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Research article

A novel approach to studying enclosure and support usage in siamangs (*Symphalangus syndactylus*): using a 3D computer model

Colleen Goh[1], Mary L. Blanchard[2], Karl T. Bates[1], Phillip L. Manning[3,4], and Robin. H. Crompton[1]

[1]*Department of Musculoskeletal Biology, Institute of Ageing and Chronic Disease, University of Liverpool, The William Henry Duncan Building, West Derby Street, Liverpool L7 8TX, United Kingdom*
[2]*School of Biosciences, University of Birmingham, Birmingham B15 2TT, United Kingdom*
[3]*Department of Geology and Environmental Geosciences, College of Charleston, 66 George Street, Charleston, South Carolina, 29242, USA*
[4]*School of Earth, Atmospheric & Environmental Sciences, University of Manchester, Oxford Road, Manchester, M13 9PL, United Kingdom*
Correspondance: Colleen Goh; E-mail: coll0003@liverpool.ac.uk; Telephone: 07450220831

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Abstract
This study set out to gain preliminary data to: (1) assess the accuracy of a computer-aided design (CAD) approach in recording the full 3D geometry of a zoo primate enclosure, and (2) evaluate the possibility of using the CAD approach to extract patterns of enclosure use (eg. quantify support availability and preference, and map behavioural data within the 3D enclosure model to visualise, identify and investigate spatial enclosure usage trends). We created two 3D models of the same enclosure in a zoo in the UK housing an adult male, an adult female and a juvenile siamang (*Symphalangus syndactylus*) using a generic CAD approach and a long-range laser scanner (LiDAR). The CAD model yielded an average geometric error of ~15% in terms of position, height and diameter of structures relative to the LiDAR model. The CAD model was divided into zones to create colour maps of enclosure usage during behaviours such as feeding and foraging, inactivity and locomotion/posture. The CAD model permitted accurate quantification of support availability and identification of exact supports and zones most frequently used for given behaviours. Using the CAD model, apparently underused supports and zones were also identified. We then attempted to determine possible reasons for such infrequent usage. Electivity indexes, a measure of support preference within a particular zone, permitted us to explore why specific supports were preferred over others in the immediate proximity. Electivity indexes were higher for strong horizontal initial supports (mainly poles) during richochetal brachiation indicating they were chosen despite having other support types in close proximity. This suggests the need for a strong horizontal support to generate sufficient propulsive force during push off, to create the flight phase characteristic of richochetal brachiation.

Introduction

Arboreal primates interact with, and locomote within, complex 3D environments both in captivity and in the wild. It is difficult to quantify the role of support availability and distribution when studying positional behaviour and support usage (Crompton 1980; Cannon and Leighton 1994; Warren 1997; Thorpe and Crompton 2006; Blanchard et al. 2015). For example, if a species uses vertical supports more in leaping, it is difficult to know if this is a result of higher vertical support availability or a behavioural preference or adaptation [see eg. in Blanchard and Crompton (2011)]. Further, primates often favour specific routes, feeding locations and/or resting places, so it is important to consider all available structures before drawing conclusions about their behaviour. This problem has not yet been fully addressed (Cannon and Leighton 1994), and no standardised method exists to quantify support availability and distribution. Previously employed methods (see eg. Whitten 1982; Crompton 1984a; Cannon and Leighton 1994; Balko and Brian Underwood 2005; Manduell et al. 2012) include measuring support diameter in quadrats or transects at breast height or at multiple levels in the wild to quantitatively estimate support distribution and availability of the whole forest range being used by the subjects. However, detail (such as extremely small supports) is often missed and supports in close proximity at the moment of the locomotor event cannot be taken into account, and thus support type arrangement, proximity and density cannot always be quantitatively assessed.

A potential solution is to create a 3D digital representation of the environment using ground-based laser scanning (Nilsson 1996; Zimble et al. 2003; Goodwin et al. 2006; Hyde et al. 2006) or photogrammetry (Sellers and Hirasaki 2014). One of the most accurate methods of obtaining data for a 3D model of a scene is by using Light Detection And Range (LiDAR) scanning (Bates et al. 2010). Ground-based LiDAR technology has been used widely in geology (Bates et al. 2008b), palaeontology (Bates et al. 2008a; Bates et al. 2009a; Bates et al. 2009b), engineering (Liu et al. 2010), space travel (Johnson et al. 2002) and forest structure studies (Zimble et al. 2003; Goodwin et al. 2006; Hyde et al. 2006). However, this technique is relatively expensive and may be impractical in certain field situations. In recent years, computer-aided design (CAD) approaches have been used as a low cost alternative to direct digitisation technologies, wherein easy-to-take physical measurements are used to reconstruct simplified 3D models of an environment for further interrogation and manipulation (Hong et al. 2008; Singh et al. 2013; Ying et al. 2011).

