A Review of Literature and Animal Welfare/Regulatory Requirements and Guidance Pertaining to the Space Density Needs of Captive Research Chimpanzees

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Introduction

The Institute of Medicine (IOM) Committee on the Use of Chimpanzees in Biomedical and Behavioral Research, in its 2011 report, set forth a series of principles and criteria that were to be followed for National Institutes of Health (NIH)-funded research with chimpanzees. These were accepted by NIH, which subsequently assembled, and charged an NIH Council of Councils' Working Group to provide advice on the implementation of the principles and criteria in the IOM report. One of the IOM Committee recommendations was that chimpanzees used in research "must be maintained either in ethologically appropriate physical and social environments or in natural habitats", which was based on the need to "minimize potential sources of stress on the chimpanzee" in order to perform replicable and reliable research (IOM, 2011, p27).

The Working Group delivered its report and recommendations to the Council of Councils in 1/2013 and included their working definition of 'ethologically appropriate physical and social environments' (EAE). After review of the report, NIH accepted all the Working Group recommendations except Recommendation EA2, which read: "The density of the primary living space of chimpanzees should be at least 1,000 ft^2 (93 m^2). Therefore the minimum outdoor enclosure size for a group of 7 animals should be 7,000 ft^2 (651m^2)" (WG Report, 2013, p3). NIH decided to review available data to clarify the minimum space density needed to provide an EAE for captive research chimpanzees. This document forms a part of that review.

Scope of Work for this report:

(1) Identify and review the published literature, and write a literature review on the space density needed to provide an ethologically appropriate physical and social environment (EAE) for captive chimpanzees in a research environment.
(2) Identify, review, and summarize relevant parts of published U.S. regulations and requirements.

As guidance in the performance of this review, 5 questions were listed under the Scope of Work, which were expected inform the review of space density needs for captive research chimpanzees:

(1) What is the minimum space density that promotes species-typical behavior of the captive chimpanzee and what is the evidence in support of this answer?

(2) What criteria are appropriate for determining the type(s) of enclosures to surround the space (e.g., moats, walls, primadomes)?

(3) Do the space density needs of captive research chimpanzees participating in a protocol differ from the space density needs for captive research chimpanzees not participating in a protocol? If so, how do these needs vary and what is the rationale?

(4) Is the space density influenced by special requirements/facilities that are necessary to conduct research?

(5) What alternatives exist for providing and accomplishing the minimum space density, e.g., rotation schedule through larger enclosures?

U.S. Regulations and Requirements Relevant to Captive Chimpanzees

The Animal Welfare Act
http://www.aphis.usda.gov/animal_welfare/downloads/awr/awr.pdf

The Animal Welfare Act of 1966 regulates the care and use of captive animals in a number of different situations including research. The United States Department of Agriculture (USDA) Animal and Plant Health Inspection Service (APHIS) oversees compliance with the Act.

The Act has been modified and updated several times since its adoption, including the addition of provisions for enhanced standards for the humane care and use of laboratory animals, and the requirement for research facilities to set up an Institutional Animal Care and Use Committee (IACUC).

Subpart D, Section 3.80 of the Animal Welfare Regulations lists the minimum space requirements for the nonhuman primate (NHP) weight category that includes chimpanzees as 25 ft^2 (2.32 m^2) for floor area per animal, and 84 in. (213 cm.) for enclosure height (page 107). They do point out however, that many of the NHP requirements are generic and that "the conditions appropriate for one species do not necessarily apply to another. Accordingly, the minimum specifications must be applied in accordance with the customary and generally accepted professional and husbandry practices considered appropriate for each species, and necessary to promote their psychological well-being" (page 100). Coe (1992) noted that research facilities tend to focus on maximizing standardization and hygiene in order to meet the standards set by the Animal Welfare Act, as administered by USDA, in contrast to Zoological displays which generally present a more diverse environment that promotes the expression of species typical behaviors. The constraints of rigidly enforced standards, without due consideration of basic animal needs, may be a factor for consideration when providing EAEs for captive chimpanzees.

Public Health Service Policy
http://grants.nih.gov/grants/olaw/references/phspol.htm

Institutions receiving support through the US Public Health Service (PHS) for research, testing and training involving animals must provide detailed documentation ("assurance") in respect to their compliance with the "PHS Policy on Humane Care and Use of Laboratory Animals". The NIH Office of Laboratory Animal Welfare (OLAW) provides guidance and interpretation of the PHS Policy, and monitors Policy compliance by participating institutions to ensure humane care and use of animals in PHS supported activities. OLAW relies on the Guide for the Care and Use of Laboratory Animals (the Guide) in respect to issues such as animal housing and psychological well-being.

