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Research article

Enclosure use as a measure of behavioural welfare in three zoo-housed African wild dogs *Lycaon pictus*

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Abstract

African wild dogs *Lycaon pictus* are a popularly exhibited zoo animal, frequently housed in groups to represent their natural packs in the wild. While such group housing is common, the effects of changes to that group are seldom directly investigated. This study examined the enclosure use of three African wild dog siblings located at the Woodland Park Zoo. The wild dogs were observed during a period of several weeks, during which one of the dogs was periodically removed from the group. Groupings of the wild dogs were examined during three conditions: (1) ALL 3, when all three dogs were on-exhibit, (2) MIXED, when one of the dogs was held off-exhibit, and (3) ALL 2, when only two animals remained in the enclosure and on-exhibit. Removal of one of the dogs from the on-exhibit portion of the enclosure (MIXED and ALL 2 conditions) significantly modified overall area usage and variability in enclosure use (as measured via Entropy, a single measure of area use variability) for the two remaining on-exhibit wild dogs. The results suggest that overall enclosure use, with attention to variability in enclosure areas used, can function as a relevant behavioural welfare measure for group-housed zoo animals, particularly when direct measures of behaviours are inconclusive.

Introduction

The African wild dog *Lycaon pictus* is a wide-ranging carnivore of sub-Saharan Africa (Woodroffe and Sillero-Zubiri 2012). This canid is highly social with complex pack dynamics, living in family groups of two to over 20 adults (Maddock and Mills 1994; de Villiers et al. 2003). They are listed as Endangered with ongoing decline in population due to habitat range fragmentation, infectious disease and human-livestock conflict (Woodroffe and Sillero-Zubiri 2012). Additional pressure on the essential resources of wild dogs is due to intraguild competition and kleptoparasitism from lions *Panthea leo*, spotted hyenas *Crocuta crocuta*, and other large predators (Carbone et al. 1997; Creel and Creel 2002; Swanson et al. 2014). Wild dogs avoid this competition and are thus forced into areas with lower resource availability year-round (Vanak et al. 2013). Their range formerly included most of sub-Saharan Africa, although it is now restricted to areas in southern Africa and southern East Africa (Woodroffe and Sillero-Zubiri 2012).

In zoo enclosures, stereotypic behaviour in carnivores have been correlated with natural foraging and ranging behaviour, based on both home-range size and daily distances travelled (Clubb and Mason 2003; 2007). Links between foraging, food-searching/hunting and stereotypic behaviours have been established in numerous zoo-housed carnivores (Carlstead and Seidensticker 1991; Carlstead et al. 1991; Shepherdson et al. 1993; Godinez et al. 2013; Fernandez and Timberlake 2019a; Fernandez 2021). It has been suggested that a large variety in enclosure structure and stimuli would be ideal for maintaining ranging carnivores in captivity, especially those allowing for animal control of variation (Clubb and Mason 2003; Mason et al. 2007). In the wild, African wild dogs move on to different parts of their range almost every day and cover great distances (Creel and Creel 2002). Studies on forms of enrichment for wild dogs indicate the use of husbandry training, faecal odour cues from natural prey species and food delivery devices, are beneficial for increasing activity, reducing stereotypic behaviours and increasing species-specific behaviours (Price 2010; Rafacz and Santymire 2010; Shyne and Block 2013). Overall, a flexible and variable approach to enrichment for African wild dogs, including social, food and sensory enrichment categories, is ideal in maintaining naturalistic wild dog behaviours (Cloutier and Packard 2014).

Thus, aside from direct measures of activity budgets, a critical factor in examining the behavioural welfare of zoo-housed carnivores, and specifically African wild dogs, is overall enclosure use. Enclosure use has been examined in zoo studies using Zone Occupancy, Spread of Participation Index (SPI) and Electivity Index measures (for a review, see Brereton 2020). SPI has been useful in producing a single measure of the variability of enclosure use, although traditionally this has required areas or zones of equal size. Plowman's (2003) modified SPI allows for assessing the variability in enclosure use of unequal zone sizes. However, this requires an estimate of the different enclosure zone sizes that can be particularly difficult for zoo exhibits, which often utilise non-conforming three-dimensional spaces. Another variability measure is Entropy, which has been effectively used to study overall enclosure use of zoo-housed animals (Fernandez and Timberlake 2019b). Entropy has the benefit of producing a single measure of enclosure variability, like SPI, but without assumptions of the parameters being measured, such as equal zone size (Shannon 1948).

