

RESEARCH ARTICLE

Environmental Conditions Associated With Repetitive Behavior in a Group of African Elephants

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Repetitive movement patterns are commonly observed in zoo elephants. The extent to which these behaviors constitute a welfare concern varies, as their expression ranges from stereotypies to potentially beneficial anticipatory behaviors. Nevertheless, their occurrence in zoo animals is often viewed negatively. To better identify conditions that prompt their performance, observations were conducted on six African elephants (*Loxodonta africana*) at the North Carolina Zoo. Individuals spent most of their time engaged in feeding, locomotion, resting, and repetitive behavior. Both generalized estimating equation and zero-inflated negative binomial models were used to identify factors associated with increased rates of repetitive behavior. Time of day in conjunction with location on- or off-exhibit best explained patterns of repetitive behavior. Repetitive behaviors occurred at a lower rate in the morning when on-exhibit, as compared to afternoons on-exhibit or at any time of day off-exhibit. Increased repetitive behavior rates observed on-exhibit in the afternoon prior to the evening transfer and feeding were possibly anticipatory responses towards those events. In contrast, consistently elevated frequencies of repetitive behavior off-exhibit at all times of day could be related to differences in exhibit complexity between off-exhibit and on-exhibit areas, as well as a lack of additional foraging opportunities. Our study contributes valuable information on captive elephant behavior and represents a good example of how behavioral research can be employed to improve management of zoo animals. *Zoo Biol.* 34:201–210, 2015. © 2015 Wiley Periodicals, Inc.

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INTRODUCTION

A primary concern of zoos is to ensure the animals under their care experience good welfare—i.e., positive mental states—while minimizing suffering [Dawkins, 1990; Hosey et al., 2009]. Conspicuous repetitive behaviors (e.g., pacing, rocking, swaying) are commonly observed in zoo animals, but their relationship to welfare is complex. At one extreme lies stereotypic behavior, defined as “repetitive behaviors induced by frustration, repeated attempts to cope, or central nervous system dysfunction” [Mason, 2006]. These behaviors arise through redirected appetitive behaviors that cannot be completed (e.g., foraging with no food available) or by an inability to exert control over the environment [Carlstead, 1998; Broom and Kirkden, 2004]. Whether stereotypies are a behavioral pathology or a coping behavior is unclear; however, they indicate a past or present failure to address an animal’s psychological needs and can be considered an indicator of poor welfare [Broom and Kirkden, 2004].

Not all repetitive behaviors are suggestive of compromised welfare. Anticipatory behaviors are elicited by predictable events and can prepare an animal for the

anticipated event, either enhancing a positive experience’s rewarding nature (e.g., salivation prior to feeding) or decreasing aversiveness of a negative one (e.g., postural changes prior to a floor-mediated shock) [Badia et al., 1979; Spruijt et al., 2001; Basset and Buchanan-Smith, 2007]. Furthermore, when the expected event is positive, the actual experience of anticipation can also be positive due to the activation of neurochemical reward systems [Berridge and Robinson, 1998]; this suggests that the expression of anticipatory behaviors can serve as real-time indicators of positive welfare [Spruijt et al., 2001; van der Harst and

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Spruijt, 2007; Watters, 2014]. Anticipatory behaviors are commonly seen prior to predictable feedings and examples include pacing in carnivores, wheel-running in rodents, and increased arousal and activity [Mistlberger, 1994; Carlstead, 1996; Basset and Buchanan-Smith, 2007; Mistlberger, 2009].

Anticipatory behavior is not always beneficial or benign, however. Increased aggression occurs in chimpanzees prior to temporally-predictable feedings [de Waal and Hoekstra, 1980], and anticipatory activity can involve self-mutilation or abnormal behaviors [Bassett and Buchanan-Smith, 2007]. Additionally, even when anticipatory behavior is a positive experience, van der Harst and Spruijt [2007] suggest that the frequency and intensity of its expression can reveal whether an animal perceives its life as being dominated by negative events. When positive events are frequent, anticipatory behavior toward those events will also be frequent, though each bout should occur at a low intensity. Since positive experiences are common, each will have less individual importance to the animal and elicit a less intense response. Conversely, when negative experiences outweigh positive ones, anticipatory behavior will be less frequent. However, when it does occur, it should be particularly intense or vigorous since the individual value of each positive event to the animal has increased.

