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Captive chimpanzee (*Pan troglodytes*) behavior as a function of space per animal and enclosure type

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Abstract

Space per animal, or animal density, and enclosure type are important elements of functionally appropriate captive environments (FACEs) for chimpanzees. The National Institutes of Health (NIH) recommends that captive chimpanzees be maintained in areas of >250 ft²/animal. Several studies have investigated chimpanzee behavior in relation to space per animal, but only two studies have examined these variables while attempting to hold environmental complexity constant. Both have found few, if any, significant differences in behavior associated with increased space per animal. The NIH does not provide recommendations pertaining to enclosure type. Although PrimadomesTM and corrals are considered acceptable FACE housing, no studies have investigated chimpanzee behavior in relation to these two common types of enclosures. We examined the NIH space per animal recommendation, and the effects of enclosure type, while maintaining similar levels of environmental complexity. We used focal animal observations to record the behavior of 22 chimpanzees in three social groups following within-facility housing transfers. Chimpanzees that were moved from an area with space below the NIH recommendation to the same type of enclosure with space above the recommendation (dome to double dome) exhibited significantly more locomotion and behavioral diversity post-transfer. Chimpanzees that were moved from an area with space below the recommendation to a different type of enclosure with space above the recommendation (dome to corral) exhibited significant increases in foraging and behavioral diversity, and a decrease in rough scratching. Lastly, chimpanzees that were moved from an area above the recommendation to a different enclosure type with space equal to the recommendation (corral to double dome) exhibited an increase in behavioral diversity. These results add to the body of literature that addresses the concept of specific minimum space requirements per chimpanzee, and highlight the need for more empirical investigation of the relationship between space per chimpanzee, behavior, and welfare.

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CONFLICTS OF INTEREST

The authors have no conflicts of interest to declare.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

Keywords

behavior; chimpanzee; enclosure; housing; space per animal

1 | INTRODUCTION

There has been an increasing focus on the refinement of functionally appropriate captive environments (FACEs) for captive chimpanzees (*Pan troglodytes*) that simulate natural conditions and promote opportunities to engage in species-typical behaviors. One aspect of these FACEs is the amount of space to which chimpanzees have access, often referred to as animal density (total space/number of animals in the group) or space per animal. Space per animal for captive nonhuman primates has been regulated by governmental agencies for decades (Else, 2013; Hau & Bayne, 2017), including regulations put forth by the Animal Welfare Act of 1966 (25 ft² of floor area per ape, Animal Welfare Act, p 107, 2008). Various guidelines also exist. For example, the *Guide for the Care and Use of Laboratory Animals* states that there is no formula for calculating space needs based on body size and weight, and that animals housed in social groups should have sufficient space and complexity in enclosures to allow escape from aggression and areas in which to hide (National Research Council, 2011). The *Chimpanzee Care Manual* recommends at least 2,000 ft² for groups of five or fewer apes, plus an additional 1,000 ft² for each additional chimpanzee in groups of more than five (AZA Ape TAG, 2010).

One of the most recent guidelines pertaining to space per animal was put forth by the NIH. In 2011, the Institute of Medicine (IOM) Committee on the Use of Chimpanzees in Biomedical and Behavioral Research announced several principles and regulations concerning captive chimpanzees, including the recommendation that they be maintained in ethologically appropriate physical and social environments, or EAEs (Institute of Medicine & National Research Council, 2011). In 2013, a Council of Councils working group charged by the NIH provided 10 recommendations pertaining to captive environments (NIH, 2013). The NIH, at the time, accepted all but one of these recommendations; the one that suggested that *each* chimpanzee should have access to 1,000 ft². Using a literature review by Else (2013) and input from experts, the NIH eventually settled on a recommendation of 250 ft²/chimpanzee for an EAE (NIH, 2014). Although the NIH (2013) and Else (2013) use the term “ethologically appropriate environment (EAE),” the more descriptive term “functionally appropriate captive environment (FACE)” is becoming more commonly used among behavioral management scientists (Bettinger, Leighty, Daneault, Richards, & Bielitzki, 2017; Dye, 2017; Honess, 2017; Reamer, Haller, Lambeth, & Schapiro, 2017; Williams & Ross, 2017) due to various shortcomings of the term “EAE” (Blooms Smith, Hasenau, & Bohm, 2017). As such, “FACEs” will be used throughout this paper in place of “EAEs.”

