## The Welfare of Chimpanzees at the Alamogordo Primate Facility

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**Executive Summary.** Chimpanzees are long-lived animals and the chimpanzee population at the Alamogordo Primate Facility has minimally 18 years remaining by the best available estimate. That timeline offers a great opportunity to enhance the lifetime welfare of the chimpanzees. I have considered all available data and specifically discuss how the small group sizes, single-sex compositions of the groups, and the quantity and complexity of the space are likely to affect the chimpanzees' current welfare. I also comment on the implications of the information that is missing without making assumptions about the content, specifically recent monitoring records, the environmental enrichment program, and the positive-reinforcement-training program. I find that the Alamogordo Primate Facility environment and management strategy may encourage chimpanzees to meet criteria that lead to a euthanasia decision. Acknowledging that transfer and acclimation to a new environment can be stressful, the available information suggests that the long-term benefits of relocating the chimpanzees would outweigh the short-term costs. The chimpanzees at the Alamogordo Primate Facility would likely experience a substantial improvement in welfare if transferred to an environment such as the national sanctuary.

I am an animal welfare scientist with 20 years of experience conducting primate research in laboratories, zoos and chimpanzee sanctuaries in North America, Europe and Africa. My primary focus for the past several years has been scientifically evaluating the welfare of animals in human care. To provide a report on the welfare of chimpanzees at the Alamogordo Primate Facility (APF), I reviewed the following materials:

- a) The behavioral records APF made available for 44 chimpanzees (most ending in 2009)
- b) The euthanasia criteria ("Humane Endpoints") for the same 44 chimpanzees
- c) The Monthly Progress Reports submitted to the National Institutes of Health (NIH) for the year of 2019
- d) The Annual Contract Report submitted to NIH covering the period of September 26, 2017, to September 25, 2018, which included the quarterly Institutional Care and Use Committee (IACUC) minutes from that period
- e) The Final Progress Report submitted to NIH covering the period of September 26, 2014, to September 25, 2019, which included the quarterly IACUC minutes from the final year
- f) A Population Model predicting the number of years of life remaining for the APF chimpanzees<sup>1</sup>
- g) A 2020 letter from Dr. James Anderson, NIH Deputy Director for Program Coordination, that provided some care and husbandry information in response to an inquiry from Senator Udall (D-NM), Senator Cassidy (R-LA) and Senator Heinrich (D-NM)
- h) Hour-long interviews with three people who had visited APF within the last year and an additional person who visited in 2013, all of whom received tours from APF staff. Two of these people had advanced degrees related to chimpanzee health or welfare.
- i) The brief video provided by NIH in May 2012<sup>2</sup>
- j) The information available in peer-reviewed journals that provided dimensions of housing conditions and basic management practices at APF<sup>3,4</sup>
- k) The scientific literature relevant to the chimpanzees' welfare, referenced within the report below

### Background on Animal Welfare as it Relates to the APF Chimpanzees

The intention of the Chimpanzee Health Improvement, Maintenance, and Protection (CHIMP) Act Amendments of 2013 (S. 252) was to offer chimpanzees who were no longer necessary for medical research the opportunity for a better quality of life than would be afforded in the laboratory environment. That intention is made clear in the letter from Senators Udall (D-NM), Cassidy (R-LA) and Heinrich (D-NM) written to Dr. Francis Collins, Director of NIH, In December of 2019. The Senators reiterate that the goal of the CHIMP Act was to maximize not only the physical but also the psychological well-being of chimpanzees who have retired from research. This equates to maximizing the retired chimpanzees' welfare.

Simply stated, animal welfare refers to the quality of life an animal is experiencing. Animal welfare is measured on a continuum, and modern animal welfare scientists talk about "a life worth living<sup>5</sup>" or ensuring that animals are "thriving<sup>6</sup>," acknowledging the absence of suffering does not equate to acceptable levels of welfare. Although earlier considerations of animal welfare prioritized physical health, nearly all animal welfare scientists now consider psychological well-being (alternatively referred to as mental health, emotional state, or affective state) as the key determinant of an animal's welfare state<sup>7,8,9,10,11</sup>. Reflecting this movement, the current, predominant model of animal welfare is the Five Domains Model<sup>12,13,14</sup> that has influenced how people consider the welfare of animals in human care across many sectors<sup>15,16,17,18,19</sup>.

