Development of bed-building behaviors in captive chimpanzees (*Pan troglodytes*): Implication for critical period hypothesis and captive management

Yumi Yamanashi[1,2]
Haruna Bando[3]
Masayuki Matsunaga[3]
Masayuki Tanaka[1,2]
Etsuko Nogami[2]
Satoshi Hirata[2]

[1] Center for Research and Education of Wildlife, Kyoto City Zoo, Okazakikouen, Okazaki-hosshoujicho, Sakyo-ku, Kyoto 606-8333, Japan

[2] Wildlife Research Center, Kyoto University, Kyoto, Japan

[3] Animal Husbandry and Conservation Section, Kyoto City Zoo, Okazakikouen, Okazaki-hosshoujicho, Sakyo-ku, Kyoto 606-8333, Japan

Abstract

Wild great apes build beds for sleeping by combining tree branches or other vegetation, but the development of this behavior is poorly understood. We investigated the development of bed-building behaviors by conducting complementary cross-sectional and longitudinal studies of captive chimpanzees. In the cross-sectional study, we created an ethogram of behaviors related to bed-building by observing 59 chimpanzees living at the Kumamoto Sanctuary, Kyoto University, and the Kyoto City Zoo. In the longitudinal study, we installed bed-building platforms, provided branches on the platforms on a regular basis, and recorded behaviors of five chimpanzees (including an infant born in 2013) over a 3-year period from February 2015 to February 2018 at the Kyoto City Zoo (total 490.7 h). We found that all the chimpanzees performed some form of bed-building behavior but wild-born chimpanzees possessed more sophisticated techniques than captive-born chimpanzees. We also found that although the offspring of a wild-born female only showed simple techniques at the beginning of the longitudinal study, his repertoire of bed-building behaviors became as complex as that of his mother by the age of five. Our results suggest that improved bed-building behaviors can be supported in captive-born great apes by providing learning opportunities during appropriate stages of development.

Keywords Chimpanzee · Bed-building · Nest · Development · Zoo · Critical period · Animal welfare

Introduction

All wild great apes build beds for sleeping (also referred to as nests) by combining tree branches and/or vegetation together (Goodall 1962; Koops et al. 2012; Prasetyo et al. 2009; Zamma 2015). Beds enable chimpanzees to obtain a safe and deep sleep (Fruth et al. 2018). Although bed- building is universal in great apes, not all captive apes build well-constructed beds for sleeping. In fact, some studies have revealed that bed-building ability depends on early rearing conditions and that bed-building techniques differ between wild-born and captive-born chimpanzees (Bernstein 1962; Morimura and Mori 2011; Videan 2006). Some orangutans raised in a rehabilitation center report- edly did not build any type of bed for sleeping after being released into the forest, which has potential negative health consequences including parasite infestation (Grundmann 2006). Our recent survey of 217 chimpanzees in Japa- nese zoos revealed that complex bed-building behaviors depended on rearing history. Wild-born individuals exhibited more sophisticated skills than captive-born chimpanzees, regardless of whether they were reared by humans or by other chimpanzees (Kyoto City Zoo 2018). There- fore, although bed-building behavior may be partly innate (Anderson et al. 2019), learning the skill during infancy is important for becoming proficient at it (Fruth et al. 2018). Studies of captive chimpanzees and wild orangutans suggest that social learning might play an important role in acquiring bed-building skills (Prasetyo et al. 2009; van Noordwijk and van Schaik 2005; Videan 2006). How- ever, as no studies have focused on the development of bed-building behaviors, it is uncertain which aspects are socially learned and which are innate or a result of individual learning.

In contrast to the wide variability in tool-use repertoires observed across chimpanzee field sites (Whiten et al. 1999), chimpanzees at all known sites build beds for sleeping (Fruth et al. 2018), and the latter can involve actions that are more complex than some forms of tool use. Social learning in chimpanzees is thought to be emulative (Tomasello 1998). In contrast to the true imitation often observed in humans (Whiten 2017), social learning in chimpanzees focuses more on the behavioral outcomes than on the specific motor skills involved in reaching an outcome. Indeed, some studies in captive chimpanzees have revealed difficulties in acquiring novel behaviors, including novel actions associated with those behaviors (Hayashi et al. 2005). Chimpanzees reportedly showed less attention toward their own or another's actions in contexts of imitation and self-monitoring of behaviors compared with humans (Kaneko and Tomonaga 2012; Myowa-Yamakoshi 2006). It is still not fully under- stood how behaviors requiring complex patterns of actions are acquired by chimpanzees.