Studies on space per chimpanzee have suggested that smaller spaces, or higher animal densities, are related to social conflict and tension (de Waal, Aureli, & Judge, 2000; Judge, 2000). To cope with high animal densities, chimpanzees have been observed to use tension-reduction strategies (i.e., increased affiliation in response to increased aggression; Duncan, Jones, van Lierop, & Phillip, 2013; Nieuwenhuijsen & de Waal, 1982; Videan & Fritz,

2007), conflict-avoidance strategies (i.e., reductions in both aggressive and affiliative behaviors; Duncan et al., 2013; Videan & Fritz, 2007), and overall decreased activity levels, including reduced allogrooming and pantgrunt greetings (Aureli & de Waal, 1997; de Waal, 1989). Chimpanzees have also been observed to exhibit increased abnormal behaviors and undesirable self-directed behaviors as a result of increased density (Duncan et al., 2013).

These studies provide invaluable data concerning captive chimpanzee behavior across differing quantities of available space. However, they often have a confounding variable of environmental complexity: the apes are typically moved to spaces that are larger, but also more environmentally complex (i.e., given access to outdoor areas in addition to indoor enclosures, or transferred to newer, more naturalistic enclosures) (Aureli & de Waal, 1997; Brent, Lee, & Eichberg, 1991; Clarke, Juno, & Maple, 1982; Duncan et al., 2013; Jensvold, Sanz, Fouts, & Fouts, 2001; Nieuwenhuijsen & de Waal, 1982; Ross, Wagner, Schapiro, & Hau, 2010; Videan & Fritz, 2007). Given that there is a general consensus that the quality and complexity of space in which chimpanzees are maintained is just as important, if not more important, than the amount of space per chimpanzee (AZA Ape TAG, 2010; Brent, 2001; Hosey, 2005; Reamer et al., 2015, 2017; Reinhardt, Liss, & Stevens, 1996; Ross, Calcutt, Schapiro, & Hau, 2011; Ross, Wagner, Schapiro, Hau, & Lukas, 2011; Stoinski, Hoff, & Maple, 2001; Wilson, 1992), it is difficult to separate behavioral effects due to changes in space per animal from those due to changes in environmental complexity.

Studies that have maintained comparable levels of environmental complexity across different quantities of available space seem to reveal few, if any behavioral changes related to animal density. Ross, Wagner, et al. (2011) found “conservative, but positive,” changes in behavior, including decreases in abnormal behaviors (from 1.80% pre-transfer to 0.49% post-transfer) and human-directed visual attention (from 15.78% pre-transfer to 2.92% post-transfer, likely due to the change in facility design that was specifically intended to decrease this behavior) when five chimpanzees were moved from a complex 131 ft²/animal enclosure to a new, similarly complex, 162 ft²/animal enclosure. The authors suggest that there may be a minimum size threshold (the original 131 ft²/animal), beyond which increases in space have little effect on behavior. Similarly, Reamer et al. (2015) (a study performed at the same facility as the current study) found no significant differences in behavior between chimpanzees housed in complex enclosures providing less than 250 ft²/animal and those housed in complex enclosures providing more than 250 ft²/animal. Although environmental complexity was similar across both housing situations, this study was based on retrospective group scan data from previous studies conducted over a 9-year period, and, more notably, enclosure type (corrals vs. Primadomes™, see below) and space per animal were confounded (Reamer et al., 2015). Chimpanzees that had access to more than 250 ft²/animal were almost always housed in a corral, and chimpanzees that had access to 250 ft²/animal or less were almost always housed in a Primadome™ (hereafter referred to as a dome). Therefore, in the Reamer et al. (2015) study, we could not tease apart influences on behavior due to space per animal from those due to enclosure type. Nonetheless, both of these studies seem to support the idea of a behaviorally-relevant minimum size threshold, wherein enhancements to welfare occur when space is increased beyond a suboptimal minimum, but increases in space beyond this minimum lead to smaller and smaller changes in behavior and increases in welfare (Appleby, 1997; Reamer et al., 2015; Ross, Wagner, et al., 2011).