According to the Five Domains Model of animal welfare, an animal's physical and functional domains – nutrition, environment, health, and behavior – matter to the extent that they influence the animal's mental domain either positively or negatively<sup>13</sup>. What defines the animal's welfare state is the animal's subjective experience, or, simply put, how the animal *feels*. Additionally, welfare is considered over a period of time; it is the long-term balance of positive and negative experiences that characterize an animals' lifetime welfare. If an action generated a brief period of moderately poor welfare followed by several years of mostly positive animal welfare, taking this action would improve the animals' welfare from a lifetime perspective.

Therefore, evaluating whether the APF chimpanzees, or any chimpanzees, should transfer to sanctuary based on physical health alone is not a valid way to evaluate whether the chimpanzees' welfare would be enhanced by the move. What one must consider is what the current mental experiences of the chimpanzees likely are, as impacted by their physical and functional domains, in their current environment, and what the mental experiences would likely be in an alternative environment. Given that population modeling¹ suggests that the APF chimpanzee population will persist for at least another 18 years (and maximally 33 years), there is a lot of potential to affect the overall lifetime welfare of the APF chimpanzees by making changes that would improve their welfare.

# What Do We Know About the Lives of the APF Chimpanzees that Can Inform Our Understanding of Their Welfare?

**Group Sizes.** The size of the chimpanzee groups at APF is available, non-disputed information. Early in 2020, the largest group size was five individuals and the smallest "group" was comprised of a single individual. Scientific publications reporting on the APF population indicate group sizes of six as the historical norm<sup>3,4</sup>. Interviews conducted with people who had recently received tours from the APF Director revealed that there is no intention of increasing group sizes, and this is consistent with the information in Dr. Anderson's letter from earlier this year.

Social environments that allow the fullest range of a species' natural behavior will typically ensure the best welfare<sup>8,10,13</sup>. Ensuring the opportunity to engage in behaviors that chimpanzees are naturally motivated to perform allows for the chimpanzees to seek out rewarding opportunities that stave off frustration, and, importantly, promote positive mental states that characterize good animal welfare. Chimpanzees have evolved living in large, mixed-sex social groups of 20-100 individuals, and are adapted for navigating complex social interactions that include forming and re-establishing social bonds and navigating social hierarchies<sup>20,21</sup>.

The NIH recommends that captive chimpanzees be maintained in ethologically-appropriate environments, defined as conditions that promote a full range of behaviors that are natural for chimpanzees. Specific characteristics of ethologically-appropriate environments, including minimum group sizes, have been accepted by NIH<sup>22</sup> based on recommendations made by an NIH working group that considered the available scientific evidence. All current group sizes at APF are below the recommended minimum size that is advised by the NIH Council of Councils to support good animal welfare. The NIH Council of Councils recommends<sup>22</sup>, "Chimpanzees must have the opportunity to live in sufficiently large, complex, multi-male, multi-female social groupings, ideally consisting of at least seven individuals. Unless dictated by clearly documented medical or social circumstances, no chimpanzee should be required to live alone for extended periods of time. Pairs, trios, and even small groups of four to six individuals do not provide the social complexity required to meet the social needs of this cognitively advanced species." Since the release of this recommendation, two recent studies have demonstrated behavioral differences indicative of better welfare for chimpanzees living in mixed-sex groups of seven or more<sup>23,24</sup>.

**Welfare Implication of Group Size:** There is a clear opportunity to enhance the welfare of the APF chimpanzees by integrating chimpanzees into larger social groups.

**Solitary Housing.** It is well established that single-housing is associated with extremely compromised welfare in chimpanzees <sup>25, 26</sup>. At the time of this report, records indicate one known singly-housed chimpanzee, a 29-year-old male named Lester, who has been singly-housed since his cagemate Martin died six months earlier. The Chimpanzee Medical and Behavioral Profile completed by APF notes Lester's distinguishing characteristics as "friendly, gets along with group, playful." On his Chimpanzee Personal Data Form there is the comment, "gets along well with all cagemates." His young age and historical personality suggest that it should be possible to integrate Lester with other chimpanzees, and this should be done as soon as possible to avoid prolonged welfare compromise.

Lester's case serves to highlight two additional considerations relevant to the welfare of chimpanzees at APF in the future. First, small group sizes pose a risk not only because of the reduced social complexity described above but also because the increased likelihood that chimpanzees will be reduced to solitary living, even temporarily. Lester's case also illuminates that introductions to new chimpanzees, which APF has stated concern about in the case of transferring the animals to a sanctuary, are inevitable at APF if the facility plans to avoid compromising welfare through solitary housing.

