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Evaluating the activity patterns and enclosure usage of a little-studied zoo species, the sitatunga (*Tragelaphus spekii*)

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Abstract

Ungulates can be underrepresented in zoo animal behaviour and welfare research, yet they comprise some of the most widely-kept captive species and as such, their lives within the zoo are worthy of closer investigation. Sitatunga (*Tragelaphus spekii)* are kept in numerous zoological collections globally yet current information on species-specific husbandry requirements and captive behaviour patterns appears limited. Many enclosures for ungulates can be uninspiring and generic; this study was designed to gain a better understanding of daily activity and enclosure use of a species that, in the wild, has a very particular habitat choice. Data were collected at the former Cricket St Thomas Wildlife Park, Chard, UK on eight sitatunga to determine overall daily activity patterns and usage of all available areas of their exhibit. Instantaneous scan sampling of the whole herd during three periods each day (morning, midday and afternoon) allowed for changes in behaviour patterns to be assessed over time. The enclosure encompassed both biologically-relevant (long grasses, reeds and shallow water) and less relevant (open, short-grassed) areas; these were zoned according to features considered useable to the sitatunga and that could influence behaviour and time spent within that zone. Zone usage was analysed using a modified Spread of Participation Index (SPI) which indicated a significant preference for biologically-relevant spaces. Significantly enhanced behavioural repertoires occurred in the "natural" zones of the enclosure and three behaviours (standing, sitting/ruminating and eating) showed significant differences in performance between natural and artificial zones, and between time of day. Captive sitatunga display a daily rhythm in their activity, however comparison with wild data in the literature shows only few similarities in daytime activity budget and analysis reveals a significant difference between daily feeding patterns. Overall, enclosure design based on facets of natural ecology is important for the expression of a "wild-type" behaviour pattern in captive ungulates and sitatunga will actively choose more biologically-relevant areas of their exhibit when these are available. It is suggested that alterations to husbandry regime and management style of such specialised ungulates could help improve captive behavioural repertoires and enhance the display of such animals in the zoo.

Introduction

When designing zoo animal enclosures it is important to have knowledge of the activity budgets of the species intended for exhibition to determine optimal furnishing and size allocation, thus providing quality space for the animal (Estevez and Christman 2006; Ross *et al.* 2009). Simple methods of space-use evaluation and assessment have been applied to several commonly held zoo taxa (e.g. Hedeen 1983; Hebert and Bard 2000; Mallapur *et al.* 2002; Ross and Lukas 2006; Ross *et al.* 2011) and it is understood that the design of enclosures (and hence the environment created for a species) plays an important role in determining the overall diversity of activity budgets shown by captive species (Reinhardt *et al.* 1996; Seidensticker and Forthman 1998; Clark *et al.* 2012; Rose and Roffe 2012). Species-appropriate exhibitory that facilitates the performance of self-fulfilling behaviours (e.g. appetitive behaviours, as per Day *et al.* 1995; Duncan 1998) is enriching to the animal and may ultimately provide a better quality experience for the zoo visitor (Blowers *et al.* 2012; Fabregas *et al.* 2012).

It is well-known that measurement of such "useable space" can be undertaken via a calculation of Spread of Participation Index (SPI), either in its traditional or modified form (see Hedeen 1983; Plowman 2003). SPI results enable those providing care, designing enclosures and manipulating social groupings to have quantifiable data on which to base decisions pertinent to individual species. Evaluation of captive provision is required for species commonly kept but perhaps overlooked; animals that may not outwardly show signs of stress but who may benefit from an assessment of husbandry, management and provision within their collection. Such an evidence-based approach (Melfi 2009) is a useful direction for zoos to travel in to make substantial and long-term changes to husbandry and enclosure design. This evidence-based style has been the subject of the research project presented here.

The sitatunga (*Tragelaphus spekii*) is an example of a species held in captivity at a range of institutions (being kept in 78 animal collections throughout the world, see ISIS as of February 2012) but where little research into captive need has been conducted. Wild sitatunga face a current downward population trend although they are not currently classed as threatened on the IUCN Red List (IUCN SSC Antelope Specialist Group 2008). A semi-aquatic antelope occupying marshes and swamps, papyrus beds and the wetter areas of savannah and rainforest habitats (Kingdon 1982; Estes 1991; MacDonald 2001; Robinchaud 2011), the wild activity budget of the sitatunga can be difficult to define, posing a challenge to those seeking the "evidence-basis" for zoo husbandry.