PHS also oversees the CHIMP Act, which includes the standards of care for chimpanzees held in the federally supported sanctuary system. The Act does not specify enclosure size, but rather stipulates that the facilities must meet USDA and PHS compliance standards. However the Act does require that the facility design should be in accordance with the Guide, and that the "facility must be designed to provide sufficient space and variety of natural and artificial objects to accommodate natural activities of chimpanzees while restricting their movement and range to the defined area" (Federal Register, 2008 - page 60418).

The Institutional Animal Care and Use Committee
http://www.iacuc.org

As stated above, the Animal Welfare Act requires U.S. Institutions to have an IACUC to review all institutional activities involving animals. The IACUC plays a major role in ensuring that research animals are being responsibly used, and cared for in a humane manner. The Committee is the ultimate authority and, depending upon the circumstances and appropriate justification, can waive or impose stricter regulatory requirements than are listed in the Guide and Animal Welfare Act. For example, space allocations should be assessed, reviewed, and modified by the IACUC, which should consider performance indices (e.g., health, reproduction, growth, behavior, and use of space) (Guide, page 56).

The Guide for the Care and Use of Laboratory Animals
http://www.nap.edu/catalog.php?record_id=12910

The Guide contains relatively extensive discussions on animal space needs, noting "there is no ideal formula for calculating an animal's space needs based only on body size or weight (page 55), and that performance indices should be taken into consideration". The Guide also notes that "socially housed animals should have sufficient space and structural complexity to allow them to escape aggression or hide from other animals in a pair or group" (page 55). The recommended minimum space requirement for adult chimpanzees housed in pairs or groups is the same as stipulated in the Animal Welfare Act - 25 ft^2 (2.32 m^2) of floor area per animal, and 84 in. (213 cm.) in height (Table 3.5, page 61).

In respect to behavioral and social management, the Guide notes that animal activity includes cognitive activity and social interaction as well as motor activity, and that "animals' natural behavior and activity profile should be considered during evaluation of suitable housing" (page 63). In respect to social environment the Guide notes that appropriate social interactions among conspecifics are essential to normal development and well-being, and that "an understanding of species-typical behavior (e.g. natural social composition, population density, ability to disperse, familiarity, and social ranking) is key to successful social housing. However concern has been expressed about the lack of control NHPs have on their environment, including the provision of uniform levels of temperature, illumination, etc. as dictated by USDA and AAALAC standards, vs. facilities that offer gradients and diversity (Coe, 1992).

Association of Zoos and Aquariums
http://www.aza.org

The Association of Zoos and Aquariums (AZA) offers an accreditation program for its members who must go through an accreditation process that is similar to AAALAC. The members must be in compliance with AZA accreditation standards. However, given the diverse species covered, AZA also produces Animal Care Manuals for select species, including for the chimpanzee: 'Chimpanzee (*Pan troglodytes*) Care Manual' (AZA Ape TAG, 2010). These manuals are compiled by recognized experts, and are looked upon as "work in progress" in an evolving field. The recommendations are not necessarily mandatory, and may require adaption to the specific needs of individual animals, and particular circumstances in each institution.

The Chimpanzee Care Manual's recommended minimum exhibit size for small groups of chimpanzees (5 or fewer individuals) is: "indoor and outdoor space of at least 2000 ft^2 (185 m^2), and usable vertical heights of over 20ft (6.1m)" (page 16). For larger groups, there should be at least "an additional 1000 ft^2 (92.9 m^2) for every additional individual over a group size of 5" (page 16). Following these guidelines, a group of 7 chimpanzees would require a combined indoor and outdoor space of at least 4000 ft^2.

Literature Review on Minimum Space Density Needed to Provide Ethologically Appropriate Environments:

All literature reviewed in preparation for this report is listed in Appendix A: Literature Review, and those cited in the actual report are also listed under

References, at the end of this report. Every effort has been made to cite the main publications that summarize current research relating to the issues identified in the Scope of Work, as well as to represent the varying different perspectives held by experts working with both captive and wild chimpanzees.

Background to Recommendation EA2

In their 2013 report, the Working Group defined the IOM Committee term "ethologically appropriate physical and social environments" as "environments that not only *allow* but importantly, *promote* the full range of natural chimpanzee behaviors" (p. 13). The definition was a product of extensive deliberations, including visiting facilities and sanctuaries maintaining chimpanzees, and interviewing experts on ethologically appropriate environments (WG Report, 2013, p. 61). The Working Group noted that: "In the tradition of modern ethology, the behavioral repertoire of free-ranging wild chimpanzees is used as the model, or gold standard, toward which facility management should aspire when developing captive environments." (p. 20), and therefore "The environment and behavior of wild chimpanzees must be understood before determining how to recapitulate the most important aspects of the natural behavioral repertoire of chimpanzees in captive settings" (p. 20).