One final comment regarding solitary housing at APF is needed. There is mention throughout the historical records of moving solitary chimpanzees to a "time out" or, more frequently and recently, to "the sick room." The records indicate that chimpanzees are housed in isolation for multiple days. From my reading of the records, it seems the chimpanzees are sometimes in isolation not to protect the chimpanzee's own physical health or the health of other chimpanzees (this is not a quarantine or recovery situation), but

rather to be conveniently accessible for observation or potential follow-up veterinary procedures. In the records, chimpanzee demeanors are documented as depressed in the sick room. In some but not all cases, there is mention of minimally engaging enrichment (e.g., offering a pumpkin or a piece of cardboard to shred). The practice of isolating chimpanzees poses a significant welfare concern.

**Welfare Implication of Solitary Housing:** Social isolation at APF, regardless of the duration, is a current and significant welfare concern.

**Group Sex Ratios.** The sex ratio of the chimpanzee groups at APF is available, non-disputed information. As of July 2020, all chimpanzees were housed in single-sex groups. This is consistent with the historical behavioral records that also indicate single-sex housing. Scientific publications reporting on the APF population indicate single-sex groups as the historical norm<sup>3,4</sup>. Interviews conducted with people who had recently received tours from the APF Director report that they were informed there is no intention of integrating sexes, and intentional single-sex housing is indicated in Dr. Anderson's letter from earlier this year.

As explained above, social environments that allow the fullest range of a species' natural behaviors will typically ensure the best welfare. This relates to group size (above) and group composition. Chimpanzees navigate complex social interactions between and within sexes <sup>27</sup>, and negotiating these dynamics is undoubtedly mentally stimulating for chimpanzees, requiring the use of their advanced socio-cognitive skills <sup>28,29,30</sup>. Not engaging in these dynamics would lessen the number of enriching experiences available to enhance mental states, or welfare. The group compositions at APF do not adhere to the NIH Council of Councils recommendation<sup>22</sup> to house chimpanzees in multi-male, multi-female groups to support good animal welfare. Not only does not housing chimpanzees in mixed-sex groups limit the diversity and complexity of their social interactions, but research has shown that single-sex groups are characterized by more aggression than mixed-sex groups<sup>31</sup>.

The letter from Dr. Anderson indicates that the reason for housing chimpanzees in single-sex groups is to avoid reproduction. However, there are several established approaches available to control reproduction in mixed-sex groups<sup>32,33</sup> that are successfully employed in zoos and sanctuaries.

**Welfare Implication of Group Sex Ratios:** There is an opportunity to enhance welfare by integrating chimpanzees into multi-male, multi-female groups. Temporary stress associated with integration does not negate the potential welfare benefit from a lifetime perspective.

Amount of Space. Available information suggests that the housing space available to the chimpanzees at APF is the same across groups: all chimpanzee groups have access to an indoor cage (180 ft², 9-foot height), an outdoor cage (242 ft², 12-foot height), and a Primadome³⁴ (800 ft², 25-foot height at tallest point). It is my understanding from interviews conducted with people who have recently visited that the chimpanzees have access to these three spaces nearly 24 hours a day. Other reports suggest it is during daytime hours. Either case reflects an increase in regularly available space from previously published accounts in which the chimpanzees reportedly had only weekly access to Primadomes.

The indoor, outdoor and Primadome spaces combined equate to 1222 ft<sup>2</sup> per social group, or, in the case of the largest social group (five individuals), 244 ft<sup>2</sup> per individual. This is just below the NIH-recommended ethologically-appropriate space of 250 ft<sup>2</sup> per individual<sup>22</sup>. It is worth noting that the recommendation of

250 ft<sup>2</sup> per chimpanzee is only 25% of that originally recommended to NIH by the Working Group, and far less than what is recommended in the *Chimpanzee Care Manual* <sup>32</sup>. Specifically, the current available space is only 61% of the minimum space (2000 ft<sup>2</sup>) recommended in the *Chimpanzee Care Manual* for a social group of five or fewer individuals.