Information presented in Delany and Happold (1979) and Kingdon (1982) states that animals prefer to browse in low-growing thicket in and around marshy areas, as well as entering deeper water to consume vegetation. Owen (1970) details foraging patterns with sitatunga consuming a wide variety of wetland plants, and again, Kingdon's (1982) review of sitatunga grazing behaviour in wetland areas details animals regularly leaving resting areas of dense cover to forage on new-growth grass. Consequently, for a meaningful exhibit to be constructed in the zoo, key aspects of evolutionary biology, ecological niche and behavioural ecology must be incorporated. The minimum husbandry guidelines developed by the Association of Zoos and Aquaria (AZA) do provide basic husbandry needs for the keeping of Tragelaphine antelopes (Antelope TAG 2006) but no specialist requirements are stated for individual species. These AZA guidelines, together with some detail on the World Association of Zoo and Aquariums (WAZA) website, are only minimum standards and zoos are expected to expand on them to incorporate biologically-important features within species-specific exhibits.

Data presented here will hopefully enable those managing sitatunga populations to have a greater understanding of captive needs and show an example of evidence-based animal management whereby changes can be implemented from a sound understanding of need and requirement. Whilst complete re-creation of the biome so favoured by this antelope (Plate 1) may not always be totally feasible, key facets of this biome could be included to remove the generalised look of an exhibit (e.g. Plate 2).

Plates 1 (left) and 2 (right). A replication of the sitatunga's natural habitat in the American Museum of Natural History, and a familiar, less diverse, habitat provided for the same species in captivity (author's photographs, 2011).

Data were collected to answer the hypotheses a) sitatunga will preferentially favour specific areas of an exhibit that best mimic wild-type conditions and that b) time budgets / behavioural repertoires of sitatunga in the zoo will mirror those of wild, free-living animals.

Methods

Behavioural data were collected at Cricket St Thomas Wildlife Park, Chard, UK in July 2009 for ten consecutive days. The study location was chosen due to the perceived quality of the sitatunga paddock, which contained a range of different "habitats" for the antelope to use and showed environmental heterogeneity not always that evident for captive ungulates. Observations were made in three time periods (09:00-11:00, 12:00-13:00 and 14:00-16:00 BST) using instantaneous scan sampling with an interval time of two minutes. A total of 50 hours of data was gathered on each individual antelope. These three observation periods were selected to best replicate the division of daytime activity that would be seen in the wild (and hence to allow for differences in behaviour at varying time periods to be recorded) and to work around the husbandry regime at the collection at that time. Animals were individually identifiable via different coloured ear tags so that, with the aid of binoculars, identification was always possible. The sitatungas' paddock was divided up into zones (Table 1) with some areas containing features that replicated biologically-relevant habitats and others that were deemed less ecologically important. These zones were designated and mapped using a satellite picture of the paddock obtained from Google Earth™ Pro with the areas (m^2) of each section being calculated. At the same time as behavioural sampling, location of each animal within the exhibit was. recorded

Zone	Name	Area (m^2)
1	Back grassed area	3754
2	End waterfall	102
3	Deep pool	311
4	Pool with trees	271
5	Centre waterfall	153
6	Shallow pool	682
7	Bank with reeds and grass	1181
8	Start waterfall	46
9	Front grassed area	3403
10	Housing	166
11	Marshy area	243
Total area of enclosure = 10312m^2		

Table 1. Designated zones with the sitatunga enclosure and the area of each.

Behaviour		Description
	Standing	The animal is upright on all four limbs, not moving, with its torso raised off ground, eyes open and observant of the immediate environment.
Grouped into sit / ruminate for analysis.	**Sitting**	The animals is conscious and in a ventral recumbent position on the ground.
	Rumination	Jaw movements associated with mastication of food or a bolus for the process of digestion of plant material. Normally performed sitting down, quietly, in a sheltered area of the enclosure.
Grouped into feeding for analysis.	**Feeding and foraging**	The action of eating or consuming forage, browse or grass using the tongue, teeth and mouth. The animal can be upright or sitting.
	Foraging	The animal is actively seeking and searching for food using its senses to search out food. The animal is moving purposefully around the exhibit sniffing, tasting and exploring different foodstuffs.
Grouped into other state behaviour for analysis.	**Sleeping**	The animal is in a complete or partial state of unconsciousness; in a dormant state, with eyes closed, resting on the ground.
	Aggression	Any antagonistic interaction between or directed to other individuals; this can include clash fighting where horns are used against another animal, chasing of one animal by another in a threatening manner, pushing, shoving or displacement of one individual by another.
	Walking	The animal is travelling on foot, advancing the feet alternately so that there is always two or more feet on the ground at any one time, either individually or as a herd.
	Scratching	The animal uses horns, mouth or limbs to manipulate or rub a part of its body in a short, sharp rhythmic pattern.
	Play	The animal engages in physical activity that is undertaken purely for enjoyment or amusement; this can include skipping, "gambolling", running, chasing or cavorting with other individuals in the enclosure. There is no associated aggressive response. In male animals only, sparring ("play fighting") may be performed between two individuals.
	Vigilance	The animal, whilst standing, assumes an alert posture and stares fixedly on a specific point with both ears forward; the animal may produce an alarm snort or stamp the ground with one leg.
	Territorial actions	A directed social interaction of one individual towards another to denote possession of a specific area of ground. Once the targeted animal moves away, the interaction ceases. In a male animal only, the antelope may "horn" the ground or associated enclosure furnishings.