In defining 'ethologically appropriate social and physical environments' (also referred to as 'ethologically appropriate environments', or EAE), the Working Group noted that "chimpanzees in the wild live in large fission-fusion communities"(p. 20), and that "daily travel is an essential aspect of chimpanzee life" (p. 21). Their recommendation EA2, on the minimum density of the primary living space, was prefaced by the statement: "The space available to captive chimpanzees should be large enough to support their complex social structures and sufficiently dense to allow functional subgroup behaviors. More specifically, spaces should be large enough for chimpanzees to demonstrate their natural tendencies to range, travel, patrol, and separate from their social group completely when necessary." (WG Report, p. 22).

1. *What is the minimum space density that promotes species-typical behavior of the captive chimpanzee and what is the evidence in support of this answer?*

This review has demonstrated that there is little published literature containing quantitative scientific data that can be used to support a determination of the minimum space density (horizontal surface area per animal) needed to provide an EAE for captive chimpanzees. Furthermore, other aspects of enclosure design, such as complexity and vertical height, are considered by many to be more important

species specific behavior (Wilson, 1982, Hosey, 2005, Morgan and Tromberg, 2007).

Given the emphasis placed by the IOM Committee and the Working Group on providing for the replication of wild chimpanzee behavior in the management of captive chimpanzees, a brief review of current literature on relevant wild chimpanzee behavior is provided below. Additionally, a brief review of various captive chimpanzee behaviors monitored by investigators as indicators of psychological well-being is also included.

Chimpanzee behavior in the wild

Replication of wild chimpanzee behavior in captive populations is a commonly used yardstick in assessing chimpanzee well-being in captivity (Wrangham, 1992), and was referred to by the NIH Working Group (2013) "as a model, or gold standard, toward which facility management should aspire when developing captive environments". The Working Group definition of an EAE is one that would "*promote* the full range of natural chimpanzee behaviors". However a number of investigators do not consider the full range of wild chimpanzee behaviors, including many of those reflected in a 'fission-fusion society', to be necessary or desirable in captive populations. Wrangham (1992) notes that "normal chimpanzee behavior, i.e. behavior in the wild, is not always necessarily desirable in captivity because it includes responses to environmental hardships, including food shortages, predation attempts, disease, and climatic extremes, as well as competitive and occasionally violent social behavior."

Wild chimpanzees' propensity to live in fission-fusion societies, whose members form temporary parties that vary in size and composition, is a frequently referenced species typical behavior (Nishida, 1968). This social strategy helps balance the advantages and disadvantages of group living, by allowing flexible responses of group size to external conditions, while at the same time retaining group stability (Lehmann and Boesch, 2004).

Fission-fusion in chimpanzees in the wild is reported to be driven by external factors such as food availability (they tend to fragment during times of food scarcity and coalesce into larger groups in times of good food availability – Chapman & Chapman, 2000; Chapman et al., 1995; Symington, 1990; Mitani et al., 2002; Anderson et al., 2002), reproduction (formation of large groups when a female is in estrous – Boesch & Boesch-Acherman, 2000; Anderson et al., 2002), and perceived threats from neighboring troops (leading to aggressive territorial behavior and patrols (Goodall, 1986; Boesch & Boesch-Acherman, 2000). However, as dictated by various U.S. regulations and requirements, chimpanzees in captivity do not

Furthermore, it would be unwise to encourage some chimpanzee fission-fusion society behaviors in a captive environment, due to their potential dire consequences (Wrangham, 1992). Examples include territorial behavior and patrols where: "Lethal intergroup aggression is a characteristic feature of chimpanzee territorial behavior" (Wilson and Wrangham, 2003). Likewise, other behaviors such as fission during food scarcity (Chapman & Chapman, 2000; Chapman et al., 1995; Symington,

1990) have limited relevance to captive chimpanzees, as food cannot be withheld (Animal Welfare Act, 2008).