Chimpanzees use floor space and vertical space to the extent that it is offered. The ability to climb, swing on limbs and vines (or their replicates), and socialize at heights is essential for normal development of chimpanzees<sup>35</sup>. The height of the Primadomes at their tallest point suggests the potential for rewarding opportunities up high which would be fitting with chimpanzee natural history, but the realization of this space as a welfare benefit for the chimpanzees depends entirely on how the space is furnished. I have only been informed of two platforms per enclosure (per Dr. Anderson's letter) and have no report of flexible furnishing that allows stimulating reconfiguration of space (e.g., with hoses, hammocks, ropes that are sufficient for promoting locomotion or providing spaces to rest or socialize). The heights of the indoor and outdoor cages (not the Primadomes) are concerning; at their tallest, they are only 60% of the height recommended in the *Chimpanzee Care Manual*.

It has historically been difficult to quantify the welfare value of some amount of space for a chimpanzee, largely because it is the characteristics of the space that are so influential on welfare. However, a recent study evaluated the behavioral changes in chimpanzees that transitioned from a housing space that was below the NIH-recommended space per chimp to a space that was above the recommendation while holding the complexity of the space constant. The study reports that the larger space is associated with behavioral indicators of improved welfare, including, but not limited to, increased locomotion by chimpanzees<sup>36</sup>. This finding is directly relevant to the potential increase in welfare that could be afforded to the APF chimpanzees if they were to be provided more space, given that the health assessments repeatedly report concern for cardiac health.

**Welfare Implication of the Amount of Space:** Chimpanzees are living in spaces smaller than is recommended to promote good welfare. There is an opportunity to enhance welfare by providing more space.

**Complexity of Space.** The complexity of a habitat encompasses a broad suite of characteristics that are distinct from the absolute quantity of space available. For example, complexity can refer to the topography, trees, shade, sunny spaces, climbing structures, termite mounds, tall grass, bare areas, swampy areas, streams, pools, large rocks, smooth areas, rough areas, and various sights and sounds<sup>32</sup>. At APF, it is established that the chimpanzee groups can access an indoor and outdoor cage, and have access to a Primadome.

The chimpanzees have the choice between being indoors and outdoors, and the control this offers, as well as the exposure to the outdoors, is a benefit to their welfare <sup>37,38</sup>. In addition to this choice, which should bring some welfare benefit, they have access to fresh air and sunlight. However, many features that tend to be associated with positive welfare outdoors are limited or lacking at APF; the May 2012 NIH video<sup>2</sup> and interviews with recent visitors indicate that the features of the chimpanzees' space are hard, sparse, and static. There are neither plants nor trees, nor was there any apparent natural substrate with which the chimpanzees could physically interact. The NIH recommendations<sup>22</sup> are for chimpanzees to have outdoor access year-round, with access to natural substrates such as grass, dirt and mulch to enhance the complexity of the environment. Given the information available, this recommendation

appears to either be not met, or to be minimally met, indicating that there is ample opportunity to enhance the welfare of these chimpanzees in a more complex and dynamic environment.

The Primadome structures themselves are designed in a way that allows the chimpanzees to utilize the walls and ceilings for climbing, which is a potential benefit<sup>36</sup> if the chimpanzees use them in this manner. As mentioned above regarding the quantity of space, there is a great deal of potential that may not yet be realized for maximizing the degree to which chimpanzees can move dynamically within the volume of the dome at elevations. The NIH advises that the environment must provide enough vertical space to allow all members to travel, feed, and rest in elevated spaces<sup>22</sup>. Given the information on the number of resting structures available per group (2 spaces) reported in Dr. Anderson's 2020 letter, along with the interview of recent visitors, it seems the NIH recommendation has not been met and again there is ample opportunity to enhance welfare in an environment that utilized vertical space effectively.

**Welfare Implication of the Complexity of Space:** The complexity of the chimpanzee space, both in terms of the features and how they change, as well as the utilization of vertical space, indicates ample opportunity to improve welfare.

#### Consideration of the "Humane Endpoints" (Euthanasia Criteria)

The Humane endpoints for all 44 chimpanzees consisted of lists of behavioral or physiological criteria that, if observed, would signal to APF that the chimpanzee's quality of life had declined to a point that euthanasia would be the most probable humane choice. The primary health concerns for the chimpanzees included chronic renal failure, metabolic syndrome, hypertension, advanced cardiovascular disease, anemia, or some combination of these conditions. The criteria for euthanasia, which varied systematically by health concern, typically included weight loss of 25% or weight falling below 42 or 45 kg, low body condition scores, unresponsive anorexia for four days, signs of stroke (lack of coordination, weakness in arms or legs), and signs of cardiac failure (exercise intolerance, respiratory distress).

