

Article

# Impacts of Socialization on Bull Asian Elephant (*Elephas maximus*) Stereotypical Behavior

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**Abstract:** There is a growing need for animal care institutions to house multiple bull elephants as the population increases due to transfers from private ownership and the births of male offspring in managed care. Elephants in North American, European, and Latin American zoos exhibit stereotypies—repetitive, fixed behaviors. Previous research demonstrated that housing Asian elephants alone increased stereotypic behavior. Therefore, for animals in managed care, social restriction can contribute to stereotypy and, by extension, reduce welfare. In this study, we examine how being alone affects stereotypic behavior by monitoring pacing and head-bobbing in individual bull Asian elephants at Denver Zoo when housed alone as well as with other bulls. Two young males arrived at Denver Zoo in September 2018 and joined an existing all-male group of three elephants that were previously socialized and housed together. From July 2018 to December 2019, we used instantaneous scan sampling to collect data on stereotypic behavior of focal bulls when they were housed alone and socially. The frequency of pacing and head-bobbing significantly decreased when the elephants were housed socially compared to when they were housed alone; these stereotypies were lower when elephants were housed with at least one other bull and were in close proximity to a conspecific. Additionally, pacing decreased as the proportion of affiliative behaviors increased, and the amount of agonistic behavior did not significantly affect stereotypic behavior. When housed alone, bulls in musth engaged in significantly more pacing behavior than when they were out of musth. Our results indicate that housing bull Asian elephants in all-male groups substantially improves their welfare by reducing stereotypies and provides a basis for future evidence-based management.

**Keywords:** animal welfare; stereotypy; bachelor herd; musth



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## 1. Introduction

Male elephants are now known to regularly socialize, including with other bulls [1,2]. However, of the 33 institutions participating in AZA's Asian Elephant Species Survival Plan [3] at the outset of this study in 2018, only 18 were holding more than one bull and only three were routinely housing bulls together [4]. To date, there have been few studies on the management of bachelor groups of zoo elephants [5–7] and thus there are gaps in knowledge about the effects of sociality on bull welfare in zoos. This study examines how all-male socialization impacts stereotypic behavior among bull Asian elephants at Denver Zoo, Colorado, USA.

Stereotypic behaviors are repetitive, fixed, and serve no discernable purpose [8]. In elephants, these behaviors can manifest as pacing, swaying, rocking, bobbing, or chain biting, among others [9,10]. Both semi-captive elephants in range countries and elephants in North American, European, and Latin American zoos exhibit stereotypic behaviors [9–11]. In many cases, these stereotypic behaviors persist for years, well beyond the existence of

the original potentiating condition or event [10,12]. Stereotypy can become entrenched in the elephant's behavioral repertoire and lead to neurophysiologic changes that allow the animals to cope with frustration even when the causal factor no longer exists [12]. Stereotypy can be distinguished from anticipatory behavior in that the latter is goal directed and generally occurs prior to acquiring rewards [13], typically preceding predictable positive events (e.g., feeding time, keeper interaction, and location shifts) [14,15]. Stereotypy, by contrast, is not related to rewards, nor does it typically occur in relation to an upcoming external event [8]. Stereotypy may be mitigated by housing elephants in social groups [9,10].

Once considered solitary, the sociality of free-ranging Asian elephant bulls (*Elephas maximus*) is now well documented [2,3,5,16,17]. Social learning plays an important role in elephants' lives and adolescent males benefit from social proximity to mature males in order to learn social skills important for social and reproductive success later in life [18]. Long-term studies of social dynamics of Asian elephants in Ruhuna National Park, Sri Lanka, for example, revealed that bulls do have regular contact with other elephants, including other bulls [19,20]. Social opportunities are also critical for captive Asian elephants and are considered an important welfare priority [21]. It is widely thought that behavioral restriction, including reduced foraging and social opportunities, can lead to stereotypic behavior in elephants and that these abnormal behaviors indicate compromised welfare [10,22–25]. In a study across 194 institutions, 20% of all elephants were housed alone or with only one conspecific, contrary to management recommendations for females, which advise that they be housed in groups; recommendations for social housing of male elephants are not provided [26,27].

Several studies have demonstrated a relationship between stereotypy and socialization among captive elephants [9,10,23]. At the Pinnewela Elephant Orphanage of Sri Lanka, for example, socially integrated individuals exhibited fewer stereotypies than socially isolated elephants [10]. Housing elephants alone also increased stereotypy in zoos. Meehan et al. [28] observed less daytime stereotypy when North American zoo elephants interacted more with staff or juvenile elephants and stereotypic behavior increased when elephants were housed alone. A North American study of zoo elephants found that pacing increased as elephants spent more time housed alone or indoors and showed that stereotypy was the second-most observed behavior (after feeding) [9,23]. The same study indicated that pacing similarly increased when elephants encountered more, different social groups [9,23]. Limiting positive social opportunities negatively affects captive elephant welfare [9,21,29].

As long-lived, social mammals, elephants develop extensive social networks and institutional transfers of individuals for breeding or space can disrupt these social bonds [30]. In North America, 84% of zoo elephants experienced at least one inter-zoo transfer [30]. Furthermore, two multi-institutional studies reported that increased inter-zoo transfers were correlated with increased stereotypic behaviors [23,28]. However, planning institutional transfers at biologically appropriate times, such as when adolescent males would naturally disperse from their natal herds, aligns these periods of stress with the life histories of free-ranging elephants [30–34]. The average age of separation for male elephants in North American zoos was 9.7 years old, which corresponds with the period of natural dispersal [30–34]. The present study paralleled the process of social integration of two new adolescent bull elephants into an existing bull group at Denver Zoo [35,36]. The adolescent males were 9 and 10 years old at the time of transfer [35,36], mirroring the age of natural dispersal [33,34]. The existing group at Denver Zoo consisted of three unrelated bulls across a broad age range (11, 14, and 49 years old) who were socialized together beginning in 2016 [35,36].

In the present study, we specifically examine how being alone affects stereotypic behavior by monitoring each type of stereotypy (i.e., pacing and head-bobbing) in individual elephants, both when housed alone and with other bulls. We hypothesized that the odds of exhibiting each type of stereotypy will be significantly lower when elephants are housed socially compared to when housed alone. When housed with other elephants, opportunities for social interactions are most likely when in close proximity to a conspecific, although

this has not yet been specifically studied. Therefore, we also predicted that when housed with at least one conspecific, odds of each type of stereotypy will be significantly lower when elephants are in proximity (i.e., within two body lengths) to other bulls compared to when they are not in proximity (i.e., more than two body lengths) to another bull.