Table 2. Ethogram of captive sitatunga behaviour observed in the study

The eight sitatunga (two adult males, five adult females, one juvenile of unknown gender) were all ear-tagged. The two male antelope, one older than the other, could be identified by their physical size and horn length. All five females were identifiable by the position and colour of their ear tags. The juvenile sitatunga was identifiable due to its size in comparison to other members of the study group.

Behavioural recording, undertaken by the same sole researcher for the duration of the observation period, took place from a small hide placed in the enclosure in a position that provided an uninterrupted view of all animals in all areas of the enclosure. A seven day pilot study and acclimatisation period were instigated before the main data collection period commenced. Using Popp (1982) and Estes (1991) as a main guide, an ethogram of key behaviours was created to categorise activity observed (Table 2). To enable clarity in analysis of the results, observed behaviours were grouped into four main categories, which also facilitated the comparison of sitatunga behaviour with that in published work.

Data were analysed using Microsoft Excel© 2008 and Minitab© Statistical Software, version 16. Evaluation of zone usage was undertaken using the Modified SPI formula (Plowman 2003). A value of 0.0 suggests equal use of all zones whereas a value of 1.0 suggests use of only one zone, with the formula for calculation of zone use being: SPI = (S | f_o - f_e |) / [2 (N - f_e min)] whereby f_o is the observed frequency in each zone, f_e is the expected frequency for each zone and f_e min the expected frequency in the smallest zone.

Behavioural data were normally distributed and a two-way ANOVA was used to determine differences between wild and captive time budgets, and for analysing differences between the animals' behaviour at different sample points. Analysis of enclosure zone use (non-parametric data) was conducted with one-factor Chi-squared tests. Wild/captive activity comparisons were analysed using tabulated behavioural data published by Owens (1970) from a group of free-living sitatunga.

Results

Analysis of time spent by each animal in the different zones showed an overall preference to spend time in the more biologically-relevant areas of the exhibit. In total, 27.5% of the enclosure falls into biologically-relevant areas (zones 3, 4, 5, 6, 7 and 11) and 54% of the total study time showed animals to be in these zones. A one-factor Chi-squared analysis confirmed a significant difference between zone uses for the group as a whole; $\chi^2_{[1]}$ =86.9, p< 0.005.

All sitatunga appeared to favour zone 7, the "river bank" area with long grass and reeds (Table 3). The male animals also spent more time in the house than the females. The juvenile spent more time out on the short grass areas than the rest of the herd. No animals were seen to use zone 8, the waterfall at the start of the exhibit. Figure 1 shows the total time (as a % of the overall observation period) that each individual spent in the biologically-relevant zones.

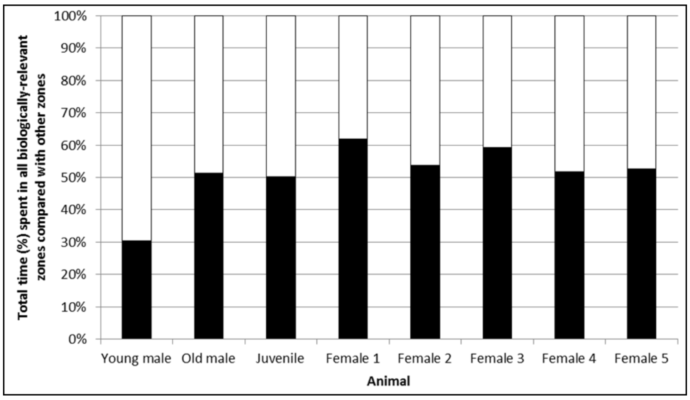

Figure 1. Total time spent by individual sitatunga at Cricket St Thomas Wildlife Park in two main classes of zone in the enclosure. Black = all biologically-relevant zones; white = all other zones.

