

Structural analysis of behavioral freedom in free-ranging and captive chimpanzees

Naruki Morimura 

Kumamoto Sanctuary, Wildlife Research Center of Kyoto University, Kumamoto, Japan

Correspondence

Naruki Morimura, 990 Ohtao, Uki, Kumamoto, 869-3201, Japan.
 Email: morimura.naruki.5a@kyoto-u.ac.jp

Funding information

the Great Ape Information Network; the IDEAS of Chubu University, Grant/Award Number: IDEAS201714/201918 to NM; the JSPS KAKENHI, Grant/Award Number: 15K12048 to NM; the JSPS to the Leading Program in Primatology and Wildlife Science, Grant/Award Number: JSPS-LGP-U04; the MEXT, Grant/Award Number: 16H06283 to Tetsuro Matsuzawa; The Mitsui & Co. Environment Fund, Grant/Award Number: K18-0098 to NM

Abstract

Behavioral freedom is becoming an increasingly important issue bridging animal welfare and conservation biology. This study focused on range size and spatiotemporal variation in Western chimpanzees, creating a novel index for behavioral freedom. Direct observations were conducted on a group of seven free-ranging chimpanzees in Bossou, Guinea, during 10-hr observation periods over 10 days, and on a group of five captive individuals at the Kumamoto Sanctuary during 7-hr observation periods over 7 days. Bossou chimpanzees showed dynamic ranging patterns; their range size was larger, and their day and time-of-day ranges did not generally overlap. Additionally, the average time-of-day range was 5.2 times greater than the day range. In contrast, sanctuary chimpanzees showed a static ranging pattern, with a smaller range size and a time-of-day range to day range ratio of 1.0. Therefore, the time-of-day range to day range ratio is a suitable quantitative index of behavioral freedom in chimpanzees.

KEY WORDS

animal captivity, animal welfare, conservation, habitat fragmentation, ranging behavior

1 | INTRODUCTION

Behavioral freedom, defined operationally here as the extent of choice and behavioral change for coping with challenges over time and space in daily life (Broom, 2001), is the subject of considerable debate over conflict between humans and non-human animals (hereafter “animals”) in captivity as an animal-welfare issue (Broom, 2011; Hosey, Melfi, & Pankhurst, 2009). Under care and management by caretakers, which aim to promote the well-being of captive animals, animals rarely have control over access to space, temperature and humidity conditions, food, conspecifics, and other resources, in daily life. In contrast, wild animals compete

for space, food, and various other resources with humans over different spatiotemporal scales. Linear infrastructures such as highways, power lines, and gas lines have created habitat fragmentation and loss (Crooks et al., 2017). By accelerating habitat degradation, these anthropogenic impacts are highly related to extinction risk, especially in terrestrial mammals (Wilson et al., 2016). Human presence can also significantly affect the distribution and/or behavior of wild animals in their natural habitat (e.g., bears: Olson, Gilbert, & Squibb, 1997; Rode, Farley, & Robbins, 2006; elk: Whittaker & Knight, 1998; howler monkeys: Grossberg, Treves, & Naughton-Treves, 2003; and gibbons: Reisland & Lambert, 2016). Thus, anthropogenic disturbances confronting wild animals

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2021 The Author. Conservation Science and Practice published by Wiley Periodicals LLC. on behalf of Society for Conservation Biology

can also be detrimental to the degree of behavioral freedom in the wild.

Additionally, recent increases in the number of wildlife rehabilitation and reintroduction projects imply that behavioral freedom is becoming a new issue bridging animal-welfare science and conservation biology (Fraser, 2010; Paquet & Darimont, 2010). Rehabilitation and reintroduction projects subject animals first to a captive life according to welfare considerations and then to a natural life under conservation protection (Bradshaw, Schore, Brown, Poole, & Moss, 2005; Humle, Colin, Laurans, & Raballand, 2011; Teixeira, De Azevedo, Mendl, Cipreste, & Young, 2007). The success of reintroduction programs is linked to free-range survival and reproduction, which, in turn, are subject to the quality of the captive environment where animals engage in problem-solving via cognitive competences, such as physical or spatial cognition, memory, planning, manipulating objects and tools, and cooperative or competitive social interactions. Most captive facilities for wild animals, including zoos, sanctuaries, and laboratories, have been mainly designed for complete life care. Exploring the behavioral freedom of wild animals in captivity could offer in-depth insights into their behavior and potentially increase their rehabilitation and reintroduction; however, only few studies have been conducted on this subject.

