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Examination of enrichment using space and food for African elephants (Loxodonta africana) at the San Diego Zoo Safari Park

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Abstract

*Concern for elephant welfare in zoological facilities has prompted a number of exhibit and management modifications, including those involving enrichment. Knowledge of how these changes impact indicators of welfare, such as elephant movement and behaviour, is crucial for continued improvement of elephant husbandry and care. The present study used observations and GPS-collected data to determine the effects of available space and food presentation on the walking distance and behaviour of thirteen African elephants (*Loxodonta africana*), which had a dominance structure ascertained by animal care staff at the San Diego Zoo Safari Park (SDZSP). This facility has two exhibits of approximately equal size. Three treatments were created to assess the effects of food and space enrichment: (i) access to half of the exhibit with food (Half); (ii) access to the entire exhibit with food in one yard (Both/Half); and (iii) access to the entire exhibit with food in both yards (Both). For Half and Both/Half, food was presented in each yard for an equal number of trials. Significant differences across treatments were revealed for average total walking distances but this was not found between any two given treatments. Walking distance varied among elephants belonging to different dominance groups, with middle-ranked elephants taking the most advantage of a larger available space. Behaviour did not differ across treatments, but the change in behavioural diversity from one treatment to another was significant for subordinate elephants. The information obtained from this study has direct implications for the management of the SDZSP elephants and for other facilities looking to increase walking distance or subordinate behavioural diversity.*

Keywords: *African elephant, animal behaviour, animal welfare, enrichment, GPS technology, zoo studies*

Introduction

Zoological institutions housing elephants are working diligently to improve elephant management and care in accordance with current policies set by the Association of Zoos and Aquariums (Olson 2004; AZA 2012). An integral component of elephant welfare involves physical and mental stimulation through enrichment (AZA 2012). A recent multi-institutional study funded by the Institute of Museum and Library Services (IMLS) entitled 'Using science to understand zoo elephant welfare' collected various data measurements among 68 North American zoos. A plethora of information pertaining to elephant welfare has emanated from the IMLS project, including research on walking distances (Holdgate *et al* 2016b), recumbence behaviour (Holdgate *et al* 2016a), factors impacting foot and musculoskeletal health (Miller *et al* 2016), body condition scores (Morfeld *et al* 2016), reproductive health (Brown *et al* 2016), demographics (Prado-Oviedo *et al* 2016), stereotypic behaviour (Greco *et al* 2016a), and enrichment use (Greco *et al* 2016b). This multi-institutional study provides context to which detailed examinations of individual zoos and their elephants can be compared to assist with site-specific management assessments. This is especially valuable because variation in enrichment practices exist across zoos (Greco *et al* 2016b), and thus continued experimental analyses on the effects of enrichment are valuable and warranted.

The addition of enrichment into an exhibit area can increase behavioural choices for animals and encourage species-appropriate behaviours, ultimately enhancing their welfare (Laule 2003). According to AZA, enrichment is defined as "a dynamic process for enhancing animal environments within the context of the animals' behavioural biology and natural history" (Colbert 2010). Care must be taken in the creation of an enrichment programme as it can be costly, deplete resources, and/or not have a lasting benefit (Cipreste *et al* 2010). To be successful over the long term, programmes must also be variable and unpredictable to the animals of concern (Cipreste *et al* 2010). This is particularly important for elephants, as they are cognitively advanced (Bates *et al* 2008). Past enrichment studies with elephant subjects have examined the effects of enrichment diversity

(Greco *et al* 2016b), housing (Posta *et al* 2013), feeder balls (Rees 2009), water spray devices (Mellen *et al* 1981), and feeding (Stoinski *et al* 2000; Björk 2011; Posta *et al* 2013; Greco *et al* 2016b; Holdgate *et al* 2016b) on overall activity budgets, walking, animal visibility to zoo guests, and stereotypic behaviour (ie stereotypies, see Mason 1991). Physiological responses, such as female cycling (Brown *et al* 2016) have also been examined.

One of the more consistent forms of enrichment for elephants includes socialisation (Veasey 2006). Elephants display a high level of social complexity (Payne 2003). Within zoological institutions they are housed in a greater range of group sizes, ages, and degrees of relatedness than they would be in the wild (Schulte 2000). Elephants may interact with each other differently depending on their level of relatedness, animal density, and their place in the dominance hierarchy (Archie *et al* 2006). In zoos, dominance rank has been found to positively correlate with acyclicity, behavioural measures such as willingness to share preferred or novel objects (Freeman *et al* 2004), and aggression (Hambrecht & Reichler 2013).

Elephants cover vast distances in their native habitat when they need to access resources such as food, water, and shelter, to avoid threats (ie aggressive conspecifics, predators, or humans), and to locate conspecifics (Wittemyer *et al* 2007). Despite resources being regularly provided to elephants, Miller *et al* (2016) found that elephants in one zoo walked comparable distances to elephants in Botswana during the rainy season (9.82 and 8.65 km per day, respectively).

Activity levels in zoo settings may be altered by the manipulation of resources. Holdgate *et al* (2016b) found that elephants in larger enclosures did not walk longer distances than their counterparts did in smaller enclosures, but elephants did walk more when given a greater diversity of food and were fed on more unpredictable schedules. Movement is an important aspect to consider when managing elephants as numerous ailments, such as foot issues, arthritis, and obesity, are linked to a lack of exercise (Clubb & Mason 2003; Veasey 2006; Miller *et al* 2011). More active animals may also have enhanced appeal to zoo visitors as shown by Margulis *et al* (2003) with felids. However, it is important that movements and activity are species-appropriate and not stereotypic motions (Altman 1998), especially because zoos provide opportunities for people to view endemic and non-endemic animals up-close and inspire conservation of the natural world (Beardsworth & Bryman 2001). Miller (2012) found that guests who saw a video of a tiger engaging in the stereotypic behaviour of pacing were less likely to state that the tiger had good welfare, and thus less likely to support such a zoo, than guests who saw a video of an inactive tiger. Enrichment has been considered vital in reducing stereotypic behaviours and increasing overall animal welfare (Mason *et al* 2007), and its application in the form of space and food may encourage species-appropriate movement and behaviour (Dulong *et al* 2005).

The goal of the present study was to determine the effects of exhibit space availability and food distribution on thirteen African elephants (*Loxodonta africana*) at the San Diego Zoo Safari Park (SDZSP). To our knowledge, this is the first study to manipulate space and food simultaneously and then measure the responses of walking and elephant behaviour. Overall, the expectation was that elephants in the treatment with the greatest amount of space and most widely distributed food (termed 'Both') would exhibit the longest walking distances, with the largest behavioural measures (behavioural diversity and richness), and elephants in the treatment with the least amount of space and distributed food would exhibit the shortest walking distances and behavioural measures. Walking was expected to vary among elephants belonging to different dominance groups, as motivations for the movement of subordinate animals is likely impacted by those more dominant. Dominance was also predicted to affect behaviour across treatments, and between individuals.