It would be interesting to investigate further any social or hierarchical influences that were reducing the time the young male was able to spend in areas that were preferentially frequented by the other antelope. A modified SPI analysis for each demographic provides the following results; for the adult male sitatunga SPI = 0.64; for the young male = 0.74; and for female sitatunga SPI = 0.59. For the group as a whole, an SPI value of 0.61 was calculated for zone usage for the entire observation period. A one factor Chi-squared analysis was also used to analyse the number of behaviours performed in either category of zone and this showed there to be a significant difference in the total number of behaviours recorded between the different zones ($\chi^2_{[1]}$ = 104.11, p<0.05). Similar analyses were conducted for three key behaviours (standing, sitting and feeding), and sitting and eating behaviours were found to be performed for significantly different amounts of time between natural and artificial zones ($\chi^2_{[1]}$ = 609.64, p<0.05; $\chi^2_{[1]}$ = 143.18, p<0.05) respectively.

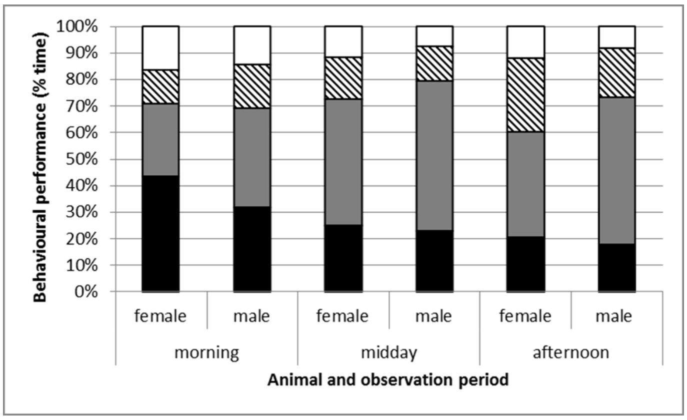

Figure 2. Daily activity pattern of both female and male sitatunga over an average day of the study period. Black =standing; grey = sitting / ruminating; dashed black = feeding; white = other state behaviour. Sitting has been grouped with ruminating as this the common position that this behaviour was observed in.

	Biologically-relevant Zones					Other Zones					
	Zone 3	Zone 4	Zone 5	Zone 6	Zone 7	Zone 11	Zone 1	Zone 2	Zone 8	Zone 9	Zone 10
Young male	0	10	4	38	860	10	24	0	0	298	1776
Old male	8	4	2	42	1482	10	4	224	0	272	972
Juvenile	24	94	0	120	1270	6	74	0	0	1228	204
Female 1	28	16	22	138	1662	0	146	134	0	508	366
Female 2	18	8	0	72	1522	0	32	306	0	232	830
Female 3	22	4	4	80	1678	2	40	48	0	358	784
Female 4	0	8	56	142	1360	0	284	0	0	336	834
Female 5	0	118	4	180	1256	30	102	10	0	780	540

Table 3. Time (in minutes) each individual sitatunga spent in each zone of the enclosure for the total duration of the study. See Table 1 for a description of each zone.

Figure 2 shows fluidity in behaviour across the observation period for the group of sitatunga, as well any differences in behavioural performance between the sexes. Inferential analysis shows there to be a significant difference between gender and time spent sitting ($F_{[1]}$=182.28, p=0.005) as well as for time of day when animals were observed sat down ($F_{[2]}$=474.04, p=0.002). Likewise, the same differences but analysing when animals chose to feed, also showed a significant relationship ($F_{[1]}$=18.30, p=0.051 and $F_{[2]}$=49.61, p=0.02).

Figure 3 provides an interesting comparison between wild and captive sitatunga behaviour as it shows only limited similarity in the activity budget of both populations, especially concerning time spent performing “other” behaviours in the morning and at midday. Deviations away from the natural activity pattern of the wild individuals are seen in this captive group concerning performance of key appetitive behaviours such as feeding and sitting/ruminating. Wild animals stand more in the middle of the day and feed more in the morning.