The findings of other studies in West Africa may throw light on the applicability or otherwise, of some other aspects of wild chimpanzee fission-fusion behavior to populations of captive chimpanzees. Lehmann and Boesch (2004) analyzed the extent to which fission-fusion patterns are influenced by changes in demographic variables like community size and composition of the chimpanzee groups. Data were collected from a habituated chimpanzee group in Tai Forest, Cote d'Ivoire over a 10-year period, during which time the group decreased in size from 51 to 21 individuals, and the number of males decreased from 9 to 2. While the community size declined during this period, ecological parameters such as food availability and predation pressure remained relatively constant (Lehmann and Boesch, 2003). As the community (total group size) decreased in size there was greater group stability, an increased cohesiveness between the sexes and a reduction in fission-fusion behavior, leading the authors to conclude that, "small communities are more cohesive and have a less flexible fission-fusion system". Essentially all captive research chimpanzee groups would be classified as "small communities", which draws into question the relevance of fission-fusion systems to captive chimpanzees.

Similar findings were observed in another long-term study in Bossau, Guinea. Here an isolated chimpanzee group has been studied for 26 years, during which time the group size has remained relatively stable, at approximately 20 individuals, and fission fusion does not exist (Sugiyama, 2004). The chimpanzee group's home ranges is restricted in size due to agricultural development on the periphery, but has a relatively rich and constant food supply, and there are no neighboring chimpanzee groups, nor predators (Sugiyama, 1999 and 2004). The physical characteristics (small, relatively stable group) and environmental conditions (restricted range, constant food supply, and no threats from the outside) of this population of animals are remarkably similar to the captive situation, thus the apparent consequential lack of fission-fusion behavior is of interest.

Chimpanzee behavior in captivity

Observing levels of select chimpanzee normal (species-typical) and abnormal/stereotypical behaviors is an essential tool in the estimation of minimum space densities needed for an EAE for captive chimpanzees. For example, changes in normal chimpanzee social behaviors, such as play, and affiliative, agonistic and submissive behaviors, may be used to indicate relative states of well-being, anxiety, and social tension (Aureli and de Waal, 1997; Clarke et al, 1982; Ross et al., 2011b). Agonism in captive chimpanzees is influenced by many factors, including lack of space and inability to escape from others, contributing to the general pattern of greater aggression in captive than in wild groups (Bloomsmith and Baker, 2001).

significant stressor, eliciting anxiety from the increased risk of intragroup aggression (Baker and Aureli, 1997, Aureli et al., 2001), thus should be avoided where possible.

Abnormal or stereotypic behaviors among captive animals are generally defined as those that are atypical of wild-living individuals (Birkett and Newton-Fisher, 2011),

Herndon, 1992; Birkett and Newton-Fisher, 2011). Thus a decline in abnormal

minimum space density is lacking.

Some of the normal and abnormal chimpanzee behaviors frequently monitored to assess captive chimpanzee well-being (in many cases resulting from changes in enclosure design and characteristics or, in some cases, space density) are well described in the literature and cited below:

- agonistic such as (hooting, bluff, charge, fighting, biting) and submissive (grinning, hunching) behaviors (Aureli and de Waal, 1997; Clarke et al, 1982; Ross et al., 2011b)
- afilliative behaviors such as allogroming and play (Aureli and de Waal, 1997; Martin, 2005)
- activity and exploration (Ross et al., 2011b; Clarke et al., 1982; Jensvold et al., 2001),
- displacement activities which may indicate anxiety and social stress. Examples include self-grooming; self–scratching and yawning (Aureli and de Waal, 1997; Baker and Aureli, 1997)
- stereotypic behaviors generally indicate physical or psychological distress. Examples include pacing, coprophagy, rocking, regurgitation, spitting, etc.) (Fritz and Howell, 1993; Goff et al., 1994; Birkett and Newton-Fisher, 2011)

The impact of enclosure size and animal density on chimpanzee behavior.

Although there is a wealth of published literature on captive chimpanzee behavior and well-being in various enclosures, relatively few studies include detailed space density data, and an even smaller subset have used space density as a variable. However, Ross et al. (2011b) do report a series of behavioral data sets, aimed at identifying positive and negative behavioral changes resulting from moving chimpanzees from a traditional hardscape setting, to a modern, more spacious naturalistic environment. He compares behavioral data sets collected from 2001-02 for 5 chimpanzees, when they were housed in a 73 m^2 indoor enclosure at a space density of 12.2 m^2/individual (GAH facility – enclosure dimensions and space density data from Ross et al. 2009), with data collected from 2004-07 when the same 5 animals occupied a new, naturalistic facility (RCAA), an indoor/outdoor enclosure which provided a combined space density of 36.9 m^2/individual (RCAA enclosure space density data from Ross et al. 2009). Both the GAH and the RCAA indoor enclosures had substantial vertical height and spatial complexity, and RCAA comparative behavioral data was only collected when the chimpanzees did not have access to the outdoor area (indoor space density was 14.5 m^2/individual) to provide a more equal comparison. The authors did not find significant indications of improved chimpanzee behavior and welfare subsequent to the move, a fact they attributed to the successful design attributes of original (GAH) enclosure, and they postulated: "We may predict the most robust effects of increasing usable space to occur when individuals are maintained in an enclosure at the minimal size threshold. Once this threshold is crossed – as was the case in GAH – we would then expect diminishing behavioral and welfare benefits with further increases" (Ross et al., 2011b: p. 113). A similar observation was made by Wilson (1982), who noted that increasing space beyond that required, may have little effect on activity.