The present study examined the enclosure use of three zoo-housed African wild dogs. Originally, both the behaviours and area usage of all three wild dogs were studied during three different grouping conditions of the wild dogs on- and off-exhibit. However, few differences were observed in their behavioural distributions during these conditions, even though there appeared to be differences across the conditions based on their area usage. Therefore, the study focussed directly on both overall enclosure use of each observed on-exhibit area and the variability in overall enclosure use as a result of the different grouping conditions. It was hypothesised that variability in enclosure use would be lowest for all the wild dogs when they were on-exhibit with one of the dogs that appeared to remain almost exclusively in one of the areas observed.

Methods

Subjects and housing

Subjects were three African wild dogs *Lycaon pictus* housed at the Woodland Park Zoo in Seattle, Washington. The three dogs (Bakari, Jalen and Mtima) were all brothers from the same litter, born in captivity, and 11 years old at the time of the study. They had lived at the Woodland Park Zoo in the same exhibit for the preceding 10 years. All three African wild dogs were considered advanced in age compared to their wild counterparts (Creel and Creel 2002; Creel et al. 2004). Mtima, who was chronically ill, was occasionally separated from the group (i.e., held off-exhibit) and was later euthanised during the study.

The African wild dog enclosure at the Woodland Park Zoo was comprised of two major sections: (1) the indoor, non-public feeding cages and open-air area (e.g., off-exhibit section), and (2) the outer, publicly viewed, open-air exhibit (e.g., on-exhibit section). The off-exhibit section was approximately 42 m2 and included heated dens and a digging mulch area. The on-exhibit section was approximately 465 m2 and consisted of natural grass, vegetation, sand, trees and tree stumps, as well as artificial rock, boulders, tree limbs and regularly placed environmental enrichment.

Materials

Data were collected using either handheld personal computers (PalmOne Zire 21™) with Event-PC software developed by Dr. James Ha at the University of Washington, or pre-printed ethogram data sheets. In addition, a notebook was used to record field observations such as any potential errors during a session.

Data collection procedure

Prior to its implementation, the study was approved through Woodland Park Zoo's Research Committee, as well as the University of Washington's Institutional Animal Care and Use Committee (IACUC #2858-06). All three African wild dogs were observed in the on-exhibit section of the enclosure for three weeks, from 27 June to 15 July 2011. Mtima was occasionally held off-exhibit, and later euthanised, resulting in three conditions:

ALL 3 – All three wild dogs present and on-exhibit.

MIXED – Bakari and Jalen in the on-exhibit section, Mtima held off-exhibit.

ALL 2 – Mtima no longer present on- or off-exhibit (post-euthanasia).

A modified scan sampling procedure (Altmann 1974) was used to record behaviour and exhibit location during all observation sessions. Behaviours comprised 12 mutually exclusive responses (e.g., lying down; locomoting), but were not included in the analyses due to few observed differences (see Introduction). Exhibit location was divided into four possible coding areas. Figure 1 shows the on-exhibit section of the enclosure, with the coding areas labelled A through D. A session comprised of recording each individual dog's behaviour and location every 30 sec for 30 min with instantaneous, pinpoint sampling. The exhibit was observed for eight sessions per day in half-hour blocks per hour (e.g., 30 min of observation between 10.00 and 11.00), between 09.30 and 17.00. A total of 17 days of recording took place, giving a total of 136 sessions (68 hr) observed. For 111 sessions, at least one of the animals was in sight (for 25 sessions, all dogs were out of sight) for a total of 55.5 hr of observed on-exhibit enclosure use (see Table 1).

Statistical analyses

Data for each subject was independently analysed by combining each subjects' session data across a time or condition and then using number of sessions for each time/condition as the blocking/subject variable. Statistical analyses were performed using SigmaStat™, version 11.0 (Systat Software Inc., San Jose, CA, USA). All the data failed to meet normality and/or equal variance assumptions; therefore, non-parametric Kruskal-Wallis ANOVAs with Bonferroni-corrected Dunn's post hoc tests were performed. Data were presented graphically by summing all session results per time/condition, regardless of when the condition was presented within the study.

Table 1. Number of sessions for each condition and each African wild dog, as well as the total number of sessions for each dog.