Investigating bed-building behavior is relevant for improving animal welfare and visitor education. Providing apes with opportunities to acquire new behaviors enhances their cognitive development (Yamanashi et al. 2016), which is now an important component of enhancing the mental health of captive species (Clark 2017; Meehan and Mench 2007). In addition, because primates' sleep quality is related to the physical and mental health of primates (Martin-Ordas and Call 2011), acquiring adequate bed-building skills can contribute toward high-quality sleep. Better-built beds have been shown to improve the quality of sleep in orangutans (Samson and Shumaker 2013; Samson and Shumaker 2015a). Moreover, one important educational focus of zoos is to display diverse natural behavioral repertoires in their animals, and so zoos should strive to facilitate natural behaviors whenever possible. Videan (2006) reported that no captive-born chimpanzees performed weaving of branches given as bedding material. Creating beds from branches requires particular expertise because chimpanzees have to adjust their motor output when weaving and pay careful attention to how materials are joined. Can such sophisticated bed-building behaviors in captive chimpanzees be promoted? The purpose of this study is to investigate how bed-building behaviors are acquired by captive chimpanzees and better understand the developmental processes involved in acquiring these behaviors.

Methods

Study 1: variations of bed-building techniques in captive chimpanzees

Our subjects were 59 chimpanzees inhabiting either the Kyoto City Zoo (KCZ), or the Kumamoto Sanctuary, Kyoto University (KS) (Supplementary Table 1). Established in 2007, KS was the first chimpanzee sanctuary in Japan. It was originally called the Chimpanzee Sanctuary Uto (Morimura et al. 2010). The subjects included wild-born and captive-born individuals, including zoo-born and laboratory born chimpanzees that were either mother-reared or human-reared.

We first created a baseline ethogram of behaviors related to bed-building. To do this, we recorded bed-building behaviors exhibited before nighttime and daytime resting periods. We conducted behavioral observations between June 2014 and April 2017. We recorded individual behaviors in the compartments used by the chimpanzees for nighttime sleeping by observing their behaviors after their evening meal. We used a tripod-mounted video camera to record the behaviors when possible. Daytime behaviors were recorded ad libitum with a video camera during previous studies (Yamanashi et al. 2018a, b). We defined a bed-building behavior as actions performed just prior to lying down to rest. We included behaviors that involved manipulation of materials, as well as behaviors seen in the context of bed- building but without the specific manipulation of materials (Supplementary video 1). Therefore, we divided bed-building behaviors into two categories: bedding and air-bedding behaviors. Air-bedding was defined as unnecessary behaviors associated with bedding but without manipulation of materials. Because chimpanzees often slept on the sleeping platforms, it was not always possible to know whether the materials were really weaved together or not. Therefore, we scored the occurrence of weaving based on the complexity of the individuals' combinatory actions and previous observations of clear examples of weaving. We observed bed- building-related behaviors on 126 occasions (1–6 times per individual). The specific bedding materials varied; however, all subjects had free access to the materials, which included burlap sacks, branches, hay, and firehoses. The bedding materials were not novel and had previously been introduced since 2008, or earlier. Despite our efforts, we were unable to record the behaviors of some KS individuals because they reacted to the presence of the video camera or observer by not building a bed or lying down. These included four hand- raised individuals and one wild-born individual.

Study 2: longitudinal observation of bed-building behaviors in captive chimpanzees

Our second study was a longitudinal observation of bed- building by five chimpanzees at KCZ, between February 2015 and February 2018, including a 2-year-old male born February 12, 2013. The mother of the infant was wild-born and the other

three adults were captive-born (Supplementary Table 1). We installed two sleeping platforms (Fig. 1): a flat one (with locations to put branches), built in February 2015 (modified in July 2017 for ease of maintenance), and a wire- mesh one (rectangular with a depression to emulate the central bowl of real chimpanzee beds), built in May 2015. The wire-mesh platform design was based on a platform used in the Edinburgh zoo (Scotland). The platforms were about 0.63 m^2 and 0.70 m^2, respectively, and about 2.5–3.0 m above the ground. Branches were replenished by zoo keepers about 2–3 times per week. The number of branches and amounts of other materials provided, such as hay and burlap sacks, fluctuated daily; importantly, chimpanzees always had access to branches, mostly stems of the common camellia (*Camellia japonica*), cut to about 1–2 m in length. KCZ had provided other materials, such as burlap sacks, hay, and fire hoses since 2010, when the zoo received a group of chimpanzees from another facility.

