest. American Journal of Physical Anthropology 124:81–92.

Tarou LR, Kuhar CW, Adcock D, Bloomsmith MA, Maple TL. 2004. Computer-assisted enrichment for zoo-housed orangutans (*Pongo pygmaeus*). Animal Welfare 13:445–453.

Veasey JS, Waran NK, Young RJ. 1996. On comparing the behaviour of zoo housed animals with wild conspecifics as a welfare indicator, using the giraffe (*Giraffa camelopardalis*) as a model. Animal Welfare 5:139–153.

Washburn DA, Rumbaugh DM. 1992. Investigations of rhesus monkey video-task performance: evidence for enrichment. Contemporary Topics in Laboratory Animal Science 31:6–11.

Whiten A, Goodall J, McGrew WC, Nishida T, Reynolds V, Sugiyama Y, Tutin CEG, Wrangham RW, Boesch C. 1999. Cultures in chimpanzees. Nature 399:682–685.

Wrangham RW. 1977. Feeding behaviour of chimpanzees in Gombe National Park, Tanzania. In: Clutton-Brock TH, editor. Primate ecology: studies of feeding and ranging behaviour in lemurs, monkeys and apes. London: London Academic Press. p 504–538.

Yamakoshi G. 1998. Dietary responses to fruit scarcity of wild chimpanzees at Bossou, Guinea: possible implications for ecological importance of tool use. American Journal of Physical Anthropology 106:283–295.

Yamanashi Y, Matsuzawa T. 2010 Emotional consequences when chimpanzees (*Pan troglodytes*) face challenges: individual differences in self-directed behaviours during cognitive tasks. Animal Welfare 19:25–30.

Young RJ. 2003. Environmental enrichment for captive animals. Oxford: Blackwell Publishing.