Other studies that focus more on aggression, and that report quantitative space density data, include Aureli and De Waal (1997) who studied the effects of short-term high population density in 45 chimpanzees housed in 5 groups at the Yerkes Primate Center. The "control" indoor/outdoor density was 5.5 m^2 per individual. When animals were locked into "high density" (2 m^2/individual) indoor enclosure during cold weather they exhibited (behaviorally) increased social tension/anxiety, but also a general decrease in social activities, including antagonistic behavior, thought to be an inhibition strategy to reduce opportunities for conflict when inter-individual distances are decreased". Such a strategy was thought to be effective only for short time periods.

Nieuwenhuijsen and de Waal (1982) reported earlier on a group of 22 chimpanzees held at Arnheim Zoo in an outdoor summer enclosure of 7,000 m^2 (318 m^2/individual) and an indoor enclosure of 432 m^2 (19.6 m^2/individual, where the chimpanzees resided during the winter. Increased aggressiveness during the winter months was noted, although the aggression frequencies did not rise by a very high factor, and they did not find any increase in intensity of aggressive acts due to crowding. There was also a reduction in vertical structures and complexity in the indoor enclosure, which is a significant confounding variable (see environmental complexity and vertical height section below), but again the chimpanzees appeared to behaviorally adapt to increased density through a reduction of intense agonistic interactions.

Caws and Aureli (2003), studying the effect of reduced escape opportunities in a large group of chimpanzees at the Chester Zoo, suggested that chimpanzees may adopt a selective inhibition strategy when escape opportunities are limited, and speculated that the inhibition of aggressive tendency may be related to how chimpanzees in a captive environment respond to the natural challenges by subgroup membership changes, characteristic of their fission-fusion organization. As such, the inhibition of aggression in select situations may well be a normal species typical behavior.

Jensvold et al. (2001) compared the effect of enclosure size and complexity on chimpanzee behavior when five chimpanzees were moved to a new 587m^2 indoor/outdoor enclosure with an exceptionally high degree of environmental complexity, and introduced the concept of 'climbable surface area', which underlies the importance of considering the physical complexity of enclosures as well as surface space. While not defining the term, nor providing any calculation details, she asserted that the climbable surface area of the new enclosure was more than 7-fold that of the actual surface area.

Ross and Lukas (2002) reported that when two small groups of chimpanzees were combined to create a more complex multi-male group, social play and proximity increased significantly, despite the fact that proportionately more enclosure space had been made available. This could indicate that (minimum) space density requirements do not increase linearly with increased group size and social complexity.

AZA accreditation requires indoor and outdoor space of at least 2000 ft^2 (185 m^2) for up to 5 chimpanzees (or 400 ft^2/18.6m^2 per individual), and then an additional 1000 ft^2 (92.9 m^2) for every additional individual (AZA Ape TAG, 2010). Though not stated it might be assumed that increased space density requirement for the additional individuals was to accommodate the projected need to travel and escape as the group increased in size and complexity. However, from much of the literature reviewed it would appear that the same effect could be accomplished through the provision of a high level of enclosure complexity, including adequate above ground surface area, multiple visual barriers and escape opportunities.

Space preferences and use

Measuring how animals choose to utilize their space is a common method to determine both positive and negative aspects of captive environments (Ross et al., 2009). Although space use is influenced not only by environmental preferences, but also by social and biological factors (Ross et al., 2009; Bettinger et al., 1994), studying the way in which animals use and choose different features in their enclosure is a valuable way to measure the appropriateness of their environment and maximize animal welfare (Ross et al., 2009).

Effective use of space provided for captive chimpanzees is an issue that needs to be considered in conjunction with space density. A number of studies as well as opportunistic observations indicate that, even in relatively large compounds, chimpanzees tend to preferentially utilize specific enclosure attributes such as perimeter walls and climbing structures, and favor doorways and corners (Clarke et al., 1982; Traylor-Holzer and Fritz, 1985; Ross et al, 2009) and essentially all space use studies report significant underutilization of open space. The ideal is for the chimpanzees to use all available space evenly (Traylor-Holzer & Fritz, 1985; Ross et al., 2009), but this is rarely the case and most if not all space use studies report marked disparities (Ross et al., 2009 and 2011a; Ross and Lukas, 2006; Stoinski et al., 2001; Traylor-Holzer & Fritz, 1985; Bettinger et al., 1994).