During all observational periods (between February 2015 and February 2018), behaviors were recorded using an infrared camera installed in the corner of the indoor enclosure to monitor chimpanzees' behaviors on the two sleeping platforms (see Supplementary Videos). We randomly selected 1 day per month to record videos. The total duration of all video recordings was 490.7 h. We analyzed the portions of videos that were recorded from about 16:00–07:00 (the following morning), including the start and end times for the use of each platform. In addition to bed-building behaviors, we recorded platform use and peering behaviors. Peering was scored when one individual was bed-building and another on the same platform visually oriented toward it. Peering ended when the observing chimpanzee left the platform or the bed-builder stopped building. We counted the frequency of the peering bouts. We also categorized the infant's bed-building behaviors according to the ethogram in Supplementary Table 2 using the one-zero sampling method for each month (Martin and Bateson 2007). In addition, we calculated the proportion of 10-s intervals during which each bed-building behavior occurred. We analyzed rates of bed- building, peering, and platform use starting after May 2015, when both platforms were installed. However, we analyzed bed-building techniques using all video records from February 2015 onward. Beds made by chimpanzees were often destroyed; however, we were occasionally able to measure bed dimensions in the morning, after the introduction of new branches. We noted bed length, width, thickness, and the number of parts. Length, width, and thickness were measured based on the definition of Samson (2012). The number of parts was recorded by simply counting the number of materials remaining in the beds.

Data analysis

For study 1, we used a proportion test for analyzing the relationship between each type of bed-building behavior and rearing history [wild-born, captive-born (at a biomedical facility), captive-born (other facility)]. We excluded individuals whose rearing history was unknown (n = 2). For study 2, we used a Wilcoxon's signed-rank test to test which platform was preferred by each chimpanzee. We compared the proportion of time spent on the sleeping platforms. We did not analyze data from the two adult males we studied at the KCZ because their rates of platform use were very low. We used a Mann–Whitney U test to assess changes in the rate of bed-building behaviors over time in the mother- reared infant. We compared the proportion of time spent bed-building between the first half (until 16 months after the introduction of the platforms) and the second half of the study period (17 months after the introduction of the platforms). We compared the proportion of time spent bed- building between the mother and infant by a Wilcoxon's signed-rank test. We used R v3.5.2 software (R Development Core Team 2019) for statistical analyses with an alpha level of 0.05. We used a package "exactRankTests" (Hothorn et al. 2006). Interobserver reliability was assessed using ten video clips of several different individuals and situations. Two observers (Y.Y. and a second observer not listed in the author list) independently categorized the action patterns using the ethogram in Supplementary Table 2. The rate of concordance was 90.8%.

Results

Study 1: variations in bed-building techniques in captive chimpanzees

The details of observed behaviors by category are summarized in Supplementary Table 2. All studied chimpanzees showed at least one bed-building behavior; however, details differed according to their rearing histories. Table 1 shows the number of individuals that performed each main type of bedding-behavior. We found significant differences in three behavioral categories: weaving, bending, and air bedding. The complex techniques (weaving and bending techniques) were executed mostly by wild-born chimpanzees, whereas air-bedding behaviors only occurred among captive-born individuals,

especially those born in biomedical facilities. There were no statistically significant differences in the pro- portion of individuals exhibiting “placing large materials around”, the simplest technique, among the three groups of chimpanzees.

Study 2: longitudinal observation of bed-building behaviors in captive chimpanzees

Study 2.1: use of sleeping platforms

The two platforms were mostly used by the mother–infant pair (percent of observation time: Koiko (mother) 91.5%, Niini (infant) 86.8%, followed by Lora 20.1%, James 1.09%, and Takashi 0.15%. The wire-mesh platform was preferred by Koiko ($V = 126$, $p = 0.009$) and Niini ($V = 71$, $p > 0.001$), whereas Lora showed no preference between the two plat- forms ($V = 157$, $p = 0.895$). Details on the beds built by wild-born chimpanzees and their infants are shown in Supplementary Figs. 1.