Generally, animals restrict their movement to specific areas that are much smaller than one might expect from its observed mobility, although some animals can migrate for thousands of kilometers (Börger, Dalziel, & Fryxell, 2008; White & Garrot, 1990). Ranging behavior represents a fundamental characteristic of wild animal movement corresponding to the extent of choice and behavioral change, which is a consequence of problem-solving in numerous ecological processes, such as the distribution and abundance of fauna and flora (Gaustestad & Mysterud, 2005), habitat selection (Boyce et al., 2016), and predator-prey dynamics (Fryxell, Mosser, Sinclair, & Packer, 2007). Moreover, animal location based on its

movement can be described in the form of a matrix (Figure 1(a)). The day range is one of the major characteristics varying across species (Carbone, Cowlishaw, Isaac, & Rowcliffe, 2005; Clutton-Brock & Harvey, 1977). Understanding relative location distributions within a day and across days facilitate the evaluation of the extent of spatiotemporal variation in ranging behavior under various conditions, for a broad range of species, by eliminating the influence of the absolute value of range size in a day. Few studies have focused on ranging behavior from a behavior freedom perspective, while feeding, traveling, playing, and abnormal behavior have been recognized as candidates of behavioral freedom (Held & Špinka, 2011; Hosey et al., 2009; Kagan, Carter, & Allard, 2015; Wickins-Dražilová, 2006).

Therefore, the present study focused on range size and its spatiotemporal variation in Western chimpanzees (*Pan troglodytes verus*). The aim was to create a novel index using ranging behavior that represents behavioral freedom under both free-ranging and captive conditions. Direct observations from the wild and captivity were compared to understand range size variation within and across observation days. The comparison was expected to illuminate differences in behavioral freedom (as represented by ranging patterns) between free-ranging and captive conditions.

2 | METHODS

2.1 | Study site and subjects

Pan troglodytes verus (Western Chimpanzee) is a critically endangered species found only in West Africa (Humle, Maisels, Oates, Plumptre, & Williamson, 2016; Kühl et al., 2017). Most captive chimpanzees are Western chimpanzees in zoos, sanctuaries, and institutions around the globe (Morimura, Idani, & Matsuzawa, 2011), which indicates that Western chimpanzees are one of the species that is most influenced by anthropogenic

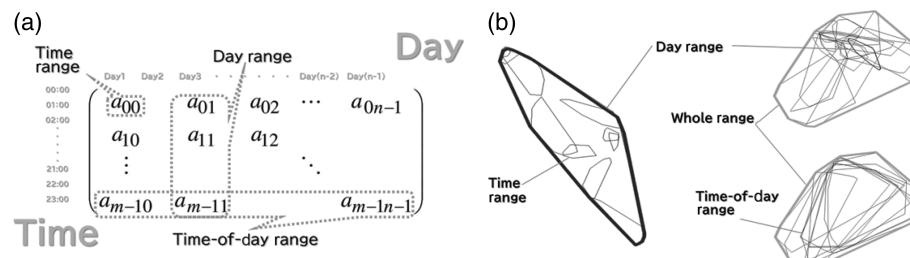


FIGURE 1 (a) A sample of matrix describing the animal range structure. In the sample, time range is calculated from the 1-hr animal location data. The column represents a day range described from the time ranges within a day. The row represents a time-of-day range described from the time ranges across days. The whole range is calculated based on the entire the matrix. (b) A schematic of animal range structure corresponding to the matrix

activities. Therefore, the study was conducted at a natural habitat and at a captive facility for Western chimpanzees.

2.1.1 | Field study

Guinea provides a habitat for the largest population of Western chimpanzees (Tweh et al., 2015). Free-ranging chimpanzees in Bossou, Guinea, have coexisted with the local Manon people for many generations (Matsuzawa, Humle, & Sugiyama, 2011). The subjects of this study were a group of seven chimpanzees, including two adult males (21 and 37 years old), four adult females (estimated to range from 21 to 62 years old), and one juvenile (7 years old). Chimpanzees living in this region have a home range of approximately 15–20 km², with a core area of approximately 6 km² (Sugiyama, 1984). The landscape is composed of small hills (70–150 m high) covered in primary and secondary forests, along with cultivated areas (including orchards) and abandoned fields. Agriculture is currently and was previously practiced within reserve forests.