This study has two objectives: First, to compare the accuracy of low-cost 3D CAD reconstruction with a sub-millimetre accurate LiDAR model of a primate enclosure. Demonstrating accuracy and reliability of CAD modelling in this context could potentially stimulate wider use of this approach in other captive positional behaviour and support usage studies and in the planning stages of enclosure development. Second, the 3D models are exploited to gain preliminary data on a range of aspects relevant to understanding behaviour of captive siamangs (*Symphalangus syndactylus*), such as positional and non-positional behaviour and apparent support choice, while considering the influence of habitat structures by quantifying support availability and preference. Siamangs are arboreal (Chivers 1977) and known to repeatedly use aerial pathways (Fleagle 1976), but their positional behaviour has only been studied once in the wild (Fleagle 1976) and not yet in captivity. Few studies have investigated captive siamang behaviour patterns (Fox 1972; Fischer and Geissmann 1990). The 3D enclosure models will allow us to combine quantification of support availability, preference and enclosure usage patterns with 3D visualisation, permitting a greater understanding of the impact that captivity has upon the behaviour of this species and leading to wider implications for the future design and construction of captive primate habitats. For example, by identifying which exact supports and areas are favoured for certain positional and non-positional behaviours, and why, zoos can aim to: 1) encourage those behaviours and hence activity and 2) avoid stress by making sure there are sufficient suitable supports and areas to carry out those behaviours and avoiding the removal of favoured supports during enclosure redesign. In addition, knowing which supports are underused and why, can contribute to enclosure redesign which encourages maximal use of the enclosure. In particular, there is a lack of documented studies on siamang enclosure usage and captive siamang positional behaviour (and support usage).

Materials and methods

LiDAR model

A portable Z+F IMAGER 5010C medium-range near infrared laser-scanner (LiDAR), that can achieve sub-millimeter accuracy, was used to digitally capture the siamang enclosure. A series of scans were collected from multiple scan stations, and combined to provide a full 3D point cloud for each enclosure. A point cloud is a set of data points in a 3-dimensional coordinate system. Scans were spatially aligned using the automated cloud-to-cloud registration tool in ReCap360 (www.recap.autodesk.com). Aligned point clouds were imported into Geomagic Studio, where they were cropped so only points within the enclosure fences were retained. Remaining points were meshed using Geomagic Studio's surfacing tool (Figure S1 shows the LiDAR model).

CAD model

Measurements of diameter, height and angle of structures were taken using a measuring tape (accurate to 1 mm) on all possible structures in the enclosure. Total length, width and height measurements of the enclosure were provided by the Zoo. When supports were not within reach because of health and safety constraints, an estimation of dimensions was made based upon similar support structures within the enclosure that could be reached and measured. Architect Michelle Wong created the CAD model in SketchUp (Figure 1) by manually building each structure into a 3D model, based upon dimensions taken in this study. This CAD model has been made freely available in supplementary information.

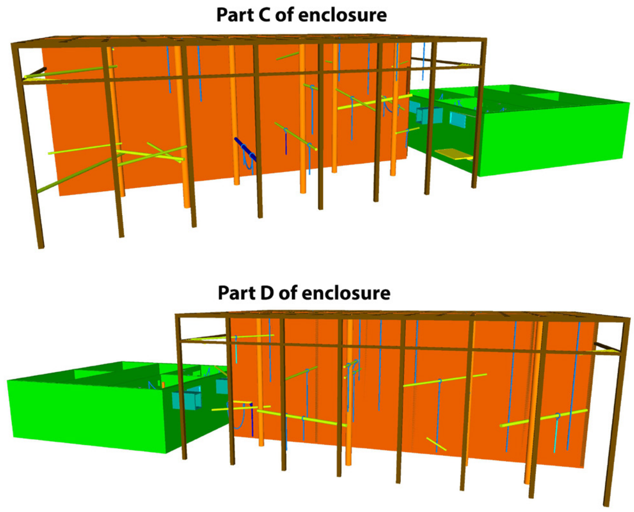

Figure 1. SketchUp model of outside enclosure (orange) with division of enclosure longitudinally into parts C and D. The inside enclosure (green) has not been included in this study.