Study 2.2: developmental changes in bed‑building behaviors of an infant chimpanzee

Table 2 details the behaviors exhibited by the five chimpanzees at KCZ. The adults’ data were derived from study 1. It also includes the emergence of each behavioral action in infants from the ages of 2–5 years. The infant of the wild-born mother already showed some actions related to bed-building behaviors at the beginning of the study (e.g., folding, stepping, and rotating), and he displayed the full bed-building repertoire by 3 years of age (Supplementary Video 2). This infant acquired not only the same techniques as his mother, but also the air-bedding behaviors seen in the two adult males. We did not observe the infant performing behaviors that were only seen at KS in study 1. The pro- portion of time the infant spent bed-building also increased from the first to the second half of the study period (Fig. 2a: $W = 72.5$, $p = 0.036$), whereas that of the mother did not change (Fig. 2a: $W = 137$, $p = 0.738$). In the first half of the study period, the infant devoted significantly less time than the mother to bed-building ($V = 120$, $p < 0.001$), but this difference disappeared by the latter half of the study ($V = 115$, $p = 0.071$). Peering behavior was observed throughout the study in this young individual (Fig. 2b). He almost exclusively watched his mother’s bed-building behaviors (46 bouts), but he once watched Lora build a bed. Peering behaviors between adults were never observed.

Discussion

In agreement with previous studies (Bernstein 1962; Videan 2006), we found that the early rearing conditions impact bed-building behaviors in captive chimpanzees, indicating importance of the post-natal environment for acquiring the necessary skills. This study complements earlier ones by showing that captive zoo-born chimpanzees can acquire skills comparable to those of wild-born chimpanzees, if learning opportunities are provided at an appropriate development stage. At the onset of study 2, our focal infant displayed only some basic behaviors associated with bed building. As he grew older, he acquired more sophisticated behaviors, including weaving branches and adjusting beds by adding or rearranging small materials, and his bed-building behaviors generally became similar to his mother’s. Although previous studies have used various bedding materials to promote bedding behaviors in captive great apes (Lukas et al. 2003; Samson and Shumaker 2015b; Videan 2006), we focused more on providing natural bed- ding material (branches) to the chimpanzees. Supporting the expression of sophisticated natural behaviors is important for great ape welfare and for improving visitor experiences. Both platforms used in the study 2 were effective in that they were used for bedding, but the wire-mesh platform was clearly preferred by the wild-born female and her infant, possibly because it more readily afforded construction of a more naturalistically formed bed. The beds built by the wild-born chimpanzee resembled those measured by Samson (2012) in overall dimensions, except that the zoo-built beds were shallower than those in the wild (Supplementary Figure 1). The only chimpanzees to exhibit complex bed-building weaving techniques with the branches provided were the wild-born mother and her offspring. Despite having opportunities to do so, none of the other adults (all more than 25 years old) watched the wild-born female’s bed-building. Another adult female also made beds on the platform, but she used less complex techniques.

The techniques seen in the offspring of the wild-born mother were a mixture of those exhibited by other members of the same group. Notably, he also exhibited the unnecessary action pattern "air-bedding" behaviors shown by the two adult males in the group. Other air-bedding patterns were observed in other groups of chimpanzees (Table 2); however, the young male acquired specifically patterns shown by the adult males of his group, suggesting social learning; indeed, he was sometimes observed to peer at the adults as they air bedded (Supplementary Video 1). How- ever, alternative explanations may be proposed (e.g., individual learning). The development of the young male's bed- building recalls other examples of complex actions being acquired during infancy. For example, Bossou chimpanzees learned to nut-crack by the age of 4–5 years, whereas older, naive chimpanzees had difficulty with the task (Matsuzawa 1994). Our project started when the wild-born mother's off- spring was 2 years of age. Videan (2006) proposed that the first few years of life is critical for acquiring bed-building skills. More studies are needed to clarify the optimal timing for learning behaviors and their subsequent generalization. Although post-natal learning is important, our study also supports the view that the chimpanzees have an innate motivation to perform bed-building behaviors (Anderson et al. 2019). All subjects in study 1, regardless of their rearing history, performed behaviors related to bed-building (including air-bedding behaviors). Although we lack details of rearing environments for all the chimpanzees in our study, we recorded air-bedding behaviors in individuals reared in biomedical facilities, where bedding materials were not pro- vided to infants (pers. comm. from staff working at the facilities). These behaviors might be a form stereotypic behaviors (Birkett and Newton-Fisher 2011), repetitive behaviors induced by, and used to cope with suboptimal environments, (Mason et al. 2007). Therefore, providing suitable bedding materials during infancy to encourage proper bed-building acquisition and accommodate adult chimpanzees' abilities and preferences can also be important from a welfare perspective.