Elephants' social environments can be negative (stressful) or positive depending on the amounts of affiliative or agonistic social interactions that occur among individuals, and stress due to negative social interactions may increase stereotypy [9]. Due to the potential for both positive (i.e., affiliative) and negative (i.e., agonistic) social experiences, we hypothesized that when bulls were housed with at least one conspecific, stereotypy would decrease as affiliative behaviors increased. Additionally, we predicted that stereotypy would increase as agonistic behaviors increased between bulls. Our work with the Denver Zoo bull group previously documented that affiliative behavior significantly increased during the last five months of the study period compared to before and during the introductions of the new bulls, and non-contact agonistic behavior was highest during the introductions [35]. We therefore hypothesized that the odds of engaging in stereotypic behavior would decrease during the last five months of our study compared to before and during introductions of the new bulls, as their arrival and physical introductions likely represent time periods with increased acute stressors.

Finally, we examined the influence of musth on stereotypic behavior. Musth is a heightened hormonal state leading to physical and behavioral changes that mature bull elephants (over 20 years old [33,34]) undergo 1–2 times per year [37,38]. We used well-documented physical and behavioral changes such as temporal gland swelling and drainage, urine dribbling, and increased agonism to determine if and when a bull was in musth during our study [37–40]. Free-ranging bull elephants in musth spend more time travelling and less time feeding as they search for estrous females [40–42]. Musth bulls in managed care may thus be more prone to stereotypic behavior, such as pacing, compared to when they are not in musth since their space is restricted and may not accommodate the increased drive to travel typically observed during musth. Furthermore, spending less time feeding during musth frees up a component of their activity budget which might be filled in part with increased stereotypy. Finally, potentially aggravating aspects of musth itself, such as increased testosterone levels, may trigger stereotypic behavior. Therefore, we hypothesized that when housed alone, the odds of stereotypic behavior will be significantly higher when elephants are in musth compared to out of musth.

## 2. Materials and Methods

This study focused on a bachelor group of five bull Asian elephants housed at Denver Zoo, Colorado, USA [35,36]. Three bulls were unrelated (Individuals 1–3; 11, 14, and 49 years old at time of introduction) and were previously socialized together at Denver Zoo, and two were half-brothers (Individuals 4–5; 9 and 10 years old) that arrived at Denver Zoo in September 2018. Five months after arrival (following quarantine and time spent in the yards where initial introductions occurred), the new elephants had some auditory, olfactory, and limited visual and tactile contact through vertical stall bollards with the other bulls over a three-day period before sharing the same physical space (i.e., howdy). After howdy, the two new bulls (Individuals 4 and 5) were first physically introduced to the two oldest bulls (Individuals 2 and 3). Individual 1 was initially introduced to the new bulls when Individuals 2 and 3 were present so that he could rely on their pre-established relationships if necessary. Initial physical introductions occurred in an outdoor yard (0.135 hectares) and were kept short (30–60 min) before gradually increasing to full days together. Prior to the first introductions, animal care staff and veterinarians agreed to separate elephants if they were visibly seriously injured or stressed (e.g., broken tusks, limb injuries thought to compromise mobility, open-mouth breathing, liquid diarrhea, inappropriate physical aggression that continues even after the recipient submits or attempts to disengage). During the course of the introductions there was never a situation that necessitated separation. Once all elephants had been introduced to one another, keepers gradually integrated

the bulls into social units of 2–5 animals, depending on stage of integration, musth, and environmental conditions. Elephants were also sometimes alone, particularly when in musth [35,36]. Animal care staff always separated the elephants overnight until February 2019 when staff determined that beginning occasional overnight socialization could be appropriate for some pairs of elephants based on the bulls' social integration and daytime behavior [36].

From July 2018 to December 2019, we collected behavioral data on each of the original three bulls, both when alone and when in various social combinations [35,36]. We began behavioral data collection on the two other bulls at the end of September 2018, shortly after they arrived at Denver Zoo, and continued through December 2019. Behavioral data were collected several days per week between 9:30 and 11:30 and 13:30 and 15:30. These time periods were chosen to coordinate with the keepers' and elephants' schedules to minimize interference due to elephant–human interaction aside from occasional reprovisioning of food. Elephants were housed across five outdoor yards as well as indoor stalls, and they sometimes had access to multiple yards and stalls at a given time [35,36]. In total, we collected 519 h (1039 30 min sessions) of observational data: 130.5 h (261 30 min sessions) when the elephants were housed alone and not in musth, 55.5 h (113 30 min sessions) when they were alone in musth, and 333 h (666 30 min sessions) when they were housed socially. A team of six trained observers from Denver Zoo collected data: one primary observer contributed 79% of the data, a second observer collected 8% of the data, and the remaining 13% of observations were split between animal care staff. Observers used video clips from prior introductions between the original three bulls to identify each behavior from the ethogram (Table 1) for training purposes. Interobserver reliability was 95% and was assessed using simultaneous observations of the bulls.

**Table 1.** Ethogram of Behaviors for a Bachelor Group of Five Bull Asian Elephants at Denver Zoo [35,36]. Reprinted by permission of the publisher (Taylor & Francis Ltd., <http://www.tandfonline.com> accessed on 28 January 2022).

Behavior Category	Behavior	Definition
Agonistic	Approach head high	Actor moves toward recipient to within two body lengths with head above shoulders and ears out perpendicular
	Charge	Rapid forward lunging or rapid gait by actor towards a stationary conspecific starting from more than two body lengths away
	Chase	Actor rapidly pursues recipient, who is moving away from actor, for at least 5 s
	Head shake	Actor holds head above shoulders and moves vigorously from side to side, up and down, or in circular motion
	Supplant	Actor approaches to within two body lengths of conspecific without making contact, causing recipient to turn away or yield ground
	Grasp tail	Actor places tail of conspecific into its own trunk while recipient attempts to move away from focal animal
	Kick	Actor strikes at recipient with rear limb
	Mount	Actor rears up on hind legs and places forelegs on recipient for 5 s or more
	Push	Actor contacts conspecific with enough force to displace recipient
	Spar	Two elephants mutually and simultaneously push one another backwards with force with heads and/or heads and trunks and this is sustained for at least 5 s
	Trunk over back	Actor places 2/3 or more of its trunk firmly over the back or head of a conspecific

Table 1. Cont.