Materials and methods

Study site and subjects

Data for the present study were collected between March and July 2014 at the SDZSP in Escondido, CA, USA (33.099703° N/113.001525° W). The elephant enclosure measured 2.23 hectares and consisted of two exhibits of approximate equal size that were dividable into east and west yards by a remote-controlled gate (for more details, see Andrews *et al* 2004). At the time of the present study, the herd included thirteen African elephants: four adults, one sub-adult, three juveniles, and five calves (for age determinations, see Loizi *et al* 2009), all managed via protected contact. General management protocols provided the elephants with varied access to the east yard, west yard, or both yards depending upon the keepers' and elephants' needs. For example, while the keepers cleaned the west yard, the elephants were housed in the east one. The elephants would then be shifted to the west yard while keepers cleaned the east one, and after cleaning the elephants could then be provided with both yards, split into family groups between the two yards, or housed together in one yard.

Design and procedure

Ethical statement

The methods outlined in this study were approved by the Institutional Animal Care and Use Committees (IACUC) of both the San Diego Zoological Society (#12-022) and Western Kentucky University (#13-06).

Treatments

The study design included five treatments, with two pairs of mirrored designs (Figure 1). Treatment Half-West provided access to the west yard of the exhibit with food throughout. Treatment Half-East, provided access to the east yard of the exhibit with food throughout. Treatment Both/Half-West provided the elephants with access to both yards and with food in only the west yard. Treatment Both/Half-East provided access to both yards with food in only the east

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Figure 1

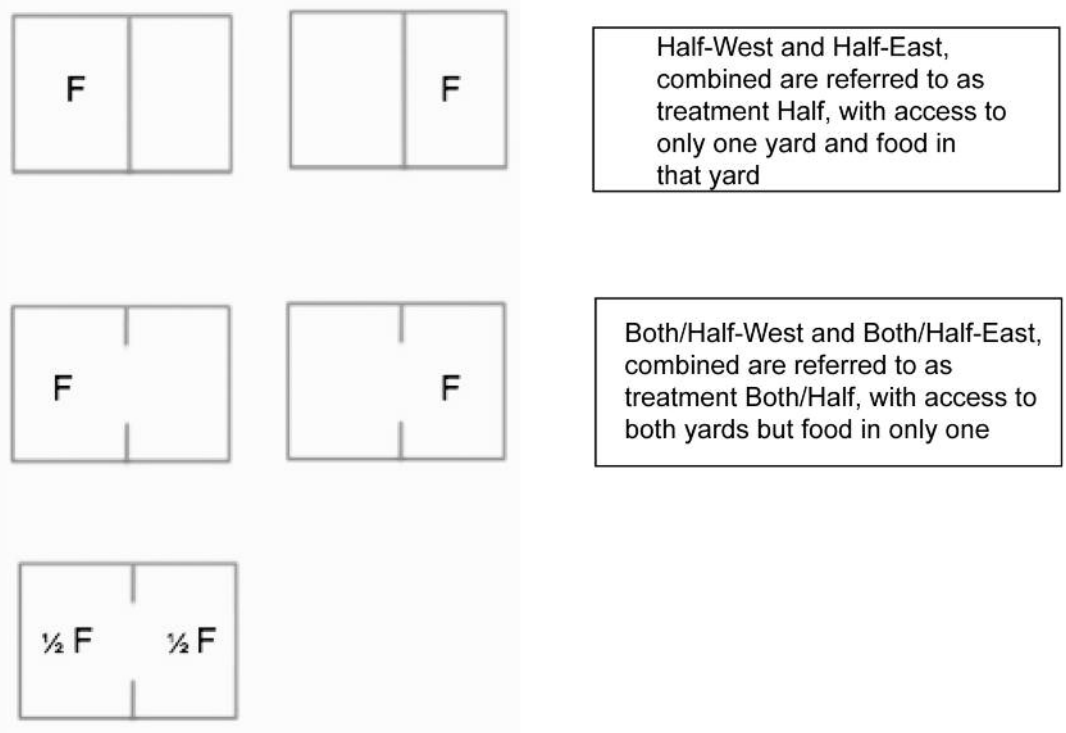

Exhibit treatments of space and food (F). The top row shows treatment Half-West (access to the west yard of the exhibit with food in that yard) and its mirrored counterpart, Half-East. The second row shows treatment Both/Half-West (access to both yards of the exhibit with food in the west yard) and its mirrored counterpart, Both/Half-East. The bottom row shows treatment Both (access to both yards of the exhibit with food in both). The ½ is to clarify that the same amount of total food (F) was used in treatment Both but was distributed over a greater area.

yard. Treatment Both provided access to both yards with food throughout (no mirrored treatment was possible). Treatments lasted for 22 h and started on various days of the week depending on the keepers' schedules until three trials of each treatment were completed. The order of treatments was selected randomly without replacement. Treatments ran from 1100h until the following day at 0900h. All 13 elephants were housed as one social group except from 1500 to 0800h in which the bull was housed in the west bull yard (all treatments) for standard management practices with male elephants to reduce prolonged interactions between sub-adult or adult males and female groups. The sub-adult male was housed in the opposing yard when the herd had access to only one yard (for example, for treatment Half-West, he was moved to the east yard to be kept overnight and *vice versa* for treatment Half-East) following similar management protocol.

Each trial started with four bales of Bermuda grass hay (*Cynodon dactylon*), two bales of Sudan grass hay (*Sorghum* × *drummondii*), and one cart of browse. To ensure consistency, the principle investigator on the project (CH), with occasional help from keepers, was responsible for setting food items prior to elephant access. Each bale weighed approximately 25 kg and all six were collectively distributed into 16 approximately equal piles throughout the pre-determined space for each treatment. Pile location and type (Bermuda, Sudan, Bermuda/Sudan mix) were recorded onto a Google Earth image of the elephant exhibit. One cart of browse occupying roughly 0.5 m^3 of space was then scattered equally throughout the same space as the hay piles. Browse generally consisted of woody plants from the genus *Ficus*, though some of the treatments involved bird-of-paradise (*Stelitzia reginae*) or panaceum (*Poganatherum panaceum*) due to reduced availability of *Ficus*. Supplemental food products were supplied at two different times. Celery (*Apium graveolens*), romaine lettuce (*Lactuca sativa* L var *longifolia*), cucumbers (*Cucumis sativus*) and alfalfa pellets (primary ingredient: alfalfa [*Medicago sativa*], San Diego Zoo Global Herb Supp Pits ½", Western Milling LLC, Gosen, CA, USA) were tossed into the exhibit space at 1500h (4 h into treatment) respective of where hay piles and browse were initially placed. One bale of Sudan hay was tossed into the exhibit the following morning at 0800h (21 h into treatment) respective of the yard or yards where hay piles and browse had initially been placed. No additional food was provided to the elephants for the 22-h duration of the study period.

Walking activity

A leather anklet (Excelsior Leather, Fallbrook, CA, USA) with Global Positioning System (GPS) technology was used to monitor walking distances. Both GPS collars and anklets have been used previously to study elephant movement and

behaviour (Theiss *et al* 2005; Leighty *et al* 2010; Miller *et al* 2011; Holdgate *et al* 2016b). Horback *et al* (2012) examined the effects of GPS collars on elephant behaviour at the SDZSP and found no behavioural differences. Since collars are bulkier and heavier than anklets, it was anticipated that GPS anklets would also reliably measure elephant movement. Four adults, one sub-adult, two juveniles, and one calf were conditioned to wear anklets. One keeper stationed the elephant while another secured the anklet. A GPS tracking unit (Qstarz BT-Q1000X, Taipei, Taiwan) was encased in a waterproof OtterBox™ (DryBox 1000, Fort Collins, CO, USA) and secured in a pouch in the middle of the anklet. The manufacturing company of the GPS units reported the devices to be accurate within 2.5 m. An earlier study found the units to be reliable except during severe weather (Miller *et al* 2011), which did not occur during the time-period of this study. Anklets were put on the elephants by 1100h the day of the trial and were removed soon after 0900h the following morning after collecting 22 h of data. Keepers inspected the elephants' ankles during a testing period prior to the start of the study to ensure the absence of any visible discomfort such as marks or sores caused by the GPS anklets. GPS location points were collected every 5 s and included time of day, co-ordinates, and related accuracy measures. The data were downloaded from the unit to a PC computer and opened using the GPS device's accompanying software (QTravel V1, Taipei, Taiwan). Data were revised by removing any points with fewer than six satellites in view or a horizontal position (HDOP) score greater than two to increase the accuracy of the data set (Holdgate *et al* 2016b).

