

Investigating the behaviour and enclosure use of zoo-housed Cuvier's dwarf caiman *Paleosuchus palpebrosus*

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ABSTRACT - The welfare needs of reptiles in zoological collections are generally less well understood than those of other taxa. Crocodylians represent an excellent opportunity to study a commonly-housed, conservation-dependant zoo animal. We studied the behaviour and enclosure use of five dwarf caimans *Paleosuchus palpebrosus* through day and night, at two British zoological collections; the enclosures had either six or seven identifiable zones. Time of day, mean temperature and collection were used as predictors of behaviour and enclosure usage. Camera traps recorded the position and behaviour of caimans at 30-second intervals. At each zoo, 80 hours of data were collected from which we constructed activity budgets and calculate a relativised Electivity Index of enclosure usage. The results identified that water-based perching, floating, swimming, immobile water behaviour and underwater behaviour were significantly affected by time of day, and that collection and temperature were good predictors of some behaviours. As for enclosure use, zone 3 (shallow water) was slightly overutilised in both collections, while all other zones were underutilised. Time was a significant predictor of the use of zones 3, 5, 6 and 7. There is considerable scope for future research on crocodylians in zoos.

INTRODUCTION

Modern zoological collections are united in their aim to champion both conservation and education (Hosey, 2005). It is important to ensure that animal welfare is optimised, both for the zoo and the general public (Melfi, 2009; Moss & Esson, 2010). However, not all zoo-housed species are equally well studied. Despite being frequently housed in zoological collections, reptiles have been researched less frequently (Brereton & Brereton, 2020; Moszuti et al., 2017). Reptiles are cognitively more complex than is often acknowledged, with many reptile species showing evidence of problem-solving ability, personality and social learning (Learmonth et al., 2021). Applying an evidence-based approach to future studies could help develop the husbandry and welfare of unrepresented taxa such as reptiles (Melfi, 2009).

One Order of reptiles that is well-represented in zoos is the Crocodylia (Ziegler et al., 2017) and there have been several zoo-based studies on crocodylian welfare. Enrichment has been shown to have a positive impact on the behaviour of African dwarf crocodiles *Osteolaemus tetraspis* (Uwakaneme et al., 2004) and in the case of broad-snouted caimans *Caiman latirostris* it was found that only 53 % of their husbandry requirements were being met in captivity (Prystupczuk et al., 2019; Verdade et al., 2006). Studies of the behaviour and enclosure use of Nile crocodiles *Crocodylus niloticus* in the presence of visitors demonstrated no effect from the visitors (Riley et al., 2021) but visitors significantly increased inactive behaviours in dwarf caiman (Hamilton et al., 2022). These studies show the feasibility of welfare research for zoo-housed crocodylians and the opportunity

for further research. It is in this context that we investigated the behaviour and enclosure use of dwarf caimans in two zoological collections

METHODS

Study subjects and location

Following University Centre Sparsholt ethical approval (UCS050520) observations were made on two Cuvier's dwarf caiman *Paleosuchus palpebrosus* at The Living Rainforest and three individuals at Crocodiles of the World (see Table 1). The enclosures at Crocodiles of the World (Fig. 1A) and The Living Rainforest (Fig. 1B) are similar in design and contain a basking area, bank area, open water and a zone out of sight of the public. At Crocodiles of the World the caimans shared their enclosure with two male South American river turtles *Podocnemis expansa*.

Behaviour

The objective of the study was to build an understanding of dwarf caiman behaviour and enclosure usage at different times of the day (Plowman, 2008). Data collection was completed between 23 August 2020 and 5 October 2020, making up 160 hours; 80 hours per collection (for five whole days). Camera traps (Bluesmart trail camera, 4K 20MP IP66) (wide angle, infrared, set at 20MP) allowed the behaviour to be recorded without the observer effect, which has been reported in reptiles (Riley et al., 2021). Two camera traps were placed in each enclosure to ensure animals were always visible. Eight time codes were used to define different times of the day and to reduce pseudo replication effects (Plowman, 2008) (see Table 2). Time of day and

Table 1. Dwarf caiman sex, hatch date, and origin from two zoo collections

Collection	Sex	Hatch date	Origin
Crocodiles of the World	Male	Between April 2005 and April 2006	Undetermined
	Female	Between April 2000 and April 2001	Private British collection
	Female	15 September 1987	Cologne Zoo
The Living Rainforest	Male	17 August 2014	Undetermined
	Male	16 July 2015	Undetermined