Behavior Category	Behavior	Definition
<b>Affiliative</b>	Approach relaxed	Actor moves to within two body lengths of recipient with head low and ears lying flat against its head, not associated with any other behavior
	Body contact	Body contact unspecified in any other behavior (e.g., side-to-side rubbing or touching)
	Play	Actor voluntarily spars, wrestles with, mounts, or chases recipient without obvious intent to do harm or display dominance or for less than 5 s; does not include when following agonistic interaction
	Shares food/object	Actor either feeds or uses an object in concert with another elephant that is within one body length
	Trunk tangle	Actor loosely entwines its trunk with that of recipient
	Trunk to mouth	Actor places its trunk in another elephant's mouth
	Trunk touch/toward	Actor extends trunk toward recipient with or without touching; not associated with any other behavior
<b>Submissive</b>	Allow	Actor remains still and calmly permits physical contact by conspecific, including genital investigation
	Back into/toward	Actor takes two steps (minimum) backward towards another elephant to within one body length, with or without touching
	Lower head or ears	Actor quickly drops head and/or ears in response to approach by another elephant
	Run away	Actor flees from conspecific in response to its agonistic contact, display, or approach
	Turn away/yield	Actor turns body away from or yields ground as a result of actions or encroachment by another elephant
<b>Other</b>	Bathe/swim	Actor lies, stands, or submerges in pool (includes spraying water on self); not associated with any other ethogram behavior
	Drink	Actor uses trunk to bring water to its mouth and drink
	Dust/mud	Actor uses trunk to throw dirt, sand, shavings, or mud onto body while standing
	Enrichment interaction	Actor interacts with provided non-food enrichment items
	Feed	Actor ingests presented diet items; includes manipulating food items
	Follow	Actor closely trails behind recipient, who is moving away from actor (at normal walking speed)
	Genital investigation	Actor sniffs or touches genitals of another elephant with its trunk
	Locomotion	Actor moves directionally along a horizontal surface (not while feeding); can include slow or fast walking or running
	Rest	Stationary; lying down or standing with trunk resting loosely on the ground; eyes open or closed; not performing any other behavior
	Head-bob	Actor displays repetitive head rotation/movement from side to side, at least two repetitions within 10 s
	Pace	Actor repeatedly walks the same line of travel, at least three times
	Wallow	Actor lies or rolls in mud or dirt
	Other	Actor performs any behavior not on ethogram
<b>Out of View</b>	Out of view	Actor cannot be seen or cannot be distinguished from other elephants

We included displaced aggression, knock down, and trunk slap in our data collection protocol. However, we never observed any of these behaviors.

We used instantaneous scan sampling [43] of focal elephants over 30 min periods, recording behavior every minute including agonistic, affiliative, stereotypic, and non-social behavior (Table 1) [35,36]. We defined stereotypy as repetitive, fixed behaviors without an apparent purpose [8]. When performing stereotypic behavior, we noted the type of stereotypy; over the course of the study period, we observed two types: pacing (repeatedly walking the same line of travel, at least three times) and head-bobbing (repetitive head rotation/movement from side to side, at least two repetitions within 10 s; Table 1). These never preceded predictable events such as feeding, shifting across yards/stalls, or keeper interaction [14,15], and thus we are confident they were not instead anticipatory behaviors. When housed with at least one other elephant, at each scan, we also recorded whether the



focal bull was in proximity (defined as within two body lengths) to another bull [35,36]. In order to investigate changes in stereotypic behaviors due to the arrival and introduction of Individuals 4 and 5 into the existing bachelor group, we separated observations into three time periods: before introductions (July 2018–January 2019), during introductions (February 2019–July 2019), and end of study (August 2019–December 2019) (Table 2) [35,36]. We used the Zoomonitor® mobile application created by Lincoln Park Zoo and Zier Niemann Consulting to record elephant behavior. The study protocol was reviewed and approved by Denver Zoo’s Research and Animal Welfare Committees (DZ#2018-008).

**Table 2.** Description of Variables Considered in Our Generalized Estimating Equations (GEE) [35,36]. Reprinted by permission of the publisher (Taylor & Francis Ltd., <http://www.tandfonline.com> accessed on 28 January 2022).

Variable	Description	Reference Level
HeadBobProp	Numeric (binomial proportion) variable indicating proportion of scans that the focal animal was engaging in head-bobbing ( $x/30$ )	NA—response variable
PaceProp	Numeric (binomial proportion) variable indicating proportion of scans that the focal animal was engaging in pacing ( $x/30$ )	NA—response variable
TimePeriod.5mos	Categorical variable indicating which 5 month time period the observation fell within (Before, Intro.5mos, End.5mos)	Before
Relevel.5mos	Categorical variable indicating which 5 month time period the observation fell within (Before, Intro.5mos, End.5mos); relevelled to compare Intro.5mos to End.5mos	Intro.5mos
Socialized	Binary variable indicating if the focal animal was house alone (0) or with at least one conspecific (1)	Alone (0)
FocalMusth	Binary variable indicating if the focal animal was in musth (1) or not (0) during the time of the observation session	No musth (0)
AccessArea	Continuous variable indicating the size of the area that the focal animal had access to (per 1000 ft <sup>2</sup> ); 2.00–47.37	2000 ft <sup>2</sup>
InOutAccess	Categorical variable indicating if focal animal had access inside (in), outside (out), or both (both)	Both
AMPM	Binary variable indicating if observations took place in the afternoon (1) or morning (0)	Morning (0)
AffiliativeProp	Numeric (binomial proportion) variable indicating proportion of scans that the focal animal was engaging in affiliative behavior ( $x/30$ )	0.10 increase in proportion
AgonisticProp	Numeric (binomial proportion) variable indicating proportion of scans that the focal animal was engaging in agonistic behavior ( $x/30$ )	0.10 increase in proportion
NearProp	Numeric (binomial proportion) variable indicating the proportion of scans that the focal animal was within two body-lengths of a conspecific ( $x/30$ )	0.10 increase in proportion
InOutAccess*AccessArea	Interaction term between InOutAccess (in, out, both) and AccessArea (2.00–47.37)	Both:AccessArea
Socialized*FocalMusth	Interaction term between Socialized (alone/0, social/1) and FocalMusth (no musth/0, musth/1)	Alone(0):No Musth(0)
Socialized*AccessArea	Interaction term between Socialized (alone/0, social/1) and AccessArea (2.00–47.37)	Alone(0):AccessArea
IndivGroup	Categorical variable indicating observations on a focal animal within a specific social unit; used for clustering observations with an independent correlation matrix	N/A—(used for clustering data)

We used binomial Generalized Estimating Equations (GEE) with a logit link function [44–46] to compare (1) odds of each type of stereotypic behavior (i.e., pacing and head-bobbing) when each elephant was alone (and not in musth) vs. when he was with one or more other bulls; (2) when housed with other bulls, odds of each type of stereotypic behavior when in proximity to another bull vs. when they were farther than two body

lengths from a conspecific; (3) odds of each type of stereotypic behavior compared to the amount of affiliative or agonistic social interactions when housed socially; (4) odds of each type of stereotypic behavior before introduction, during the five-month introduction period, and during the final five months of our study; and (5) when alone, odds of each type of stereotypic behavior when in musth vs. not in musth (Tables 2–4).