Behaviour

Behavioural data were collected from 1100 to 1330h, 1430 to 1700h, and 0630 to 0900h the following morning culminating in a total of 6.5 h. Observations were recorded on a data sheet and included observing focal animals using continuous sampling (states) and all occurrence sampling (events) via an ethogram (see Appendix in the supplementary material to papers published in *Animal Welfare* on the UFAW website: https://www.ufaw.org.uk/the-ufaw-journal/supplementary-material) modified from the Elephant Husbandry Resource Guide (Olson 2004). Elephants were selected at random without replacement for order of observations. Each animal was observed for 10 min three times per trial for a total of 30 min per elephant per trial. Total time of observations for all elephants extended to 130 min per observation period and 390 min for each trial.

Dominance

Elephant care personnel who had worked with the elephants for time-periods ranging from one to eleven years ascertained the dominance order of the herd via a majority rules vote. A previous study at SDZSP corroborated the keepers' perception of dominance with behavioural data (Hacker *et al* 2015). Therefore, the decision was taken to use keeper knowledge as opposed to traditional time-consuming behavioural observations.

Data analysis

Euclidean distances between successive longitude and latitude readings measured at 5-s intervals were calculated from the GPS devices (Leighty *et al* 2010). The walking distances of each elephant for each of the three trials were summed and averaged into a value for each of the five treatments.

Behavioural data were examined by using rates for all occurrence event behaviours (frequency divided by total duration of focal length) (Martin & Bateson 2007). Since enrichment increases behavioural opportunities, enrichment effectiveness can be measured by behavioural diversity (Shepherdson 2010). The Shannon-Wiener index (S-W index) (Shannon & Weaver 1949) is a diversity index used in ecology that has been modified for animal behaviour with nocturnal mammals (Clark & Melfi 2011) and small cats (Shepherdson *et al* 1993). This modified S-W index (Stokke & Du Toit 2002) was used to assess elephant behavioural diversity with the equation:

$$\text{S-W Index} = -\Sigma\,[(p_i)\ln(p_i)];$$

where p_i is a proportion of the number of times an event behaviour was performed divided by the total number of event behaviours observed, and Σ is the sum of those proportions. The larger the resulting value, the greater the diversity of behaviour displayed. Richness refers to the number of different event behaviours witnessed by the observer from the constructed ethogram. Richness was converted into a rate per minute to account for time an elephant was not visible. For example, an elephant in view for the entire 10-min observation may show an increased variety of behaviours to those in view for 2 min. Behavioural richness rate was examined with the equation:

$$\text{Richness rate} = p_i/\text{time visible};$$

where p_i is the number of event behaviours observed out of the number of behaviours possible divided by time visible. Evenness reflects the distribution of behaviours and was calculated using the equation:

$$\text{Evenness} = \text{S-W Index}/\ln(r);$$

where behavioural diversity was divided by the natural logarithm of the number of different completed behaviours. Evenness scores range from 0 to 1, with 0 indicating that a behaviour was witnessed by the observer many more times over any other behaviour, and 1 indicating that each behaviour was viewed the same number of instances. This score allows for investigation of the impact of each treatment on how often behaviours are completed. Behavioural diversity, richness rate, and evenness for each of the three trials for each elephant were averaged to produce one value for each of the five treatments.

SPSS (version 21.0, Chicago, IL, USA) was used for all statistical tests. Non-parametric tests were used when assumptions for parametric tests were not met (ie small sample size, unevenly distributed data, non-independent data). To ensure that treatments Half-West and Half-East as well as Both/Half-West and Both/Half-East could be

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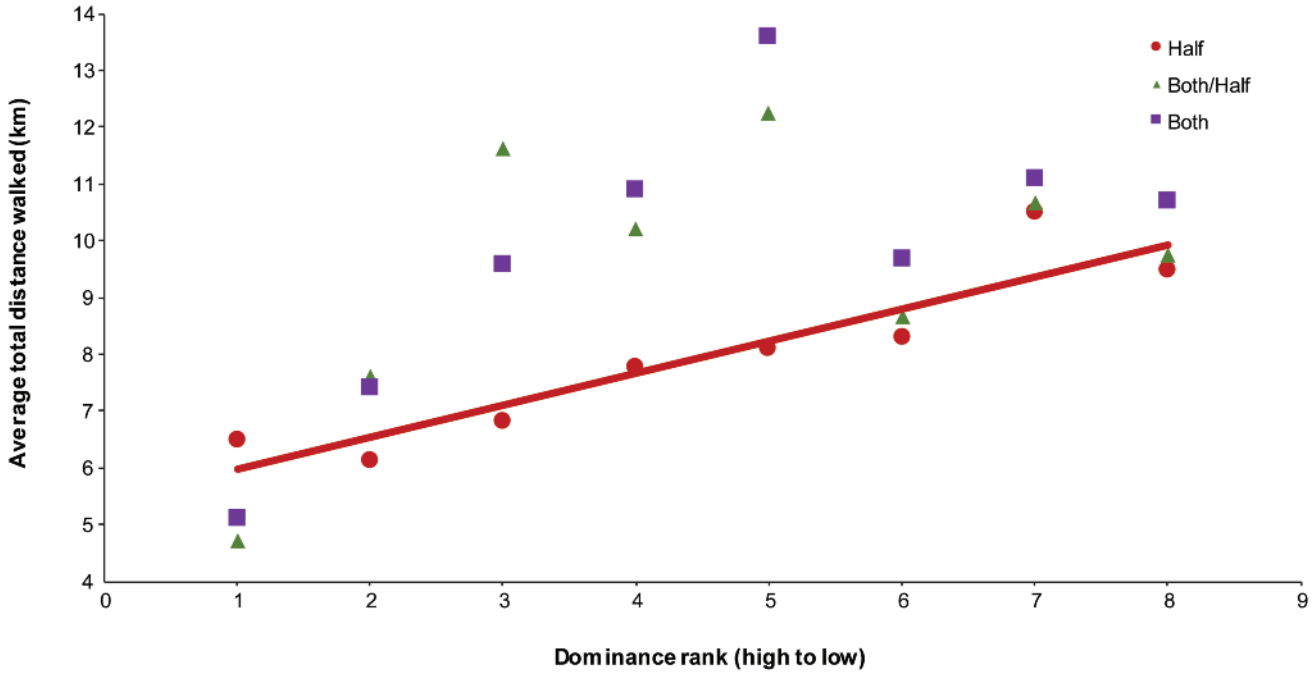
Figure 2



The total average distance walked relative to the rank of the elephant from most to least dominant for each of the three treatments. The red line is representative of treatment Half.

combined into one group, a paired Wilcoxon rank sum test was completed to confirm no significant differences. This allowed for their combination (average total walking distance: $P = 0.78$ and $P = 0.33$; average behavioural diversity: $P = 0.70$ and $P = 0.65$; average behavioural evenness: $P = 0.59$ and $P = 0.74$; average behavioural richness rate: $P = 0.48$ and $P = 0.78$), yielding three treatments for analysis. A Friedman's test was performed to assess the variation in average total distance walked, average behavioural diversity, evenness, and richness rate. A Pearson correlation was used to investigate the relationships between dominance and behavioural diversity as well as dominance and total distance walked. A Spearman's *rho* was used to investigate possible relationships between dominance and richness rate. A Pearson correlation was used to examine changes in behavioural diversity between any two given treatments for each elephant and dominance. Since age is reflective of dominance in elephants, a '1' was coded for adults and a '0' for the remaining elephants to control for age.