Verification of the CAD model

The LiDAR model was used herein as the benchmark to assess the accuracy of the CAD model generated in SketchUp. All support heights and diameters (total of 10 supports) that were captured in the LiDAR model were measured in Meshlab and compared to those within the CAD model. The percentage errors and average percentage errors for each support were calculated.

Data collection and transcription

All work was conducted under ethical permission from the Zoo and the University of Liverpool. Data were collected via videography by Colleen Goh and Mary Blanchard from an adult male (14 years old) and an adult female (14 years old) siamang that were housed together with their son (5 years and 6 months old). Data were collected by focal, all-occurrence sampling (Altmann 1974);

Table 1. Definitions of each behaviour type recorded

Behaviour	Definition
Feed and forage	All food gathering and intake activities, fruit and non-fruit
Travel[1]	Any physical displacement that takes place, e.g. walking, climbing, running, with or without carrying objects
Inactivity[1]	Sleeping, reclining with eyes opened or closed, being stationary when not feeding or socialising
Auto-groom	Grooming oneself
Rocking	Repetitive forward and backward movmeent of torso
Allo-play[2]	Non-aggressive activities with more than one individual, such as play, groom, chase or engaging in body contact
Aggression[2]	Hitting surfaces, bluff charges, chasing, physical fighting. submission and fleeing
Repetitive-swinging	Swinging back and forth on mobile support

[1]Modified from Blaney and Walls (2004); [2]Modified from Kuhar (2008)

each sample lasted for two minutes. In total, 94 samples were collected over nine days. The date, time and number of samples are shown in Figure S2 ; S denotes supplementary materials. The variables collected were name, positional behaviour, behaviour, height, initial support zone, initial support of forelimbs and hindlimbs, terminal support zone and terminal support of forelimbs and hindlimbs. Behaviour was classified into “feed and forage”, “travel”, “inactivity”, “auto-groom”, “rocking”, “allo-play”, “aggression”, “repetitive swinging” and “calling”. Definitions for each classification can be found in Table 1. Using Hunt et al. (1996) as a guide, positional modes and submodes were separated and classified into individual locomotor/postural behaviours that were relevant to this study. Initial and terminal supports refer to specific structures used at the beginning and end of each locomotor event. A locomotor event was considered to end when the subject changed support. For example, if the siamang stood bipedally on the ground and used a robe to swing himself up onto a platform, the initial supports would be the ground and the rope, and the terminal support would be the platform. A locomotor event was also considered to end when the subject moved by more than 1 m on a support. For example, if the siamang brachiated on a pole for more than 1 m, each arm swing would be considered as a new locomotor event as each arm swing spanned more than 1 m. For postural events, only initial supports were recorded as no movement was involved. Descriptions of each locomotor/postural behaviour can be found in Table S1. Behaviour and height were recorded at the start of each positional event. The outside enclosure (orange) was divided longitudinally into two halves, C and D, on the left and right, respectively, if standing at the indoor enclosure (green) (Figure 1). Each half was subsequently divided vertically (4 levels: a, b, c and d) and horizontally (14 rectangles: CC1-14 and DD1-14 for parts C and D, respectively) into “zones” (Figure 2). Hence, “initial support zone” refers to the specified “zone” where the subject is found at the beginning of each locomotor/postural event. Each zone and support was assigned a code. Hence the CAD model could display the supports and zones corresponding to certain positional and non-positional behaviours. The top and bottom vertical levels were 1 m from the ground and ceiling, respectively. These divisions were chosen based on the height of a siamang when orthograde (~1 m), so the bottom level almost always meant the subject was terrestrial, while the top level almost always meant that the subject was in close proximity to the ceiling. The remaining levels (middle two) were divided equally into two for simplicity. These superficial vertical levels were added to the model to enable accurate vertical height recording during data transcription while watching the videos. Data were analysed using SPSS version 22.