Table 2. Eight time codes altered from Chapman et al. (2018)

Day/Night	Time code	Time of observation
Night	Late night	01:00-03:00
Night	Dawn	04:00-06:00
Day	Morning	07:00-09:00
Day	Late morning	10:00-12:00
Day	Afternoon	13:00-15:00
Day	Evening	16:00-18:00
Night	Dusk	19:00-21:00
Night	Early night	22:00-00:00

Table 3. Ethogram of state behaviours

Behaviour	Description
Terrestrial locomotion	Travelling taking place on land
Immobile land behaviour	The individual is not in the pool and is resting, thermoregulating or gaping
Surface swimming	Swimming on the surface of the water. Eyes and back above the water surface.
Floating	Individual immobile on the surface of the water or only the top of the head is showing
Perched in water	Individual head above the water with limbs resting on a surface/object under the water; absence of any other behaviour
Underwater	Completely immersed under the water
Out of sight	Unable to identify the location of the individual or determine the behaviour accurately

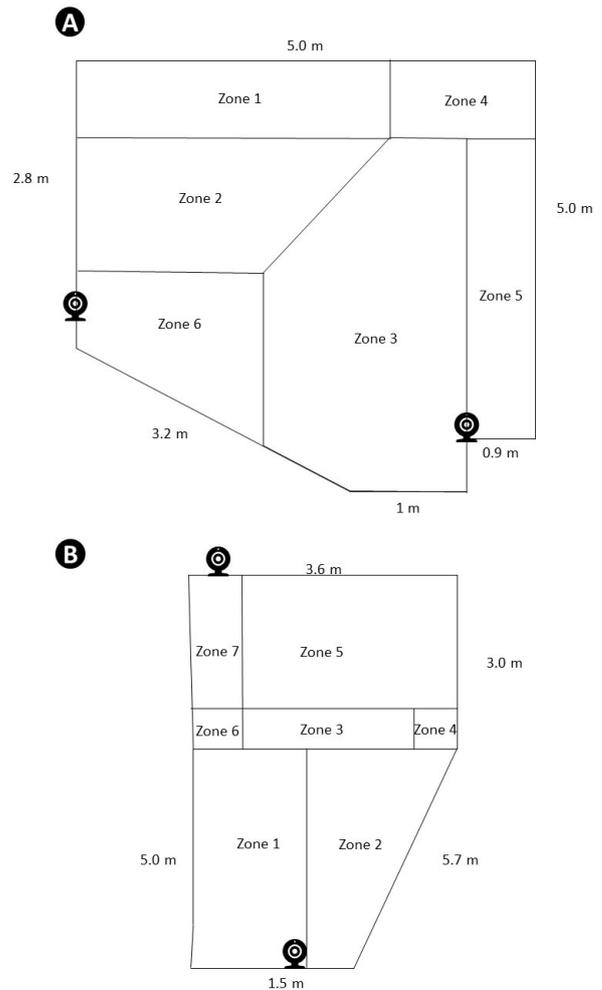


Figure 1. Dwarf caiman enclosures with zones, measurements, and camera trap positions (camera symbols) - **A.** Crocodiles of the World, basking is available in zone 2, and **B.** The Living Rainforest, basking is available in zone 1

mean environmental temperature (from the camera trap’s internal temperature gauge) were recorded as predictors of behaviour and enclosure usage. The cameras were set to take photographs automatically every 30 seconds (categorised as instantaneous scan sampling). When an individual was located between two or more zones, the location of the head and forelimbs was used to identify the zone occupied. An ethogram was devised to describe the various behaviours displayed by the caimans (Bateson & Martin, 2021) (Table 3) and the observed behaviours were subsequently summarised in activity budgets (Fig. 2).