The NIH does not provide specific recommendations pertaining to enclosure type for captive chimpanzees. However, Else (2013) mentions aspects of various housing structures, noting that domes are acceptable in creating EAEs because of their low cost and increased usable volume (IOM, 2011), and that the use of concrete walls with the addition of ground-level windows, characteristic of corrals, is also acceptable. Domes and corrals are two common types of housing for captive chimpanzees, and can be found at multiple facilities across the United States and abroad (including, but not limited to: Chimp Haven, the National Chimpanzee Sanctuary, Louisiana; Yerkes NPRC Field Station, Georgia; New Iberia Primate Center, Louisiana; Alamogordo Primate Facility, New Mexico; Primarily Primates, Texas; Texas Biomedical Research Institute, Texas; Center for Great Apes, Florida; Primate Research Institute, Japan; as well as the National Center for Chimpanzee Care, Texas in the current study), but they do differ in certain aspects. Corrals have open tops and concrete walls, whereas domes are fully-enclosed with wire mesh. These structural variations create differences in functional space (volume), and the ability of the animals to use the volume. In general, domes allow utilization of much of the structure's volume, because practically all surfaces, including the walls and ceilings, are climbable. Corrals typically have more area at ground level, but less utilizable volume than domes, due to the corrals' open top and concrete walls, which constrain the placement of climbing structures too close to the walls for safety and containment reasons. Despite the common use of these enclosures and the differences between them, captive chimpanzee behavior has not been examined in relation to these enclosure types. Furthermore, as mentioned previously, enclosure type and space per animal were confounded in Reamer et al. (2015), making it difficult to determine whether the absence of statistically significant changes in behavior were due to differences in space per animal or differences in enclosure type.

Given the lack of data to support a specific minimum space density or enclosure type for captive chimpanzees, we aimed to empirically examine potential differences in chimpanzee behavior as a function of differing amounts of space per animal, and/or different enclosure types, with comparable environmental complexity across experimental conditions. We used a repeated-measures design in which chimpanzees experienced within-facility transfers, resulting in (1) differing amounts of available space per animal and (2) either a change in, or no change in, enclosure type. Three stable social groups of captive chimpanzees were moved to different enclosures in three types of "transfers" (note that $\text{ft}^2/\text{animal}$ was calculated by dividing the total amount of inside and outside horizontal square footage by the number of chimpanzees in the group): (a) from a dome ($\sim 142 \text{ ft}^2/\text{animal}$) to a double dome ($\sim 284 \text{ ft}^2/\text{animal}$); (b) from a dome ($\sim 142 \text{ ft}^2/\text{animal}$) to a corral ($\sim 645 \text{ ft}^2/\text{animal}$); or (c) from a corral ($\sim 564 \text{ ft}^2/\text{animal}$) to a double dome ($\sim 250 \text{ ft}^2/\text{animal}$). Although we were not interested in the behavioral effects of the transfer process itself, we used this within-subjects transfer paradigm to assess differences in chimpanzee behavior in areas less than, equal to, or greater than the NIH space recommendation, while attempting to tease apart the effects of space per animal from those of enclosure type.