**Table 3.** Model Comparison Table for GEE of Head-Bobbing. Bold Indicates the Final Model.

Model	QIC	QICu	p-Value	Mean Effect Parameters	Corrected QIC
<b>All Data (Alone and Social)</b>					
TimePeriod.5mos + Socialized + FocalMusth + InOutAccess + AccessArea + AMPM + InOutAccess * AccessArea + Socialized * AccessArea + Socialized * FocalMusth	1475.4	143.3	-	13	1475.7
<b>TimePeriod.5mos + Socialized + FocalMusth + InOutAccess + AccessArea + AMPM + InOutAccess * AccessArea + Socialized * FocalMusth</b>	<b>1844.0</b>	<b>141.4</b>	<b>0.43</b>	<b>12</b>	<b>1844.3</b>
<b>Social Data Only</b>					
NearProp + AffiliativeProp + AgonisticProp + FocalMusth + InOutAccess + AccessArea + AMPM + TimePeriod.5mos + InOutAccess * AccessArea	32.98	32.55	-	13	33.53
<b>NearProp + FocalMusth + InOutAccess + AccessArea + TimePeriod.5mos + InOutAccess * AccessArea</b>	<b>112.13</b>	<b>31.34</b>	<b>0.19</b>	<b>12</b>	<b>112.60</b>
<b>Alone Data Only</b>					
<b>TimePeriod.5mos + FocalMusth + InOutAccess + AccessArea + AMPM + InOutAccess * AccessArea</b>	<b>1782</b>	<b>128</b>	<b>-</b>	<b>10</b>	<b>1783</b>

All GEE included an independent correlation matrix that clustered observations of each focal animal within every specific social group (Table 2). To control for the temporal correlation between scans in the same observation session, we used the binomial proportions of scans within the observation session (i.e., out of 30 possible scans) that the focal animal exhibited pacing or head-bobbing stereotypies as our response variables (Table 2). Our model selection process involved hypothesis testing: we initially fit a complex model, removed individual terms that did not serve as significant predictors, and then compared our final, reduced model to the original, complex model using ANOVA with a Wald test (Tables 3 and 4). Fixed effects for all models (i.e., predictions) included the time period (i.e., before introduction, five-month introduction period, final five months of study), if the focal animal was in musth, whether the focal animal had access indoors, outdoors, or both, total area that the focal animal could access (per 1000 ft<sup>2</sup>), and whether the observation session occurred in the morning (9:30–11:30) or the afternoon (13:30–15:30) (Tables 2–4). To assess the impact of social interactions within an observation session on stereotypic behaviors, we used a 0.10 (10%) increase in scans when focal animals were in proximity to a conspecific, engaged in affiliative interactions, or exhibited agonistic behaviors as our unit of analysis (Table 2). We did not include data collected during howdy in our analyses. We conducted all analyses in open-source statistical software R [47] and RStudio [48] and values  $p < 0.05$  were considered statistically significant.

**Table 4.** Model Comparison Table for GEE of Pacing. Bold Indicates the Final Model.

Model	QIC	QICu	p-Value	Mean Effect Parameters	Corrected QIC
<b>All Data (Alone and Social)</b>					
TimePeriod.5mos + Socialized + FocalMusth + InOutAccess + AccessArea + AMPM + InOutAccess*AccessArea + Socialized*FocalMusth + Socialized*AccessArea	1317.7	190.6	-	13	1318.1
<b>TimePeriod.5mos + Socialized + FocalMusth + InOutAccess + AccessArea + AMPM + InOutAccess*AccessArea + Socialized*AccessArea</b>	<b>1323.0</b>	<b>188.6</b>	<b>0.43</b>	<b>12</b>	<b>1323.3</b>
<b>Social Data Only</b>					
NearProp + AffiliativeProp + AgonisticProp + FocalMusth + InOutAccess + AccessArea + AMPM + TimePeriod.5mos + InOutAccess*AccessArea	273.8	51.9	-	13	274.4
NearProp + AffiliativeProp + AgonisticProp + FocalMusth + InOutAccess + AccessArea + AMPM + TimePeriod.5mos	427	48	0.98	11	428
NearProp + AffiliativeProp + AgonisticProp + FocalMusth + InOutAccess + AccessArea + AMPM	492.3	44.3	0.99	9	492.5
NearProp + AffiliativeProp + AgonisticProp + FocalMusth + InOutAccess + AccessArea	475.3	42.5	0.96	8	475.5
<b>NearProp + AffiliativeProp + AgonisticProp + FocalMusth + InOutAccess</b>	<b>309.4</b>	<b>40.5</b>	<b>0.99</b>	<b>7</b>	<b>309.6</b>
<b>Alone Data Only</b>					
<b>TimePeriod.5mos + FocalMusth + InOutAccess + AccessArea + AMPM + InOutAccess *AccessArea</b>	<b>−1107.2</b>	<b>153.5</b>	<b>-</b>	<b>10</b>	<b>−1106.5</b>

### 3. Results

Socialization, proximity, affiliative social interactions, study period, and musth substantially impacted the percentage of scans during which the elephants engaged in stereotypy. While all bulls that exhibited stereotypic behavior paced (Individuals 1, 2, 3, and 4), only Individual 3 demonstrated head-bobbing. Stereotypic behavior was relatively rare: across all behavioral scans recorded for each elephant, on average, Individual 3 head-bobbed during 7.35% of scans and Individuals 1, 2, 3, and 4 paced during 0.5–6.2% of scans (Table 5). Individual 5 did not engage in any stereotypy during our observations (Table 5).

