JOURNAL OF APPLIED ANIMAL WELFARE SCIENCE
https://doi.org/10.1080/10888705.2025.2481883

Routledge
Taylor & Francis Group

RESEARCH ARTICLE

OPEN ACCESS Check for updates

Evaluating Qualitative Behavioral Assessment and Ethogram Techniques for Captive Black Rhinoceros (*Diceros bicornis*)

Emily J. Hughes [a], Tony King [b,c], and Todd R. Lewis [d]

[a]Bristol Veterinary School, University of Bristol, Langford, UK; [b]The Aspinall Foundation, Port Lympne Reserve, Kent, UK; [c]Durrell Institute of Conservation and Ecology, School of Anthropology and Conservation, University of Kent, Canterbury, Kent, UK; [d]School of Architecture and Environment, University of the West of England, Bristol, UK

ABSTRACT

Maintaining high animal welfare in zoos is a persistent concern for practitioners and regulators, yet assessing welfare remains challenging. Welfare assessment techniques should be rapid and noninvasive, as traditional methods are often invasive, time-consuming, or costly. Qualitative Behavioral Assessment (QBA) is a promising alternative to ethograms. This study evaluated QBA's usefulness in assessing behavior in ten captive black rhinos in a UK zoo by comparing it with ethogram data. QBA descriptors meaningfully overlapped with ethogram behaviors, for example, agonistic behaviors like horn clash aligned with Angry, Startled, and Nervous, while playful behaviors like head fling matched Lively and Excited. Correlations emerged between techniques; for instance, naso-nasal greeting and environmental investigation correlated with Active and Interested, while tactile contact negatively correlated with Angry and Nervous. Individual rhinos accounted for ~35% of (co)variation, with coefficient plots identifying significant key ethogram behaviors/QBA descriptors. The strong overlap within a joint model suggests QBA is a valuable welfare assessment tool that complements ethogram data collection for this species.

ARTICLE HISTORY
Received 14 September 2024
Accepted 12 March 2025

KEYWORDS
Rhino; qualitative behavioural assessment; ethogram; generalized linear latent variable model; welfare assessment

Introduction

In recent years zoos have redefined their role to try to focus on education, research, and the support of biodiversity conservation, while remaining attractive to paying visitors (Carr & Cohen, 2011; EAZA Executive Office, 2013). The value to biodiversity conservation of captive-breeding in zoos is under increasing scrutiny (Alroy, 2015; Brichieri-Colombi et al., 2019; Conde et al., 2013; Lees & Wilcken, 2009) and the challenges of maintaining high levels of animal welfare in zoos have been of mounting concern (Hosey, 2005; Melfi, 2009; Spooner et al., 2021; Yon et al., 2019). Therefore, the need to assess welfare within zoos has become pertinent (Ward et al., 2018).

Welfare assessment techniques should be rapid and noninvasive to minimize disturbance and stress to the animal (Wolfensohn et al., 2018; Yon et al., 2019). While physiological parameters such as stress hormone levels in blood or feces can provide insights into welfare status, these methods are often invasive, require specialized equipment, and can be costly and time consuming (Palme, 2019). However, welfare is not solely determined by the absence of stress or negative experiences but also by the presence of positive experiences, which contribute to overall well-being (Dawkins, 2004; Temple et al., 2011; Watters, 2014; Yon et al., 2019). Behavioral assessments, including qualitative

CONTACT Todd R. Lewis Todd.Lewis@uwe.ac.uk School of Architecture and Environment, University of the West of England, Frenchay Campus, Coldharbour Ln, Bristol BS16 1QY, UK

This article has been corrected with minor changes. These changes do not impact the academic content of the article

Supplemental data for this article can be accessed online at https://doi.org/10.1080/10888705.2025.2481883

behavioral assessment (QBA), have the advantage of capturing both negative and positive welfare indicators, providing a more holistic understanding of an animal's welfare state.

Quantitative behavioral assessments using predefined ethograms for species' behaviors are utilized to determine the variety, and frequency, of different behavior types, which are then used to determine welfare status (Binding et al., 2020). However, quantitative behavior studies are time consuming and require substantial data collection to accurately surmise welfare status (Williams et al., 2012).