Anticipatory behaviors can also develop into stereotypes, though the relationship between stereotypic behaviors and welfare is not always clear [Mason and Latham, 2004; Bassett and Buchanan-Smith, 2007]. Stereotypes can be a coping response in stressful environments, such that individuals displaying the highest frequencies of stereotypic behavior can experience less stress than individuals not performing them [Mason and Latham, 2004]. Additionally, behavioral repetition during stereotypic behavior can result in permanent central nervous system changes, leading to stereotypes that are difficult to extinguish and are displayed in situations that normally would not induce their performance [Mason and Latham, 2004]. For the above reasons, it can be difficult to assess the influence repetitive behavior, either anticipatory or stereotypic in nature, has on welfare.

Repetitive behavior is commonly observed in zoo elephants (Clubb and Mason, 2002; Harris et al., 2008). Its proximate causes are uncertain, but likely include: restricted movement, social factors, reduced physical environment complexity, and inability to fulfill foraging motivations [Clubb and Mason, 2002]. Elephants performed stereotypic behavior more frequently when chained [Friend and Parker, 1999; Gruber et al., 2000] and in colder temperatures [Rees, 2004]. Higher repetitive behavior frequencies also occurred prior to routine husbandry events [Friend, 1999; Wilson et al., 2004, 2006]. In contrast, the amount of time engaged in foraging is negatively associated with repetitive behavior frequency [Friend and Parker, 1999; Rees, 2009]. A review of various population-wide indices of elephant welfare identified the occurrence of repetitive behaviors as suggestive of compromised welfare [Mason and Veasey, 2010].

The current study had two main objectives. First, we quantitatively assessed patterns of behavior in African elephants (*Loxodonta africana*) at the North Carolina Zoo relative to behavior of elephants in other published reports. Second, we identified factors associated with increased rates of repetitive activity performed by elephants under captive conditions. Two non-mutually-exclusive hypotheses were tested. First, increased repetitive behavior frequencies would occur off-exhibit due to the substantially smaller and less complex nature of the off-exhibit areas compared to the larger, more naturalistic public display spaces. Secondly, depletion of preferred foraging items and/or anticipation of the evening feeding would result in increased repetitive behavior frequencies in the afternoon. Elephants in the wild can spend over half their day foraging on a variety of vegetable matter [Poole and Granli, 2009]. Higher nutritional content and caloric density of food items fed in captivity (e.g., concentrates, domestic produce) result in an elephant's nutritional needs being satisfied with relatively low volumes of food consumed over short time periods. Rapid consumption of available food can leave elephants with significant periods of the day where food-oriented behaviors cannot be performed. Additionally, animals can easily become entrained to predictable daily events (e.g., feedings), potentially resulting in anticipatory behaviors [Bassett and Buchanan-Smith, 2007].

MATERIALS AND METHODS

Study Animals and Site

This study was conducted between June 4th and July 26th of 2011 on six African elephants kept at the NC Zoo. The study group consisted of four adult cows, one juvenile female, and one adult bull. The bull was kept physically isolated from the other elephants, though often in visual contact. The females were divided into two groups, one mother-daughter pair and a group of three, unrelated adults. Personal histories, social groups, and the number of hours each elephant was observed are given in Table 1.

Daily elephant husbandry involved an initial cleaning and inspection by keepers, followed by a feeding consisting of pellets and fresh produce. Two groups (Table 1) were released each day into two separate on-exhibit enclosures around 8:30 AM. Each enclosure was approximately 14,000 m² with primarily grassy ground cover and contained several trees offering shade and a pool deep enough for an adult elephant to submerge itself. Elephants in separate exhibits could maintain visual, but not physical, contact. Hay was spread throughout each area prior to releasing the elephants. Animals also foraged on grass and other vegetation within the exhibits. Elephants were brought off-exhibit around 4:30 PM. Usually one or two groups were given night-time access to the on-exhibit spaces.

The remaining group was kept off-exhibit for the day. These areas consisted of paddocks with sand substrate and a

TABLE 1. Personal history and hours of data collected for each elephant

Elephant	Sex	Age	Hours of data collected				Time at NC zoo	Social grouping	Relatedness to other individuals
			Morning/ On-exhibit	Afternoon/ On-exhibit	Morning/ Off-exhibit	Afternoon/ Off-exhibit			
1	M	28	14	18	14	7	3yr., 7mth.	A	None
2	F	33	15	11	16	11	3yr., 7mth.	B	Mother to 3
3	F	9	14	13	12	9	3yr., 7mth.	B	Daughter to 2
4	F	30	15	18	11	7	7yr., 8mth.	C	None
5	F	33	14	13	13	7	16yr., 1mth.	C	None
6	F	23	17	19	7	4	3yr., 8mth.	C	None

concrete strip adjacent to the elephant barn. Each paddock was 240 m² and adjacent paddocks could be combined into one. A variety of enrichment devices (e.g., logs, tires, and balls) were provided. Animals off-exhibit were periodically provided hay and browse by keepers, but had limited additional foraging opportunities.