In conclusion, our study demonstrates that sophisticated bed-building behaviors can be promoted in captive chimpanzees by providing learning opportunities at an appropriate developmental stage. Our study also suggests that wild-born individuals retain the ability to perform sophisticated behavioral techniques that they might have learned as infants in the wild (e.g., complex bed-building), as suggested by Bern- stein (1962) and Videan (2006). Therefore, before wild-born chimpanzees in the captive population die, efforts should be made to pass on their complex behaviors to captive-born young generations. Creating bedding platforms and regularly providing branches (as done here) could prove effective in this context. However, building beds in the wild requires additional problem-solving skills, such as selecting appropriate locations and ensuring that beds are sufficiently strong and stable. How to address these aspects of this complex behavior is for future work.

Acknowledgements

The care of the chimpanzees and the present study were supported financially by grants from the Japan Society for the Promotion of Science (#13J04636 and #17K17828 to YY, 18H05524 to SH, JSPS-LGP-U04, JSPS core-to-core CCSN) and also by Itochube foundation and Great Ape Information Network. We are grateful to the following people and program for their support of our study: Fumio Ito, Kanae Shimada, Akihiro Mizuno, Ryuichiro Kado, Motoharu Sato, Tomoko Matsusaka and the staff at the Kyoto City Zoo, Yusuke Mori, Toshifumi Udono and the staff at the Kumamoto Sanctuary, Nobuaki Yoshida and Great Ape Information Network. We thank the editor and two anonymous reviewers for providing valuable suggestions to improve the previous version of this manuscript.

References

Anderson JR, Ang MYL, Lock LC, Weiche I (2019) Nesting, sleeping, and nighttime behaviors in wild and captive great apes. Primates 60:321–332. https://doi.org/10.1007/s10329-019-00723-2

Bernstein IS (1962) Response to nesting materials of wild born and captive born chimpanzees. Anim Behav 10:1–6. https://doi. org/10.1016/0003-3472(62)90123-9

Birkett LP, Newton-Fisher NE (2011) How abnormal is the behaviour of captive, zoo-living chimpanzees? PLoS ONE 6:e20101. https ://doi.org/10.1371/journal.pone.0020101

Clark F (2017) Cognitive enrichment and welfare: current approaches and future directions. Anim Behav Cogn 4:52–71

Fruth B, Tagg N, Stewart F (2018) Sleep and nesting behavior in pri- mates: a review. Am J Phys Anthropol 166:499–509. https://doi. org/10.1002/ajpa.23373

Goodall JM (1962) Nest building behavior in the free ranging chimpanzee. Ann NY Acad Sci 102:455–467. https://doi. org/10.1111/j.1749-6632.1962.tb13652.x

Grundmann E (2006) Back to the wild: will reintroduction and reha- bilitation help the long-term conservation of orang-utans in Indo- nesia? Soc Sci Inform 45:265–284. https://doi.org/10.1177/05390 18406063643

Hayashi M, Mizuno Y, Matsuzawa T (2005) How does stone-tool use emerge? Introduction of stones and nuts to naïve chimpanzees in captivity. Primates 46:91–102. https://doi.org/10.1007/s1032 9-004-0110-z

Hothorn T, Hornik K, van de Wiel M, Zeileis A (2006) A Lego sys- tem for conditional inference. Am Stat 60:257–263. https://doi.org/10.1198/000313006X118430

Kaneko T, Tomonaga M (2012) Relative contributions of goal repre- sentation and kinematic information to self-monitoring by chim- panzees and humans. Cognition 125:168–178

Koops K, McGrew W, de Vries H, Matsuzawa T (2012) Nest-building by chimpanzees (*Pan troglodytes verus*) at Seringbara, Nimba Mountains: antipredation, thermoregulation, and antivector hypotheses. Int J Primatol 33:356–380. https://doi.org/10.1007/ s10764-012-9585-4

Kyoto City Zoo (2018) Prevalence of species-specific behaviors in cap- tive zoo-housed chimpanzees (*Pan troglodytes*) in Japan: effects of rearing history and sex on behaviors. J Japan Assoc Zoo Aquar 60:36–52