Results

Walking distance

Walking distances varied significantly across treatments for GPS-wearing individuals (n = 8, df = 2, $\chi^2 = 7.75$; $P = 0.02$). However, pair-wise comparisons showed no significant differences (Half and Both/Half; $P = 0.07$, Half and Both; $P = 0.07$, Both/Half and Both; $P = 0.21$). The mean (± SEM) total walking distance for treatment Both was 9.77 (± 0.90) km (range 4.45 to 17.4 km), for Both/Half, a mean of 9.45 (± 0.85) km (range 3.80 to 15.46 km), and for treatment Half an average of 7.96 (± 0.53) km (range 5.57 to 12.01 km).

Behavioural diversity (S-W Index)

Behavioural diversity did not vary significantly across treatments (n = 13, df = 2, $\chi^2 = 5.69$; $P = 0.06$) for all animals. The mean (± SEM) behavioural diversity for treatment Both was 1.84 (± 0.51) (range 1.59 to 2.11), for Both/Half, 1.79 (± 0.50) (range 1.43 to 2.01), and for treatment Half 1.75 (± 0.48) (range 1.56 to 1.94).

Behavioural richness rate

Richness rate did not vary significantly across treatments (n = 13, df = 2, $\chi^2 = 0.45$; $P = 0.80$) for all animals. The mean (± SEM) richness rate for treatment Both was 1.18 (± 0.05) behaviours per minute (range 0.98 to 1.51), for Both/Half a mean of 1.15 (± 0.08) behaviours per minute (range 0.84 to 1.41) and for treatment Half, a mean of 1.13 (± 0.37) behaviours per minute (range 0.93 to 1.34).

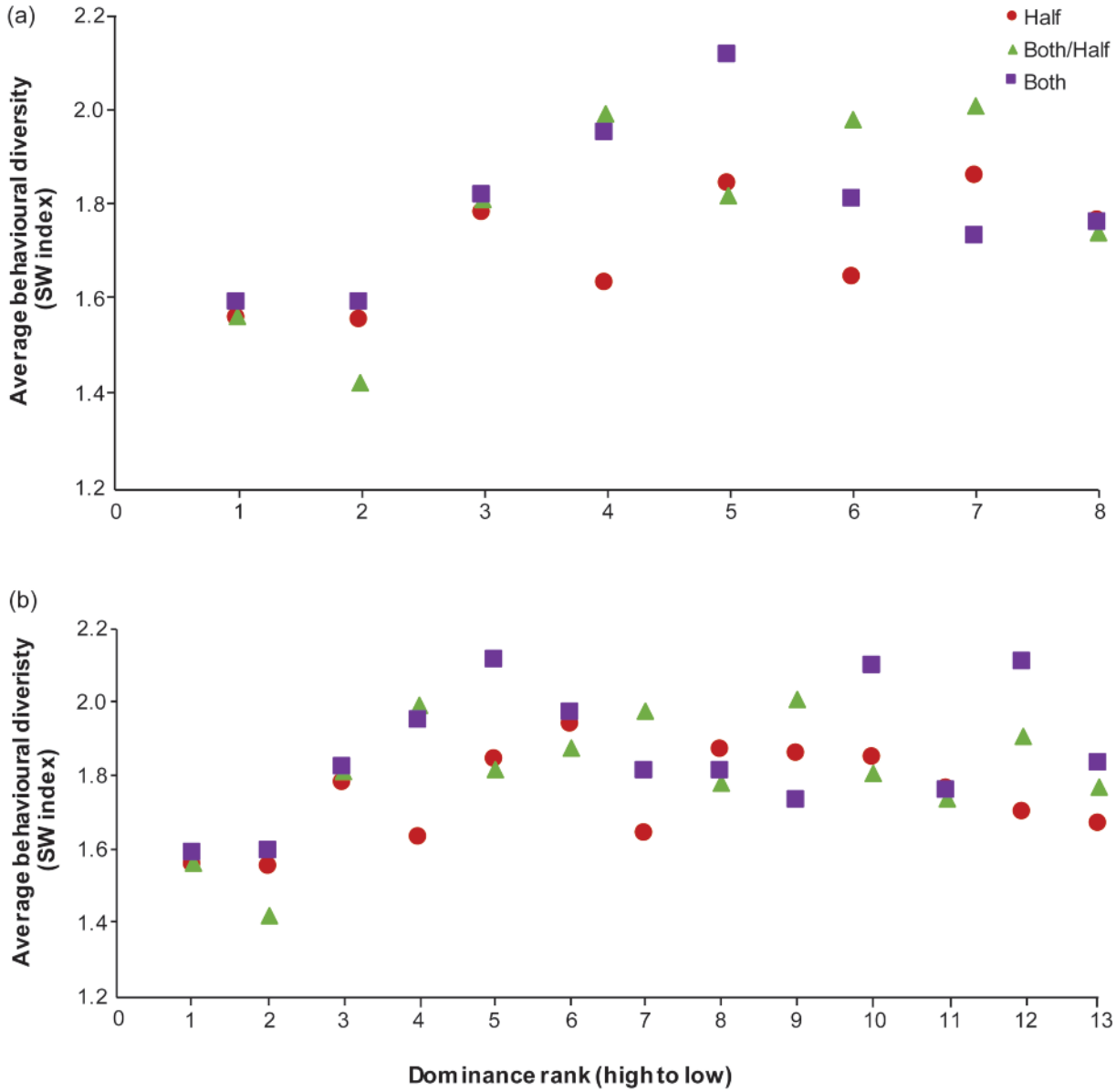
Behavioural evenness

Evenness did not vary significantly across treatments (n = 13, df = 2, $\chi^2 = 0.46$; $P = 0.79$) for all animals. Treatment Both had a mean (± SEM) of 0.81 (± 0.01) (range 0.71 to 0.90), treatment Both/Half had a mean of 0.82 (± 0.02) range (0.68 to 0.87), and treatment Half had a mean of 0.80 (± 0.01) (range 0.74 to 0.86).

Dominance and total distance walked

For the eight elephants outfitted with GPS devices, dominance and average total distance walked showed a significantly positive correlation with treatment Half ($P = 0.001$; $R = 0.92$), but not for treatment Both/Half ($P = 0.18$; $R = 0.53$) or treatment Both ($P = 0.06$; $R = 0.69$) (Figure 2). Three elephants in the middle of the hierarchy

Figure 3



Showing (a) the average behavioural diversity relative to the rank of the elephant from most to least dominant for each for the three treatments for the eight elephants equipped with GPS anklets and (b) the average behavioural diversity relative to the rank of the elephant from most dominant to least dominant for each of the three treatments for all 13 elephants.

were removed from analysis after it was determined these data may be heavily influencing the correlation. Dominance and average total distance walked were significantly correlated for treatment Half (P = 0.03; R = 0.87), treatment Both/Half (P = 0.02; R = 0.90), and treatment Both (P = 0.01; R = 0.94).