2.1.2 | Captive study

As of 2021, 301 captive chimpanzees (mostly *P. t. verus*) reside in Japan, with 50 of them found in the Kumamoto Sanctuary (KS), the first in the nation to be established for retired laboratory chimpanzees (Morimura et al., 2011). The subjects were a group of five individuals, comprising two subadult females (both 11 years old), one adult male (24 years old), and three adult females (14–23 years old). The individuals were housed in large social cages. The outdoor compound consisted of a complex of three cages with different areas: 69 m² ($W \times D \times H = 6.5 \times 12.5 \times 5.4$ m), 81 m² ($W \times D \times H = 6.5 \times 12.5 \times 5.4$ m), and 145 m² ($W \times D \times H = 8.0 \times 16.0 \times 5.4$ m). Indoor housing consisted of a complex of eight rooms of various sizes, ranging from 3.6 m² ($W \times D \times H = 2.0 \times 1.8 \times 3.5$ m) to 22 m² ($W \times D \times H = 7.5 \times 3.0 \times 3.5$ m). The total indoor area was 58 m². In both the outdoor and indoor cages, environmental enrichment comprised climbing logs, used fire hoses, burlap hammocks, and several feeding devices. Food and water were provided ad libitum.

2.2 | Data collection

From December 2018 to January 2019, daily location data for the Bossou chimpanzees were collected between 07:00 and 18:00 with the help of five local research assistants. Location data were collected using a GPS receiver

(GPS status & Toolbox ver. 9.2.192) for Android OS, with an accuracy of less than 10 m. During travel, these data were recorded once per minute. When chimpanzees split into several parties, the largest party was followed to acquire location data that represented the largest number of individuals.

From August 12–21, 2019, a research assistant (XC) at KS collected location data daily between 10:00 and 17:00, because chimpanzees stayed in specific sections of outdoor or indoor cages between 08:00–09:30 and 17:00–18:00 during cleaning routines. On the sixth day, observations were limited to 11:00 to 16:00 (August 20, 2019). A 45-min observation session was repeated seven times per day. Instantaneous sampling at 1-min intervals and focal sampling were performed concurrently using a tablet PC with Surface Go (Microsoft Co. Ltd., Redmond, Washington).

2.3 | Data analysis

2.3.1 | Range calculation

The observation data of free-ranging and captive chimpanzee were modified to establish the 10-hr × 10-days and 7-hr × 7-days datasets, respectively, for balancing the observation effort in the range size calculations both within a day and across days. Location (GPS) data collected in Bossou were in both longitude–latitude and Universal Transverse Mercator systems. Range sizes and overlapping areas were calculated using a minimum convex polygon (MCP) method from the adehabitatHR spatial analysis package (Calenge, 2011) in R version 3.5.0 (R Development Core Team, 2018). Location data at KS were X-Y coordinates representing the relative position in pixels. After converting these values to meters, the range size was calculated using the following formula:

$$\frac{1}{2} \left| \sum_{j=1}^n (x_j - x_{j+1}) \times (y_j + y_{j+1}) \right|. \text{ Overlapping area was calculated using the "PBSmapping" R package (Schnute, Boers, & Haigh, 2017). The "leaflet" R package (Cheng, Karambelkar, & Xie, 2018) generated figures showing GPS points at Bossou, which were then overlaid on the Open Street Map.}$$

2.3.2 | Structural analysis of ranges

Location data in both the wild and captivity were analyzed to calculate four types of ranges: whole, time, day, and time-of-day (Figure 1b). The whole range was described using all the location data by the MCP method.

The time range was defined as the MCP range for each single observation session in the wild (1 hr) and captivity (45 min). The day range was calculated based on the sum of the location data within a day. Time-of-day range was defined as the MCP area covered for 1 hr across 10 days (e.g., 7:00–8:00 every day for 10 days) in the wild and for 45 min across 7 days (e.g., 10:00–11:00 every day for 7 days) in captivity.