Dog / Condition	All three	Mixed	All two	Total sessions
Bakari	66	18	27	111
Jalen	65	16	27	108
Mtima	67	N/A	N/A	67

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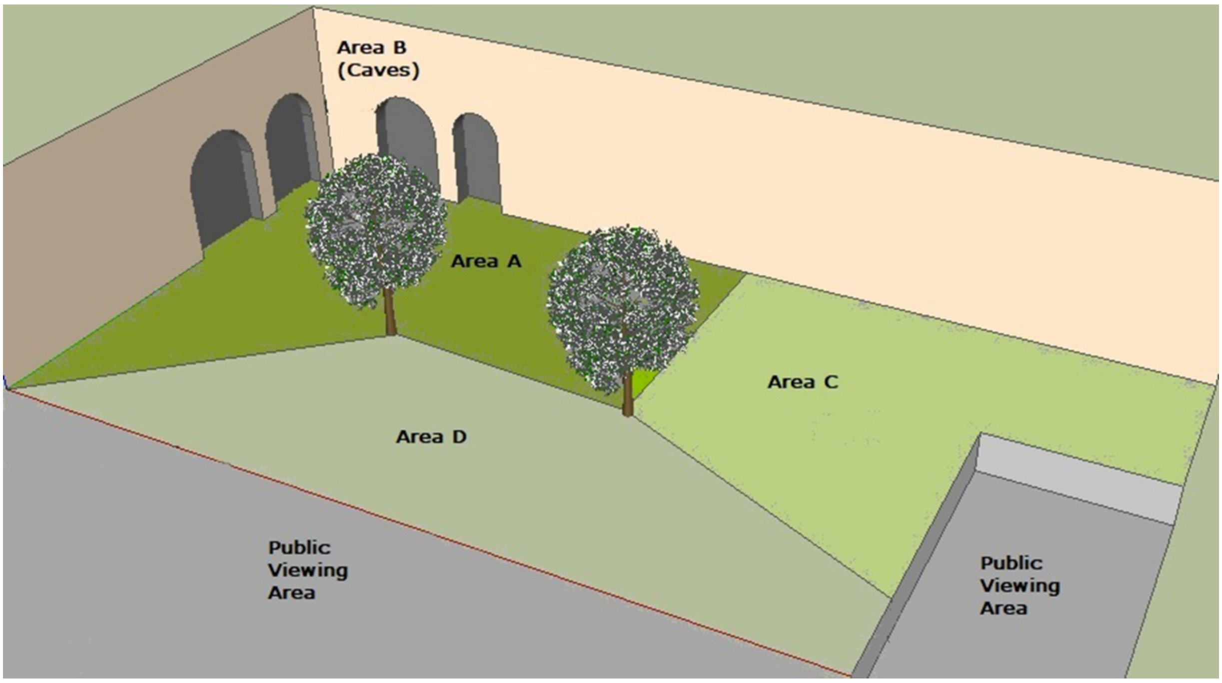

Figure 1. On-exhibit section of the African wild dog exhibit with each coding area (A, B, C and D) and public viewing areas labelled.

To examine overall enclosure use, a measure of Entropy (Shannon 1948) was generated for each observation session. Entropy measures randomness across a set of variables and therefore produces a single measure of the total variability of enclosure use across the four possible areas. The measures of Entropy were calculated by the formula

$$H = -\Sigma \quad p(i) \log p(i),$$

where $p(i)$ is the proportion of time spent in ith area. This formula produces a number from 0 to 1, with a higher value of H demonstrating more variability in overall enclosure use. Entropy was selected as a measure of variability in enclosure use (over a spread of participation index [SPI]; Dickens 1955; Hedeen 1982; Plowman 2003) because it is sensitive to small sets of variables and does not require a modified formula to accurately handle unequal enclosure zones. The same Kruskal-Wallis ANOVA tests were then applied to differences in the three conditions.

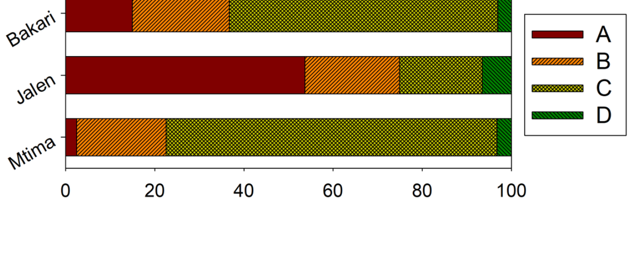

Figure 2. Total percentage of area use for all four areas (A, B, C and D) and for all three African wild dogs during the ALL 3 condition.