2 | METHOD

2.1 | Subjects and housing

Subjects included 22 captive chimpanzees living in three stable social groups at the National Center for Chimpanzee Care (NCCC), Michale E. Keeling Center for Comparative Medicine and Research of The University of Texas MD Anderson Cancer Center (UTMDACC) in Bastrop, Texas. The Keeling Center has been continuously accredited by AAALAC since 1979. There were 14 females and eight males in the study that ranged from 14 to 51 years of age (mean age = 29 years). One group ($n = 8$) was housed in a corral with access to indoor space, measuring approximately 4,518 ft² total, or 564 ft²/animal. Two groups ($n = 7$ each) were housed in a dome with access to indoor space, each measuring approximately 1,000 ft² total or 142 ft²/animal (Figure 1). Domes and corrals, while perhaps not equal in terms of functional space (volume), were quite similar in terms of structural and environmental complexity. Both domes and corrals adhere to our facility's environmental enhancement plan, with each enclosure containing 19–22 telephone poles, 2–3 wooden platforms, 2–4 culvert sections, one tractor tire, two large plastic balls, one or two 55-gallon barrels, and 3–6 fire hose/rope swings. Additionally, highly similar foraging enrichment strategies and Positive Reinforcement Training programs are employed in both domes and corrals. The research conducted in this study complied with the approved protocols of the UTMDACC Institutional Animal Care and Use Committee, and complied with the legal requirements of the United States and the American Society of Primatologists' Principles for the Ethical Treatment of Primates.

2.2 | Design

To help distinguish the influences on behavior of space per animal from the effects of enclosure type, three chimpanzee groups moved through three space and enclosure type scenarios (Figure 2). In scenario (a), one group housed in a dome was moved to double domes, thus moving from less space per animal than recommended by the NIH (142 ft²/animal) to more space than recommended (284 ft²/animal), while keeping enclosure type (dome) constant. In scenario (b), a second group housed in a dome (142 ft²/animal) moved to a corral (~645 ft²/animal), an increase in space of approximately four and a half times per animal. This move was from below the NIH recommendation to far above it, and included a change in enclosure type as well. In scenario (c), a third group, housed in a corral (~564 ft²/animal), was moved to double domes (~250 ft²/animal), a decrease in space of about one-half, as well as a change in housing type. In this last scenario, animal density was *increased* by approximately 200%, yet post-transfer space per animal still met the NIH's minimum recommendation.

2.3 | Procedure

Chimpanzee groups were temporarily moved to different enclosures in order to complete a building renovation project, beginning in late October, 2016. Baseline data collection began approximately four months prior to transferring the animals for renovations and post-transfer data were collected for an additional 5 months, commencing 1 day after the animal moves were completed. Animal moves consisted of each chimpanzee voluntarily entering a transport box (an approximately 1.5 × 1.5 × 1 m enclosure on wheels). Two trainers then

wheeled the chimpanzee to the post-transfer enclosure, where the door to the transport box was opened and the chimpanzee was free to enter the enclosure. This was repeated for each chimpanzee in the social group (although sometimes two chimpanzees were transported together). The longest individual transport lasted approximately 8 min and the longest distance traveled was 121 m.

Behavioral data were collected using 15-min focal animal observations (Altmann, 1974). Each chimpanzee was a focal animal between 2 and 4 times per week, for a total of 320 hr of observations (160 hr pre- and 160 hr post-transfer) across all individuals in the three social groups. Focal animal observations were collected on a laptop computer running Noldus Observer XT 10 (2010) between 0700 and 1600 hr and were equally distributed across AM and PM. Categories of behavior included locomotive, aggressive, submissive, self-directed, abnormal, sexual, affiliative, object manipulation, and other (Supplementary Table S1). The proximity of focal animals to other animals within the group (i.e., touching, near, or distant) was simultaneously recorded (Supplementary Table S1). Lastly, we included a behavioral diversity score that served as a measure of the average number of different behaviors exhibited by the subjects during an observation period. Behavioral diversity scores were determined by counting the number of different behaviors that each animal exhibited during each observation and then calculating the average pre- and post-transfer.