2.4 | Statistics

Standardized observations of range size were compared within and across days using Welch's two-sample *t*-tests. All statistical tests were performed in R. Significance was set at $p < .05$.

2.5 | Ethics statement

Field observations and research protocols were noninvasive, complied with the laws of Guinea, and were approved by the Direction General de la Recherche Scientifique et l'innovation Technologique (DGERSIT). Animal husbandry and research protocols in KS were approved by the Ethics Committee of the Wildlife Research Center (WRC-2019-KS010A) and the Animal Research Committee of the author's university.

3 | RESULTS

In Bossou, a total of 6,000 GPS points were collected to reveal a range size of 2,450,066 m² (Figure 2). The mean range size from the 1 hr observation sessions from 7:00 to 18:00 was $9,982 \pm 1,624$ m² (mean \pm SEM). The average day range after 10 hr/day was $304,371 \pm 64,833$ m² across the entire study period. The average time-of-day range was $1,583,306 \pm 168,542$ m². The time-of-day range was greater than the day range (Welch's two-sample *t*-test; $t = -7.08$, $df = 11.6$, $p < .001$). Additionally, the mean overlap area in the time range from 7:00 to 18:00 across 10 days (90 overlaps in total) was 336 ± 215 m², corresponding to 3.4% of the average time range. Overlaps in the day (9 overlaps from 1st to 10th day) and time-of-day ranges (9 overlaps from 7:00 to 16:00) were $50,495 \pm 31,709$ m² and $1,483,440 \pm 163,424$ m², respectively. The values corresponded to 16.6 and 93.7% of the average day and time-of-day ranges, respectively.

At KS, the overall range size was 295 m², as obtained from 10,800 location points. The mean range during 45 min was 182 ± 7 m². The mean day range (from 7 hr consecutive observation) was 279 ± 5 m². The mean time-of-day range (from the same time of day across multiple days for 7 hr) was 281 ± 4 m². The time-of-day range did not differ significantly from the day range (Welch's two-sample *t*-test; $t = -0.26$, $df = 11.8$, $p = .80$). Additionally, the mean overlap area (41 overlaps total)

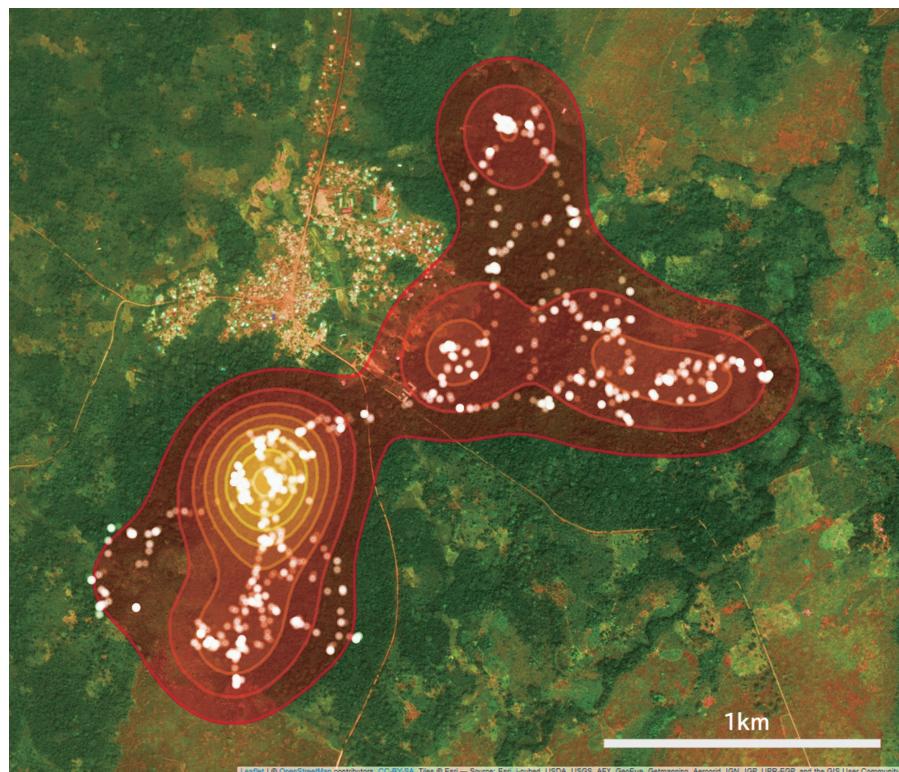


FIGURE 2 Heatmap overlaid with GPS locations of Bossou chimpanzees in field observations. A plot indicates 300 m² and corresponds to the whole range size at the Kumamoto Sanctuary