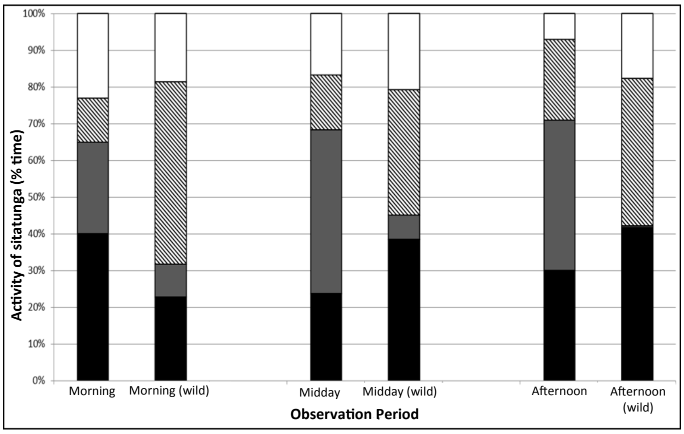

Figure 3. Overall group time budget for the whole observation period, split into the three specific sampling times. Black =standing; grey = sitting / ruminating; dashed black = feeding; white = other state behaviour. Wild data adapted from that published in Owens (1970), page 186, table 3. Data used is from time periods that compared to those used for the captive study. Sitting is compared to Owens' category of “lying” and other (for both captive and wild) includes other normal state behaviours (e.g. grooming, locomotion).

Wild sitatunga also display 1% of their time lying / sitting / ruminating in the afternoon whereas this behaviour comprises a substantial proportion of the activity budget of the captive animals (41%). Captive sitatunga show a less defined rhythm to their feeding activities, which is perhaps to be expected in an artificially managed environment. A two-way ANOVA shows there to be a significant difference for time spent feeding between each population at each time of day ($F_{[1]}$=29.56, p=0.032).

Numerous authors expand on the sitatunga's preference for long grass and reedy habitats. The biologically-relevant areas of the enclosure included only one section (zone 7) of long grasses/reeds; 11% of the total space available to the sitatunga. Figure 4 shows the time each sitatunga spent this zone; there is no significant difference between individuals in time spent in zone 7 ($\chi^2_{[7]}$ = 7.57; p<0.05), so

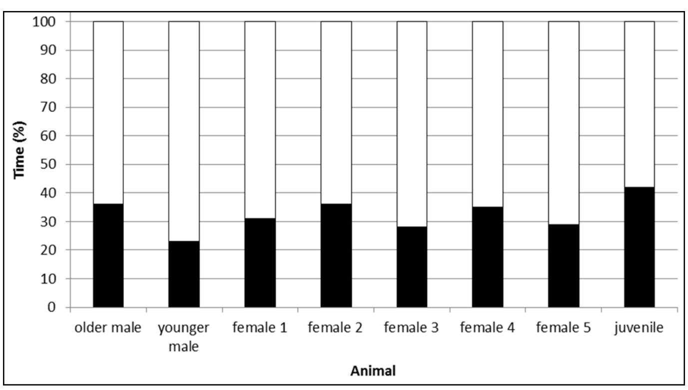

Figure 4. Comparison of time spent in a biologically-important area, long grass and reeds (black section) compared to time spent in the rest of the enclosure (white section).

it could assumed to be equally important to all animals in this herd. The importance of “natural” zones for performance of behaviours with a strong motivation is illustrated by Figure 5.

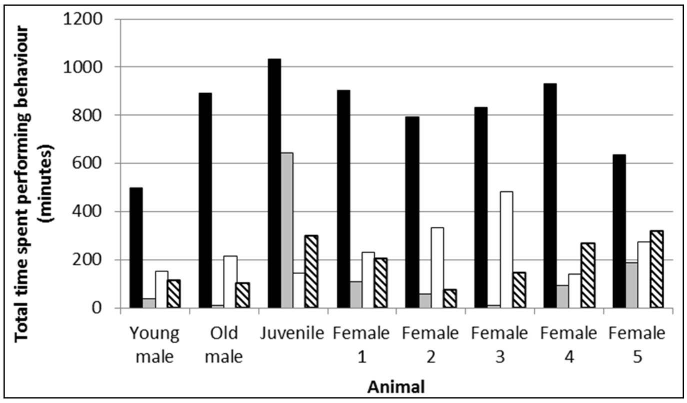

Figure 5. Performance of key appetitive behaviours by individual sitatunga in biologically-relevant and other enclosure zones. Black = sitting/ruminating (biologically-relevant zones); Grey = feeding/foraging (biologically-relevant zones); White = sitting/ruminating (other zones); Dashed line = feeding/foraging (other zones).