Data Collection

The ethogram consisted of 23 behaviors, some of which were combined for data analysis due to infrequency (e.g., agonism) or equivalence for analysis purposes (e.g., repetitive behavior; Table 2). When an animal was engaged in both repetitive behavior and another behavior simultaneously (e.g., eating), it was recorded as the respective repetitive behavior. Keeper-elephant interaction was exclusively via a protected contact system. This could consist of delivering browse, hay, and running water to off-exhibit elephants, or providing produce to on-exhibit elephants during public interaction sessions. Data collection did not halt during these often-spontaneous interactions; keeper interaction took precedence over all other behaviors when classifying a behavior.

Observations occurred between 8:00 AM and 5:00 PM each day. Instantaneous focal animal sampling was used at two-minute intervals over the course of one hour [Altmann, 1974]. Animals were watched continuously for a number of seconds prior to and after a sampling instant in order to correctly classify behaviors whose identification could not be made at a single instance in time (e.g., repetitive behaviors). When multiple elephants were present, the identity of each animal and the initiator and recipient of any behavior involving multiple individuals was recorded. Two observers were responsible for data collection. Prior to beginning the study, joint recordings ensured that inter-observer agreement was greater than 90%.

Multiple data hours were collected on each animal (Table 1). Observation times were not randomized. Rather, we attempted to observe each animal at least once per day and sought to balance observation sessions for each elephant across contexts (on- or off-exhibit; morning or afternoon). While the total data hours per elephant were consistent, fewer observations were made off-exhibit in the afternoon compared to the other three combinations of location and

time of day (Table 1). This discrepancy arose due to external events (e.g., animals brought within the barn, veterinary visits) that decreased sampling opportunities during this context.

Statistical Analysis

All observations for each hour-long session were collapsed to provide the proportion of repetitive behavior per session [Martin and Bateson, 1993]. These proportions were used as our response variable in a generalized estimating equation (GEE) using a binomial distribution [Zuur et al., 2009; Smithson and Merkle, 2014]. Sessions can be considered reasonably independent if the amount of time between successive sessions was longer than the average bout length of a given behavior [Martin and Bateson, 1993]. While this assumption should hold for our data, multiple data hours on the same elephant are still likely correlated to some extent. Using a GEE allowed us to incorporate a covariance structure accounting for this non-independence [Zuur et al., 2009].

The model fitted by the GEE takes the form of:

$$\mu_{is} = \frac{e^{\alpha + \beta_1 * X_{1is} + \dots + \beta_n * X_{nis}}}{1 + e^{\alpha + \beta_1 * X_{1is} + \dots + \beta_n * X_{nis}}}$$

$$var(Y_{is} | X_{1is} + \dots + X_{nis}) = \phi * \mu_{is} * (1 - \mu_{is}), \text{ and}$$

$$cor(Y_{is}, Y_{it}) = \alpha,$$

where μ_{is} is the predicted proportion of repetitive behavior for elephant i during session s given explanatory variables $X_{1is} + \dots + X_{nis}$, $var(Y_{is} | X_{1is} + \dots + X_{nis})$ is the predicted variance of μ_{is} given those same variables, and $cor(Y_{is}, Y_{it})$ describes the correlation between sessions s and t on elephant i . For μ_{is} , α indicates the intercept, and the coefficient for each predictor variable, X , is given by its respective β . An estimated scale parameter, ϕ , is used to calculate the variance.

Our model included two categorical predictors: time of day (morning/afternoon) and location (on- or off-exhibit), as well as their interaction. Additionally, temperature was recorded at the start of each session, as it could potentially influence behavior [Rees, 2004]. Since temperature effects