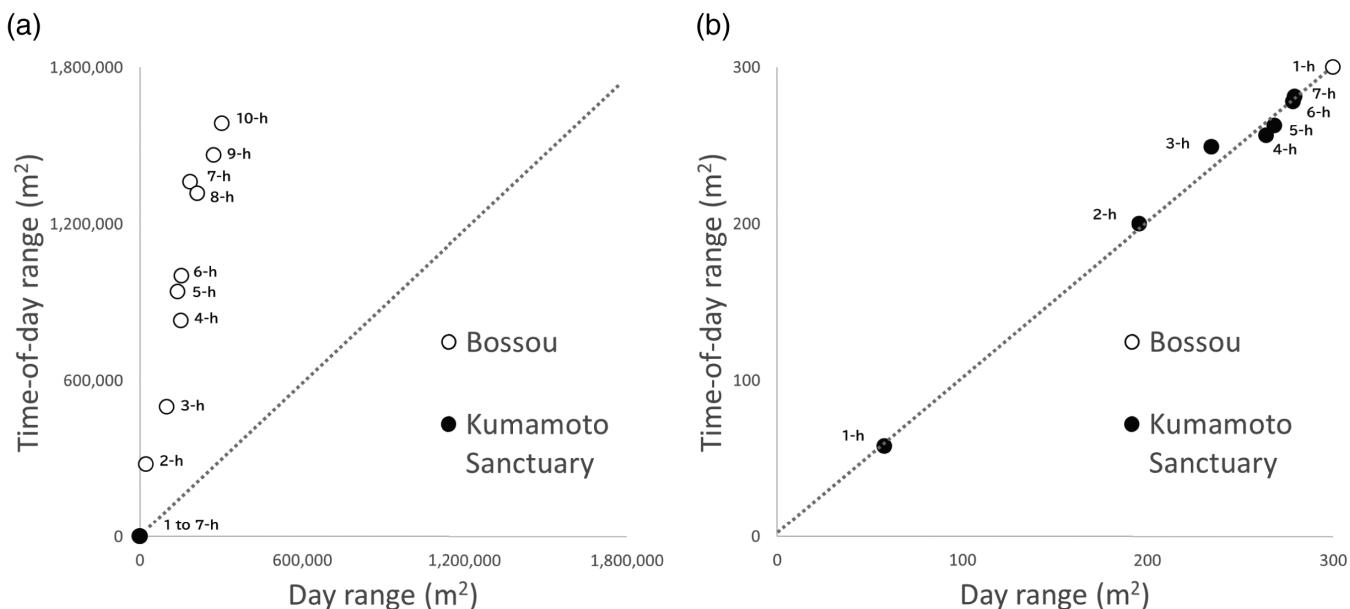


FIGURE 3 (a) Correlation of day range and time-of-day range at Bossou and the Kumamoto Sanctuary (KS). “1 hr” refers to a plot of both ranges calculated from 1 hr observation blocks. (b) Enlargement of 1-hr block in Bossou and 1-hr to 7-hr blocks at KS with a smaller size scale. The plots at KS are mostly close to the dot-line of direct proportion between day and time-of-day ranges, regardless of observation efforts

was $147 \pm 8 m^2$, corresponding to 80.8% of the average. Overlaps in the day and time-of-day ranges were 277 ± 2 and $267 \pm 4 m^2$, respectively, corresponding to 99.3 and 95.0% of their respective averages.

When the day range was plotted against the time-of-day range across multiple blocks of observation time for Bossou and KS, the plots showed that the time-of-day range increased more than the day range as the observation effort increased in the Bossou range (Figure 3a), while the plots at KS stayed close to zero in all time blocks (Figure 3b). The comparison illustrated that the relationship between the two types of ranges varied continuously but was still sensitive to the environmental difference between captivity and the wild, regardless of observation efforts. Under a comparable observation effort (e.g., 7 hr blocks), the ratio of day range to time-of-day range was 7.3 in Bossou and 1.0 at KS.