Dominance and behavioural diversity (S-W Index)

Dominance and behavioural diversity were not significantly related for treatments Half (P = 0.34; R = 0.29), Both/Half (P = 0.15; R = 0.42), or Both (P = 0.18; R = 0.40) for all animals. As a result of the impact of the three GPS-wearing animals on walking, it was elected to additionally run analyses with only the GPS-wearing animals to better tease out any other unexpected patterns in the data sets surrounding behaviour. For the eight elephants with GPS anklets, dominance and behavioural diversity were again not significantly related for treatments Half, Both/Half and Both (P = 0.15; R = 0.56, P = 0.11; R = 0.61 and P = 0.37; R = 0.36, respectively) (Figure 3).

Dominance and behavioural richness rate

Dominance and behavioural richness rate were significantly positively correlated for treatment Both/Half (P = 0.02; R = 0.30) but not for treatments Half (P = 0.10; R = 0.38) or Both (P = 0.16; R = 0.30) for all animals. There were no significant relationships between behavioural richness rate and dominance for data pertaining to

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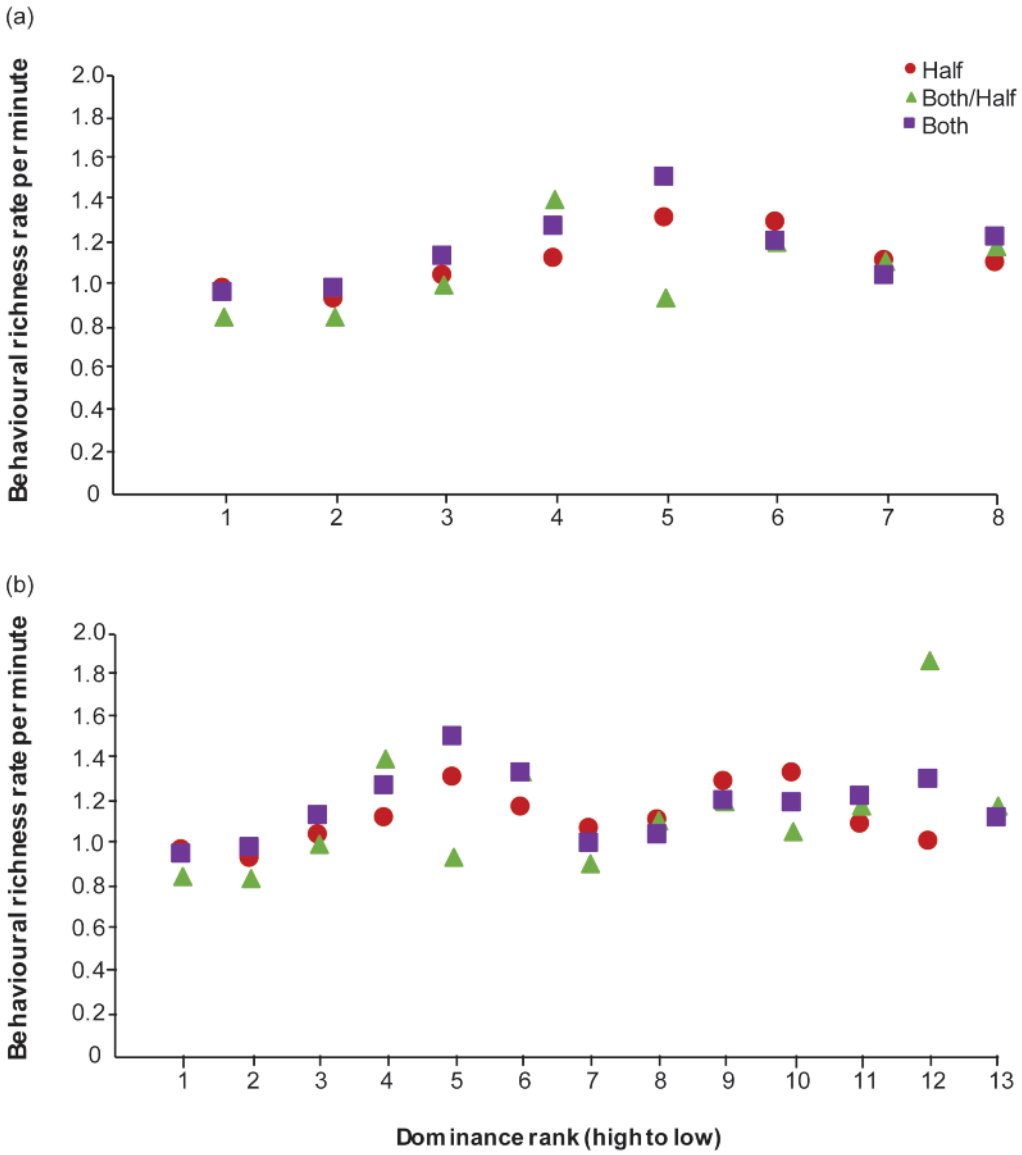
Figure 4



Showing (a) the average behavioural richness rate relative to the rank of the elephant from most to least dominant for each of the three treatments for the eight elephants equipped with GPS anklets and (b) the average behavioural richness rate per minute relative to the rank of the elephant from most dominant to least dominant for each of the three treatments for all 13 elephants.

only those elephants wearing GPS anklets for treatments Half, Both/Half, and Both ($P = 0.08$; $R = 0.57$, $P = 0.06$; $R = 0.62$, $P = 0.10$; $R = 0.52$) (Figure 4).

Dominance and differences in behavioural diversity (S-W Index)

The difference in behavioural diversity between treatments Half and Both was significantly positively correlated with dominance ($P = 0.002$; $R = 0.80$) for all animals. No significant correlations between treatments Half and Both/Half and between treatments Both/Half and Both with dominance ($P = 0.518$; $R = 0.207$ and $P = 0.927$; $R = 0.030$, respectively) for all animals.

Discussion

For the 13 elephants housed at the SDZSP, walking distances and behavioural values were predicted to be greatest when both space and food distribution were greatest. Walking varied significantly across treatments indicating that space and food did impact elephant movement; however, no pairwise comparisons were significant as a potential result of small sample size. Differences in behavioural diversity between treatments Half and Both were significantly correlated with dominance, suggesting that subordinate animals may benefit from the combination of increased physical space without an increase in food distribution. Although not

statistically significant, behavioural diversity and richness rate were lowest in treatment Half and highest in treatment Both while behavioural evenness was highest in treatment Both/Half and lowest in Both.