TABLE 2. Ethogram of African elephant behavior

Behavior	Description	Behavioral categories for analysis
Self-maintenance	Rubbing, scratching, throwing sand/dirt/hay/water/fecal material onto body, mudding, dusting, or digging	Self-maintenance
Resting	No interactions with conspecifics, environment, or keepers; no bodily movement. Can be asleep or awake, standing up or lying down	Resting
Pacing	Pacing back and forth between point A and B or in a circle. May include eating	Repetitive Behavior
Rocking	Swaying back and forth with no locomotion. May include eating	Repetitive Behavior
Other repetitive behavior	Other repetitive behavior whose cause and function are unknown. May include eating	Repetitive Behavior
Locomotion	Walking or running non-repetitively	Locomotion
Forage—exhibit vegetation	Browsing on trees/shrubs/grass	Forage-Exhibit Vegetation
Forage—prepared diet	Eating prepared diet (hay/grain/vegetables)	Forage-Prepared Diet
Forage—browse	Eating cut browse	Forage-Prepared Diet
Drinking	Drinking from pool or drinker	Other
Interacting—exhibit structure	Interacting with permanent exhibit structures. Does not include eating	Abiotic Interaction
Interacting—caging	Interacting with cage bars/fencing, both on- and off-exhibit	Abiotic Interaction
Interacting—temporary enrichment	Manipulating any temporary non-food enrichment item, such as tires or barrels	Abiotic Interaction
Bathe	Bathing in exhibit pond. Does not include splashing water while standing at the pool edge	Self-Maintenance
Other solitary behavior	Other solitary behaviors (e.g., moving trunk, defecating, etc.).	Other
Agonism—non-contact	Threats (ears extended, charging, head shake, pursuit). No physical contact between individuals	Other
Agonism—contact	Aggressive behavior involving physical contact between individuals; can include biting, head-butting, poking, striking with the trunk, or pushes	Other
Affiliative—contact	Behaviors that involve any non-aggressive physical contact; includes trunk intertwining, trunk placed within another elephant's mouth, contact with another elephant without obvious use of force	Other
Displace	Focal elephant approaches another elephant which then leaves its position; the focal elephant takes up the vacant position	Other
Displaced	Focal elephant moves from its position as another elephant approaches it; the other elephant then takes up the vacant position	Other
Keeper interaction	Interacting with a keeper	Keeper Interaction
Not visible	Elephant or its behavior is not visible to the observer	Other
Other	Elephant engages in any behavior that does not meet the above behaviors	Other

might vary with location on- or off-exhibit due to differing thermal properties of the enclosures, an interaction between these terms was included. Hour-long sessions were clustered by elephant and assigned the exchangeable covariance structure in which the parameter α describes the correlation between two sessions from the same elephant [Zuur et al., 2009].

We applied an information-theoretic approach to our analysis, using information criteria to evaluate the importance of potential models and variables [Burnham and Anderson, 2002]. This approach provides a formal theoretic framework for model selection absent from stepwise-

selection methods that use significance-testing of null hypotheses. Rather than assessing significance via p -values, a model or variable's importance is assessed via Akaike weights, parameter estimates and 95% confidence intervals [Burnham and Anderson, 2002].

All subsets of the global GEE model that included both the interactions between time of day and location and between location and temperature were evaluated, resulting in 12 candidate models. Support was assessed using QIC (quasilikelihood under the independence model criterion) with a lower QIC indicating a more parsimonious model [Pan, 2001]. Akaike's Information Criterion (AIC) cannot be

used with the non-likelihood based GEE. The difference, Δ_i , between each model's QIC and the best model's QIC were used to calculate Akaike weights, w_i [Burnham and Anderson, 2002]. These weights ($0 \leq w_i \leq 1$) estimate the relative likelihood that a given model is the "best" among the models considered.

Model validation was visually assessed for the global model by plotting Pearson residuals against fitted values and against each predictor variable [Zuur et al., 2009]. Plotting against fitted values indicated poor model fit with significant positive skew. While this pattern could be due to negative residuals having a lower magnitude due to the imposed lower boundary of zero for a session (i.e., a negative value cannot be assigned to repetitive behavior), positive residuals often exceeded two standard deviations from zero.

Another possible cause for the strong positive skew observed in the GEE residuals could have been excessive zeroes in the data. We therefore repeated our analysis using a zero-inflated, negative-binomial (ZINB) model with the number of repetitive behavior observations per session as our response. We included the same predictor variables as in the global GEE model.

The model fitted by the ZINB takes the form of:

$$E(Y_i) = \mu_i * (1 - \pi_i) = \left([e]^{\alpha + \beta_1 * x_{i1} + \dots + \beta_n * x_{in}} \right) * \left(1 - \frac{e^v}{1 + e^v} \right), \text{ and}$$

$$var(Y_i) = (1 - \pi_i) * \left(\mu_i + \frac{\mu_i^2}{k} \right) + \mu_i^2 * (\pi_i^2 + \pi_i),$$

where $E(Y_i)$ is the expected number of repetitive observations during session i and $var(Y_i)$ is the variance for that session. α indicates the intercept, β is the coefficient for its respective predictor variable, and v represents the intercept for the zero-inflation portion of the model. For $var(Y_i)$, k equals the dispersion parameter, \emptyset .