4 | DISCUSSION

To the best of our knowledge, this study is the first to develop a scalable index for behavioral freedom. Although the results of the study are promising, the present study is preliminary because of limited observation periods, sites, group size, and less systematic comparisons in terms of climate and environmental conditions, resource availability and its seasonal variation, population structures, social relationships, and anthropogenic impact, which can substantially influence the ranging behavior of chimpanzees. The Bossou chimpanzees

showed a dynamic ranging pattern that was large and rarely overlapped across three time frames (60 min, 1 days, and 1 hr over multiple days). The dynamics were especially clear when comparing the time-of-day and day ranges. On average, the time-of-day range was 5.2 times greater than the day range at Bossou, suggesting that chimpanzees in a larger habitat have multiple core areas that they use intensively. In contrast, the KS chimpanzees showed a static ranging pattern with a smaller range size that largely overlapped (>80%) across three time frames (45 min, 1 days, and 1 hr over multiple days). This pattern suggests that the KS chimpanzees stayed mostly in the same limited area. The difference between the day and time-of-day ranges under standardized observation highlighted a distinctive difference between wild and captive environments: the former allows for multiple core areas, while the latter typically contains only one. A similar tendency is present in the day and home ranges of 79 primate species (Pearce, Carbone, Cowlishaw, & Isaac, 2013), namely the dynamic variation of day range within home range, which support the findings of this study.

The results also showed that a higher ratio of time-of-day range to day range, with limited overlap, indicates that an individual has more options when choosing where to be, which is beneficial after a negative event caused by natural processes in ecological and climate dynamics and human activity in logging, cultivation, and other developments. This suggests that the degree of behavioral freedom increases with large differences between day and time-of-day ranges. This study also demonstrated that the ratio of the time-of-day range to

the day range is a valid quantitative index for representing the behavioral freedom. The index is simple enough to be applied to a variety of animal species in the comparison of the spatiotemporal variation of animal movement between different species, across different environmental conditions for the same species, and different periods in a specific area for a certain species.

Considering the static ranging pattern at KS, such as greater than 80% overlapped across three time frames, KS chimpanzees had few spatial options for coping with negative events in their environment caused by different climate and ecological conditions from the natural habitat, care management, or human presence (Figure 2b). These findings enable the clear distinction of ranging patterns between free-ranging and captive chimpanzees, namely the differences in dynamic and static ranging patterns, based on range size variation, regardless of the absolute value of range size. In turn, a captive environment could be developed that is qualitatively comparable to the wild, where an animal has a larger time-of-day range than day range. Animal-welfare efforts in captivity could focus on the gap between day and time-of-day ranges by providing living area rotations that create multiple core regions, even if the overall living space is limited. Zoo animals tend to stay in a single location (Ross, Calcutt, Schapiro, & Hau, 2011), suggesting that having one primary caretaking site may be responsible for creating a single-core lifestyle. Environmental enrichment practices for enhancing a multicore lifestyle can lead to an increase in animal space use and activity level (Lukas, Hoff, & Maple, 2003) and improve quality of life with high controllability over the surrounding environment. Rehabilitation centers could potentially take inspiration from precision agriculture science, which has already tackled the challenge of establishing a multicore lifestyle in captivity (Munksgaard, Rushen, De Passillé, & Krohn, 2011). Preserving the number of cores in a whole range, at least comparable to the current status, is a potential goal in wildlife conservation, while a comparable counting method for the core area in the animal range remains unknown. Further comprehensive studies for a deeper understanding of behavioral freedom in a variety of environments in chimpanzees and other species can bring a significant benefit for promoting a symbiotic existence between humans and wildlife.

ACKNOWLEDGMENTS

The author thanks the staff at the Kumamoto Sanctuary of Kyoto University (Japan), Institut de Recherche Environnementale de Bossou, and DGERSIT (Guinea). This research was financially supported by grants from the JSPS KAKENHI (15K12048), the IDEAS of Chubu University (IDEAS201714/201918), and Mitsui & Co. Environment

Fund (K18-0098) to Naruki Morimura, the MEXT (16H06283) to Tetsuro Matsuzawa, the JSPS to the Leading Program in Primatology and Wildlife Science, and the Great Ape Information Network. Thanks are extended to the anonymous reviewers for their many insightful comments.