Enclosure use

The enclosures were divided into zones based on the useable space for the caimans and the biological use of each area (Fig. 1 A & B, Table 4). Both zoos were open to the public seven days week, with visitor hours for The Living Rainforest being 09:30–16:00 and for Crocodiles of the World from 10:00–17:00. The two exhibits were indoors with limited natural lighting. Both collections controlled their heating provisions through a thermostat, and the UV lighting provisions were on a timer. For the Living Rainforest they turned on at 08:00

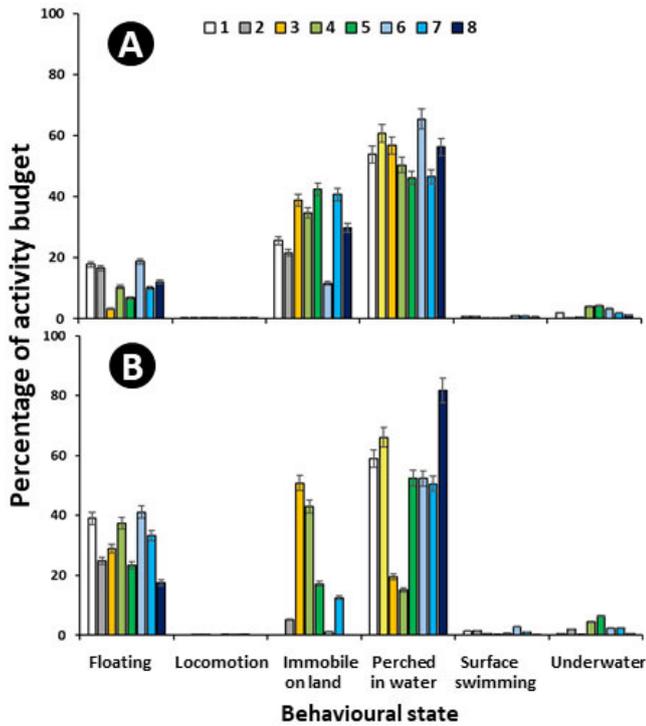


Figure 2. Activity budget for caimans housed at - **A.** Crocodiles of the World, **B.** The Living Rainforest, across all time periods (+/- standard error), Key: 1. Late night, 2. Dawn, 3. Morning, 4. Late morning, 5. Afternoon, 6. Evening, 7. Dusk, 8. Early night

h and off at 16:30 h, and for Crocodiles of the World turned on at 08:00 h and off at 17:00 h. Sizes of each respective zone were calculated based on exhibit blueprints.

Once data were collected, a relativised Electivity index (E^*) was used to express the relative zone usage (Brereton, 2020). Electivity index values range between a maximum of 1 (overutilisation) and a minimum of -1 (underutilisation) of each zone. A value of 0 indicates use that an animal is neither overutilising nor underutilising a zone (i.e. the zone makes up 50 % of the exhibit, and the animal spends 50 % of its time in that area). The values were estimated from the formulae below taken from Vanderploeg & Scavia (1979), where r_i refers to the observed use of a zone, p_i refers to the expected use of a given zone (generated using the proportional size of the zone in comparison to the total available space). The letter n denotes the total number of zones or resources available to the study species.

$$E^* = (W_i - (1/n)) / (W_i + (1/n)) \text{ where } W_i = (r_i/p_i) / \sum (r_i/p_i)$$

Data analysis

Behavioural and enclosure use data were collated in a Microsoft Excel 2019© spreadsheet and statistical analyses undertaken using Minitab® 19. Prior to testing of behaviour and enclosure use data, normality of the residual errors was confirmed. Checks were also made using general linear models to determine whether the collection (as a random effect) had high standard deviation (SD) values. As the SD values were consistently low, collection was discounted as a random effect. Behavioural data were analysed using a series

Table 4. Zone sizes and their definitions for dwarf caiman enclosures at The Living Rainforest and Crocodiles of the World

The Living Rainforest	Definition
Zone 1 (5.92m ²)	Open land with a basking area
Zone 2 (3.6m ²)	Capture cage area
Zone 3 (1.04m ²)	Shallow bank water area
Zone 4(0.37m ²)	Deepwater with cover
Zone 5 (4.89m ²)	Open water
Zone 6 (0.46m ²)	Water/land combination with cover
Zone 7 (1.5m ²)	Waterfall
Crocodiles of the World	Definition
Zone 1 (2.04m ²)	Land with cover
Zone 2 (3.35m ²)	Open land basking area
Zone 3 (5.48m ²)	Open water with a shallow bank and perching areas
Zone 4 (0.82m ²)	Open water with land access
Zone 5 (1.93m ²)	Open water with access to the shallow bank
Zone 6 (1.55m ²)	Open water with land access