Discussion

The results show that various aspects of the sitatungas' behaviour are significantly different between biologically-relevant and other enclosure zones. The frequencies of three behaviours (standing, sitting/ruminating and feeding) were significantly different from morning to afternoon, thereby reflecting, in part, natural activity patterns. The modified SPI value (0.61) indicates that the sitatunga were not utilising all aspects of their enclosure equally and the sitatungas' significant preference for reedy / long-grassy areas is supported by the inferential analysis and by Figure 5. The herd spent 54% of its time in only 28% of the enclosure, suggesting that improvements to the remaining 72% encourage more widespread movement and a fuller development of a daily activity pattern.

The increased usage of these natural areas may also be explained by the behavioural ecology of the sitatunga and the need to conduct important state behaviours (feeding, resting, standing) in an environment most suitable for their performance. Comparing with observations from Owen (1970), Kingdon (1982), Games (1983), Estes (1991), Starin (2000) and Robinchaud (2011), sitatunga were observed to remain sedentary in reedy, or long-grass beds during the day; such habitats were reflected in this captive setting and the same behaviours were observed within them. Important functions of long-grass for sitatunga in the wild include places to hide from predators, provision of shelter from high temperature and sites for rumination (Estes 1991; Wronski *et al.* 2006). Figure 4 shows the relative proportion of time spent in a relatively small area of the enclosure (11%) compared to all of the other space available to the animals. Whilst not all behavioural functions are required per se in a captive setting, it is important to provide animals with the choice to perform behaviour that has a high motivational value (Duncan 1998); such activities can be reliable indicators of positive welfare (de Jonge et al. 2008). It is recommended that sitatunga be given more areas of long grass and reeds to facilitate their apparent preference for this type of “habitat”.

None of the sitatunga in this study displayed any form of stereotypy, such as repetitive oral movements or pacing (Bashaw *et al.* 2001; Baxter and Plowman, 2001). As stated by Mason and Mendl (1997) many stereotypical behaviour patterns are linked to an inability to perform appetitive foraging behaviours. Sitatunga are both grazers and browsers, and as a result spend long periods of time foraging for specific plant materiel (Estes 1991; Skinner and Chimimba 2006). As no stereotypies were displayed it can be deduced that the area of, and resources within, the natural zones were currently sufficient to prevent the need for the display of unnatural behaviours. To further support the high-quality aspects of this enclosure the sample population had no access to enrichment devices or routines, consequently the need to substitute "add-in" enrichment items is not always required in biologically-relevant, species-specific enclosures that provide sufficient enrichment in their own right.

Robinchaud's (2011) review of several data on sitatunga activity states that the majority of a daily time budget is spent within a wetland habitat, and only a fraction of this is spent on drier areas of grassland. The same author explains that open grassland is the sitatunga's least preferred habitat, but that animals will also avoid excessively boggy areas, presumably because these are open and devoid of cover. Interestingly, to support this, the adult male studied here spent less than 0.3% of the observation period in the open marshy zone, and the adult females showed a slight preference (out of all fully aquatic areas) for zone 6, the shallow pool. Plate 3 illustrates the social and investigative behaviour that can take place when sitatunga are provided with an expanse of shallow wetland areas with a zoo enclosure.

Plate 3. Example of shallow wetlands recreated in captivity that provides an opportunity for increased behavioural diversity (author's photograph, 2011).

The structure and type of wetland habitat created for sitatunga will influence time spent within it, as well as how animals divide their time between other areas of their exhibit and the range of behaviour they perform. As highlighted by Figure 2, captive sitatunga changed their rates of feeding, resting and moving throughout the day but in an apparently different manner to that observed in the wild (Figure 3). There may be a simple explanation for the differences between resting and standing behaviour as illustrated by Figure 3. Wild sitatunga have been observed to stand motionless in reeds during midday (Owen 1970; Kingdon 1982; Robinchaud 2011); if such "habitat" is not readily available in captivity, the animals may be expressing the need to be motionless but in a different form. Therefore the function of the behaviour carries the same important need for the animal. However, removal of any threat of predation could also result in more time spent relaxed across a range of the day that would not be seen in wild animals. Similarly, climatic differences may also account for altered activity patterns in zoo housed animals in temperate parts of the world. Differences in when feeding occurs (again illustrated in Figure 3) could be used as evidence for a change in how and when captive sitatunga are fed; provision of forage in the early morning and late in the afternoon may allow for a more natural activity pattern to emerge. However, the logistics of keeper routines and the climate that zoo animals are kept in may not always allow this to be practicable.