Studies of space use patterns can reveal the environmental preferences of captive primates and can be useful for establishing detailed housing guidelines to assure housing does not negatively impact psychological well-being (Goff et al., 1994). Ross and Lukas (2006) studied patterns of space use by 6 chimpanzees at Lincoln Park Zoo and then incorporated this information in the design of a new great ape exhibit. Follow up space use studies showed that the chimpanzees utilized all areas of the new facility more evenly than in the older previous exhibit (Ross et al., 2009).

Environmental complexity and vertical space

Morgan and Tromberg (2007) in their comprehensive review the various causes of stress in captive animals concludes that "it may well be that it is not the quantity of space available to the animal which is important, but its quality – what it affords animals (including great apes) in the way of behavioral opportunity". They highlight the importance of complexity, escape opportunities, and the animals' ability to make choices and have some control over environmental stressors.

Vertical space adds diversity, increases the available space, allows the entire enclosure to be more efficiently utilized, and provides platforms, exercise opportunities, and a means of increasing social distance. (Traylor-Holzer and Fritz, 1985). Vertical space is a particularly important component of chimpanzee space utilization as chimpanzees spend approximately half of their time off the ground both in the wild (Reynolds & Reynolds, 1965) and in captivity (Olleta & Baró, 2006; Ross & Lukas, 2006; Bloomsmith et al. 1999, Goff et al., 1994).

Environmental enrichment (enhancement) is used to encourage natural behaviors and promote an animal's psychological and physiological well-being (Caws et al., 2008). Three-dimensional structures can increase interest in, and use of, all available space and thus, are an important source of enrichment for a wide range of species (Maple and Perkins, 1996). Stoinski et al., (2001) reported that gorillas spent 50% of their time in less than 15% of their exhibit, concluding that the quality of space rather than the quantity of space was important. Ross et al. (2011a) reported an even more striking finding from analyzing four years of chimpanzee and gorilla space use data in a modern indoor-outdoor zoo enclosure: "We found that both species used relatively little of their available space: chimpanzees and gorillas spent half of their time in only 3.2 and 1.5% of their usable three-dimensional space respectively"; and they went on to conclude: "The fact that the apes in this study were highly selective in the use of their enclosure underscores the importance of the quality of space over the quantity of space".

The lack of three-dimensional space and escape routes may increase aggressive behavior in captive settings (Caws et al., 2008; Bloomsmith and Baker, 2001). A number of investigators believe that escape opportunities such as platforms and visual barriers allow animals the opportunity to avoid contact with each other, reducing excessive aggression and social stress (Traylor-Holzer & Fritz, 1985). Caws et al. (2008) ranked and recorded agonistic encounters in a stable chimpanzee group of 29 individuals, housed in a spacious indoor-outdoor enclosure. The encounters were ranked before and after a large and complex vertical structure was added to the outdoor enclosure, and they found a reduction of serious injuries, with no episodes of severe aggression initiated while individuals were on the vertical structure. The investigators concluded that the vertical structure appeared to function as a deterrent of aggression and apparent escape route during aggressive interactions (Caws et al. 2008).

It is clear from the literature that vertical space and environmental complexity have a highly significant impact on captive chimpanzee space use. Many investigators believe that they should be taken into account when space density is being considered. Hosey (2005) goes so far as to conclude that restricted space *per se* need not be a welfare problem and need not lead either to the loss of species typical behaviors or the acquisition of abnormal behaviors provided that the components of the space (particularly structural complexity) are appropriate and give behavioral opportunities.

Ross et al. (2011a), noting that there was a tremendous range of enclosure guidelines for chimpanzees from different agencies (e.g. USDA, AZA and Pan African Sanctuary Alliance), commented that: "While each of these documents specifically notes the importance of other considerations such as vertical height and environmental complexity, it is clear that there is very little consensus on how much space is necessary to provide to this (chimpanzees) and other animals". He concluded that "Given the push to formulate scientifically based management standards, further research that accounts for a range of environmental variables is necessary, especially studies that help elucidate the value of all the space that captive primates are not using". Wilson (1982) completed an excellent comparative study in which she quantified space provision against a panel of behaviors of 43 gorilla and 68 orangutan groups from 41 different zoos in 7 European countries. In her assessment she used 'usable surface area', which she defined as "all of the usable or functional surface in an enclosure. The value, calculated in square meters, included the floor, all above-ground objects in the cage, and any 'usable' walls or ceilings, such as those made of wire or bars. In all cases, the measurement was made as if the objects were flat planes, including ropes, poles and chains. The purpose of this value was to represent the proportion of the cage that actually could be used by the animals, and the major determinant of the differences in these values for various enclosures was the construction material of the wall(s) and or ceilings." It is somewhat surprising that very few investigators adopted this or similar approaches over the next three decades.