Model selection for the global model and all its subsets proceeded by obtaining AIC values corrected for sample size (AIC_c) and using them to assign Akaike weights. We next applied model averaging to account for the large amount of model uncertainty present in our data [Burnham and Anderson, 2002]. First, a 95% confidence set of models was

selected by summing w_i starting with the top model until cumulative weight was ≥ 0.95 . Weights were then renormalized for this model subset. Parameter estimates for each model were multiplied by these weights and summed across all included models to obtain a single, model-averaged estimate for each predictor variable. An unconditional variance estimator was used to calculate 95% confidence intervals [Burnham and Anderson, 2002]. Each variable's strength of support (i.e., the likelihood it should be included in the best model) was obtained by summing the Akaike weights of each model in which it was included [Burnham and Anderson, 2002]. Models including an interaction term were not counted towards the overall support for the individual variables making up that interaction.

Residual plots for the global ZINB model indicated a greatly improved fit compared to the GEE. However, the ZINB prevented us from including a covariance structure to account for non-independence between sessions from the same elephant. Additionally, since we used repetitive behavior counts rather than the proportion of behavior per session, an additional source of autocorrelation may have been introduced [Martin and Bateson, 1993]. We therefore decided to present results from both approaches. Analyses were carried out using the packages *geepack* [Højsgaard et al., 2006] and *pscl* [Zeileis et al., 2008; Jackman, 2012] in the statistical program R ver. 3.1.2 [R Core Team, 2014].

RESULTS

Activity Budget Overview

Individual activity budgets are provided in Table 3. All elephants displayed repetitive behavior to some extent with elephants 1 and 4 being observed most often engaging in these behaviors and elephant 5 performing them the least. Only 26 out of 1,359 instances of repetitive behavior involved another behavior being performed simultaneously. We are therefore confident that our scoring of these simultaneous occurrences as repetitive behavior did not bias our data. About a third to one-half of observations on each elephant involved foraging, divided amongst hay, browse, and other prepared foods, as well as grasses and

TABLE 3. Proportion of observations for each behavioral category out of all observations (mean (SD))

Elephants	Behavioral Categories								
	Self-maintenance	Foraging (Prepared)	Foraging (Exhibit)	Keeper interaction	Abiotic interaction	Locomotion	Repetitive behavior	Resting	Other
1♂	0.026(0.04)	0.303(0.38)	0.179(0.30)	0.028(0.10)	0.043(0.12)	0.042(0.04)	0.277(0.34)	0.086(0.10)	0.018(0.03)
2♀	0.038(0.07)	0.253(0.26)	0.236(0.30)	0.023(0.06)	0.019(0.03)	0.116(0.11)	0.125(0.18)	0.153(0.16)	0.036(0.09)
3♀	0.054(0.09)	0.274(0.29)	0.293(0.34)	0.019(0.05)	0.032(0.06)	0.106(0.10)	0.113(0.19)	0.058(0.10)	0.051(0.06)
4♀	0.035(0.05)	0.192(0.25)	0.154(0.20)	0.011(0.03)	0.041(0.08)	0.065(0.05)	0.267(0.28)	0.194(0.18)	0.041(0.07)
5♀	0.062(0.06)	0.113(0.16)	0.241(0.27)	0.033(0.10)	0.026(0.05)	0.099(0.06)	0.074(0.12)	0.289(0.20)	0.060(0.06)
6♀	0.055(0.06)	0.175(0.21)	0.179(0.25)	0.028(0.10)	0.045(0.10)	0.109(0.07)	0.127(0.18)	0.249(0.23)	0.033(0.04)

TABLE 4. GEE summary statistics

Coefficients	Estimate	Standard error	95%CI
Top model (83.7% support)			
Intercept	-1.607	0.221	(-2.04, -1.18)
Temperature	0.074	0.041	(-0.01, 0.15)
Scale parameter	0.421	0.087	(0.25, 0.59)
Correlation structure (exchangeable)	0.081	0.031	(0.02, 0.14)
Second-highest model (16.2% support)			
Intercept (Afternoon)	-1.240	0.261	(-1.75, -0.73)
Time of day (Morning)	-0.689	0.229	(-1.14, -0.24)
Scale parameter	0.413	0.066	(0.28, 0.54)
Correlation structure (exchangeable)	0.073	0.026	(0.02, 0.12)

shrubs found in the exhibits. Locomotion and resting behavior were also frequently observed.

Associations Between Repetitive Behavior and Captive Conditions

Generalized estimating equation (GEE) approach.