Humane endpoints identified in advance can serve to avoid unnecessary suffering for animals in human care. Those caring for the animal can specify, before decisions are impacted by emotion or conflicting motivations, thresholds that are probabilistically related to unacceptable future welfare.

I am concerned that some of the criteria, specifically the unresponsive anorexia for four days which is included in nearly every animal's Humane Endpoints document, is too low of a threshold to cross and could be induced by the APF environment. Related to my concerns about the "sick room" above (see section Solitary Housing), when a chimpanzee is isolated at APF for observation, it is likely that the individual will become depressed and have reduced interest in food. In my experience, overcoming the inappetence of chimpanzees who are ill or depressed requires a great deal of effort tailored to the individual. Familiar and trusted staff will often spend hours with the chimpanzee, offering favorite foods and drinks along with potentially appealing novel foods to encourage eating. I would feel more confident in this specific criterion if there were no risk of isolation-induced anorexia and if there was an indication that staff go beyond normal feeding efforts to encourage consumption. An individualized approach that involves increased staff effort is not mentioned in the records I reviewed. With the current practices at APF, loss of appetite seems inevitable for many chimpanzees, inviting early euthanasia.

This concern was underscored in the recent necropsy report for Danny, a 37-year-old male who was moved to the "sick room" and isolated from conspecifics for intensive observations on November 12,

2019, after staff noted that he was moving slower and was less interested in food. Necropsy records indicate that while in the "sick room," Danny was provided "free access to biscuits, fruits, vegetables and offered various types of liquids." The next day he was reported to be poorly responsive to the environment and refusing food, and was euthanized.

**Welfare Implication of the Humane Endpoints:** The current criteria for euthanasia may set too low of a threshold. The APF environment and management strategy may encourage chimpanzees to meet some criteria that lead to a euthanasia decision.

#### **Consideration of Information That Was Not Provided**

Three pieces of information were <u>not</u> available for review that would have provided valuable insight into the probable welfare of the APF chimpanzee population. These include:

- a) The environmental enrichment plan. The IACUC minutes state that there was a standard operating procedure (SOP) for the Environmental Enrichment Plan reviewed and accepted by the IACUC on December 15, 2017, and again on December 14, 2018. In the latter, the IACUC comments on material mentioned on page 8 of the SOP, so this is at least an 8-page document with information directly relevant to the psychological well-being of the APF chimpanzees. It is my understanding that a request for this information has been made several times without success.
- b) The positive reinforcement training protocol. In the Final Progress Report, APF states that all animals have been trained using positive reinforcement techniques (Section: Developments in the APF Veterinary Care and Animal Husbandry Program, Point G.). In the records available that pre-date 2010 there is some mention of positive reinforcement training methods being applied (e.g., for heel sticks), but also mention of negative reinforcement (e.g., reducing cage squeeze restriction upon compliance) that induces animals to cooperate to avoid an even more aversive stimulus. Any mention of training in the records provided was at least 10 years old.
- c) The monitoring records. APF referenced monitoring records in the Monthly Progress Reports submitted to NIH. Specifically, APF states monthly that "all animals are monitored 16 hours per day, seven days per week by the APF animal care staff" (Section: Developments in the Veterinary Care and Animal Husbandry Programs). Related, the Final Progress Report explains that a technician observes all chimpanzees at least every 2-4 hours daily for "undesirable behavior." No documentation of that monitoring program was available for review. All behavioral data provided were at least 10 years old.

The absence of protocols or data associated with these three key pieces of information is notable and unfortunate from the perspective of evaluating animal welfare. Behavioral monitoring programs, environmental enrichment programs, and positive reinforcement training programs are central to all modern approaches to promoting good animal welfare for animals in human care. I expand upon why each of these are so relevant below.

**Behavioral monitoring programs** are typically designed to track individual behavioral patterns so that deviations from an animal's baseline that may indicate a decline in welfare (such as an increase in abnormal behaviors), or an improvement in welfare (such as an increase in affiliative interactions) are evident. Behavior provides the best insight into animals' mental or emotional states<sup>39</sup>. Ideally, behavioral data are regularly reviewed and the information is acted upon to improve welfare<sup>40,41</sup>.