Lukas KE, Stoinski TS, Burks K, Snyder R, Bexell S, Maple TL (2003) Nest building in captive *Gorilla gorilla gorilla*. Int J Primatol 24:103–124. https://doi.org/10.1023/A:1021450613272

Martin P, Bateson P (2007) Measuring behaviours: an introductory guide, 3rd edn. Cambridge University Press, Cambridge

Martin-Ordas G, Call J (2011) Memory processing in great apes: the effect of time and sleep. Biol Let 7:829–832. https://doi.org/10.1098/rsbl.2011.0437

Mason G, Clubb R, Latham N, Vickery S (2007) Why and how should we use environmental enrichment to tackle stereotypic behaviour? Appl Anim Behav Sci 102:163–188

Matsuzawa T (1994) Field experiments on use of stone tools by chim- panzees in the wild. Chimpanzee cultures. Harvard University Press, Cambridge, USA, pp 351–370

Meehan CL, Mench JA (2007) The challenge of challenge: can problem solving opportunities enhance animal welfare? Appl Anim Behav Sci 102:246–261

Morimura N, Mori Y (2011) Effects of early rearing conditions on problem-solving skill in captive male chimpanzees (*Pan trog- lodytes*). Am J Primatol 72:626–633. https://doi.org/10.1002/ ajp.20819

Morimura N, Idani GI, Matsuzawa T (2010) The first chimpanzee sanc- tuary in Japan: an attempt to care for the "surplus" of biomedical research. Am J Primatol 73:226–232. https://doi.org/10.1002/ ajp.20887

Myowa-Yamakoshi M (2006) How and when do chimpanzees acquire the ability to imitate. In: Matsuzawa T, Tomonaga M, Tanaka M (eds) Cognitive development in chimpanzees. Springer, Tokyo, pp 214–232

Prasetyo D, Ancrenaz M, Morrogh-Bernard HC, Utami Atmoko S, Wich SA, van Schaik CP (2009) Nest building in orangutans: geographical variation in behavioral ecology. Oxford University Press, Oxford, pp 269–277

R: A language and environment for statistical computing (2019) https ://www.R-project.org/.

Samson DR (2012) The chimpanzee nest quantified: morphology and ecology of arboreal sleeping platforms within the dry habitat site of Toro-Semliki Wildlife Reserve Uganda. Primates 53:357–364

Samson DR, Shumaker R (2013) Documenting orang-utan sleep archi- tecture: sleeping platform complexity increases sleep quality in captive. Pongo Behav 150:845–861

Samson DR, Shumaker R (2015a) Orangutans (*Pongo* spp.) have deeper, more efficient sleep than baboons (*Papio papio*) in captiv- ity. Am J Phys Anthropol 157:421–427. https://doi.org/10.1002/ ajpa.22733

Samson DR, Shumaker R (2015b) Pre-sleep and sleeping platform construction behavior in captive orangutans (*Pongo* spp): impli- cations for ape health and welfare. Folia Primatolog 86:187–202 Tomasello M (1998) Emulation learning and cultural learning. Behav Brain Sci 21:703–704. https://doi.org/10.1017/S0140525X98441748

van Noordwijk MA, van Schaik CP (2005) Development of ecologi- cal competence in Sumatran orangutans. Am J Phys Anthropol 127:79–94. https://doi.org/10.1002/ajpa.10426

Videan EN (2006) Bed-building in captive chimpanzees (*Pan troglo- dytes*): the importance of early rearing. Am J Primatol 68:745– 751. https://doi.org/10.1002/ajp.20265

Whiten A (2017) Social learning and culture in child and chimpanzee. Annu Rev Psychol 68:129–154

Whiten A et al (1999) Cultures in chimpanzees. Nature 399:682–685 Yamanashi Y, Matsunaga M, Shimada K, Kado R, Tanaka M (2016) Introducing tool-based feeders to zoo-housed chimpanzees as a cognitive challenge: spontaneous acquisition of new types of tool use and effects on behaviours and use of space. J Zoo Aquar Res 4:1–9

Yamanashi Y, Nogami E, Teramoto M, Morimura N, Hirata S (2018a) Adult-adult social play in captive chimpanzees: is it indicative of positive animal welfare? Appl Anim Behav Sci 199:75–83. https ://doi.org/10.1016/j.applanim.2017.10.006