The top GEE model included only temperature as a predictor and was strongly supported based on its Akaike weight (Table 4). The second-highest model included only time of day and received some support (Table 4), while all other models had little support (<1%). According to the top model, the estimated repetitive behavior rate was 0.17 at the mean recorded temperature (i.e., the intercept) (Table 4). Each °C changed the repetitive behavior rate by ~0.01, with higher temperatures associated with increased rates. Over the observed temperature range (21–37°C), the estimated repetitive behavior rate ranged from 0.095–0.258. However, the 95% confidence interval for temperature provides insufficient evidence to conclude that a temperature effect truly exists (Table 4).

In the second-best model, the intercept represents afternoon conditions while the time of day parameter represents mornings (Table 4). Confidence intervals for both the intercept and parameter provide strong support that time of day influenced the frequency of repetitive behavior. Though elephants consistently performed repetitive behavior

throughout the day, they were less likely to engage in these behaviors in the morning compared to the afternoon (Table 5).

Zero-inflated negative binomial (ZINB) approach.

The 95% confidence set used for model averaging included the top seven out of 12 candidate models. Inclusion of the interaction between time of day and location in the “best” model was strongly supported (0.88 cumulative weight), with all other variables receiving far less support (0.017–0.117 cumulative weight). Model-averaged parameter estimates and associated confidence intervals are provided in Table 6. The intercept represents conditions off-exhibit in the afternoon and serves as a baseline to which other conditions are compared. The intercept’s confidence interval provides strong evidence that elephants on average engaged in repetitive behavior at a substantial rate during afternoons off-exhibit (Table 6). Additionally, the confidence interval for the interaction between time of day and location suggests these variables together influenced repetitive behavior rates (Table 6). Elephants on-exhibit in the morning performed fewer bouts of repetitive behavior compared to other times and locations (Table 5). Confidence intervals for all other variables included zero (Table 6). Repetitive behavior frequency did not vary over the course of the day when off-exhibit, nor did it differ comparing afternoons on-exhibit to

TABLE 5. Comparison of observed and expected proportions of repetitive behavior (mean ± SD)

GEE (based on the 2nd highest model)				
	Morning		Afternoon	
Observed	0.121 ± 0.211		0.220 ± 0.265	
GEE expected values	0.127 ± 0.214		0.224 ± 0.268	
ZINB (based on model-averaged estimates)				
	On-exhibit		Off-exhibit	
	Morning	Afternoon	Morning	Afternoon
Observed	0.045 ± 0.116	0.223 ± 0.285	0.214 ± 0.259	0.216 ± 0.219
ZINB expected values	0.082 ± 0.156	0.209 ± 0.384	0.173 ± 0.320	0.161 ± 0.299

TABLE 6. ZINB Model-averaged estimates

Count model coefficients	Estimate	Standard error	95%CI
Intercept (Afternoon, off-exhibit)	2.124	0.189	(1.75, 2.49)
Time of day \times location (Morning, on-exhibit)	-1.004	0.486	(-1.96, -0.05)
Temperature \times location (On-exhibit)	-0.005	0.013	(-0.03, 0.02)
Time of day (Morning)	0.068	0.261	(-0.44, 0.58)
Location (On-exhibit)	0.257	0.236	(-0.20, 0.72)
Temperature (Off-exhibit)	0.013	0.022	(-0.03, 0.06)
Log(θ)	0.179	0.229	(-0.27, 0.63)
Zero-inflation model coefficients	Estimate	Standard error	95%CI
Intercept	-0.318	0.183	(-0.68, 0.04)

off-exhibit conditions. Temperature also did not influence repetitive behavior performance, even in conjunction with location. Based on these model-averaged estimates, the expected proportion of time elephants engaged in repetitive behavior assuming 30 observations per hour are provided in Table 5.

The intercept from the zero-inflation portion of the ZINB provides the probability of a false zero for a session in which no repetitive behavior was recorded. No covariates were included in this model, since we were confident that behaviors were correctly classified as repetitive or otherwise during data collection and that repetitive behavior detectability during a session did not vary according to time of day or location. To calculate the probability of a false zero, π_i , the intercept, v , is used in the equation $\pi_i = e^v / (1 + e^v)$, yielding a probability of 0.42. This can be interpreted as for every hour-long observation session in which no repetitive behavior was recorded, there is a 42% chance that repetitive behavior actually occurred during that hour (e.g., between sampling instants). This probability was taken into account when calculating the expected values displayed in Table 5.