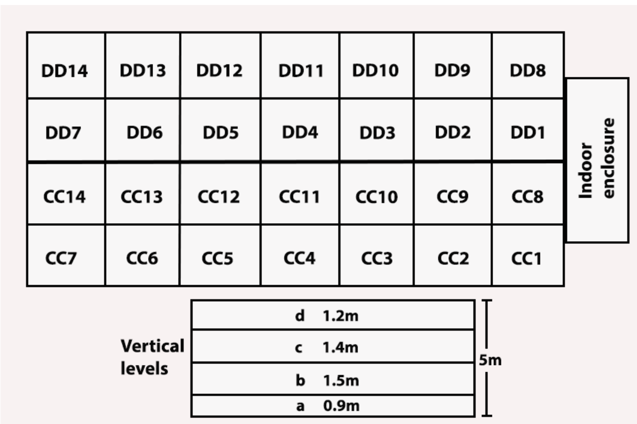

Figure 2. Division of enclosure into horizontal (top) and vertical (bottom) levels. Height of each vertical level is given in metres. Each area is given a horizontal code, i.e. CC1, and a vertical code, i.e. CC1d therefore refers to the area CC1 at level d.

Analysis of enclosure usage zones

The frequency and percentage of use of each enclosure zone, with corresponding behaviour, was calculated using SPSS. Colour maps in the CAD model were then created using SketchUp to show, out of all the zones that were used, the least and most used zones overall, and for specific behaviours such as feed and forage, and inactivity, for visual identification of trends (see for example Figures S3 , S4 and S5). For simplification, only the least and most used zones were focused on in this study to enable us to easily identify factors that could have led to any differences.

Analysis of support availability

Support availability for a specified zone was calculated by:

Support availability = $\Sigma SE / V$

ΣSE = sum of surface areas of each support (e.g. ropes, shelves) in the zone; V = volume, which is product of height, width and length of the zone.

The surface area of shelves (considered as rectangular prisms) and that of ropes and poles (considered as cylinders) were calculated by:

Surface area of shelf = 2(wl+hl+hw)

Surface area of rope or pole = 2πrh+2πr2

w = width; l = length; h = height; and r = radius of support.

Thus, if a zone had a height, width and length of 1 m each, and there was a rope or pole with surface area of 1.5 m^2 and a shelf with surface area of 2 m^2, the support availability would be: (1.5 m^2 + 2 m2)/1 m^3 = 2.5 m-1. All calculations were taken from the CAD model in metres. For simplification, the surface area of the outside mesh was considered as a single, solid support.

Analysis of support preference

In order to measure support preference within a zone (i.e. if one support was favoured over others for a specific behaviour), electivity indexes (E) were calculated for each support in a zone following Ross et al. (2009). Therefore, the electivity index takes into account the presence of other supports in close proximity, which is important as a siamang would have to decide which supports to use based on availability and accessibility (within the proximity). The index (E) can range from −1 to 1, a high E indicates a strong support preference and is calculated using Ross et al. (2009) thus:

$$E = [Wi - (1/n)] / [Wi + (1/n)]$$
$$Wi = (ri/pi)/\Sigma ri/pi$$

ri = proportion of time of observed use of support; pi = proportion of time of expected use of support; n = number of supports in the specified zone.

For feed and forage, and inactivity, electivity indexes were calculated for each of the three most frequently used supports (along with the remaining supports in their corresponding zones). These electivity indexes were plotted onto the supports in the CAD model, to aid in visual identification of any patterns in support preference (see Figure S6 for example).

Table 2. Comparison of measurements of supports from LiDAR and SketchUp models.

Support	LiDAR	SketchUp	Error (%)
Position			
D9 hortizontal pole	1.45 m from ground	1.34 m from ground	7.6
D10 horizontal pole	1.24 m from ceiling	0.7 m from ceiling	43.5
D11 horizontal pole	2.08 m from ceiling	1.88 m from ceiling	9.6
D12 horizontal pole	2.03 m from ceiling	1.88 m from ceiling	7.4
D13 horizontal pole	1.54 m from ceiling	1.38 m from ceiling	10.4
D37 ledge	1.42 m from ground	1.41 m from ground	0.70
Diameter			
D10 horizontal pole	0.06	0.06	0.0
D11 horizontal pole	0.103	0.077	25.2
D13 horizontal pole	0.08	0.07	12.5
Length			
D19 vertical rope	0.904	1.18	30.5
D22 vertical rope	1.95	2.2	12.8
D24 vertical rope	1.49	1.69	13.4
D26 vertical rope	1.4	1.09	22.1

Results

Quantifying accuracy of the CAD model

The diameters, relative positions and lengths of all accurately measurable supports (10) that were captured in the LiDAR model, were measured and compared directly with the CAD model (see Table 2). It was found that the recorded diameters, positions and lengths of structures based on the CAD model differed from those of the LiDAR model by an average of 15%. The minimum and maximum percentage differences were 0% and 43.5%, respectively, with the maximum percentage error resulting from a support position that had to be estimated, for health and safety reasons. Percentage error was greater for supports that were higher and had to be estimated by eye (e.g. horizontal pole D10), as compared to supports that were measured manually (e.g. horizontal pole D9 and ledge D37). Longer supports had lower error margins. However, percentage error was greater for bigger supports (e.g. horizontal pole D11) than smaller supports (e.g. horizontal poles D11 and D13). This unexpected discrepancy could be due to the small sample size.