Yamanashi Y, Teramoto M, Morimura N, Nogami E, Hirata S (2018b) Social relationship and hair cortisol level in captive male chim- panzees (*Pan troglodytes*). Primates 59:145–152. https://doi. org/10.1007/s10329-017-0641-8

Zamma K (2015) Bed making and nocturnal behavior. In: Nakamura M, Hosaka K, Itoh N, Zamma K (eds) Mahale chimpanzees: 50 years of research. Cambridge University Press, Cambridge, pp 583–598

Fig. 1 Two types of sleeping platforms provided for chimpanzees at the Kyoto City Zoo (*left*: flat-style platform; *right*: wire-mesh plat- form)

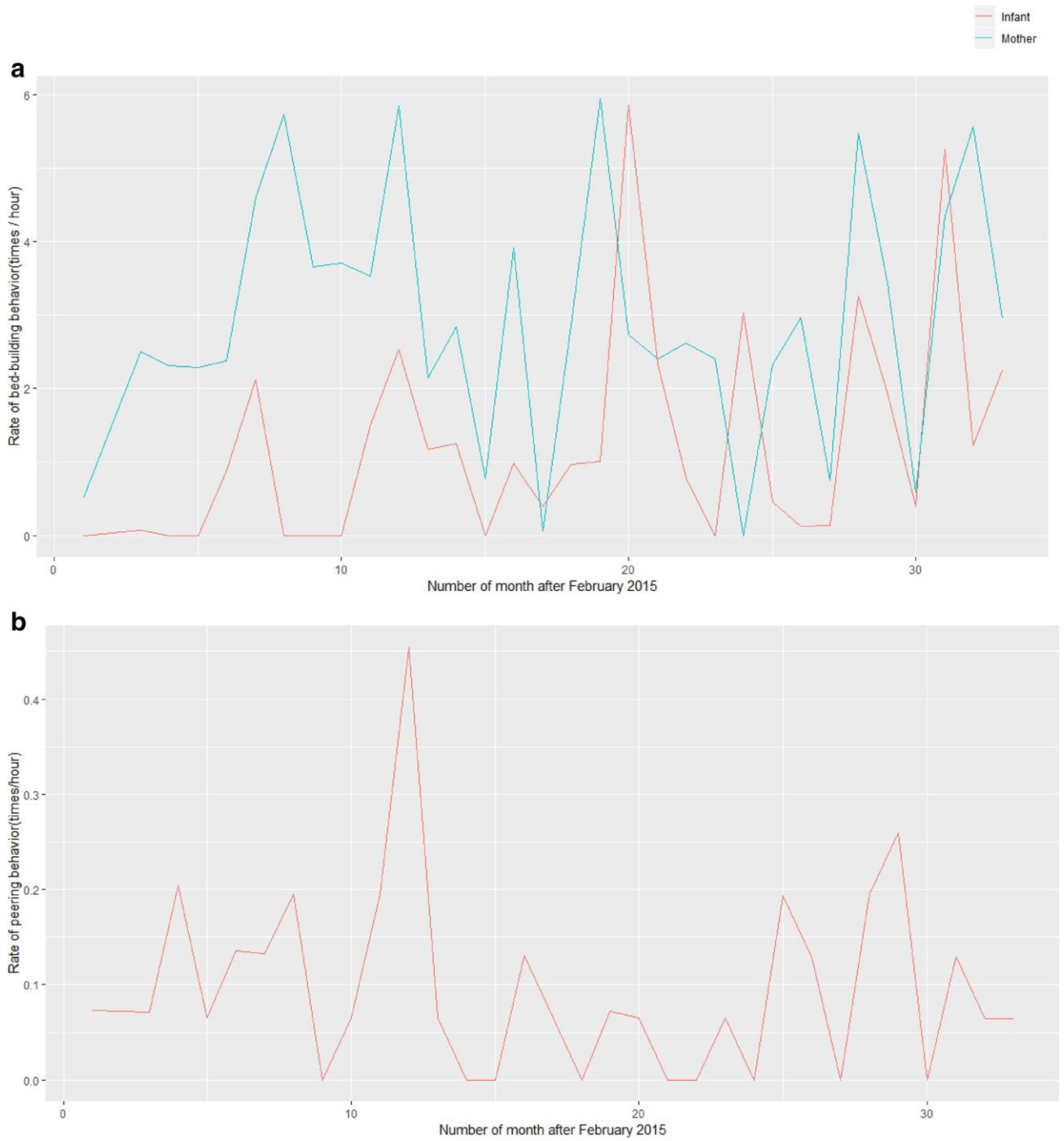

Fig. 2 Change in the rate of bed-building behaviors of a mother and infant chimpanzee (**a**) and the rate of peering behaviors of the infant chimpanzee (**b**) from May 2015 to February 2018