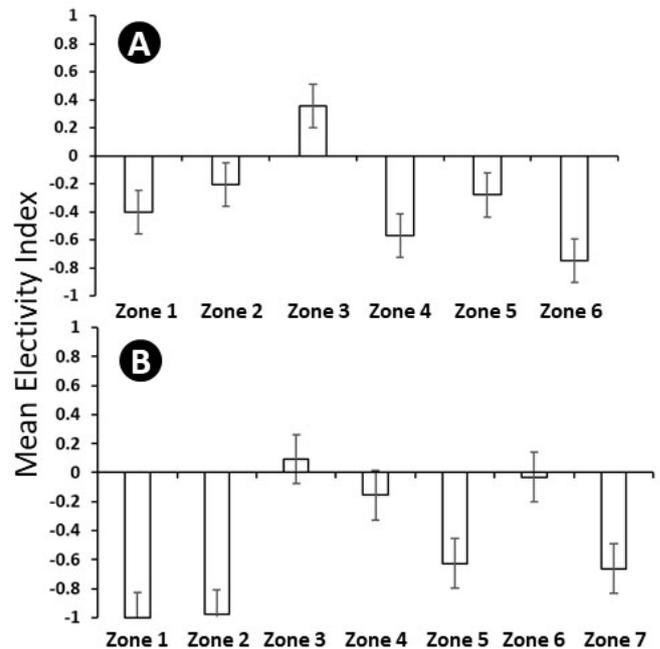


Figure 3. Mean Electivity Index values for enclosure zones - **A.** Crocodiles of the World, and **B.** The Living Rainforest, across all time periods (+/- SE)

of Poisson regressions (not general linear models), in which the variables of mean environmental temperature, collection and time of day (categorical) were inputted as predictors. For enclosure use data, regressions were run on the Electivity

Index values, with mean environmental temperature, collection and time of day (categorical) inputted as predictors. A Bonferroni correction factor was applied to account for the use of three predictors in the Poisson regression and regression models, meaning that the new, corrected alpha value was 0.016. The results of statistical modelling are presented in Supplementary material, available from the BHS website.

RESULTS

Behaviour

The activity budgets for the caimans housed at Crocodiles of the World and the Living Rainforest are shown in Fig. 2A & B respectively. Poisson regressions revealed that floating, immobile land behaviour, perched, surface swimming and underwater were impacted by time of day (See Table 1S, Supplementary Material). Collection and temperature were significant predictors for some, but not all tests.

Enclosure use

Electivity graphs were generated for Crocodiles of the World (Fig. 3A) and the Living Rainforest (Fig. 3B). Except for zone 3 in both collections, on average, all zones were underutilised.

The mean Electivity index was then calculated for each time period for each collection (Fig. 4A & B). This revealed that for both collections, zone use was not consistent throughout the day, with several zones in both collections being overutilised during specific time periods and underutilised during others. Time of day was a significant predictor of Electivity Index value for zones 3, 5, 6 and 7 (Table 2S, Supplementary Material).

DISCUSSION

Behaviour

The results of this study suggest that the behaviour and enclosure use of zoo-housed dwarf caimans can be affected by the time of day, collection, and temperature. Apart from locomotion, dwarf caimans from both collections showed differences in all other behaviours (Table 1S). Model predictive power ranged from as high as 36.37 % for immobile land behaviour, to as low as 2.68 % for terrestrial locomotion.

For both collections, immobile land behaviour and a range of water-based behaviours were observed at different times the day. Recent studies on Nile crocodiles have found comparable results, with the time of day and temperature being predicates of behaviour (Riley et al., 2021). A significant increase in immobile land behaviour during the daytime hours is expected, as this has been noted in previous studies on crocodylians (Verdale et al., 2006) and would be expected, as the dwarf caiman needs to thermoregulate during daylight hours (Lopes et al., 2021; Somaweera et al., 2020). Previous observations on broad-snouted caimans noted that they only left the water to bask in the sun during the hottest time of day (Prystupczuk et al., 2019). Little is known about the nocturnal behaviour of dwarf caimans (Campos & Magnusson, 2016). Our results indicate that the caimans display water-based