Overall enclosure usage

A total of 713 events of initial-support (IS) and 476 of terminal-support (TS) usage zones were collected. Figures S3, S4 and Table S2 show which five zones were most used (IS: 8.7%, 6.9%, 6.5%, 5.5%, 4.6%; TS: 11.6%, 6.9%, 4.2%, 4.2%, 3.4%) and which two were least used (IS: 0.1%, 0.1%; TS: 0.2%, 0.2%). In both initial and terminal support zones of C and D, the most frequently used zones were near the indoor enclosure at CC8b and DD1b (near the opening between parts C and D; however, the opening is obscured in figures).

Enclosure Use for Feeding and foraging

Sixty-eight bouts of feed and forage behaviour and 202 instances of feed and forage support use were recorded. Figure S5 shows the five most and two least commonly used zones for feed and forage at C and D. Excluding the outside mesh, average support availability (calculated from the CAD model) of the five most commonly used zones was 0.84 m^{-1} (standard deviation = 0.36) whereas that of the least was 0.11 m^{-1} (standard deviation = 0.11) (see methods section 2.6 for derivation of support availability).

The outside mesh (5.4%), shelf C45 (21.3%), horizontal pole C8 (3%) and corner ledge C1 (1.5%) were among the most commonly used supports during feed and forage. These supports (C45, C8 and C1) had a high electivity index of 0.5 whereas other supports in the same zones had a low electivity index of −1 (Figure S6).

Enclosure Use for Inactivity

A total of 142 bouts of inactivity and 506 bouts of support use during inactivity were recorded. Figure S7 shows the five most and two least commonly used zones for inactivity at C and D. The average support availability (calculated from the CAD model) of the top five zones was 1.94 m^{-1} (standard deviation = 1.25) whereas that of the least was 0.95 m^{-1} (standard deviation = 0.19).

With respect to supports used during inactivity, the outside mesh (20.8%), horizontal pole D11 (8.3%), vertical rope D22 (4.9%), and horizontal pole D8 (5.3%) were the most used. Horizontal pole D11 had electivity indexes of 0.36 (at DD9c) and 0.5 (at both DD2c and DD10c) (see Figure S8). Vertical rope D22 had an electivity index of −0.06 and horizontal pole D8 of 0.44 (Figure S8). The remaining supports had lower electivity indexes that ranged from −0.4 to −1.

Enclosure Use for Locomotion

The most commonly displayed locomotor behaviour was brachiate (24.7%), followed by unimanual swing across (18.7%), bipedal walk (8.5%), bimanual swing across (7.1%), and richochetal brachiation (5.8%) (Table S3). Table S4 shows the percentages of supports used in these five locomotor behaviours. The supports used for brachiation and richochetal brachiation were examined in detail.

Support use for 178 instances of brachiation were recorded. Both initial and terminal supports used were positioned evenly along part D of the enclosure (Figure S9). However within part C of the enclosure, initial supports were positioned at either end of the enclosure, and terminal supports were distributed nearer the indoor enclosure (Figure S9). With regards to support orientation preferences, overall horizontal supports were used more than vertical supports by 12% in initial and 16.6% in terminal supports. Also, only three of the top 10 initial supports were horizontal, compared to five of the top 10 terminal supports (Table S4). All horizontal supports used were either the wire mesh, a ledge or horizontal poles 5–10 cm in diameter.

Of the 68 instances of support use recorded for richochetal brachiation, initial and terminal supports in part D of the enclosure were distributed evenly along the middle (Figure S10) and were primarily/exclusively the same (all horizontal poles; Table S3 and Figure S10). However, in part C of the enclosure, initial supports were concentrated near the opening between parts C and D, and terminal supports were positioned at either end of the enclosure (Figure S10). With regards to support orientation preferences, for initial supports, six of the eight most used supports were horizontal and, overall, 31.2% more horizontal than vertical supports were used. However, for terminal supports, horizontal and vertical supports were used equally. As with brachiation, all horizontal supports other than the wire mesh were horizontal wooden poles between 5–10 cm in diameter.