Table 1
Number of individuals performing main types of bedding behaviors

Category	Weaving	Bending	Placing large materials around	Air-bedding	Total
Wild-born	13	22	23	0	23
Captive-born (other)	1	2	6	0	6
Captive-born (biomedical)	0	4	25	13	28
Unknown	1	2	2	0	2
p	<0.001	<0.001	0.194	<0.001	

The *p* values of proportion tests were written in the bottom row of the table

Table 2
The developmental change over time in bed-building routines of the infant chimpanzee from February 2015 to February 2018 and the techniques observed in four adult chimpanzees living in the Kyoto City Zoo

Categories			Bedding behaviors																			Air-bedding behaviors						
Name of individuals	Age (year)	Month	Weaving	Multiple bending	Adjustments after reclining	Adding small materials while reclining	Outside-in	Snapping	Splitting branches	Bend	Stepping on materials	Pushing with knuckle	Rotating body	Gathering	Ventral-dorsal translocation	Placing large materials around body	Moving small materials	Bringing materials	Sweeping with hand	Sweeping with legs	Sweeping with tools	Complex movement of arms	Stepping on substrate	Pushing substrate with knuckle	Rubbing substrate with back of the hand	Shaking materials	Clapping	Rubbing substrate with fingers
Niini	2	F								✓	✓	✓	✓															
		M					✓			✓	✓	✓	✓															
		A								✓																		
		M																										
		J		✓			✓			✓	✓	✓	✓															
		J								✓	✓	✓	✓			✓												
		A																										
		S																										
		O																										
		N								✓	✓	✓	✓			✓												
		D		✓			✓		✓	✓	✓	✓	✓			✓												
		J							✓	✓						✓												
	3	F					✓		✓	✓	✓	✓	✓			✓												
		M					✓			✓	✓	✓	✓															
		A					✓		✓	✓	✓	✓	✓			✓												
		M	✓	✓	✓		✓	✓	✓	✓	✓	✓	✓			✓	✓	✓										
		J		✓	✓	✓	✓		✓	✓	✓	✓	✓			✓						✓						
		J		✓				✓	✓		✓	✓	✓			✓												
		A		✓	✓	✓	✓			✓	✓	✓	✓			✓												
		S			✓		✓	✓	✓	✓	✓	✓	✓			✓												
		O		✓			✓		✓	✓	✓	✓				✓												
		N	✓	✓	✓		✓		✓	✓	✓	✓	✓			✓												
		D		✓	✓		✓		✓	✓	✓	✓	✓			✓						✓						
		J		✓	✓		✓	✓	✓	✓	✓	✓	✓			✓	✓											
	4	F	✓	✓	✓		✓	✓	✓	✓	✓	✓	✓			✓	✓	✓				✓						
		M	✓	✓	✓		✓	✓	✓	✓	✓	✓	✓			✓	✓	✓										
		A	✓	✓	✓		✓	✓	✓	✓	✓	✓	✓			✓												
		M	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓			✓	✓	✓				✓						
		J	✓	✓			✓	✓	✓	✓	✓	✓	✓			✓												
		J		✓	✓	✓	✓	✓	✓	✓							✓												
		A	✓	✓	✓	✓	✓	✓	✓	✓			✓			✓	✓											
		S	✓	✓	✓	✓	✓		✓	✓	✓	✓	✓			✓		✓				✓						
		O	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓			✓		✓										
		N	✓	✓			✓		✓	✓	✓	✓	✓			✓												
		D	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓			✓	✓	✓				✓						
		J	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓			✓	✓											
	5	F	✓	✓	✓		✓	✓	✓	✓	✓	✓	✓		✓	✓	✓	✓										
Keiko	Mother		✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓			✓	✓	✓										
James	Father															✓						✓						
Takashi																						✓						
Lora					✓		✓	✓		✓	✓	✓	✓	✓		✓	✓	✓										