**Environmental enrichment plans**, broadly speaking, are the set of documented strategies that can be implemented to produce relevant novelty, engaging challenges, and mental stimulation to animals. The NIH<sup>22</sup> stipulates that the program must provide relevant opportunities for choice and self-determination. The Animal Welfare Act specifies that "research facilities must develop, document, and follow an appropriate plan for environment enhancement adequate to promote the psychological well-being of non-human primates"<sup>42</sup>. The broad goal of an environmental enrichment plan is to detail how the staff will ensure a complex environment that engages the animal's senses, promotes interaction, and functionally simulates behavioral opportunities that would be found in the animal's natural habitat<sup>43</sup>. The effect of offering environmental enrichment on animal behavior should also be monitored to determine if the strategy is having the intended effect; evaluation and modification of enrichment are essential<sup>44</sup>. To be an effective, meaningful program, plans have to be updated regularly and modified based on individual animal responses. A good environmental enrichment plan has the potential to set the stage for an animal to thrive in human care; a poor plan can assure that an animal's welfare will be compromised. There is no evidence of this plan available for review.

Much like a strong environmental enrichment program, **positive reinforcement training** also has the demonstrated effect of enhancing animal welfare<sup>45</sup> and is recognized as an essential tool for the humane and effective management of captive animals. Positive reinforcement training, a training technique that relies on rewarding desirable behaviors to increase their frequency, has been shown to reduce distress in animals, mitigate social problems, increase affiliative interactions<sup>46</sup>, aid in social introductions, reduce abnormal behavior<sup>47</sup>, provide an important sense of control and predictability over the environment<sup>48</sup>, improve the human-animal bond<sup>49</sup>, and provide valuable mental challenges.

### Conclusion

Chimpanzees are long-lived animals and the chimpanzee population at the Alamogordo Primate Facility has minimally 18 years remaining by the best available estimate. That timeline offers a great opportunity to enhance the lifetime welfare of the chimpanzees. I have considered all available data and specifically discuss how the small group sizes, single-sex compositions of the groups, and the quantity and complexity of the space are likely to affect the chimpanzees' current welfare. I also commented on the implications of the information that is missing without making assumptions about the content, specifically recent monitoring records, the environmental enrichment program, and the positive-reinforcement-training program. I find that the Alamogordo Primate Facility environment and management strategy may encourage chimpanzees to meet criteria that lead to a euthanasia decision. Acknowledging that transfer and acclimation to a new environment can be stressful, the available information suggests that the long-term benefits of relocating the chimpanzees would outweigh the short-term costs. The chimpanzees at the Alamogordo Primate Facility would likely experience a substantial improvement in welfare if transferred to an environment such as the national sanctuary.