Several areas of the exhibit are poorly utilised by the sitatunga, and one zone is not used at all (see Table 3); consequently, work could be undertaken to improve the nature of these zones to the exhibit as a whole as well as further investigate the reasons for their avoidance by the antelope. The three waterfalls in the exhibit are not well-used and such a feature is not evident in the sitatunga's natural habitat. Re-modelling of defunct areas and more space given over to favoured areas (e.g. the shallow pools and reed beds) would help increase the use of more areas of the exhibit.

Social pressures on individuals within the group could also affect type and duration of behaviour performed, as well as the area of the enclosure the animal is able to frequent. The distinct difference (Figures 2 and 5) between the time spent in biologically-relevant zones by the young male and the rest of the group could be suggested of an individual being forcibly pushed out of the herd and into the remaining, unoccupied areas of the enclosure. Popp (1982) bemoans the lack of information available on sitatunga, in both a wild and captive state, and expresses his wish that captive research will lead into better husbandry and informed management of this species. Consequently, the importance of group dynamics, hierarchy and sociality is hard to infer. Thirty years later, published information is still scarce and as such it is hoped that this paper adds to a gap in our knowledge of more advanced *Tragelaphus* antelope husbandry.

Conclusions

1. The non-random distribution of sitatunga around the enclosure demonstrates a preference for specific areas that the animals consider important to them.
2. Sitatunga show a daily rhythmic change to activity that in parts is reminiscent of wild animals but that can also show deviation away from what is considered a natural time budget.
3. The welfare of the sitatunga appears good with no display of stereotypic, unwanted behaviours.
4. Feeding/foraging, resting/rumination and standing appear the most biologically-important behaviour shown by captive sitatunga, characteristics that mirror the behaviours recorded in wild animals. Behaviours that occupy the majority of the animal's time should be enabled in its enclosure both at the "normal" time of day and in a habitat that allows the behaviour to be performed in its entirety.
5. Provision of more tall grass and reedy areas in sitatunga exhibits would be beneficial to behavioural performance, sitatunga welfare and the development of a more interesting and relevant public exhibit.
6. Reduction in the area of short grass provided, or the use of short grass pathways through areas of taller vegetation could help replicate the type of environment selected by wild sitatunga.

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References

Antelope TAG. (2006). *AZA Minimum husbandry guidelines for keeping antelopes and gazelles in captivity*.

Bashaw M.J., Tarou L.R., Maki T.S., Maple T.L. (2001). A survey assessment of variables related to stereotypy in captive giraffe and okapi. *Applied Animal Behaviour Science* 73 (3): 235-247.

Baxter E., Plowman A.B. (2001). The effect of increasing dietary fibre on feeding, rumination and oral stereotypies in captive giraffe (*Giraffa camelopardalis). Animal Welfare* 10: 281-290.

Blowers T.E., Waterman J.M., Kuhar C.W., Bettinger T.L. (2012). Female Nile hippopotamus (*Hippopotamus amphibius*) space use in a naturalistic exhibit. *Zoo Biology* 31: 129-136.

Clark F.E., Fitzpatrick M., Hartley A., King A.J., Lee T., Routh A., Walker S., George K. (2012). Relationship between behaviour, adrenal activity, and environment in zoo-housed western lowland gorillas (*Gorilla gorilla gorilla*). *Zoo Biology* 31: 306-321.

Day J.E.L., Kyriazakisa I., Lawrence A.B. (1995). The effect of food deprivation on the expression of foraging and exploratory behaviour in the growing pig. *Applied Animal Behaviour Science* 42: 193-206.

de Jonge F.H., Tilly S-L., Baars A.M., Spruijt B.M. (2008). On the rewarding nature of appetitive feeding behaviour in pigs (*Sus scrofa*): Do domesticated pigs contrafreeload? *Applied Animal Behaviour Science* 114: 359-372.

Delany M.J., Happold D.C.D. (1979). *Ecology of African mammals*. London, UK: Longman Group Ltd.

Dickens M. (1955). A statistical formula to quantify the "spread of participation" in group discussion. *Speech Monographs* 22: 28–31.

Duncan I.J.H. (1998). Behaviour and behavioural needs. *Poultry Science* 77: 1766–1772.

Estes R.D. (1991). *The behaviour guide to African mammals.* Berkeley, USA: University of California Press.

Estevez I., Christman M.C. (2007). Analysis of the movement and use of space of animals in confinement: The effect of sampling effort. *Applied Animal Behaviour Science* 97: 221-240.