Discussion

The use of both LiDAR and SketchUp to generate digital enclosure models permits a quantitative approach to mapping enclosure use enabling greater insight into the key factors influencing behaviour of the captive siamangs. It must be noted that the findings here may not be directly applicable to other species of *Hylobates* (or other primates) as each primate species is likely to display varying preferences and trends with regards to enclosure and support usage based on species-specific behavioural and evolutionary ecology. Also, since data were collected from late morning to late afternoon due to access to the enclosure, it must be noted that the trends here do not represent a complete picture of enclosure usage (i.e. there is no information regarding where or on which supports the siamangs choose to sleep or spend their early waking hours).

Factors influencing enclosure usage for feed and forage and inactivity

Using the CAD model, we were able to identify which zones were used the most and least. Subsequently, we calculated the support availability in each of those zones (see methods section), which would have been almost impossible without a digital model of the enclosure. The findings suggest that support availability may play an important role in enclosure usage, as average support availability was higher in the zones that were most commonly used. Factors other than support availability were also identified by looking at the patterns displayed with the aid of the CAD model, through colour maps and the detailed visualisation of positions and proximities of structures in a selected region or for the whole enclosure. However, it must be recognised that other factors which were not taken into account in this study, could have influenced the trends identified, such as visitor proximity and number, keeper proximity and proximity to gibbons in the neighbouring enclosure.

Enclosure usage for inactivity (dominated by sitting and orthograde suspension) was influenced by support type and, to a certain extent, support orientation. With the CAD model, we were able to explore in detail the zones (DD8d, DD9c, DD8c, CC1b and CC7d) that were most commonly used for inactivity, and identified within those zones exactly which supports (e.g. D22, D11 and D8) were preferred. Such information can be used by zoos to avoid removal of favoured supports during enclosure redesign and thus reduce stress. Furthermore, we were able to distinguish between true support preference for inactivity, versus support preference as a result of prevalence (something that traditional methods have not been able to accomplish). The CAD model was used to calculate electivity indexes of supports within the zones most commonly used during inactivity, a method which takes into account other supports available within the same zone. The electivity indexes for supports D8 (0.44) and D11 (0.5 and 0.36) were much higher than for supports D21, D3, D22, D40 and D4 (−0.4, −1, −0.06, −1 and −1, respectively). Next, we used the CAD model to identify any similarities or differences that existed between those supports: those with higher electivity indexes were wooden, horizontal supports (ledges D1, C2, D37 or poles D8, D11), whereas those with lower electivity indexes were mostly vertical ropes (D21, D22, D40). A wooden support is stronger than a rope, thus making it safer for inactivity, and sitting can only occur on a horizontal support thus skewing the results to a certain extent. Nonetheless, this indicates that in the presence of varying types of supports (horizontal, vertical, wooden and rope), wooden ones and to a certain extent horizontal ones, are preferred. In addition, it was found that ledges D2 and C1 were not used for inactivity, although they were identical in size, type and orientation as preferred ledges C2 and D1. The CAD model suggests the likely cause for this discrepancy to be a difference in accessibility: ledges C2 and D1 each had a large horizontal pole (> 5 cm in diameter) leading onto them, whereas the nearest supports to ledges D2 and C1 were vertical ropes at least 1 m away, making them substantially less accessible. Such information on support preferences for inactivity and reasons for unused supports is vital during enclosure design, in order for zoos to provide sufficient accessible supports that offer adequate support characteristics for resting and nesting, and to avoid constructing unusable supports.

Using the CAD model, we identified which supports were most commonly used during feeding and foraging (ledge C45, horizontal pole C8 and the ground near ledge C45). The siamangs were often fed near or on ledge C45, or ate the grass on the ground in those zones, explaining why feeding and foraging occurred in those zones. Within the zones most commonly used for feed and forage, horizontal supports (ledge C45 and horizontal pole C8) were preferred over vertical supports (ropes C28, C27 and pole C3) as indicated by the higher electivity indexes of horizontal supports (Figure S6). Therefore, our findings suggest that besides support density, additional important factors influencing enclosure usage for feed and forage are where the siamangs were fed and the presence of horizontal supports. Such information can enable zoos to place favoured support types away from areas where the animals are fed, to encourage activity during feeding and foraging. In addition, for predominantly arboreal primates, such as siamangs, information regarding preferences for sitting and feeding on horizontal supports or suspending and moving on a mixture of vertical and horizontal supports during feeding and foraging can be invaluable to zoos.