#### References

- <sup>1</sup> Faust, L. 2020. Alamogordo Chimpanzee Population Modeling.
- <sup>2</sup> https://www.youtube.com/watch?v=6MfqunkBakc . The Alamogordo Primate Facility Research Reserve NIH B-Roll May 2012.
- <sup>3</sup> Lammey M.L., Lee, D.R., Ely, J.J., & Sleeper, M.M. (2008). Sudden cardiac death in 13 captive chimpanzees (*Pan troglodytes*). *Journal of Medical Primatology*, *37*(S1), 39-43.
- <sup>4</sup> Lammey, M.L., Baskin, G.B., Gigliotti, A.P., Lee, D.R., Ely, J.J., & Sleeper, M.M. (2008). Interstitial myocardial fibrosis in a captive chimpanzee (*Pan troglodytes*) population. *Comparative Medicine*, *58*(4), 389-394.
- <sup>5</sup> Mellor, D. J. (2016). Updating animal welfare thinking: Moving beyond the "Five Freedoms" towards "a Life Worth Living". *Animals*, *6*, 21.
- <sup>6</sup> Hill, H. M., & Nollens, H. (2019). Providing belugas (*Delphinapterus leucas*) in controlled environments opportunities to thrive: Health, self-maintenance, species-specific behavior, and choice and control. *Frontiers in Psychology*, *10*, 1776.
- <sup>7</sup> Duncan, I. J. (1996). Animal welfare defined in terms of feelings. *Acta Agriculturae Scandinavica. Section A. Animal Science. Suppl. 27*, 29–35.
- <sup>8</sup> Fraser, D. (2009). Animal behaviour, animal welfare and the scientific study of affect. *Applied Animal Behaviour Science*, 118(3-4), 108-117.
- <sup>9</sup> Hewson C. J. (2003). What is animal welfare? Common definitions and their practical consequences. *The Canadian Veterinary Journal*, 44(6), 496–499.
- <sup>10</sup> Dawkins, M. S. (2006). A user's guide to animal welfare science. Trends in Ecology & Evolution, 21(2), 77-82.
- <sup>11</sup> Fraser, D. (2008). Understanding animal welfare. Acta Veterinaria Scandinavica, 50(1), 1-7.
- <sup>12</sup> Mellor, D.J. & Reid, C.S.W. (1994) Concepts of animal well-being and predicting the impact of procedures on experimental animals. In: Baker R, Jenkin G and Mellor DJ (eds.) *Improving the Well-being of Animals in the Research Environment* pp 3-18. Australian and New Zealand Council for the Care of Animals in Research and Teaching: Glen Osmond, SA, Australia.
- <sup>13</sup> Mellor, D.J. (2017). Operational details of the five domains model and its key applications to the assessment and management of animal welfare. *Animals*, *7*(8), 60.
- <sup>14</sup> Mellor & Beausoleil (2015) Extending the five domains model for animal welfare assessment to incorporate positive welfare states. *Animal Welfare*, *24*(3), 241-245.
- <sup>15</sup> Wigham, E. E., Butterworth, A., & Wotton, S. (2018). Assessing cattle welfare at slaughter–Why is it important and what challenges are faced? *Meat Science*, *145*, 171-177.
- <sup>16</sup> Mellor, D. J., Hunt, S., & Gusset, M. (2015). Caring for wildlife: the world zoo and aquarium animal welfare strategy. *WAZA Executive Office*.
- <sup>17</sup> Sherwen, S. L., Hemsworth, L. M., Beausoleil, N. J., Embury, A., & Mellor, D. J. (2018). An animal welfare risk assessment process for zoos. *Animals*, 8(8), 130.
- <sup>18</sup> Ledger, R. A., & Mellor, D. J. (2018). Forensic use of the Five Domains Model for assessing suffering in cases of animal cruelty. *Animals*, *8*(7), 101.
- <sup>19</sup> Mellor, D. J. (2012). Affective states and the assessment of laboratory-induced animal welfare impacts. *Altex Proceedings*, *1*, 445-449.
- <sup>20</sup> Nishida, T. (2011). *Chimpanzees of the lakeshore: Natural history and culture at Mahale*. Cambridge University Press.
- <sup>21</sup> van Lawick-Goodall, J. (1968). The behaviour of free-living chimpanzees in the Gombe Stream Reserve. *Animal Behaviour Monographs*, 1, 161-311.
- <sup>22</sup> National Institutes of Health. (2013). Council of councils working group on the use of chimpanzees in NIH-supported research report. Retrieved from https://dpcpsi.nih.gov/council/chimpanzee\_research
- <sup>23</sup> Neal Webb, S. J., Hau, J., & Schapiro, S. J. (2019). Does group size matter? Captive chimpanzee (Pan *troglodytes*) behavior as a function of group size and composition. *American Journal of Primatology*, *81*(1), e22947.
- <sup>24</sup> Reamer, L. A., Talbot, C. F., Hopper, L. M., Mareno, M. C., Hall, K., Brosnan, S. F., . . . Schapiro, S. J. (2016). The effects of group size on the behavior of captive chimpanzees (*Pan troglodytes*). Joint meeting of the International Primatological Society and the American Society of Primatologists, August 21–27, 2016.