Walking distances of zoo elephants are increasingly being used as an indicator of welfare. The elephants in the current study walked an average of 9.06 km in a 22-h period. Leighty *et al* (2010) reported an average of 3.68 km walked over a 9-h period at Disney's Animal Kingdom. Holdgate *et al* (2016b) collected data from African elephants across zoological institutions and calculated an average of 5.4 km walked over a 24-h period. A previous study at the SDZSP by Miller *et al* (2011) reported an average of 8.65 km walked over a 24-h period, comparable to the current study at the same facility albeit with a somewhat different composition of elephants. In the current study, a significant difference in average total walking distance was determined across treatments, but not between any two treatments. This may be due to a lack of statistical power given the sample size, or due to dominance-related factors discussed later. However, walking distances for treatments Both/Half and Both were closer to one another than either was to treatment Half where elephants had access to only half of the exhibit with food throughout, indicating that the increased space may have encouraged walking. When placed in a larger enclosure at Disney's Animal Kingdom, the females of the largest social grouping walked significantly more than when in the smaller exhibits (Leighty *et al* 2010). These results contrast with the IMLS elephant study, which found that space was not the most significant predictor to overall walking distances and negatively correlated with night-time walking distances (Holdgate *et al* 2016b). However, that particular study compared walking across institutions; not within the manipulated space of the same institution.

Food distribution did not appear to influence walking. This was surprising as distance walked in the wild is dictated primarily by food availability (Merz 1986; Whyte 1996). However, food items may not have been far enough apart to significantly impact walking distances such as they can be in the wild. Similarly, Holdgate *et al* (2016b) were unable to find a correlation between how often food was spread throughout an exhibit and walking distances. The longer overall distances walked observed in treatments Both/Half and Both relative to Half could be due to the elephants' motivation to use the secondary resources and exhibit features in the opposing yard. For example, in treatments where elephants had access to both yards, an additional pool was available. Further investigation into space use may reveal effects of food distribution not evident in the present study.

A recent use of the S-W index was in the form of an Enrichment Diversity score calculated for the IMLS elephant study (Brown *et al* 2016; Greco *et al* 2016a,b; Holdgate *et al* 2016a,b; Meehan *et al* 2016). However, the S-W index had yet to be used in the context of elephant behaviour until this study. The S-W Index was used to examine behavioural diversity for treatments Half, Both/Half, and Both (1.75, 1.79, and 1.84, respectively) but there was no difference in behavioural diversity among treatments. Behavioural richness rates (1.13, 1.15, and 1.18 different behaviours per minute, respectively) also failed to distinguish any treatment effect. Evenness assessed the frequency of each behaviour observed, contributing to an overall distribution of behaviours (0.80, 0.82, 0.71, respectively) but, again, elephants did not differ significantly in the evenness of their displayed event behaviours across treatments. The management at SDZSP did not target any specific behaviours that they wanted to see increased or curtailed by the elephants in our study. Thus, the absence of differences in evenness among treatments indicates that neither space nor food distribution was limiting the evenness of behaviours. At SDZSP or other facilities, aligning enrichment with a targeted behavioural repertoire would be expected to elicit a different distribution of behaviours (ie a change in evenness).

Subordinate elephants give up valuable resources and space to those more dominant to avoid conflicts both in the wild (Wittemyer & Getz 2007) and in zoos (Leighty *et al* 2010). Social structures in zoos vary from those in the wild but dominance hierarchies still exist (Schulte 2000). In this study, dominance and average total walking distance were significantly related in treatment Half in that higher-ranking individuals had lower walking distances. A relationship between walking and dominance was not apparent for treatments Both/Half where elephants had access to both exhibits but food only in one side, or Both where elephants had access to both exhibits with food in each exhibit. However, three elephants in the middle of the hierarchy walked more in treatments Both/Half and Both than their conspecifics and this appeared to be skewing the correlations. When statistical analyses were repeated without those three elephants, walking and dominance were significantly correlated for all treatments. Increased space may not have had the same effect on walking for all of the elephants in this study. Rather, the elephants in the middle of the hierarchy appear to have taken the most advantage of a larger space. Dominance rank is known to influence space use (Murray *et al* 2007). In pigs, aggressive interactions and displacements decreased when there were lower densities of individuals presumably because subordinate animals could better control their proximity to dominant animals (Bryant & Ewbank 1972). Dominant animals are able to occupy areas of their choosing. Higher-ranking female chimpanzees (*Pan troglodytes*) outcompeted their subordinates for smaller spaces with better resources (Murray *et al* 2007). In the present study, walking for the elephants in the middle of the hierarchy appeared to be less influenced by dominance when given a larger space. However, space may not have been the main or only determinant of walking distances. The three elephants consisted of a sub-adult male, his mother, and an unrelated female. The male was actively pursuing the unrelated female during two Both trials. The unrelated female may have been in oestrus, prompting pursuit by the male and his mother as she tried to stay with her offspring. However, this activity was not noted during treatment Both/Half and therefore does not explain the increased walking found therein.

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In the present study, there was no relationship between overall behavioural diversity and dominance. Dominance and richness rate were not significantly correlated for treatments Half or Both but they were for Both/Half. Another significant finding was the relationship between change in behavioural diversity from treatment Half to treatment Both and dominance in that more subordinate animals experienced a greater increase in behavioural diversity. Additional exhibit features accompanied by the wider distribution of valuable food resources may have encouraged behaviours from subordinates which otherwise would not have used those features because a dominant animal was nearby or already doing so. The Greco *et al* (2013) study at the SDZSP assessed social learning using an experimental apparatus and indicated that the most dominant member of the herd was selected by the researchers because of the subordinate animals' likely apprehension to use the device in this elephant's presence. Similarly, the presence of nearby dominant animals in treatment Half because of a smaller space may have evoked hesitation to engage in particular behaviours on the part of the more subordinate animals.

Elephants that had not been previously exposed to larger spaces and/or more widely distributed food may show more significant differences in behaviour. The elephants at the SDZSP have had access to both or either side of their exhibit space since 2010, and were presumably accustomed to the space and the resources found within. Repeating this study with elephants being introduced into a larger space with or without more widely distributed food for the first time, or after a long interval of time, may show more changes in behaviour due to the novelty of the space. Posta *et al* (2013) noted that the largest change in elephant behaviour and walking came from access to an outdoor exhibit that was used less frequently during the winter months. If deemed necessary in the future, changes in behaviour may have to be induced using other enrichment strategies for the elephants at the SDZSP.

Direct outputs, such as walking distances and various behavioural measures, along with their relation to dominance, are meaningful for evaluating the success of enrichment. The present study showed that a larger exhibit space and a wider distribution of food delivered some benefits. Subordinate animals increased their behavioural diversity when food was spread throughout the larger available space, indicating that both greater space and food distribution are important for increasing behavioural diversity as measured by the S-W index. To our knowledge, this study is the first application of the S-W index to elephant behaviour. The above-mentioned result confirms the success of this measure as an added tool for assessing enrichment efficacy. Benefits were also found in the form of increased walking distances. However, it is unclear statistically whether increased space or a wider distribution of food was most beneficial due to the small sample size of the study population. Middle-ranked individuals took the most advantage of the increased space in regards to distance walked, but this interaction between walking and dominance may not translate to elephant groups at other facilities. It should be noted that a smaller exhibit may still encourage walking with a dynamic enrichment programme. For example, Hodgate *et al* (2016b) found that elephants fed on unpredictable schedules and elephants provided with various delivery methods (ie browse, puzzle feeders, hanging food items, floor feeding) walked more than those fed at predictable times or with only floor or trough feeding. It is suggested that zoos looking to increase walking should try the manipulation of both food and space, and take additional measures to tease out the potential benefits such as improvement in body index scores (Morfeld *et al* 2016), reproductive success (Carlstead & Shepherdson 1994), or more positive human-animal relationships (Hosey 2008). Projection of the current study at other facilities would aid in clarifying the weight of benefits for increased space or increased food distribution. Through experimental studies, more can be learned about the value of management and enrichment practices to enhance the welfare of elephants and other animals housed at zoological facilities.