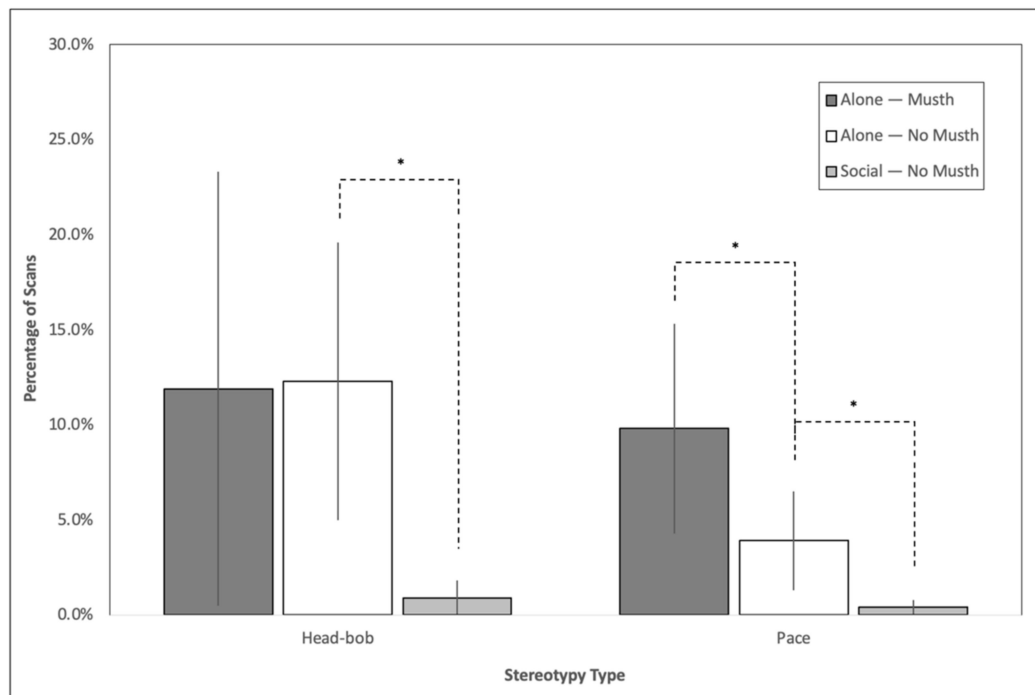
**Table 5.** Percentage of Total Scans Engaged in Stereotypic Behavior for Each Focal Animal.

Elephant	Overall Percentage of Scans Engaged in Stereotypic Behavior
Individual 1	2.4% (95% CI: 0.5–4.3%)
Individual 2	6.2% (95% CI: 3.0–9.5%)
Individual 3	Pacing: 0.5% (95% CI: 0.0–1.6%) Head-bobbing: 7.4% (95% CI: 3.7–11.1%)
Individual 4	1.3% (95% CI: 0.0–2.9%)
Individual 5	0.0% (Individual 5 did not engage in any stereotypic behaviors during our observations)



### 3.1. Impact of Social Housing on Stereotypy

When Individual 3 was not in musth, he engaged in head-bobbing during 12.3% of scans when housed alone (95% CI: 5.0–19.6%) and 0.9% of scans when housed with at least one other bull (95% CI: 0.0–3.0%). This represents a significant 98.4% decrease in the odds of Individual 3 engaging in head-bobbing while housed socially (95% CI: 83.5–99.8%;  $p < 0.001$ ; Binomial GEE; Figure 1; Table 6).



**Figure 1.** Percentage of scans engaged in stereotypy when socialized compared to alone and when in musth vs. not in musth. Only one individual (Individual 3) exhibited head-bobbing during our study, and Individuals 1, 2, 3, and 4 exhibited pacing. Individual 5 did not engage in stereotypy, and Individuals 4 and 5 did not undergo a musth period during our study. During non-musth observations, the elephants engaged in less head-bobbing and pacing when they were housed with at least one other bull compared to alone (head-bobbing  $p < 0.001$ ; pacing  $p = 0.005$ ). When alone, the elephants engaged in significantly more pacing when they were in musth than when they were not in musth ( $p < 0.001$ ). Musth did not significantly impact Individual 3's head-bobbing ( $p = 0.685$ ). Error bars represent 95% confidence intervals. \* indicates  $p < 0.050$ .

When data for all elephants who engaged in pacing (excluding when in musth) were considered together (i.e., Individuals 1, 2, 3, and 4), pacing occurred during 4.1% of scans when elephants were housed alone (95% CI: 1.5–6.7%) and 0.4% of focal scans when elephants were housed with at least one other bull (95% CI: 0.0–1.0%). When elephants were housed socially, the odds of pacing significantly decreased by 97.9% compared to when they were housed alone (95% CI: 68.7–99.9%;  $p = 0.005$ ; Binomial GEE; Figure 1; Table 6).

**Table 6.** GEE Model Parameter Estimates for All Data (Alone and Social). Generalized Estimating Equation Results of Associations between Predictor Variables (Fixed Effects) and Stereotypic Behavioral Response Variables.

Predictor	Level	HeadBobProp					PaceProp				
		Odds Ratio	$\beta$	SE	Wald $X^2$	$p$	Odds Ratio	$\beta$	SE	Wald $X^2$	$p$
TimePeriod.5mos	Before *	-	-	-	-	-	-	-	-	-	-
	Intro.5mos	0.791	-0.234	0.146	2.59	0.108	0.931	-0.071	0.292	0.06	0.808
	End.5mos	0.621	-0.476	0.344	1.92	0.166	<b>0.144</b>	<b>-1.937</b>	<b>0.454</b>	<b>18.18</b>	<b>&lt;0.001</b>
Relevel.5mos	Before	1.264	0.234	0.146	2.59	0.108	1.074	0.071	0.292	0.06	0.808
	Intro.5mos *	-	-	-	-	-	-	-	-	-	-
	End.5mos	0.785	-0.242	0.256	0.89	0.344	<b>0.155</b>	<b>-1.867</b>	<b>0.296</b>	<b>39.66</b>	<b>&lt;0.001</b>
Socialized	Alone *	-	-	-	-	-	-	-	-	-	-
	Social	<b>0.024</b>	<b>-3.735</b>	<b>0.829</b>	<b>20.32</b>	<b>&lt;0.001</b>	<b>0.021</b>	<b>-3.842</b>	<b>1.367</b>	<b>7.90</b>	<b>0.005</b>
FocalMusth	No musth *	-	-	-	-	-	-	-	-	-	-
	Musth	0.945	-0.057	0.166	0.12	0.730	<b>3.796</b>	<b>1.334</b>	<b>0.186</b>	<b>51.25</b>	<b>&lt;0.001</b>
	Both *	-	-	-	-	-	-	-	-	-	-
InOutAccess	Inside	<b>72.39</b>	<b>4.282</b>	<b>0.471</b>	<b>82.61</b>	<b>&lt;0.001</b>	1.680	0.519	1.123	0.21	0.644
	Outside	1.231	0.208	0.507	0.17	0.683	6.240	1.831	1.256	2.13	0.145
AccessArea		1.087	0.083	0.065	1.61	0.205	0.996	-0.004	0.057	0.01	0.937
AMPM	AM *	-	-	-	-	-	-	-	-	-	-
	PM	<b>2.779</b>	<b>1.022</b>	<b>0.131</b>	<b>61.32</b>	<b>&lt;0.001</b>	<b>2.586</b>	<b>0.950</b>	<b>0.317</b>	<b>8.95</b>	<b>0.003</b>
InOutAccess * AccessArea	Both:AccessArea *	-	-	-	-	-	-	-	-	-	-
	In:AccessArea	<b>0.138</b>	<b>-1.982</b>	<b>0.200</b>	<b>98.43</b>	<b>&lt;0.001</b>	<b>0.454</b>	<b>-0.790</b>	<b>0.193</b>	<b>16.76</b>	<b>&lt;0.001</b>
	Out:AccessArea	0.900	-0.105	0.067	2.46	0.117	0.897	-0.109	0.068	2.55	0.111
Socialized * FocalMusth	Alone:FocalMusth *	-	-	-	-	-	N/A				
	Social:FocalMusth	<b>&lt;0.001</b>	<b>-36.98</b>	<b>0.937</b>	<b>1557.4</b>	<b>&lt;0.001</b>					
Socialized * AccessArea	Alone:AccessArea *	N/A					-	-	-	-	-
	Social:AccessArea						<b>1.120</b>	<b>0.113</b>	<b>0.057</b>	<b>3.92</b>	<b>0.048</b>