2.4 | Data analysis

Total durations of each behavior were averaged pre- and post-transfer for each chimpanzee. Durations of time spent “out of view” were removed from total durations (the denominator) to create duration spent “in view” for all analyses. Durations were then converted into percentages [Percent Time = (Duration in seconds/“In-View” Duration in seconds) * 100], representing the average percentage of time individual subjects spent engaged in each behavior. Due to small sample size and non-normal distributions (positively skewed data), we used bootstrapped paired-samples *t*-tests (1,000 resamples) for within-subjects comparisons pre- and post-transfer. A-priori pairwise comparisons were performed for welfare-related behaviors, including locomotive, aggressive, affiliative, submissive, and abnormal behaviors, as well as rough scratching, foraging, inactive alert, behavioral diversity, and social proximity. All analyses were performed in SPSS Statistics 22 (IBM Corporation, Chicago, IL). Significance level for all analyses was set at $p < 0.05$. Corrections for multiple comparisons (e.g., Bonferroni or Šidák adjustments) were not used due to the highly conservative nature of such corrections, which reduce statistical power and increase Type II error (Nakagawa, 2004; Perneger, 1998). Means, standard errors of the means, 95% confidence intervals of mean percent changes (Table 1), and exact, bootstrapped *p* values are reported.

3 | RESULTS

Table 1 shows significant ($p < 0.05$) and trending ($0.051 < p < 0.08$) differences in behavior across transfer type. Three behaviors (rough scratching, foraging, locomoting), as well as behavioral diversity scores, were significantly different between the pre- and post-transfer periods in at least one transfer scenario. Chimpanzees exhibited no other significant or

trending behavioral differences, including no significant changes in social proximity, time spent inactive but alert, or in aggressive, affiliative, sexual, abnormal, and submissive behaviors.

Chimpanzees that were transferred from an area less than the NIH recommendation to an area greater than that recommendation, and that also experienced a change in housing type (from a dome to a corral), exhibited significantly lower percentages of time spent (mean% $\pm$ SE%) rough scratching (dome = 0.58% $\pm$ 0.09%, corral = 0.26% $\pm$ 0.04%, p = 0.05, Figure 3), significantly more time foraging (dome = 2.19% $\pm$ 0.93%, corral = 3.70% $\pm$ 1.03%, p = 0.047, Figure 4), a trend toward more time locomoting (dome = 5.44% $\pm$ 0.69%, corral = 10.57% $\pm$ 1.38%, p = 0.064, Figure 5), and significantly higher behavioral diversity scores (dome = 6.60 $\pm$ 0.17, corral = 8.35 $\pm$ 0.25, p = 0.002) following the transfer.

Chimpanzees that were moved from an area less than the NIH recommendation to the same type of enclosure with space greater than the recommendation (from a dome to a double dome) exhibited significantly higher percentages of time spent locomoting (dome = 5.65% $\pm$ 1.20%, double dome = 8.00% $\pm$ 1.35%, p = 0.024, Figure 5), higher behavioral diversity scores (dome = 6.97 $\pm$ 0.33, double dome = 8.82 $\pm$ 0.37, p = 0.02, Figure 6), and a trend toward higher percentages of time spent foraging (dome = 0.87% $\pm$ 0.52%, double dome = 1.88% $\pm$ 0.57%, p = 0.074, Figure 4) following the transfer.

Lastly, chimpanzees that were moved from an area with space greater than the NIH recommendation to an area that was equal to the recommendation (from a corral to a double dome) exhibited significantly higher behavioral diversity scores following the transfer (corral = 6.29 $\pm$ 0.20, double dome = 7.67 $\pm$ 0.33, p = 0.007, Figure 6). These chimpanzees exhibited no other significant differences in behavior.