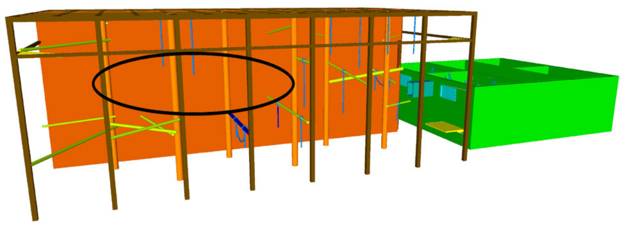

Figure 3. Part C of enclosure. Black oval indicates where there is an absence of supports.

Enclosure usage during brachiation, richochetal brachiation and bipedal walk

With the CAD model we were able to divide the enclosure into zones and visualise the entire enclosure to identify which areas were lacking certain support types; an exercise which would prove very difficult to do by eye. Thus, we were able to determine 1) why brachiation often started at one end and finished near the indoor enclosure in part C, and 2) why richochetal brachiation often started near the opening between parts C and D in part C, but started and finished throughout the same side of the enclosure in part D. We propose that this is explained by an absence of supports (vertical and horizontal) near the middle of part C of the enclosure (Figure 3) at a height where most preferred brachiation supports were positioned elsewhere in the enclosure (above ~2.5 m). Such information is important in helping zoos identify which areas of the enclosure are underused and why.

In addition, our findings suggest that siamangs prefer landing on horizontal supports during brachiation: 1) three of the 10 most commonly used initial supports were horizontal, compared to five of the 10 terminal supports, and 2) overall, 16.6% more horizontal than vertical terminal supports were used as compared to only 12% more horizontal than vertical initial supports. Using the CAD model, we were able to determine that the preference of siamangs to land on horizontal supports during brachiation was not a result of support availability, as vertical supports were available in close proximity (Figure S9). This highlights the importance of the CAD model in interpreting locomotor results; with traditional methods it would be difficult to differentiate between support availability and preference. Landing on horizontal supports is likely to provide more stability (Crompton 1984b; Crompton et al. 2010). The use of more vertical initial supports could be a result of transitioning from various different positional behaviours to brachiation, consequently creating more variation in orientation of initial supports, and the reduced need for stability at the start of brachiation. Although there were no horizontal ropes in the enclosure so no comparison can be made on support type, it is reasonable that evenly distributed horizontal wooden poles (5–10 cm in diameter) at the appropriate height (~2.5 m) should be provided to encourage brachiation throughout the enclosure, particularly given that brachiation is a key locomotor behaviour used by siamangs in the wild (Fleagle 1976) and, although it occurred in this study as the most common locomotor behaviour, is less common in captivity than in the wild (24.7%).

However, in richochetal brachiation, the siamangs preferred a horizontal initial support (unlike in brachiation): 1) 31.2% more horizontal than vertical initial supports were used; however, horizontal and vertical terminal supports were used equally, and 2) six of the eight most used initial supports were horizontal. Similarly, the CAD model revealed that the siamangs preferred to start richochetal brachiation on a horizontal support and that this was not a result of support availability. This preference can be explained by the need for producing a much stronger propulsive force on the initial support to create the flight phase (Crompton et al. 2010), which defines and differentiates richochetal brachiation from normal brachiation. This propulsive force can be generated by pushing off from a strong horizontal wooden pole. Thus, the provision of evenly distributed horizontal wooden poles (5–10 cm in diameter) at the appropriate height (~2.5 m) can encourage richochetal brachiation in captive siamangs.