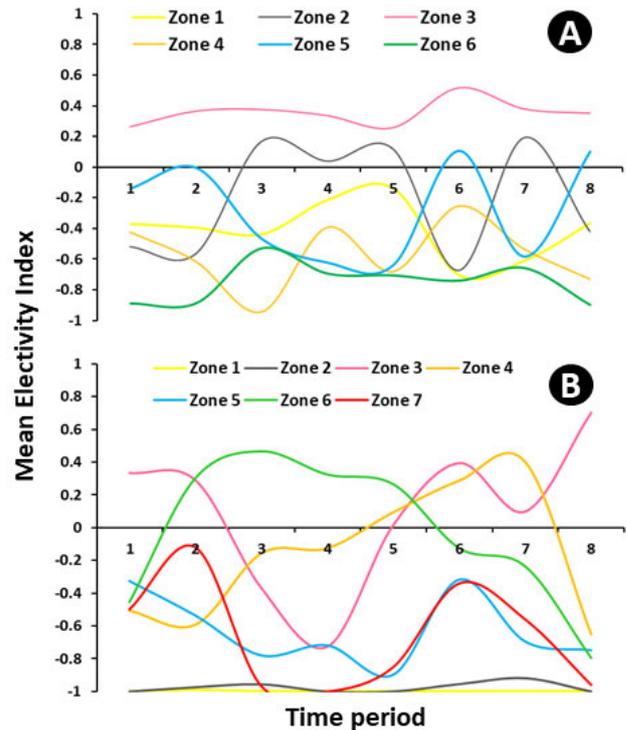


Figure 4. Mean Electivity Index in each time period for enclosure zones by time period - **A.** Crocodiles of the World, **B.** Living Rainforest, Key: 1. Late night, 2. Dawn, 3. Morning, 4. Late morning, 5. Afternoon, 6. Evening, 7. Dusk, 8. Early night

behaviours during the night; similar behaviour has been reported for captive broad-snouted caimans (Filogonio et al., 2014).

The differences between the two collections are particularly interesting, and they may reflect differences in husbandry, environmental conditions or individual background of the dwarf caiman (Marshall et al., 2016). The behaviour of zoo animals is significantly influenced by exhibit design. Increasing environmental complexity may help promote the expression of natural behaviours in zoo-housed dwarf caiman by providing different thermal zones or opportunities to express natural behaviours (Lawrence et al., 2021; Devlin & Ogle, 2022). Future research should focus on how these extraneous variables influence crocodylian behaviour in captivity.

Enclosure use

Except zones 2 and 4, regression models revealed significant predictors for the other enclosure zones. For exhibit zones 3, 5, 6 and 7, time was a significant predictor (Table 2S). The enclosure usage of the exhibits from both collections indicates a predominant use of water-based environment. Zones 3, 5, 6 and 7 are located around the margins of the water's edge in both exhibits. By using the margins, the dwarf caiman could both thermoregulate and have a sense of security by locating themselves within the water (Reber et al., 2021). This resource was apparently not scarce as agonistic interactions between individuals were not observed which could have been displayed if scarcity had resulted in competition between individuals.

In both enclosures, many zones were underutilised which may reflect the innate behaviour of dwarf caimans. Reber et al. (2021) compared the behavioural differences between two Alligatoridae species towards novel objects and found behavioural predispositional differences. They suggested that the differences were because of the species' life history. Spectacled caiman *caiman crocodilus* mothers do not protect the young, making them less bold. This safeguarding behaviour may be the case with the dwarf caiman, as they are the smallest crocodylian species and would be vulnerable to an array of natural predators in the wild (Campos et al., 2012). However, the regression outputs suggest that there are differences between collection management or temperature, which could explain why certain zones were underutilised at different times of day.

The ability of the model to account zone usage was low in the case of zone 3 ($R^2 = 16.95\%$) and zone 4 ($R^2 = 26.94\%$) where significant differences were found, suggesting other variables may be predictors for behaviour or enclosure use (Rose et al., 2021a). Among the variables in zoo studies, the presence of visitors is a factor to consider in zoo research (Hosey, 2005). The Visitor Effect (VE) has been regraded to have an overall negative effect on zoo species, associated with an increase in stereotypical and avoidance behaviours (Chiew et al., 2021). A recent study on dwarf caimans suggested they were affected by VE, as behavioural diversity was significantly reduced when visitors were present (Hamilton et al., 2022). This is an issue, as space use is a major component of crocodylians thermoregulatory behaviour, and if VE is influencing the behaviour then it may have consequences on welfare (Riley et al., 2021b). Future research should focus on how the negative impacts of VE on dwarf caiman behaviour can be mitigated.

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