4 | DISCUSSION

We were interested in examining variation in behavior as a result of differing quantities of space available and different enclosure types, and accomplished this by using a within-subjects design in conjunction with animal moves within our facility. The relationship between space per chimpanzee, behavior, and welfare has become an increasingly studied topic following the NIH's recommendations pertaining to captive environments (NIH, 2013). The current study adds to the literature that attempts to empirically evaluate space density needs in response to existing, but not empirically validated, space regulations. Our results may point to some favorable behavioral changes when chimpanzees have access to areas with more space per animal. However, the small number of significant behavioral changes per transfer scenario may lend support to the concept of a behaviorally-relevant minimum size threshold (Appleby, 1997; Reamer et al., 2015; Ross, Wagner, et al., 2011), wherein there are relatively small effects on behavior following increases in space that are already greater than a readily acknowledged suboptimal minimum. In combination with Ross, Wagner, et al. (2011) and Reamer et al. (2015) (which both found "conservative, but positive," or no significant, behavioral changes, respectively, with more space per animal), and previous findings regarding the behavioral effects of crowding (Aureli & de Waal, 1997; Brent et al., 1991; Clarke et al., 1982; Duncan et al., 2013; Jensvold et al., 2001;

Nieuwenhuijsen & de Waal, 1982; Ross et al., 2010; Videan & Fritz, 2007), our results shed light on, but do not completely clarify, the relationship between space per chimpanzee, behavior, and the 250 ft²/animal recommendation. This highlights the need for further empirical investigations of relationships among these variables.

Chimpanzees that had access to less than the NIH's 250 ft²/animal recommendation pre-transfer, and were moved to a different enclosure with more than this recommendation post-transfer, exhibited the highest number of behavioral changes, followed by chimpanzees that had access to less than the NIH's 250 ft²/animal recommendation pre-transfer, and were moved to the same type of enclosure with more than the recommendation post-transfer. A detailed look at these results reveals a few issues with applied implications. First, there were two statistically significant, positive behavioral changes with potentially practical relevance, including the significant 1.51% increase in foraging (corral to dome) and the 2.35% increase in locomotion (dome to double dome). These are beneficial increases from a behavioral management perspective, an approach which seeks to increase species-typical behaviors (such as foraging) and functionally simulate natural conditions (locomoting, traveling, and patrolling in wild chimpanzees). Second, the 5% increase in locomotion (dome to corral) and 1% increase in foraging (dome to double dome), may be seen as beneficial increases, although it is difficult, and perhaps problematic, to interpret such non-significant differences. Third, the small percentage change in rough scratching (0.32%) may not be biologically meaningful or practically relevant. From an applied welfare perspective, rates of scratching made up less than 1% of all activity pretransfer, and the decrease of a third of a percent may not have much consequence in affecting overall well-being. Last, comparable increases in behavioral diversity occurred across all transfer types, which may point to an effect of exploration of the relatively novel post-transfer environment (see below).

Chimpanzees that experienced a decrease in space per animal (a 200% increase in animal density) and a change in housing type exhibited only one significant behavioral change (an increase in behavioral diversity post-transfer). In light of previous research showing negative behavioral effects of increased animal density (Aureli & de Waal, 1997; Brent et al., 1991; Clarke et al., 1982; Duncan et al., 2013; Jensvold et al., 2001; Nieuwenhuijsen & de Waal, 1982; Ross et al., 2010; Videan & Fritz, 2007), it is possible that any changes that might have been exhibited by this group were diminished by variations in functional space (volume) between domes and corrals. There is a growing consensus of opinion that the amount of space itself seems to be less important in creating FACEs than the complexity and features of the space (AZA Ape TAG, 2010; Morgan & Tromborg, 2007; NRC, 2011; Bettinger et al., 2017; Dye, 2017; Reamer et al., 2017), including spatial topography (e.g., vertical space: Caws, Wehnelt, & Aureli, 2008; number of spaces: Herrelko, Buchanan-Smith, & Vick, 2015), available spaces to choose to occupy (Bettinger, Wallis, & Carter, 1994; Herrelko et al., 2015; Kurtycz, Wagner, & Ross, 2014; Ross, Calcutt, et al., 2011), environmental enrichment (for review, see AZA Ape TAG, 2010; Reamer et al., 2017; Wilson, 1982), escape routes (Caws et al., 2008; Ross & Lukas, 2006), and opportunities to exhibit control over the environment (AZA Ape TAG, 2010; Bloomsmith, 2017; Coe, Fulk, & Brent, 2001; Else, 2013; Herrelko et al., 2015; Reamer et al., 2017; Ross, Calcutt, et al., 2011; Schapiro, 2017; Videan, Fritz, Schwandt, Smith, & Howell, 2005). Domes and corrals are similar in these features. In the current study, although domes and corrals were