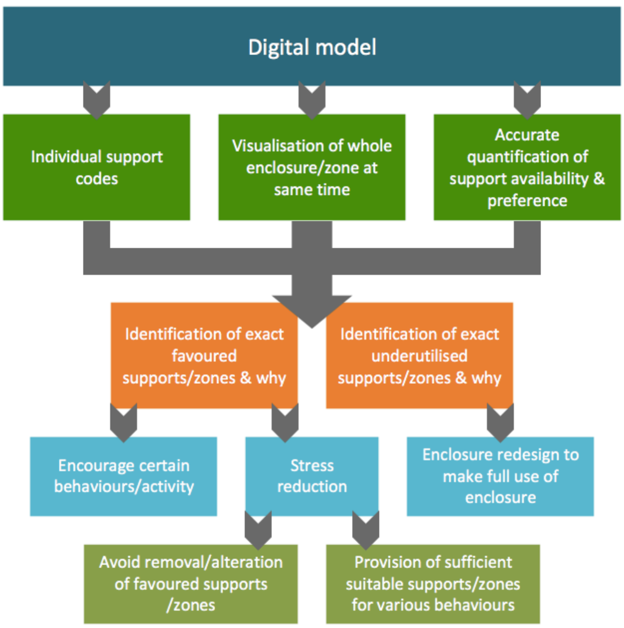

Figure 4. Schematic diagram summarising advantages of CAD method specific to this study.

Advantages and limitations of the CAD method

This study has demonstrated that there are many advantages of using the CAD method to study behaviour trends in captive primates. A variety of free CAD software packages are now available, and most (including SketchUp) allow data to be exported in generic 3D formats for use in a variety of other packages. Models are extremely flexible and easily manipulated, for example in this study we artificially split the enclosure into cubes to enable detailed study of enclosure usage. A digital model provides permanent access to the 3D architecture of the study site, allowing enhanced visualisation and communication of results and a permanent 3D record of enclosure at the time. This results in a highly reliable and flexible tool which can be adapted and widely used. Advantages specific to this study that were mentioned throughout the results/discussion above are summarised in a schematic diagram (Figure 4).

As with any method, there are limitations. The CAD model was shown to have an average of 15% error in support height and diameter when compared to the far more accurate LiDAR model. The CAD error could perhaps be reduced by training and repeated re-assessment of the accuracy of estimating dimensions by eye. The maximum percentage error arose from the position of supports that were very high and had to be estimated. There is high variability in accuracy of height/diameter estimations in the field. In Thorpe et al. (2009), estimations of support diameter were reported to be 97% accurate and in Enstam and Isbell (2004), difference between tree height estimations and measurements were found to be non-significant. However according to Nilsson (1996), in a forest with an average tree height of 12.5 m, heights measured and estimated from the ground were underestimated by 2.1–3.7 m. Also, Bezanson et al. (2012) showed that there is high variability between observers of varying amounts of training/experience (up to 28 cm difference in substrate diameter estimation and 3–11 m difference in tree height estimation). This has implications for locomotor studies in the wild (Blanchard et al. 2015; Britt 1996; Crompton 1984; Manduell et al. 2012; McGraw 1996; Warren 1997) that involve estimating and guessing support heights that are relatively much higher (e.g. > 10 m). In the future, a longer period of training and regular testing should be carried out as in Thorpe et al. (2009), to ensure more accurate estimates of support height and diameter. Additionally, LiDAR has applicability to the assessment of support availability in the wild, but the cost of the equipment may often prove prohibitive, and an alternative of assessment by photogrammetry from multiple still or video images is more practical, and involves using techniques such as those of Sellers and Hirasaki (2014). While it could not feasibly be applied to a whole forest patch, it would, however, be feasible to create a CAD model of given tree species or forest zones, to inform observational studies of locomotion and support use.

Conclusion

The use of quantitative 3D mapping, through LiDAR or CAD techniques, is a powerful approach to quantify and visualise the behaviour of captive primates within their enclosure, permitting the discrete spatial mapping of activity and locomotion. We believe that this study further demonstrates that provision of a CAD model is a simple, cost-effective way for zoos to assess enclosure usage, especially in terms of behaviour and support usage. The CAD model used here: 1) permitted relatively accurate quantification of support density and preference, which otherwise would have been almost impossible without an enclosure model; and 2) allowed identification of patterns through 3D colour enclosure maps and the ability to visualise positions and proximities of structures in detail, in a region of interest or in the whole enclosure. The use of LiDAR to generate 3D models of enclosure use might well be justified if a zoo was planning the re-development of a facility, given architect drawings would require the fidelity of resolution offered by this approach. When mapping the behaviour of a species within a 3D space, the level of error associated with the CAD approach was found acceptable in this study. Finally, digitisation or construction of a 3D digital model ensures that researchers have permanent access to the architecture of their study site, and allows sharing and modification of the 3D model by other researchers. The future evolution of the 3D enclosure space can also be mapped onto associated changes in behaviour patterns of the enclosure occupants, which could have a major impact on how enclosures are designed, managed and developed in the future.

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