Results

Figure 2 displays the total area use during the ALL 3 condition (all 3 dogs on-exhibit) for all three wild dogs. Both Bakari and Mtima spent most of their time in Area C (60.2% and 74.2%, respectively), while Jalen spent most of his time in Area A (53.7%). All three dogs spent ~20% of their time in Area B, and less than 7% of their time in Area D.

Figure 3 displays the hour-to-hour area use (09.00 to 17.00) for all three African wild dogs. Each wild dog spent the most time in Area D (range: 13.6–28.6%) during 09.00–10.00, when first entering the exhibit, decreasing to <1% by 11.00–12.00 or 12.00–13.00. This was likely in part due to enrichment being placed or thrown from the public viewing area into Area D by the keepers shortly after the wild dogs were given access to the on-exhibit portion of their enclosure. By the late morning (11.00–12.00), the wild dogs spent most of their time in one area, with Bakari and Mtima primarily in Area C and Jalen primarily in Area A.

Figure 4 displays the mean usage of each area (A, B, C and D) for each condition (ALL 3, MIXED and ALL 2 conditions) for Bakari and Jalen. There were significant effects for Bakari in the use of Area A, B and C (Area A, X^2_2=33.960, P<0.001; Area B, X^2_2=17.730, P<0.001; Area C, X^2_2=33.690, P<0.001). Post hoc tests demonstrated that Area A and B were used significantly less and Area C significantly

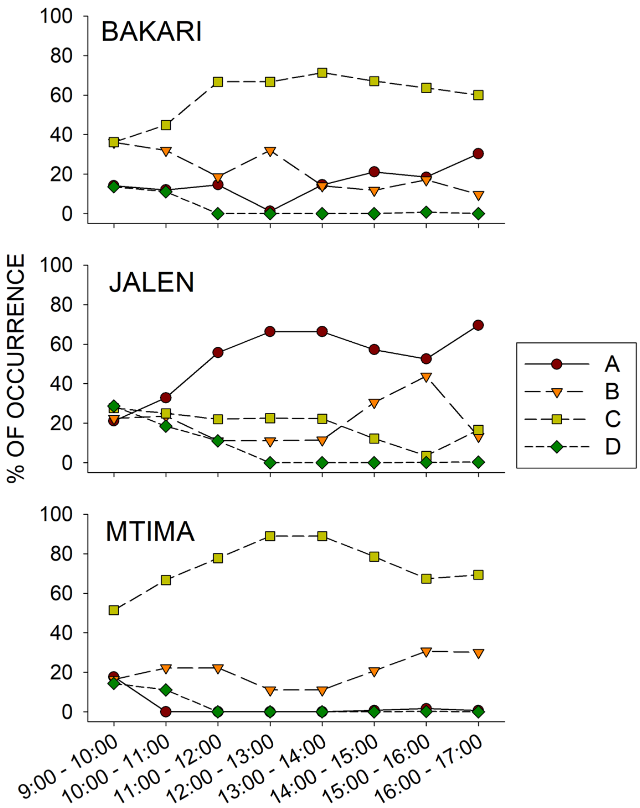

Figure 3. Hour-to-hour area use for all four areas (A, B, C and D) and for all three African wild dogs during the ALL 3 condition. Time (09.00–17.00) is displayed on the x-axis, while percentage (%) of occurrence is displayed on the y-axis.