comparable in environmental and structural complexity (i.e., similar structures, enrichment and foraging opportunities, and PRT), the fully-enclosed wire mesh of the dome may have created more *functional* space and volume (i.e., practically all surfaces are climbable, including walls and ceilings) than the concrete walls and open tops of corrals. As such, the dome's decreased horizontal, two-dimensional space may have been "equalized" by the increase in three-dimensional space (i.e., utilizability of volume). Therefore, it is possible that behavioral changes that may have occurred following a 200% increase in animal density (from a corral to a double dome) were mitigated by the increase in functional space and volume provided by the dome. However, this requires additional empirical quantification and examination.

The behavioral changes seen in the current study may also be related to the novelty of the post-transfer environment, which could have resulted in an increased motivation to engage in behaviors related to exploration. As mentioned above, the increases in behavioral diversity scores occurred regardless of increases or decreases in space per animal and changes in enclosure type. Additionally, the overall pattern of increases seen in time spent locomoting and foraging was similar across transfer types. If these changes were an effect of novelty, a return to pre-transfer levels once the novelty subsided, perhaps 2 or 3 months post-transfer, would be expected. Brief post-hoc analyses comparing the first 2 and a half months of post-transfer data to the last 2 and a half months of post-transfer data revealed no significant differences in behavior in any of the three transfer types. Additionally, comparing the last month of post-transfer data to the pretransfer data yields the same results as the original analyses. Therefore, these changes in post-transfer locomotion, behavioral diversity, and foraging seem to be relatively long-lasting. Chimpanzees were maintained in their pre-transfer enclosures for a minimum of 1–2 years prior to being transferred to their new enclosures for this study. As such, it is possible that the post-transfer environment, even 5 months later, was still relatively novel from the chimpanzees' perspective, and that this exploration effect had yet to diminish by the time data collection was complete. Given this exploratory response, it could be suggested that these transfers were enriching to the chimpanzees, and that other types of within-facility moves, or alternating between enclosures (Coe et al., 2001; Lukas, Hoff, & Maple, 2003), may be beneficial to chimpanzees, increasing complexity and novelty in the environment. Conversely, in the context of experimental control, switching between different environments can create confounds in research, which may make these types of moves unreasonable (Box & Rohrhuber, 1993). Although chimpanzees are no longer used in biomedical research, experimental control (e.g., a constant environment) is essential in the design of behavioral and welfare studies with chimpanzees, both of which are still common. Therefore, researchers and behavioral management staff may need to weigh the potential enriching and confounding effects of purposeful within-facility transfers.