- <sup>25</sup> Baker, K.C. (1996). Chimpanzees in single cages and small social groups: Effects of housing on behavior. *Contemporary Topics in Laboratory Animal Science*, *35*(3): 71-74.
- <sup>26</sup> Brent, L., Lee, D.R., Eichberg, J.W. (1989). The effects of single caging on chimpanzee behavior. *Laboratory Animal Science*, *39*(4): 345-346.
- <sup>27</sup> Cronin, K. A., van Leeuwen, E. J., Vreeman, V., & Haun, D. B. (2014). Population-level variability in the social climates of four chimpanzee societies. *Evolution and Human Behavior*, *35*(5), 389-396.
- <sup>28</sup> Cronin, K.A., Pieper, B.A., van Leeuwen, E.J.C., Mundry, R., Haun, D.B.M. (2014) Problem solving in the presence of others: How rank and relationship quality impact resource acquisition in chimpanzees (*Pan troglodytes*). *PLOS One*, *9*(4): e93204.
- <sup>29</sup> Call, J. (2001). Chimpanzee social cognition. *Trends in Cognitive Sciences*, 5(9), 388-393.
- <sup>30</sup> Byrne, R. W. (2018). Machiavellian intelligence retrospective. *Journal of Comparative Psychology*, *132*(4), 432-436.
- <sup>31</sup> Fritz, J. & Howell, S. (2001). Captive chimpanzee social group formation. In: Brent L. (*ed.*), *The Care and Management of Captive Chimpanzees*. San Antonio, Texas: The American Society of Primatologists. pp. 173-203.
- <sup>32</sup> AZA Ape TAG 2010. Chimpanzee (*Pan troglodytes*) Care Manual. Association of Zoos and Aquariums, Silver Spring, MD.
- <sup>33</sup> Personal Communication: Jocelyn Bezner, DVM, July 20, 2020
- <sup>34</sup> Brandes Brothers Constructors, Bee Cave, TX
- <sup>35</sup> Coe, J.C., Fulk, R., Brent, L. (2001). Facility design. In: Brent L. (*ed.*), *The Care and Management of Captive Chimpanzees*. San Antonio, Texas: The American Society of Primatologists. pp. 39-81.
- <sup>36</sup> Neal Webb, S. J., Hau, J., & Schapiro, S. J. (2018). Captive chimpanzee (*Pan troglodytes*) behavior as a function of space per animal and enclosure type. *American Journal of Primatology*, 80(3), e22749.
- <sup>37</sup> McMIllan, F. D. (2019). The mental health and well-being benefits of personal control in animals. In McMillan, F. D. (ed.), *Mental Health and Well-being in Animals*, 67-81.
- <sup>38</sup> Fulk, R. & Garland, C. (1992), The care and management of chimpanzees (*Pan troglodytes*) in captive environments: A husbandry manual developed for the chimpanzee species survival plan. Asheboro (NC): North Carolina Zoological Society. pp. 77-84.
- <sup>39</sup> Dawkins, M.S. (2004). Using behaviour to assess animal welfare. *Animal Welfare*, 13, S3-S8.
- <sup>40</sup> Hill, S. P., & Broom, D. M. (2009). Measuring zoo animal welfare: Theory and practice. *Zoo Biology, 28,* 531–544.
- <sup>41</sup> Brando, S., & Buchanan-Smith, H. M. (2018). The 24/7 approach to promoting optimal welfare for captive wild animals. *Behavioural Processes*, *156*, 83–95.
- <sup>42</sup> USDA (United States Department of Agriculture) 2013. Animal Welfare Act and Animal Welfare Regulations. Section 3.81 (quotation from Section 3.8.1, pg 175). Retrieved from
- https://www.aphis.usda.gov/animal\_welfare/downloads/bluebook-ac-awa.pdf . Accessed August 3, 2020.
- <sup>43</sup> Coleman, K., & Novak, M. A. (2017). Environmental enrichment in the 21st century. ILAR Journal, 58(2), 295-307.
- <sup>44</sup> Alligood, C., & Leighty, K. (2015). Putting the "E" in SPIDER: Evolving trends in the evaluation of environmental enrichment efficacy in zoological settings. *Animal Behavior and Cognition*, *2*(3), 200-217.
- <sup>45</sup> Prescott, M. J., & Buchanan-Smith, H. M. (Eds.). (2016). *Training Nonhuman Primates Using Positive Reinforcement Techniques: A Special Issue of the journal of Applied Animal Welfare Science* (Vol. 6, No. 3). Psychology Press.
- <sup>46</sup> Pomerantz, O., & Terkel, J. (2009). Effects of positive reinforcement training techniques on the psychological welfare of zoo-housed chimpanzees (Pan troglodytes). *American Journal of Primatology*, *71*(8), 687-695.
- <sup>47</sup> Bassett, L., & Buchanan-Smith, H. M. (2007). Effects of predictability on the welfare of captive animals. *Applied Animal Behaviour Science*, *102*(3-4), 223-245.
- <sup>48</sup> Prescott, M. J., & Buchanan-Smith, H. M. (2003). Training nonhuman primates using positive reinforcement techniques. *Journal of Applied Animal Welfare Science*, *6*(3), 157-161.