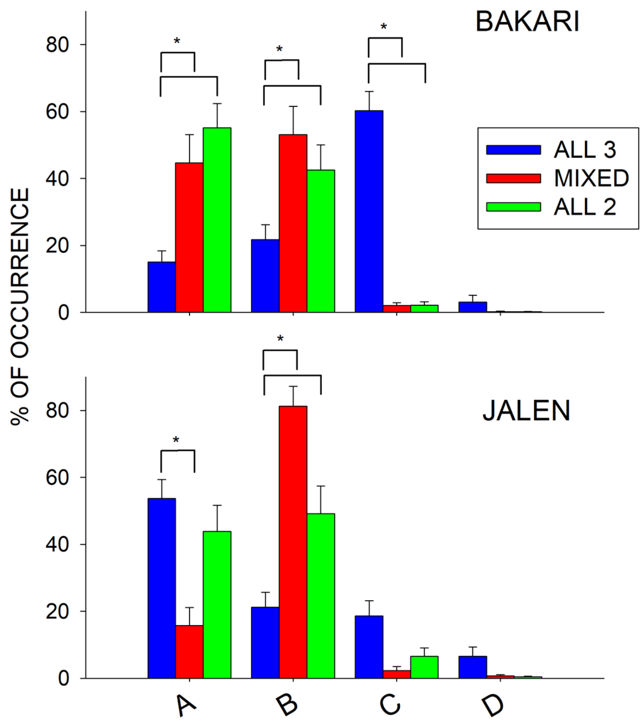

Figure 4. Percentage of area use for Bakari (top) and Jalen (bottom) across the three conditions. Area use (A, B, C and D) is displayed on the x-axis, while percentage (%) of occurrence (with SE bars) is displayed on the y-axis. Solid lines and stars represent statistically significant effects (P<0.05).

more during the ALL 3 condition when compared to the MIXED and ALL 2 conditions (P<0.05 in all cases). There were also significant effects for Jalen in the use of Area A and B (Area A, X^2_2=6.184, P=0.045; Area B, X^2_2=30.675, P<0.001). Post hoc tests demonstrated that Area A was used significantly more during the ALL 3 condition compared to the MIXED condition, and Area B was used significantly less during the ALL 3 condition when compared to the MIXED and ALL 2 conditions (P<0.05 in all cases).

Figure 5 displays the mean Entropy score for Bakari and Jalen. There was a significant effect for Bakari in his entropy score (X^2_2=14.194, P<0.001). Post hoc tests demonstrated that there was significantly less variability in the use of the enclosure during the ALL 3 condition when compared to the MIXED and ALL 2 conditions (P<0.05 in both cases). There was also a significant effect for Jalen in his Entropy score (X^2_2=7.597, P=0.022), although there were no significant post hoc effects. Finally, there was a significant effect in comparing the Entropy score for Bakari, Jalen and Mtima during the ALL 3 condition (X^2_2=8.615, P=0.013), although there were no significant post hoc effects. However, it is worth noting that, during the ALL 3 condition, Mtima showed the lowest mean Entropy score observed (M=0.043, SE=0.013) compared to the lowest mean Entropy scores recorded for Both Bakari and Jalen (M=0.081, SE=0.015; M=0.079, SE=0.015, respectively).

Discussion

During the ALL 3 condition, when all three wild dogs were on-exhibit, Bakari and Mtima spent most of their time together in Area C, with Mtima displaying the greatest use of one area by any of the wild dogs (~75%). Jalen spent much of his time (+50%) in Area A, away from the other two dogs. It is not clear why this occurred, but few acts of overt aggression were observed

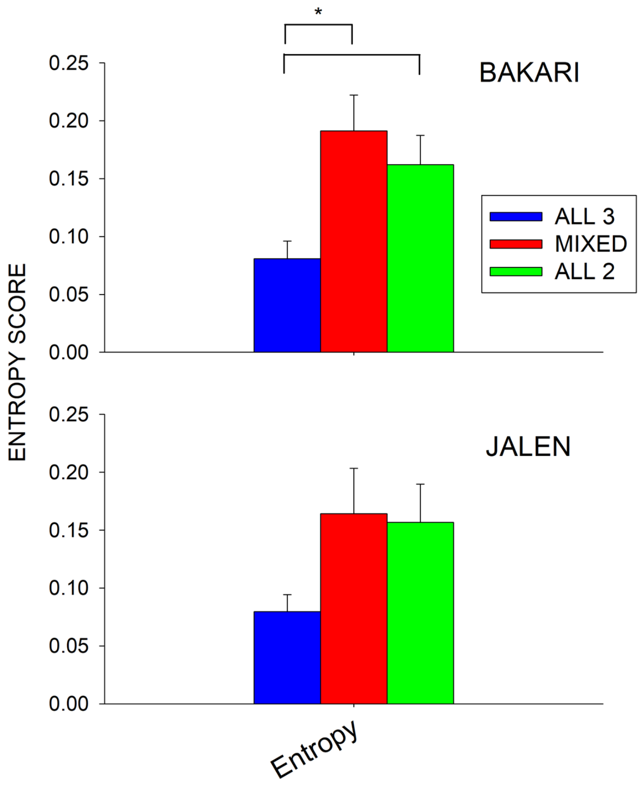

Figure 5. Entropy score (with SE bars) for Bakari (top) and Jalen (bottom) across all three conditions. Solid lines and stars represent statistically significant effects (P<0.05).