$\beta$  = beta coefficients from model outputs: positive values indicate an increase in odds compared to the reference level while negative values indicate a decrease in odds compared to reference level; SE = standard error of beta coefficients; Wald  $X^2$  = chi-squared statistic from Wald test with df = 1;  $p$  =  $p$ -value from Wald test. \* indicates reference level. Bold signifies statistical significance ( $p < 0.05$ ).

### 3.2. Impact of Social Behaviors (Proximity, Affiliative Behavior, and Agonistic Behavior) on Stereotypy

We examined the impact of proximity to a conspecific (when housed with at least one other bull) on the percentage of scans engaged in stereotypy. Individual 3 engaged in head-bobbing during 1.6% of scans when not in proximity to a conspecific (95% CI: 0.0–5.4%) and during 0.3% of scans when he was in proximity to at least one other bull (95% CI: 0.0–1.8%), which represents a significant 55.6% decrease in odds for a 10% increase in scans spent in proximity to a conspecific (95% CI: 3.9–79.5%;  $p = 0.039$ ; Binomial GEE; Table 7). Pacing occurred during 0.7% of scans when elephants (Individuals 1, 2, 3, and 4) were housed with at least one other bull but were not in proximity to a conspecific (95% CI: 0.0–1.8%) and 0.2% of focal scans when elephants were in proximity to at least one other bull (95% CI: 0.0–0.7%); however, this difference was not significant ( $p = 0.870$ ; Binomial GEE; Table 7).

The percentage of scans during which elephants engaged in affiliative behavior also significantly impacted the odds of pacing. The odds of the elephants engaging in pacing decreased significantly by 39.2% with a 10% increase in scans engaged in affiliative behavior (95% CI: 18.9–54.4%;  $p < 0.001$ ; Binomial GEE; Table 7). There was no significant change in the odds of Individual 3 engaging in head-bobbing as affiliative behaviors increased ( $p = 0.304$ ; Binomial GEE; Table 7). Additionally, the percentage of scans that elephants engaged in agonistic behavior did not significantly impact the odds of engaging in head-bobbing or pacing (head-bobbing  $p = 0.193$ ; pacing  $p = 0.114$ ; Binomial GEE; Table 7).

### 3.3. Impact of Introductions on Stereotypy

The odds of Individual 3 head-bobbing across time periods did not significantly differ (before vs. intros:  $p = 0.107$ ; before vs. end of study:  $p = 0.166$ ; intros vs. end of study:  $p = 0.344$ ; Binomial GEE; Table 6). However, the odds of the elephants engaging in pacing significantly decreased at the end of our study compared to before introductions (85.6% decrease; 95% CI: 64.9–94.1%;  $p < 0.001$ ) and during introductions (84.4% decrease; 95% CI: 72.1–91.3%;  $p < 0.001$ ; Binomial GEE; Table 6).

### 3.4. Impact of Musth on Stereotypy

When Individual 3 was housed alone, he engaged in head-bobbing during 12.3% of scans when not in musth (95% CI: 5.0–19.6%) and 11.9% of scans when he was in musth (95% CI: 0.5–23.4%), a difference that was not statistically significant ( $p = 0.685$ ; Binomial GEE; Figure 1; Table 8). When data for all musth elephants who engaged in pacing were considered together (Individuals 1, 2, and 3), pacing occurred during 3.9% of scans when elephants were not in musth and housed alone (95% CI: 1.3–6.6%) and 9.8% of focal scans when elephants were in musth and housed alone (95% CI: 4.3–15.3%). When the elephants were housed alone, being in musth significantly increased the odds of pacing by 278% compared to when they were alone but not in musth (95% CI: 147–479%;  $p < 0.001$ ; Binomial GEE; Figure 1; Table 8). Elephants were rarely housed in social groups during musth; therefore, there is not sufficient data to determine the effects of social housing on stereotypy while they were in musth. Additionally, Individuals 4 and 5 did not undergo a musth period during this study.

**Table 7.** GEE Model Parameter Estimates for Social Data. Generalized Estimating Equation Results of Associations between Predictor Variables (Fixed Effects) and Stereotypic Behavioral Response Variables.