Chimpanzees exhibited a few behavioral changes across transfer type, including rough scratching, locomotion, and foraging, in the current study. From a broad behavioral and applied perspective, these changes are potentially consistent with the idea that space available and welfare may have an asymptotic relationship, such that there are considerable advances in welfare and beneficial effects to behavior when space is increased beyond the behaviorally-relevant minimum, but increasing space beyond that minimum leads to smaller

and smaller increases in welfare and changes in behavior (Appleby, 1997; Ross et al., 2011). In combination with the effects of exploration, it is possible that these moderate, but positive, changes were observed when chimpanzees were provided with more space per animal because they already had access to complex spaces that met or exceeded a putative minimum size threshold (142 ft²/chimpanzee). Similarly, chimpanzees may have exhibited a single significant difference in behavior following a decrease in space per animal because they still had access to an amount of space that met or exceeded the behaviorally-relevant minimum after the transfer (250 ft²/chimpanzee). We are not attempting to minimize the observed behavioral changes in the current study; instead, we feel it is important to elucidate how these changes may be consistent with (a small but growing) recent line of literature that points to a behaviorally-relevant minimum size threshold (Appleby, 1997; Reamer et al., 2015; Ross, Wagner, et al., 2011).

We are not advocating for moves from one type of space or enclosure to another. Rather, we used this transfer paradigm to assess differences in chimpanzee behavior in areas below, equal to, or above the NIH recommendation (with similar levels of environmental complexity) and to attempt to separate the effects of space per animal and enclosure type. The current body of literature highlights the need for more empirical investigation of this issue. As long as chimpanzees live in captivity, empirical assessments of the amount and types of spaces in which they are maintained must be conducted. Future studies should examine how space per chimpanzee may affect individual physiology, allostatic load, social subgroupings, and chimpanzees of different temperament or rank in the social hierarchy, as well as logistical aspects of chimpanzee care, such as behavioral management and veterinary protocols. Additionally, research (1) comparing chimpanzee behavior and the aforementioned variables across other common enclosure types, such as play yards (large, enclosed indoor/outdoor rooms) and habitats (semi-free-ranging open acreage) and (2) quantifying utilizable space (volume) in these enclosures, would be valuable from behavioral management and welfare perspectives, and in further refinements to FACEs.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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FIGURE 1.
(a) Corral (~142 ft²/chimpanzee) and (b) Primadome™ (~564 ft²/chimpanzee) housing

FIGURE 2.

Transfer types in the current study. (a) From dome (142 ft²/chimpanzee) to double dome (284 ft²/chimpanzee) $n = 7$. (b) From dome (142 ft²/chimpanzee) to corral (645 ft²/chimpanzee) $n = 7$. (c) From corral (564 ft²/chimpanzee); to double dome (250 ft²/chimpanzee) $n = 8$

FIGURE 3.
Percent of time spent rough scratching pre and post transfer across transfer type.
*Significant at $p < 0.05$. Errors bars represent standard error of the mean

FIGURE 4.

Percent of time spent foraging pre and post transfer across transfer type. *Significant at $p < 0.05$. †Trending at $p < 0.07$. Errors bars represent standard error of the mean

FIGURE 5.

Percent of time spent in locomotion pre- and posttransfer across transfer type. *Significant at $p < 0.05$. †Trending at $p < 0.07$. Error bars represent standard error of the mean

FIGURE 6. Behavioral diversity scores (average number of different behaviors exhibited) pre- and posttransfer across transfer type. *Significant at $p < 0.05$. Errors bars represent standard error of the mean

Table 1

Changes in percent time and number of different behaviors

	D→C	D→DD	C→DD
Locomotion ($CI_{95\%}$)	+5.13% ** (3.93–6.31)	+2.35% * (1.74–2.95)	ns
Rough scratching ($CI_{95\%}$)	–0.32% * (0.25–0.39)	ns	ns
Foraging ($CI_{95\%}$)	+1.51% * (0.97–2.06)	+1.01% ** (0.65–1.35)	ns
Behavioral diversity ($CI_{95\%}$)	+1.75 behaviors * (1.54–1.96)	+1.85 behaviors * (1.63–2.07)	+1.37 behaviors * (1.14–1.62)

D, dome; C, corral; DD, double dome; ns, not significant; $CI_{95\%}$, 95% confidence intervals of the percent change or number of different behaviors.* Significant at $p < 0.05$.** Trending at $p < 0.08$.