DISCUSSION

Assessing whether the repetitive behaviors we observed were indicative of distress or negative affective states is difficult. However, these conspicuous behaviors can be negatively perceived by the public and be a distraction from communicating education and conservation messages, even when their impact on welfare is negligible. Identifying factors associated with repetitive behaviors in order to potentially reduce their occurrence is helpful. As this study was strictly correlative and all six elephants had demonstrated some level of repetitive behavior prior to the study's initiation, any associations do not necessarily indicate these factors lead to formation of repetitive patterns. Rather, we seek to identify conditions associated with such behavior in animals predisposed to perform them.

The conclusions that can be drawn from the current work are somewhat limited by the nature of the available data. Observations were conducted only during daylight

hours. Since elephants are active at night [Wilson et al., 2006], our study did not capture true daily activity budgets. Additionally, any potential seasonal variation would not be captured by our study which took place entirely during the summer. Average temperature (\pm SD) was $29.77 \pm 3.24^\circ\text{C}$ with a vast majority of observations made during clear, sunny conditions. While seasonal differences in North Carolina are not as extreme as in more northern regions, lower winter temperatures might still influence elephant behavior [Rees, 2004]. Additionally, our observations might not be representative of these elephants' average activity budgets if their behavior was tracked over a longer period of time. Data collected from the prior year, however, suggested that this group's behavior remained largely consistent, though slight differences in collection methods prevented formal comparison. We also acknowledge the difficulty in attempting to draw solid conclusions from a sample size of six elephants at one zoo. Our results may only apply to our study group. Nevertheless, we believe our data and analyses offer potentially valuable insights for keepers and researchers working with elephants at other zoos.

Activity budgets were comparable to those seen in other captive elephant studies. Foraging took up on average a third to one-half of each elephant's time, which is within the range recorded by others [Stoinski et al., 2000; Rees, 2009; Horback et al., 2012]. One study observed wild African elephants foraging for three-quarters of the day [Wyatt and Eltringham, 1974], though data collected on wild elephants in Amboseli National Park in Kenya found frequencies of foraging behavior more comparable to our study group (35–70% of the day; [Poole and Granli, 2009]). Average time spent in locomotion was similar to that seen in other captive groups [Stoinski et al., 2000; Rees, 2009; Horback et al., 2012], but was markedly less than that seen in the Amboseli population (15–55%). Resting behavior was also frequently observed in our study group, though at a somewhat lower rate than that seen in Rees [2009] and Horback et al. [2012]. Elephants in Amboseli were reported to spend 3–15% of the day resting with an additional 5% standing still.

Studies compiling data on UK zoos found that repetitive behaviors are common in zoo elephants; however,

African elephants in those studies performed repetitive behaviors less frequently on average than did the elephants in the current study (6–15% for Asian elephants and 1–2% for Africans; [Clubb and Mason, 2002; Harris et al., 2008]). Rees [2009] observed generally lower levels of repetitive behavior in captive Asian elephants compared to our study group; he observed a few elephants never displaying repetitive behaviors, while the rest of the herd save one spent 4–9% of their time engaged in them. One individual in his study spent 29.4% of her time performing repetitive behaviors, potentially due to arthritis limiting her movement capabilities. Wilson et al. [2004] observed low frequencies of repetitive behaviors in a group of three captive African elephants, regardless of whether the animals were on- or off-exhibit; however, the frequency of these behaviors increased to 18% (range: 0–90%) prior to shifting the animals between areas. This increase was stronger in the afternoon compared to the morning. That same elephant group spent 3.5% of the time from 5 PM to 8 AM engaged in repetitive behaviors, the majority of which involved swaying [Wilson et al., 2006]. Peak periods of swaying accompanied movement of the animals into the barn, departure of the keepers at night, and arrival of the keepers in the morning. Koyama et al. [2012] observed one captive African elephant displaying high frequencies of stereotypic pacing (up to 31%), potentially in response to unfamiliar conditions and unpredictable time schedules.

Our findings suggest time of day in conjunction with location on- or off-exhibit best explain repetitive behavior patterns. Less repetitive behavior was seen on-exhibit in the morning compared to other times and locations. The increased repetitive behavior frequency observed in the afternoon on-exhibit could be related to depletion of prepared foraging materials. Prior to releasing elephants on-exhibit, these spaces were stocked with hay piles which were easily located and usually entirely consumed in the morning. Prior studies have documented negative links between food availability and stereotypic behavior in elephants [Friend and Parker, 1999; Rees, 2009]. However, elephants still readily foraged on vegetation growing in the exhibit throughout the day, suggesting repetitive behavior was unlikely to have been prompted by restricted foraging opportunities. A more likely alternative is that repetitive behaviors were an outward expression of anticipation for the evening transfer and feeding when elephants were brought off-exhibit and provided additional, potentially preferred, forage (e.g., hay, browse, produce), as well as the possibility of interacting with keepers and other elephants kept off-exhibit that day. While location within the exhibits was not systematically recorded in this study, elephants tended to remain near transfer areas during the late afternoon when repetitive activity became more prevalent.