Predictor	Level	HeadBobProp					PaceProp				
		Odds Ratio	$\beta$	SE	Wald $X^2$	$p$	Odds Ratio	$\beta$	SE	Wald $X^2$	$p$
NearProp		<b>0.444</b>	<b>−0.812</b>	<b>0.394</b>	<b>4.25</b>	<b>0.039</b>	1.033	0.032	0.196	0.03	0.870
AffiliativeProp		0.652	−0.428	0.416	1.05	0.304	<b>0.607</b>	<b>−0.500</b>	<b>0.147</b>	<b>11.48</b>	<b>&lt;0.001</b>
AgonisticProp		2.779	1.022	0.785	1.69	0.193	0.025	−3.705	2.346	2.49	0.114
FocalMusth	No musth *	-	-	-	-	-	-	-	-	-	-
	Musth	<b>&lt;0.001</b>	<b>−40.508</b>	<b>1.809</b>	<b>501.2</b>	<b>&lt;0.001</b>	<b>17.41</b>	<b>2.857</b>	<b>0.897</b>	<b>10.14</b>	<b>0.001</b>
	Both *	-	-	-	-	-	-	-	-	-	-
InOutAccess	Inside	<b>&lt;0.001</b>	<b>−47.974</b>	<b>3.335</b>	<b>206.9</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>−41.816</b>	<b>1.274</b>	<b>1077.7</b>	<b>&lt;0.001</b>
	Outside	<b>1378.8</b>	<b>7.229</b>	<b>2.368</b>	<b>9.32</b>	<b>0.002</b>	<b>0.124</b>	<b>−2.089</b>	<b>0.901</b>	<b>5.37</b>	<b>0.020</b>
AccessArea		<b>1.310</b>	<b>0.270</b>	<b>0.120</b>	<b>5.11</b>	<b>0.024</b>			N/A		
TimePeriod.5mos	Before *	-	-	-	-	-					
	Intro.5mos	<b>&lt;0.001</b>	<b>−42.551</b>	<b>1.953</b>	<b>474.9</b>	<b>&lt;0.001</b>			N/A		
	End.5mos	0.225	−1.493	1.465	1.04	0.308					
InOutAccess * AccessArea	Both:AccessArea *	-	-	-	-	-					
	In:AccessArea	<b>23.220</b>	<b>3.145</b>	<b>0.432</b>	<b>52.90</b>	<b>&lt;0.001</b>			N/A		
	Out:AccessArea	<b>0.534</b>	<b>−0.627</b>	<b>0.218</b>	<b>8.25</b>	<b>0.004</b>					

$\beta$  = beta coefficients from model outputs: positive values indicate an increase in odds compared to the reference level while negative values indicate a decrease in odds compared to reference level; SE = standard error of beta coefficients; Wald  $X^2$  = chi-squared statistic from Wald test with df = 1;  $p$  =  $p$ -value from Wald test. \* indicates reference level. Bold signifies statistical significance ( $p < 0.05$ ).

**Table 8.** GEE Model Parameter Estimates for Alone Data. Generalized Estimating Equation Results of Associations between Predictor Variables (Fixed Effects) and Stereotypic Behavioral Response Variables.

Predictor	Level	HeadBobProp					PaceProp				
		Odds Ratio	$\beta$	SE	Wald $X^2$	$p$	Odds Ratio	$\beta$	SE	Wald $X^2$	$p$
FocalMusth	No musth *	-	-	-	-	-	-	-	-	-	-
	Musth	0.932	-0.070	0.173	0.16	0.685	<b>3.781</b>	<b>1.33</b>	<b>5.899</b>	<b>37.47</b>	<b>&lt;0.001</b>
	Both *	-	-	-	-	-	-	-	-	-	-
InOutAccess	Inside	55.757	<b>4.021</b>	<b>0.411</b>	<b>95.77</b>	<b>&lt;0.001</b>	<b>10.155</b>	<b>2.318</b>	<b>0.785</b>	<b>8.73</b>	<b>0.003</b>
	Outside	0.806	-0.216	0.324	0.44	0.506	2.512	0.921	1.229	0.56	0.453
AccessArea		1.014	0.014	0.034	0.17	0.678	0.954	-0.047	0.042	1.21	0.271
AMPM	AM *	-	-	-	-	-	-	-	-	-	-
	PM	<b>2.467</b>	<b>0.903</b>	<b>0.040</b>	<b>501.3</b>	<b>&lt;0.001</b>	<b>2.732</b>	<b>1.005</b>	<b>0.192</b>	<b>27.36</b>	<b>&lt;0.001</b>
TimePeriod.5mos	Before *	-	-	-	-	-	-	-	-	-	-
	Intro.5mos	0.892	-0.114	0.086	1.76	0.185	0.991	-0.009	0.220	0.00	0.967
	End.5mos	0.680	-0.385	0.323	1.42	0.233	<b>0.319</b>	<b>-1.144</b>	<b>0.490</b>	<b>5.46</b>	<b>0.020</b>
InOutAccess *AccessArea	Both:AccessArea *	-	-	-	-	-	-	-	-	-	-
	In:AccessArea	<b>0.144</b>	<b>-1.936</b>	<b>0.195</b>	<b>98.34</b>	<b>&lt;0.001</b>	<b>0.265</b>	<b>-1.328</b>	<b>0.398</b>	<b>11.15</b>	<b>&lt;0.001</b>
	Out:AccessArea	0.971	-0.029	0.031	0.88	0.347	0.971	-0.029	0.042	0.50	0.480

$\beta$  = beta coefficients from model outputs: positive values indicate an increase in odds compared to the reference level while negative values indicate a decrease in odds compared to reference level; SE = standard error of beta coefficients; Wald  $X^2$  = chi-squared statistic from Wald test with df = 1;  $p$  =  $p$ -value from Wald test. \* indicates reference level. Bold signifies statistical significance ( $p < 0.05$ ).



#### 4. Discussion

There are typically gaps between the experiences we offer elephants in human care versus what they experience in the wild. Closing these gaps involves providing elephants opportunities to thrive in human care with actions that promote natural behaviors and reduce or eliminate unnatural behaviors such as stereotypy. Our results show that sharing space with at least one other bull had a considerable positive impact on stereotypic behavior, with elephants engaging in substantially less pacing and head-bobbing when housed socially. Furthermore, when housed in social combinations, pacing and head-bobbing also decreased when in proximity to another bull and as affiliative behavior increased, indicating that more active, positive social interactions further contribute to a decrease in stereotypy. When housed alone, the elephants were significantly more likely to pace when in musth versus when they were not in musth, although musth did not impact Individual 3's head-bobbing behavior. Finally, diverse and abundant social opportunities with familiar social partners may further reduce stereotypy as the amount of pacing decreased at the end of our study compared to before the introduction of the new bulls and during the introductions, indicating that higher social diversity with familiar partners further decreases stereotypy. Overall, our results suggest that there are marked benefits to individual elephant welfare that stem from diverse social opportunities.

Addressing the welfare of elephants in zoological settings is our "duty of care" [49]. It requires increasing our understanding of how housing and management can impact quality of life [29]. Greco and colleagues monitored the behavior of 42 zoo-housed Asian elephants in North America for a year and results showed that including opportunities for social interaction significantly reduced stereotypic behavior [9,23]. These conclusions are consistent with the results from our study. Furthermore, Mason [24] proposed that sharing space with suitable social partners may protect against stereotypy by reducing chronic stress in social species. The lower stereotypy frequency in our study between bulls in close proximity compared to those farther apart suggests that additional positive and subtle interactions may occur when they are near each other. However, this hypothesis requires further research.