CONFLICT OF INTEREST

The author declares no conflict of interest.

DATA AVAILABILITY STATEMENT

Data requests can be made to the author.

ETHICS STATEMENT

All ethical guidelines were met.

ORCID

Naruki Morimura  <https://orcid.org/0000-0002-9117-4828>

REFERENCES

- Börger, L., Dalziel, B. D., & Fryxell, J. M. (2008). Are there general mechanisms of animal home range behaviour? A review and prospects for future research. *Ecology Letters*, 11(6), 637–650.
- Boyce, M. S., Johnson, C. J., Merrill, E. H., Nielsen, S. E., Solberg, E. J., & Van Moorter, B. (2016). Can habitat selection predict abundance? *The Journal of Animal Ecology*, 85(1), 11–20.
- Bradshaw, G. A., Schore, A. N., Brown, J. L., Poole, J. H., & Moss, C. J. (2005). Elephant breakdown. *Nature*, 433(7028), 807.
- Broom, D. M. (2001). Coping, stress, and welfare. In D. M. Broom (Ed.), *Coping with challenge: Welfare in animals including humans* (pp. 1–9). Berlin: Dahlem University Press.
- Broom, D. M. (2011). A history of animal welfare science. *Acta Biologica Theoretica*, 59(2), 121–137.
- Carbone, C., Cowlishaw, G., Isaac, N. J., & Rowcliffe, J. M. (2005). How far do animals go? Determinants of day range in mammals. *The American Naturalist*, 165(2), 290–297.
- Calenge, C. (2011). *Home range estimation in R: The adehabitatHR package*. Saint Benoist, Auffargis, France: OFFICE National de la Classe et de la Faune Sauvage.
- Cheng, J., Karambelkar, B., Xie, Y. (2018). Leaflet: Create interactive web maps with the javascript “leaflet” library. R Package Version
- Clutton-Brock, T. H., & Harvey, P. H. (1977). Primate ecology and social organization. *Journal of Zoology*, 183(1), 1–39.
- Crooks, K. R., Burdett, C. L., Theobald, D. M., King, S. R., Di Marco, M., Rondinini, C., & Boitani, L. (2017). Quantification of habitat fragmentation reveals extinction risk in terrestrial mammals. *PNAS*, 114(29), 7635–7640.
- Fraser, D. (2010). Toward a synthesis of conservation and animal welfare science. *Animal Welfare*, 19(2), 121–124.
- Fryxell, J. M., Mosser, A., Sinclair, A. R., & Packer, C. (2007). Group formation stabilizes predator-prey dynamics. *Nature*, 449 (7165), 1041–1043.
- Gautestad, A. O., & Mysterud, I. (2005). Intrinsic scaling complexity in animal dispersion and abundance. *The American Naturalist*, 165(1), 44–55.