Animal welfare implications and conclusion

This study investigated the effects of enrichment changes on elephant welfare by manipulating space and food and subsequently measuring elephant walking distances and behaviour. Increased walking distances for middle-ranked elephants, along with a significant correlation between the change in behavioural diversity among treatments Both and Half as well as dominance ranking indicates that food and space do impact both elephant walking and behaviour in this population. However, the importance of space relative to food, particularly with respect to walking distances, remains unclear. Dominance also appears to play a prominent role in the degree of change observed. While these data may not be generalisable to all facilities, the knowledge obtained herein could be used as a baseline for other facilities looking to increase elephant welfare.

Broader implications include improved enrichment programme planning across facilities housing elephants and the continued use of the Shannon-Wiener index as a tool for assessing behavioural diversity in elephants and other animals.

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References

Altman JD 1998 Animal activity and visitor learning at the zoo. *Anthrozoös 11*: 12-21. https://doi.org/10.2752/089279398787000869

Andrews J, Mecklenborg M and Bercovitch FB 2004 Milk intake and development in a newborn captive African elephant (*Loxodonta africana*). *Zoo Biology 24*: 275-281. https://doi.org/10.1002/zoo.20048

Archie EA, Moss CJ and Alberts SC 2006 The ties that bind: genetic relatedness predicts and fission and fusion of social groups in wild African elephants. *Proceedings of the Royal Society of London B273*: 513-522. https://doi.org/10.1098/rspb.2005.3361

Association of Zoos and Aquariums 2012 *AZA standards for elephant management and care*. https://www.aza.org/uploadedFiles/Conservation/Commitments_and_Impacts/Elephant_Conservation/ElephantStandards.pdf

Bates LA, Poole JK and Byrne RW 2008 Elephant cognition. *Current Biology 18*: 544-546. https://doi.org/10.1016/j.cub.2008.04.019

Beardsworth A and Bryman A 2001 The wild animal in late modernity: the case of the Disneyization of zoos. *Tourism Studies 1*: 83-104. https://doi.org/10.1177/146879760100100105

Björk K 2011 *The effect of extra feed supply on stereotypic behaviour in Asian elephants (*Elephas maximus*)*. Bachelor's thesis, Linköping University, Linköping, Sweden

Brown JL, Paris S, Prado-Oviedo NA, Meehan CL, Hogan JN, Morfeld KA and Carlstead K 2016 Reproductive health assessment of female elephants in North America zoos and association of husbandry practices with reproductive dysfunction in African elephants (*Loxodonta africana*). *PLoS One 11:* e0145673. https://doi.org/10.1371/journal.pone.0145673

Bryant MJ and Ewbank R 1972 Some effects of stocking rate and group size upon agonistic behaviour in groups of growing pigs. *The British Veterinary Journal 128*: 64-50. https://doi.org/10.1016/S0007-1935(17)37133-6

Carlstead KC and Shepherdson D 1994 Effects of environmental enrichment on reproduction. *Zoo Biology 13*: 447-458. https://doi.org/10.1002/zoo.1430130507

Cipreste CF, de Azevedo CS and Young RJ 2010 How to develop a zoo-based environmental enrichment program: incorporating environmental enrichment into exhibits. In: Kleiman D, Thompson K and Baer C (eds) *Wild Mammals in Captivity* pp 171-180. University of Chicago Press: Chicago, USA

Clark FE and Melfi VA 2011 Environmental enrichment for a mixed-species nocturnal mammal exhibit. *Zoo Biology 29*: 1-17

Clubb R and Mason G 2003 *A Review of the Welfare of Zoo Elephants in Europe*. University of Oxford: Oxford, UK

Colbert D 2010 *Enrichment.* Association of Zoos and Aquariums. www.aza.org/enrichment/

Dulong C, Graham S, Huffman B, Lympany B, Tabone G and Ward J 2005 *Suggested guidelines for captive elephant enrichment.* AAZK. https://www.aazk.org/wp-content/uploads/Suggested-Guidelines-for-Captive-Elephant-Enrichment.pdf

Freeman EW, Weiss W and Brown JL 2004. Examination of the interrelationships of behaviour, dominance status, and ovarian activity in captive Asian and African elephants. *Zoo Biology 23*: 431-448

Greco BJ, Brown TK, Andrews JRM, Swaisgood RR and Caine NG 2013 Social learning in captive African elephants. *Animal Cognition 16*: 459-469. https://doi.org/10.1007/s10071-012-0586-7

Greco BJ, Meehan CL, Hogan JN, Leighty KA, Mellen J, Mason GJ and Mench, JA 2016a The days and nights of zoo elephants: Using epidemiology to better understand stereotypic behaviour of African elephants (*Loxodonta africana*) and Asian elephants (*Elephas maximus*) in North American zoos. *PLoS One 11*: e0144276. https://doi.org/10.1371/journal.pone.0144276

Greco BJ, Meehan CL, Miller LJ, Shepherdson DJ, Morfeld KA, Andrews J, Baker AM, Carlstead K and Mench JA 2016b Elephant management in North American zoos: environmental enrichment, feeding, exercise, and training. *PLoS One 11*: e0152490. https://doi.org/10.1371/journal.pone.0152490

Hacker CE, Horback KM and Miller LJ 2015 GPS technology as a proxy tool for determining relationships in social animals: An example with African elephants. *Applied Animal Behaviour Science 163*: 175-182. https://doi.org/10.1016/j.applanim.2014.12.005

Hambrecht S and Reichler S 2013 Group dynamics of young Asian elephant bulls (*Elephas maximus* Linnaeus, 1758) in Heidelberg Zoo – integration of a newcomer in an established herd. *Der Zoologische Garten 82*: 267-292. https://doi.org/10.1016/j.zoolgart.2014.01.003

Holdgate MR, Meehan CL, Hogan JN, Miller LJ, Rushen J, de Passillé AM, Soltis J, Andrews J and Shepherdson DJ 2016a Recumbence behaviour in zoo elephants: determination of patterns and frequency of recumbent rest and associated environmental and social factors. *PLoS One 11*: e0153301. https://doi.org/10.1371/journal.pone.0153301

Holdgate MR, Meehan CL, Hogan JN, Miller LJ, Soltis J, Andrews J and Shepherdson DJ 2016b Walking behaviour of zoo elephants: associations between GPS-measured daily walking distances and environmental factors, social factors, and welfare indicators. *PLoS One 11*: 20153301. https://doi.org/10.1371/journal.pone.0150331

Horback K, Miller L, Andrew J, Kuczaj S and Anderson M 2012 The effects of GPS collars on African elephant (*Loxodonta africana*) behaviour at the San Diego Zoo Safari Park. *Applied Animal Behaviour Science 142*: 76-81. https://doi.org/10.1016/j.applanim.2012.09.010

Hosey G 2008 A preliminary model of human-animal relationships in the zoo. *Applied Animal Behaviour Science 109*: 105-127. https://doi.org/10.1016/j.applanim.2007.04.013

Laule G 2003 Positive reinforcement training and environmental enrichment: enhancing animal well-being. *Journal of the American Veterinary Medical Association 223:* 969-973. https://doi.org/10.2460/javma.2003.223.969