Fabregas M.C., Guillen-Salazar F., Garces-Narro, C. (2012). Do naturalistic enclosures provide suitable environments for zoo animals? *Zoo Biology* 31: 362-373.

Games, I. (1983). Observations on the sitatunga *Tragelaphus spekii selousi* in the Okavango delta of Botswana. *Biological Conservation* 27: 157-170.

Hebert P.L., Bard K. (2000). Orang utan use of vertical space in an innovative habitat. *Zoo Biology* 19:239-251

Hedeen S.E. (1983). The use of space by lowland gorillas (*Gorilla g. gorilla*) in an outdoor enclosure. *Ohio Journal of Science* 83(4): 183-185.

Kingdon J. (1982). *East African mammals; an atlas of evolution in Africa (volume III part C. bovids).* London, UK: Academic Press.

IUCN SSC Antelope Specialist Group. (2008). *Tragelaphus spekii*. In: IUCN 2011. *IUCN Red List of Threatened Species*. Version 2011.2. www.iucnredlist.org.

MacDonald D. (2001). *The new encyclopedia of mammals* (2nd edition). Oxford, UK: Oxford University Press.

Mallapur A., Qureshi Q., Chellam R. (2002). Enclosure design and space utilization by Indian leopards (*Panthera pardus*) in four zoos in southern India. *Journal of Applied Animal Welfare Science* 5(2): 111-124.

Mason G.J., Mendl M. (1997). Do the stereotypies of pigs, chickens and mink reflect adaptive species differences in the control of foraging? *Applied Animal Behaviour Science* 53: 45-58.

Melfi V.A. (2009). There are big gaps in our knowledge, and thus approach, to zoo animal welfare: a case for evidence-based zoo animal management. *Zoo Biology* 28: 1-15.

Owen R.E.A. (1970). Some observations of the sitatunga in Kenya. *East African Wildlife Journal* 8: 181-196.

Plowman A.B. (2003). A note on a modification of the spread of participation index allowing for unequal zones. *Applied Animal Behaviour Science* 83(4): 331-336.

Popp J.W. (1982). Observations on the behaviour of captive Sitatunga (*Tragelaphus spekii*). *Zoo Biology* 1(1): 59-63.

Reinhardt V., Liss C., Stevens C. (1996). Space requirement stipulations for caged non-human primates in the United States: a critical review. *Animal Welfare* 5: 361-372.

Robinchaud W.G. (2011). Family Bovidae (sitatunga). In: Wilson, D.E. and Mittermeier R.A (eds). *Handbook of the Mammals of the World* (volume 2). Barcelona, Spain: Lynx Edicions.

Rose P.E., Roffe S.M. (2013). A case study of Malayan tapir (*Tapirus indicus*) husbandry practice across 10 zoological collections. *Zoo Biology* (article in press), DOI: 10.1002/zoo.21018.

Ross S.R., Lukas K.E. (2006). Use of space in a non-naturalistic environment by chimpanzees (*Pan troglodytes*) and lowland gorillas (*Gorilla gorilla gorilla*). *Applied Animal Behaviour Science* 96: 143-152.

Ross S.R., Schapiro S.J., Hau J., Lukas K.E. (2009). Space use as an indicator of enclosure appropriateness: A novel measure of captive animal welfare. *Applied Animal Behaviour Science*, 121 (1): 42-50.

Ross S.R., Calcutt S., Schapiro S.J., Hau, J. (2011). Space use selectivity by chimpanzees and gorillas in an indoor-outdoor enclosure. *American Journal of Primatology* 73: 197-208.

Seidensticker J., Forthman D.L. (1998). Evolution, ecology and enrichment: basic considerations for wild animals in zoos. In: Shepherdson, D.J., Mellen, J.D. and Hutchins, M. (eds). *Second nature, environmental enrichment for captive animals.* Washington, DC: Smithsonian Institution Press.

Skinner J.D., Chimimba C.T. (2006). *The mammals of the South African Subregion* (3rd edition). Cambridge, UK: Cambridge University Press.

Starin E.D. (2000). Notes on sitatunga in the Gambia. *African Journal of Ecology* 38(4): 339-342.

WAZA (n.d.). Sitatunga in the zoo. Available from: *http://www.waza.org/en/zoo/choose-a-species/mammals/eventoed-ungulates-artiodactyla/antelopes/tragelaphus-spekii*

Wronski T., Apio A., Plath, M. (2006). Activity Patterns of bushbuck (*Tragelaphus scriptus*) in Queen Elizabeth National Park. *Behavioural Processes* 73: 333-341.