Anticipatory behavior is often expressed prior to predictable events and has been observed in several captive species [elephants: Friend, 1999; Wilson et al., 2004; felids: Carlstead, 1996; minks: Vinke, 2004, 2006; dolphins: Jensen

et al., 2013]. These behaviors are often positive experiences for the animal when the predicted event is positive in nature [Spruijt et al., 2001; Watters, 2014]. In our study, increased repetitive behavior on-exhibit in the afternoon might have been anticipatory; if so, it would likely have enhanced the rewarding nature of the anticipated transfer and feeding [Badia et al., 1979; Bassett and Buchanan-Smith, 2007]. However, further observation and experimentation (e.g., manipulation of cues and/or timing of events) would be necessary to confidently establish these behaviors as anticipatory [Watters, 2014].

Some evidence has linked anticipatory behavior to stereotypy development [Bassett and Buchanan-Smith, 2007; but see Vinke, 2004, 2006] and some anticipatory behaviors consist of stereotypic patterns [Carlstead, 1996; Ulyan et al., 2006]. Even if the behaviors we observed were stereotypic in nature, however, assessing whether these behavior patterns represent a welfare concern in the absence of physiological data or other measures is problematic [Mason and Latham, 2004].

Elephants off-exhibit engaged in repetitive behaviors at a consistently elevated rate throughout the day. Motivations underlying repetitive behavior presumably differ between elephants located on- and off-exhibit. On-exhibit areas offered elephants greater ability to control their situation (e.g., regulating distance from conspecifics, seeking additional foraging opportunities). The larger on-exhibit spaces included more varied terrain, more options for shade, pools for submersion, as well as natural vegetation to forage on. In contrast, the off-exhibit paddocks consisted of sand and concrete surfaces. Foraging material consisted entirely of prepared diet items and hay provided by keepers with limited additional foraging opportunities available outside of these instances. An inability to address behavioral motivations could prompt increased occurrence of repetitive behavior [Mason and Latham, 2004; Morgan and Tromborg, 2007] and can contribute to the development of stereotypies [Bashaw et al., 2001]. However, given our study's limitations, assessing which factors contributed to the high rates of repetitive behavior observed off-exhibit is challenging.

Over the temperature range observed in our study, temperature appeared to have no effect on repetitive behavior frequency. Additionally, any potential effect would be confounded with time of day, as temperatures tended to be lowest in the morning and rise as the day proceeded. Colder temperatures have been associated with increased repetitive behavior in elephants [Rees, 2004]. If behavior was sampled in cooler months, it would be interesting to see if that association holds for this group and others.

Repetitive behavior can have multiple underlying causes [Carlstead, 1998; Clubb and Mason, 2002]. The observed patterns in our study could have been driven simultaneously by forage availability, timing of predictable events, and variation in exhibit size and complexity. In response to our study, a number of management changes have been made to the elephant collection at the North

Carolina Zoo. Off-exhibit areas have been fitted with overhead feeding poles from which are suspended a variety of feeding devices. We have also installed a series of feeding baskets containing puzzle feeders which require extensive manipulation in order for the elephants to extract food. In order to maximize the amount of time the elephants spend on the exhibit, elephant groups are now regularly left on-exhibit overnight. During the day, the number of training sessions for off-exhibit animals has been increased in order to provide an additional source of stimulation. In addition to these changes, we plan to introduce animals who are currently housed separately in order to increase the social complexity of individual elephant groups. This will have the added benefit of further increasing the amount of time each elephant spends on-exhibit. While systematic observation of the impact of these changes has not been possible, we believe our study represents a good example of how behavioral research can be employed to improve management of zoo animals.

CONCLUSIONS

1. Elephants performed repetitive behaviors less frequently on-exhibit in the morning as compared to other times and locations. Increased rates of repetitive behavior in these other contexts likely resulted from a) depletion of preferred foraging material and/or b) anticipation of the evening transfer and feeding.
2. Smaller, less complex spaces, or an inability to seek additional foraging opportunities may have contributed to the consistent levels of repetitive behavior observed off-exhibit throughout the day.
3. Despite support by the GEE, temperature likely did not influence repetitive behavior frequency over the temperature range observed in this study.

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