Leighty K, Soltis J and Savage A 2010 GPS assessment of the use of exhibit space and resources by African elephants (*Loxodonta africana*). *Zoo Biology 29*: 220-220

Loizi H, Goodwin TE, Rasmussen LEL, Whitehouse AM and Schulte BA 2009 Sexual dimorphism in the performance of chemosensoy investigatory behaviours by African elephants (*Loxodonta africana*). *Behaviour 146*: 373-392. https://doi.org/10.1163/156853909X410964

Margulis SW, Hoyos C and Anderson M 2003 Effect of felid activity on zoo visitor interest. *Zoo Biology 22*: 587-599. https://doi.org/10.1002/zoo.10115

Martin P and Bateson P 2007 *Measuring Behaviour: An Introductory Guide, Third Edition.* Cambridge University Press: New York, USA. https://doi.org/10.1017/CBO9780511810893

https://doi.org/10.7120/09627286.27.1.055 Published online by Cambridge University Press

Mason G, Clubb R, Latham N and Vickery S 2007 Why and how should we use environmental enrichment to tackle stereotypic behaviour? *Applied Animal Behaviour Science 102*: 162-188. https://doi.org/10.1016/j.applanim.2006.05.041

Mason GJ 1991 Stereotypies: a critical review. *Animal Behaviour. 41*: 1015-1037. https://doi.org/10.1016/S0003-3472(05)80640-2

Meehan CL, Mench JA, Carlstead K and Hogan JN 2016 Determining connections between the daily lives of zoo elephants and their welfare: an epidemiological approach. *PLoS One 11*: e0158124. https://doi.org/10.1371/journal.pone.0158124

Mellen JD, Stevens VJ and Markowitz H 1981 Environmental enrichment for servals, Indian elephants and Canadian otters at Washington Park Zoo, Portland. *International Zoo Yearbook 21*: 196-201. https://doi.org/10.1111/j.1748-1090.1981.tb01981.x

Merz G 1986 Movement patterns and group size of the African forest elephant *Loxodonta africana cyclotis* in the Tai National Park, Ivory Coast. *African Journal of Ecology 24*: 133-136. https://doi.org/10.1111/j.1365-2028.1986.tb00353.x

Miller L 2012 Visitor reaction to pacing behaviour: influence on the perception of animal care and interest in supporting zoological institutions. *Zoo Biology 31*: 242-248. https://doi.org/10.1002/zoo.20411

Miller L, Andrews J and Anderson M 2011 Validating methods to determining walking rates of elephants within a zoological institution. *Animal Welfare 22*: 577-582.

Miller L, Chase MJ and Hacker CE 2016 A comparison of walking rates between wild and zoo African elephants. *Journal of Applied Animal Welfare Science 19*: 271-279. https://doi.org/10.1080/10888705.2015.1137755

Miller M, Hogan JN and Meehan CL 2016 Housing and demographic risk factors impacting foot and musculoskeletal health in African elephants (*Loxodonta africana*) and Asian elephants (*Elephas maximus*) in North American zoos. *PLoS One 11*: e0155223. https://doi.org/10.1371/journal.pone.0155223

Morfeld KA, Meehan CL, Hogan JN and Brown JL 2016 Assessment of body condition in African (*Loxodonta africana*) and Asian (*Elephas maximus*) elephants in North American zoos and management practices associated with high body condition scores. *PLoS One 11*: 20155146. https://doi.org/10.1371/journal.pone.0155146

Murray CM, Sandeep VM and Pusey AE 2007 Dominance rank influences female space use in wild chimpanzees, *Pan troglodytes*: towards an ideal despotic distribution. *Animal Behaviour 74*: 1795-1804. https://doi.org/10.1016/j.anbehav.2007.03.024

Olson D 2004 *Elephant Husbandry Resource Guide*. Allen Press: Kansas, USA

Payne K 2003 Sources of social complexity in three elephant species. In: de Waal FBM and Tyack PC (eds) *Animal Social Complexity: Intelligence, Culture and Individualized Societies* pp 57-85. Harvard University Press: Cambridge, USA. https://doi.org/10.4159/harvard.9780674419131.c5

Posta B, Huber R and Moore DE 2013 The effects of housing on zoo elephant behaviour: a quantitative case study of diurnal and season variation. *International Journal of Comparative Psychology 26*: 37-52

Prado-Oviedo NA, Bonaparte-Saller MK, Malloy EJ, Meehan CL, Mench JA, Carlstead K and Brown JL 2016 Evaluation of demographics and social life events of Asian (*Elephas maximus*) and African elephants (*Loxodonta africana*) in North American zoos. *PLoS One 11*: e0154750. https://doi.org/10.1371/journal.pone.0154750

Rees PS 2009 Activity budgets and the relationship between feeding and stereotypic behaviours in Asian elephants (*Elephas maximus*) in a zoo. *Zoo Biology 28*: 79-97. https://doi.org/10.1002/zoo.20200

Schulte B 2000 Social structure and helping behaviour in captive elephants. *Zoo Biology 5*: 447-459. https://doi.org/10.1002/1098-2361(2000)19:5<447::AID-ZOO12>3.0.CO;2-#

Shannon CE and Weaver W 1949 *The Mathematical Theory of Communication*. University of Illinois Press: Champaign, USA

Shepherdson DJ 2010 Principles of and research on environmental enrichment for mammals. In: Kleiman D, Thompson K and Baer C (eds) *Wild Mammals in Captivity* pp 62-67. University of Chicago Press: Chicago, USA

Shepherdson DJ, Carlstead K, Mellen JD and Seidensticker J 1993 The influence of food presentation of the behaviour of small cats in confined environments. *Zoo Biology 12*: 203-216. https://doi.org/10.1002/zoo.1430120206

Stoinski TS, Daniel E and Maple TL 2000 A preliminary study of the behavioural effects of feeding enrichment on African elephants. *Zoo Biology 6*: 485-493. https://doi.org/10.1002/1098-2361(2000)19:6<485::AID-ZOO1>3.0.CO;2-5

Stokke S and Du Toit JT 2002 Sexual segregation in habitat use by elephants in Chobe National Park, Botswana. *African Journal of Ecology 40*: 360-371. https://doi.org/10.1046/j.1365-2028.2002.00395.x

Theiss A, Yen DC and Ku C 2005 Global Positioning Systems: an analysis of applications, current development, and future implementations. *Computer Standards & Interfaces 27*: 89-100. https://doi.org/10.1016/j.csi.2004.06.003

Veasey JS 2006 Concepts in the care and welfare of captive elephants. *International Zoo Yearbook 40*: 63-79. https://doi.org/10.1111/j.1748-1090.2006.00063.x

Whyte IJ 1996 Studying elephant movements. In: Kangwana K (ed) *Studying Elephants* pp 75-89. African Wildlife Foundation: Nairobi, Kenya

Wittemyer G and Getz WM 2007 Hierarchical dominance structure and spatial organization in African elephants, *Loxodonta africana*. *Animal Behaviour 73*: 671-681. https://doi.org/10.1016/j.anbehav.2006.10.008

Wittemyer G, Getz WM, Vollrath F and Douglas-Hamilton I 2007 Social dominance, seasonal movements, and spatial segregation in African elephants: a contribution to conservation behaviour. *Behavioural Ecology and Sociobiology 61*: 1919-1931. https://doi.org/10.1007/s00265-007-0432-0