Behavioral enrichment that promotes effective space usage and species-typical behavior.
Behavioral enrichment can promote effective space usage and species-typical behaviors (Bloomsmith and Else, 2005). The various approaches that have been taken are well documented in the literature, including feeding enrichment (Bloomstrand et al., 1986; Nadler and Herndon, 1992), destructibles (Pruetz and Bloomsmith, 1992), positive reinforcement training (Lambeth et al., 2006; Perlman et al., 2010); problem solving (McDonald, 1994; Bloomsmith et al., 1988). Enriched physical environments may also provide opportunities for problem solving, a crucial component of enrichment (McDonald, 1994; Bloomsmith et al., 1988), as is the importance of choice (Coe, 1992).

There is a wide consensus that the behavioral enrichment activities significantly contribute to chimpanzee well-being regardless of enclosure design and space density (Bloomsmith and Else, 2005). As such it is an important consideration when promoting chimpanzee well-being but, other than perhaps enhanced enclosure complexity, should be an adjunct to, rather than a direct factor in, the calculation of space density requirements.

2. *What criteria are appropriate for determining the type(s) of enclosures to surround the space (e.g., moats, walls, primadomes)?*

The types of enclosures used for surrounding the primary living area for chimpanzees is dependent upon a number of factors including terrain, climate, and construction and maintenance costs (Gold, 1992). The main types of barriers used include walls, wet moats, dry moats, wire mesh fencing, and electric fencing (McDonald, 1994; Gold, 1992).

Walls are relatively low cost, simple to construct, and provide shade and wind barriers (Gold, 1992). Ground level visibility of the chimpanzees can be an issue, but this can be overcome through a series of viewing/ventilation windows (Riddle et al., 1982).

Moats provide an unobstructed view for the visitor, thus are popular at facilities with naturalistic enclosures (Gold, 1992). They are most practical when the terrain is level, and in a climate where freezing is not an issue. They should be at least 6.5 m in width, which is beyond the approximately 6m that chimpanzees reportedly can leap (Kortlandt, 1966). Moats are more expensive than walls or fencing, and water moats can be problematic due to chimpanzee drowning (McDonald, 1994; Adang et al, 1987). This has led to the addition of some type of underwater structures to help prevent drowning, or a deterrent (e.g. electric wires) to prevent the chimpanzees from reaching the water edge (McDonald, 1994). Dry moats can be used in climates where freezing is an concern or the terrain is not flat, but there is the risk of chimpanzees climbing out, which has led to the use of electric wires as a secondary deterrent (McDonald, 1994). Another disadvantage of moat barriers is the increased space need – space that could otherwise be used by chimpanzees or humans.

The use of wire mesh fencing as a barrier for chimpanzees greatly increases the amount of usable surface area, and is generally an inexpensive form of containment. Electric fencing or a hot wire, are generally used as a secondary or backup barrier (Gold, 1992) as discussed above. Primadomes, which were included in the IOM report (2011) as one of the examples of appropriate physical and social environments (p. 27), are perhaps the most secure in respect to containment, and offer relatively good vertical space and climbing opportunities and, while their ground surface area is limited, their usable surface area is substantial in relation to the enclosure volume.

3. ***Do the space density needs of captive research chimpanzees participating in a protocol differ from space density needs for captive research chimpanzees not participating in a protocol? If so, how do these needs vary and what is the rationale?***

Ideally, space density needs of captive research chimpanzees that are either on or off protocol should be the same. However, depending on the enclosure characteristics and the study design, it is possible that high levels of environmental complexity (which can impact space density requirements) may impair experimental observations (decreased visibility of study subject) and manipulation/separation of experimental subjects. However, in most cases, it should be feasible to train the experimental subjects for voluntary access and sample collections, using positive reinforcement techniques (Bloomsmith et al., 1998).

4**. *Is the space density influenced by special requirements/facilities that are necessary to conduct research?***

The degree of environmental complexity within an enclosure can inversely impact the absolute space density required to promote species-specific behavior. Consequently, enclosures with high levels of environmental complexity may be incompatible with specific research requirements, or may make it difficult to observe and access chimpanzees on protocol. In such instances, or when critical experimental manipulations and/or sample collections are required, it should be acceptable to move the study subjects to short term holding areas. The same approach could be used for primary enclosures with large areas that are incompatible with select experimental protocols.