- Grossberg, R., Treves, A., & Naughton-Treves, L. (2003). The incidental ecotourist: Measuring visitor impacts on endangered howler monkeys at a Belizean archaeological site. *Environmental Conservation*, 30(1), 40–51.
- Held, S. D., & Špinka, M. (2011). Animal play and animal welfare. *Animal Behaviour*, 81(5), 891–899.
- Hosey, G., Melfi, V., & Pankhurst, S. (2009). *Zoo animals: Behaviour, management, and welfare* (p. 661). Oxford: Oxford University Press.
- Humle, T., Colin, C., Laurans, M., & Raballand, E. (2011). Group release of sanctuary chimpanzees (*Pan troglodytes*) in the Haut Niger National Park, Guinea, West Africa: Ranging patterns and lessons so far. *International Journal of Primatology*, 32, 456–473.
- Humle, T., Maisels, F., Oates, J. F., Plumptre, A., Williamson, E. A. (2016). *Pan troglodytes* (errata version published in 2018). The IUCN Red List of Threatened Species 2016: E. T15933A129038584. <https://doi.org/10.2305/IUCN.UK.2016-2.RLTS.T15933A17964454.en>
- Kagan, R., Carter, S., & Allard, S. (2015). A universal animal welfare framework for zoos. *Journal of Applied Animal Welfare Science*, 18, S1–S10.
- Kühl, H. S., Sop, T., Williamson, E. A., Mundry, R., Brugière, D., Campbell, G., ... Boesch, C. (2017). The critically endangered western chimpanzee declines by 80%. *American Journal of Primatology*, 79(9), e22681.
- Lukas, K. E., Hoff, M. P., & Maple, T. L. (2003). Gorilla behavior in response to systematic alternation between zoo enclosures. *Applied Animal Behaviour Science*, 81(4), 367–386.
- Matsuzawa, T., Humle, T., & Sugiyama, Y. (2011). *The chimpanzees of Bossou and Nimba*. Tokyo: Springer.
- Morimura, N., Idani, G. I., & Matsuzawa, T. (2011). The first chimpanzee sanctuary in Japan: An attempt to care for the “surplus” of biomedical research. *American Journal of Primatology*, 73(3), 226–232.
- Munksgaard, L., Rushen, J., De Passillé, A. M., & Krohn, C. C. (2011). Forced versus free traffic in an automated milking system. *Livestock Science*, 138(1–3), 244–250.
- Olson, T. L., Gilbert, B. K., & Squibb, R. C. (1997). The effects of increasing human activity on brown bear use of an Alaskan river. *Biological Conservation*, 82(1), 95–99.
- Paquet, P. C., & Darimont, C. T. (2010). Wildlife conservation and animal welfare: Two sides of the same coin. *Animal Welfare*, 19 (2), 177–190.
- Pearce, F., Carbone, C., Cowlishaw, G., & Isaac, N. J. (2013). Space-use scaling and home range overlap in primates. *Proceedings of the Royal Society B: Biological Sciences*, 280(1751), 20122122.
- R Development Core Team. (2018). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Reisland, M. A., & Lambert, J. E. (2016). Sympatric apes in sacred forests: Shared space and habitat use by humans and endangered Javan gibbons (*Hylobates moloch*). *PLoS One*, 11(1), e0146891.
- Rode, K. D., Farley, S. D., & Robbins, C. T. (2006). Behavioral responses of brown bears mediate nutritional effects of experimentally introduced tourism. *Biological Conservation*, 133(1), 70–80.
- Ross, S. R., Calcutt, S., Schapiro, S. J., & Hau, J. (2011). Space use selectivity by chimpanzees and gorillas in an indoor-outdoor enclosure. *American Journal of Primatology*, 73, 197–208.
- Schnute, J. T., Boers, N., Haigh, R. (2017). PBSmapping: Mapping fisheries data and spatial analysis tools. R Package Version 2.70.4.
- Sugiyama, Y. (1984). Population dynamics of wild chimpanzees at Bossou, Guinea, between 1976–1983. *Primates*, 25, 391–400.
- Teixeira, C. P., De Azevedo, C. S., Mendl, M., Cipreste, C. F., & Young, R. J. (2007). Revisiting translocation and reintroduction programmes: The importance of considering stress. *Animal Behaviour*, 73(1), 1–13.
- Tweh, C. G., Lormie, M. M., Kouakou, C. Y., Hillers, A., Kühl, H. S., & Junker, J. (2015). Conservation status of chimpanzees *Pan troglodytes verus* and other large mammals in Liberia: A nationwide survey. *Oryx*, 49(4), 710–718.
- White, G. W., & Garrot, R. A. (1990). *Analysis of wildlife radio-tracking data*. San Diego, CA: Academic Press.
- Wickins-Dražilová, D. (2006). Zoo animal welfare. *Journal of Agricultural and Environmental Ethics*, 19(1), 27–36.
- Whittaker, D., & Knight, R. L. (1998). Understanding wildlife responses to humans. *Wildlife Society Bulletin*, 26, 312–317.
- Wilson, M. C., Chen, X., Corlett, R. T., Didham, R. K., Ding, P., Holt, R. D., ... Yu, M. (2016). Habitat fragmentation and biodiversity conservation: Key findings and future challenges. *Landscape Ecology*, 31, 219–227.

How to cite this article: Morimura N. Structural analysis of behavioral freedom in free-ranging and captive chimpanzees. *Conservation Science and Practice*. 2021;3:e429. <https://doi.org/10.1111/csp.2.429>