between any of the wild dogs. All three wild dogs rarely used the front of the exhibit, Area D, which was closest to the largest public viewing area. Typically, the wild dogs would only use this area of the exhibit in the mornings, when first released into the on-exhibit portion of the enclosure, and where keepers would actively place or throw enrichment to encourage increased area usage. Whether the wild dogs actively avoided this area because of the presence of visitors is not known, although other researchers have found zoo-housed leopards to distance themselves from visitors, especially on high visitor attendance days (Mallapur and Chellam 2002). Likewise, other researchers have reviewed the effects of visitors on zoo animals and found similar visitor-avoidance effects (Davey 2007; Fernandez et al. 2009; Hosey 2000; Sherwen and Hemsworth 2019).

During the removal of Mtima from the on-exhibit portion of the enclosure (MIXED condition) and later removal from the enclosure altogether (ALL 2 condition), Bakari significantly increased his use of Area A and B and significantly decreased his use of Area C when compared to the ALL 3 condition. Jalen significantly decreased his use of Area A during the MIXED condition and significantly increased his use of Area B during the MIXED and ALL 2 conditions when compared to the ALL 3 condition. Thus, the removal of Mtima from both the on-exhibit portion of the enclosure and from the enclosure altogether significantly affected the use of the enclosure by both wild dogs remaining on-exhibit. By examining overall enclosure use, the study was able to detect changes across conditions that were otherwise not directly noted by behavioural observations.

While examinations of both social dynamics and spatial distribution have been commonplace for animal behaviour research, few studies have examined the impact of changes to the group housing of zoo animals on the enclosure use of those animals. In one such study, Forthman and Bakeman (1992) were able to demonstrate that enclosure use was, in part, conditional on the group housing of zoo-housed sloth bears *Melursus ursinus*. Examinations of changes to the group dynamic of zoo-housed animals on their overall enclosure use can provide important information about that species housed, and therefore on the behavioural welfare of those individuals.

The use of Entropy as a single measure of enclosure variability demonstrated that Bakari used the on-exhibit portion of the enclosure significantly more variably when Mtima was either not on-exhibit (MIXED condition) or removed from the enclosure altogether (ALL 2 condition) when compared to when Mtima was on-exhibit (ALL 3 condition). While the post hoc tests were not significant, Jalen showed a similar trend to that of Bakari, and both animals used the on-exhibit portion of the enclosure more variably than Mtima when all three wild dogs were on-exhibit. One interpretation of these results is that the presence of Mtima on-exhibit potentially compromised the welfare of the other two wild dogs while on-exhibit. An alternative interpretation would suggest that the absence of Mtima "stressed" the two remaining on-exhibit wild dogs, thereby increasing stress-related activity. It is considered that this second interpretation is less likely, given that increased variability in enclosure use is more commonly associated with increased welfare benefits and decreased stereotypic activity (Brereton 2020). Regardless, while caution should be used in extrapolating the results of this relatively small set of observations to the greater welfare implications of these individuals, they at least provide some insight into how the removal of one individual affected the well-being of the two remaining on-exhibit wild dogs.

While it was determined that there were no conclusive differences in the direct behaviours observed across the three conditions, it is possible that a similar single measure of variability could have been applied to the behaviours observed in this study. Other researchers have demonstrated that behavioural diversity (e.g., behavioural variability) has been an effective measure for assessing the welfare of zoo animals (Shepherdson et al 1993; Clark and Melfi 2012; Miller et al. 2020). Again, while caution should be used in extrapolating the findings of any one measure to the overall well-being of zoo-housed individuals, examinations of the behavioural diversity displayed by exhibited animals is a currently under-utilised yet promising future measure of the welfare of zoo animals.

To date, only one other study has examined the enclosure use of exhibited African wild dogs, with attention to the under- and over-utilisation of specific features of the enclosure (Hunter et al. 2014). The results of the present study suggest that measurement of enclosure use, with specific attention to variability in enclosure use, is a valuable behavioural welfare metric for African wild dogs, and zoo-housed animals in general. Since African wild dogs are primarily housed in groups and because changes in how those animals are grouped are commonplace, greater attention should be given to how multiple measures of welfare, including enclosure use and variability, can aide in assessing those changes. Entropy as a measure of enclosure variability provides one of the simplest yet effective ways to assess that welfare impact. The future of zoo welfare assessment should look to multiple measures, including Entropy or other simple metrics of enclosure use, to effectively evaluate the well-being of their animals.

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