There is a substantial amount of research that supports the above approach and demonstrates that chimpanzees can be held short term (up to 30 days or longer) in restricted space with limited anxiety or stress, by behaviorally adapting to the situation through suppression of aggressive behavior and thus avoidance of serious agonistic interactions (Videan and Fritz, 2007). Many zoos hold their animals in off-exhibit holding areas, generally with reduced space density (Nieuwenhuijsen and de Waal, 1982; Aureli, 1996; McDonald, 1994) and it has been estimated that zoo housed chimpanzees typically spend up to 75% of their time in such areas, which are generally not as enriched as the exhibit areas (Ross and Wagner, 2008).

5. ***What alternatives exist for providing the accomplishing the minimum space density, e.g., rotation schedule through larger enclosures?***

The rotation of chimpanzee groups through a larger enclosure is definitely a viable option, particularly if it could be scheduled frequently (e.g. daily). Rotation of enclosures, which is a relatively common practice in zoo settings, should help meet minimum space density requirements for research chimpanzees when enclosure space is limited. It is also common in zoos located in temperate climates, to have a summer indoor/outdoor exhibit and a smaller indoor winter exhibit, and most zoos keep their chimpanzees in off-exhibit holding rooms except during opening hours (Caws et al., 2008; Nieuwenjsen and de Waal; 1982; Adang et al., 1987; Aureli, 1996; McDonald, 1994).

While perhaps not optimal, these are accepted standard operating procedures for zoological parks that have been in practice for decades. It is, however, important to provide adequate enclosure complexity in holding areas, and to include such areas when assessing chimpanzee welfare (Ross et al., 2010).

Conclusions

This literature review has revealed that very limited empirical data is available on which to base a determination of the minimum space density necessary to provide an EAE for captive chimpanzees, and no quantitative data was found to support the figure of 1000 ft^2/individual chimpanzee. Relatively few investigators have reported data that measures chimpanzee well-being using space density as a variable, with Ross and his colleagues, who have been studying enclosure design for 10 plus years, being one of the notable exceptions. Ross et al. (2011a) postulated that once the "minimal size threshold is crossed" (as they speculated could possibly be the case with their GAH facility - space density 12.2 m^2/individual) they "would then expect diminishing behavioral and welfare benefits with further increases." Wilson (1982) made a similar observation, noting that increasing space beyond that required may have little effect on activity.

There is a general consensus among essentially all investigators as to the importance of 'vertical space', 'climbable space', 'three dimensional space', 'gross usable space' and other similar enclosure parameters, and the necessity for significant environmental complexity within the enclosure. Indeed, the general impression gained from this literature review is that these parameters share equal importance with space density when captive chimpanzee well-being is considered. The difficulty is the lack of a simple, replicable way to measure them.

There is also general consensus that chimpanzees neither like nor use open spaces and that in most situations they utilize only a small proportion of their enclosure space. This is consistent with conclusions of many investigators that the overall *quantity* of cage space alone has limited value when designing an enclosure to maximize the well-being of primates because the usefulness of space depends upon its *quality* rather than quantity (Reinhardt et al., 1996; Wilson, 1982; Stoinski et al.; 2001; Ross et al., 2011a) and, having no stimulatory value, space alone does not enhance an animal's environment (Reinhardt et al., 1996).

There appears to be an urgent need for further quantitative research to fill the void in the available data informing the determination of the minimum space density required to provide an EAE of captive chimpanzees, and ascertain if the relationship between space density and group size should be linear. Of equal importance is the impact of other enclosure parameters and environmental complexity on the minimum space density, which has not been inadequately studied to date. Several investigators have started this process, noting the need for a more robust unit of measurement of space needs for captive apes than surface space density (surface area/animal) alone. It is clear that approaches beyond calculation of minimum space density must be explored in the determination of EAE for chimpanzees. The routine calculation of "usable surface area", as defined Wilson (1982), could go a long way in advancing such an approach.

This review also throws into question whether the full range of wild chimpanzee behavior, particularly some aspects of fission-fusion, are applicable to captive situations, and whether some behaviors, such as traveling long distances in search for food or patrolling the borders of their territories, may in fact not be necessary for captive group well-being, nor desirable for group stability. A wider discussion should take place on this issue, with additional views from experts studying chimpanzees in the wild, before the expression of such behaviors are adopted as indicators of an ethologically appropriate physical and social environment for chimpanzees.

JG Else
November 7, 2013

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APPENDIX A: Literature Reviewed

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