A previous study indicated that stereotypic behavior may increase in an uncertain or agonistic social environment [9]. While increased affiliative behavior was correlated with decreased stereotypic behavior, agonistic behavior did not significantly impact stereotypy in our study. This may be due to the rarity of agonistic behaviors (both contact and non-contact) observed during this study [35,36]. Since this study population consists primarily of young bulls with one older male, a low level of agonism may be biologically appropriate as younger bulls learn the bounds of appropriate social interaction. For example, wild adolescent males (ages 10–20) were more social than older and younger bulls, allowing adolescent males to develop critical social skills [1]. This age range of increased sociality corresponds with four of the five focal elephants at Denver Zoo, so the impacts of social stressors (i.e., agonism) may be limited in this group.

Stereotypy tends to manifest when animals are deprived of mental stimuli and when activities driven by instinct are constrained by environments where those activities are restricted [50]. Free-ranging bull elephants in musth spend less time feeding and more time locomoting than when they are not in musth in order to find estrous females [40–42,51]. In a zoo setting, elephants in musth are often restricted in the space they have to travel, which may lead to more pacing. Additionally, musth bulls at institutions that house only males (including Denver Zoo) will never encounter an estrous female, potentiating further frustration. Furthermore, musth bulls are usually housed alone in order to reduce conflict with conspecifics, lowering agonistic and affiliative behaviors and thus providing more available time; this may explain the increase in pacing we report when alone in musth compared to alone but not in musth.

The process of moving to a new facility and the subsequent social integration increases stress for animals [30]. As predicted, the odds of pacing were significantly lower during the final five months of our study compared to during the introduction of the new bulls,

while the odds of affiliative behavior were higher at the end of the study period [35]. This inverse relationship between pacing and affiliative behavior likely reflects decreased stress levels as the group formed a stable social dynamic and affiliative behaviors increased [35]. The odds of pacing in the final five months of the study period were also lower than before the introduction of Individuals 4 and 5 to the group. This suggests that the increased social opportunities afforded by living in a larger group with a greater number of possible social combinations serves to reduce stereotypy; bulls thus likely benefit from being members of larger groups.

Prior to our study, anecdotal observations suggested that Individual 3 engaged in substantially more stereotypy than the other bulls. However, our data do not bear out this trend. Individual 3 most often engaged in head-bobbing stereotypic behavior, which is more noticeable than pacing, the most common stereotypy for the other individuals (aside from Individual 5 who did not engage in either pacing or head-bobbing over the course of this study). Previously, animal managers underestimated the frequency of stereotypy in other individuals and overestimated the frequency of Individual 3's head-bobbing. Our results underscore the value of assessing animals objectively; data-driven management can help address the needs of every animal. In order to assess individual differences within this bachelor group, a future study will investigate individual elephant's behavior and sociality at Denver Zoo.

Our study focused specifically on the relationship between sociality and stereotypy. However, other factors may also affect stereotypic behavior in bull elephants. Space constraints, for example, may preclude far travel and thus may lead to more pacing. However, neither enclosure access size nor whether elephants had access indoors, outdoors, or both were significant predictors of pacing, showing that these variables did not influence time spent in stereotypy for the majority of this group. While there was no difference in Individual 3's pacing, he did engage in significantly more head-bobbing when he had access only indoors compared to both indoors and out (Table 6). This difference may be due to the indoor areas containing fewer enrichment items or to a stressful association with being housed indoors due to this individual's life history and requires further study. Both pacing and head-bobbing significantly increased during the afternoon observation period (13:30–15:30) compared to the morning observation period (9:30–11:30), indicating that time of day also influences stereotypic behavior in this group (Table 6). Rest, locomotion, and enrichment engagement all increased in the afternoons and the bulls exhibited decreased social behaviors in the afternoon compared to the morning [35]. This potentially reflects that the morning is a time with more novel interactions while the afternoon allows for fewer novel social experiences and more solitary activities [35].

It is also possible that stereotypy becomes less common as a consequence of other behaviors contributing to their activity budget. When elephants are housed with other bulls, they spend time socializing, leaving less time to engage in stereotypy. While the bulls spent 5.7% of their time engaged in agonistic behavior when housed with at least one conspecific, they spent twice as much time in affiliative behavior [35]. This suggests that the elephants preferentially invest time in positive behaviors when housed socially as opposed to behaviors often considered negative (e.g., stereotypy and agonism), implying that they may experience limited frustration when socially housed.

Bull Asian elephants display significant sociality, both with one another and with cow-calf herds [2,5,16,17]. From a management perspective, we need to be more attentive to the social lives of bull elephants in our care to advance best practices in their welfare [6,21]. This includes improving our willingness to provide them with social groupings that resemble those observed in the wild [52]. The Association of Zoos and Aquariums has no standards specific to bull elephant management other than to specify that males over six years of age may be housed alone, but they cannot be kept in complete isolation [3]. Housing bulls in social isolation or with only infrequent social contact with other elephants for mating represents behavioral restriction. Moving forward, zoos will increasingly need to house bulls outside of a breeding situation because the number of males born will exceed the

number that can be maintained in breeding groups and because of the expanding need to re-home bulls from the private sector. Recent studies [5,6,23,28,35,36], including the present one, provide evidence that sociality is a significant component of bull elephant welfare and support management styles that include a high degree of socialization among males.

We recommend housing bulls with more opportunities for natural social interactions, including with one another. Multiple bulls housed at the same facility should be together for a significant part of the time, while also having opportunities to separate themselves. When introducing bulls to one another, we recommend an elephant-mediated approach in which the elephants indicate when they are ready for increased social contact with other bulls, based upon observed behaviors (e.g., reduced agonism). In our all-male group at Denver Zoo, there appeared to be a benefit to having a mature bull as part of the group of younger males in that he provided opportunities for social learning, mimicking what happens in situ (e.g., [1]), and thus we encourage mixed-age groups when possible. Furthermore, institutions should not avoid housing bulls together merely because one of them is in musth as being housed alone might compound the increased likelihood of pacing during musth. After considering the personality of each bull, institutions could attempt to socialize bulls in musth in small social units in a location that allows for non-musth bulls to avoid a musth bull (e.g., an area with multiple exit routes or hiding spots). Recent trials at Denver Zoo demonstrate that it is possible to house a musth bull with other males for limited periods of time without severe or increased aggression [53]. Experimenting with introductions and time spent together, even when in musth, appears successful and can be interrupted if necessary. With the growing number of bull elephants in zoos, we must plan for their long-term management [54] while prioritizing their care and welfare. This can be addressed in part by housing bulls together in a way that considers their natural history.

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