Qualitative Behavioral Assessment (QBA) is a methodology centered around the interpretation of the expressive quality of behavior of the "whole animal" and its dynamic interaction to the surrounding environment using descriptors such as "calm" or "active" (Wemelsfelder & Lawrence, 2001; Wemelsfelder et al., 2000). The use of such descriptors, along with secondary indicators such as environmental context, physiological measures, or behavioral patterns, has the potential to determine welfare state allowing for interpretation of the animal's "mood" rather than just the activities it performs (Napolitano et al., 2012). This assessment technique relies heavily on the observer's ability to appropriately assess the body language of the animal in question and has long been criticized by skeptics as being too anthropomorphic (Wemelsfelder et al., 2001). Notwithstanding, when contrasted with quantitative behavioral assessment, QBA has the potential to complement knowledge about an animal's welfare state accurately. Due to the requirement of vast amounts of data prior to determining welfare status when utilizing quantitative methods, behaviors of small frequency may potentially become inconsequential during statistical analysis (Walker et al., 2016), despite such behaviors being potentially of paramount importance for interpretation of welfare status. QBA has been proven to allow for rapid and effective welfare assessment for domesticated animal species (Napolitano et al., 2008; Carreras et al., 2016; Ellingsen et al., 2014; Grosso et al., 2016; Walker et al., 2016), and for measuring welfare indicators of captive giraffe (Patel et al., 2019), brown and polar bear (Skovlund et al., 2023; Stagni et al., 2022), bonobo (Laméris et al., 2024) and of both wild and captive elephant (Wemelsfelder et al., 2010; Yon et al., 2019).

Our study documents, to the best of our knowledge, the first use of QBA in captive black rhinoceros (*Diceros bicornis*). Rhino populations have been under threat in the wild due to sustained high levels of poaching for many decades. Whilst the initial plummet in population numbers from the 1960s led to the black rhino being listed as critically endangered on the IUCN red list (Oginah et al., 2020; Otiende et al., 2015; van Coeverden de Groot et al., 2011), continued conservation efforts have resulted in an increase in black rhino numbers in recent years (le Roex & Ferreira, 2020). However, the recovering populations remain largely isolated, with future conservation efforts looking to move toward increased translocation of individuals to promote gene flow in geographically isolated populations (Fyumagwa & Nyahongo, 2010; Oginah et al., 2020; Stanbridge, 2020). Such translocations have previously included captive bred individuals (Fitzjohn, 2013; King & Beer, 2018).

However, historically, there has been limited success for the captive breeding efforts for black rhino, with the European captive population underperforming on all measures of reproduction when compared to wild managed populations, and only 41 of the 135 wild-caught founder individuals having contributed to the current population (Edwards et al., 2015). Moreover, the species is prone to developing diseases associated with difficulties meeting their dietary needs in captivity which are not evident in their wild counterparts (Ricketts et al., 2021). High mortality rates and low reproductive rates in captive rhinos have also been suggested to be linked to stress (Carlstead & Brown, 2005). Rapid welfare assessment for this species may therefore prove valuable in supporting successful husbandry within captivity.

Our study examines how QBA and ethogram-based behavioral methods compare in assessing the welfare of captive black rhinos. Specifically, we explore their similarities and differences, considering how each method captures behavioral expression and welfare indicators. By doing so, we aim to provide practitioners with insights into the applicability of these approaches for different welfare assessment contexts.

Materials and methods

Housing and animals

This study was carried out at Port Lympne Reserve, UK. Ten (10) eastern black rhinos were involved in this study, including one bull, seven cows (two of which were in calf) and two calves. The rhinos were managed through a variety of housing conditions, including solitarily, mixed species exhibits, female only herds and mother-offspring pairings (mean age of cows = 17.6 ± 10.1 years, bull = 17 years, calves <1 year).

The eight enclosures used for observation varied in size from 0.11 to 3.22 ha, plus additional indoor housing. Rhino distribution across the enclosures varied over time. All outdoor enclosures predominantly consisted of grassy substrates. The largest of the enclosures contained both longer grass and a variety of tree species allowing for potential grazing and visual barriers. Indoor housing consisted of concrete flooring covered with both hay and straw. All rhinos were fed twice daily, between 09:00–10:00 and 16:00–17:00. Feed included Lucerne (20–25 kg per individual), and a variety of tree branches, fruits, vegetables, and pellets. During the study, the enclosure conditions were varied due to husbandry purposes. These included the movement of the bull in with a cheetah (*Acinonyx jubatus*) for a single day, the movement of the female herd between two adjacent enclosures to regularly allow for cleaning, and the alternation of the two mother-offspring pairs between a large (1.73 ha) and small (0.11 ha) enclosure. These changes were made independently of this study and determined by zoo staff. Opening hours of the zoo were 09:30–18:30, however, due to the positioning of enclosures not all rhino observed were directly exposed to the public. Where possible, variation between the husbandry of each rhino was kept to a minimum, however, the inconsistencies between housing conditions and movement of rhino between paddocks outside of their usual routine may have impacted behavior exhibited and recorded. Because QBA strongly relies on an observer's positioning in, and perspective of, a situation, such changes and differences between husbandry conditions and animal bio-data (such as sex and age) may have skewed perceived "emotional states" during data collection. However, such limitations could be argued to be present for any, and all, QBA use and as such it was rationalized that the aforementioned uncontrollable factors did not significantly increase the limitations previously documented in the use of QBA for previous studies.

Behavioral observation method

Ethogram and QBA categories are detailed in Table 1. Data collection occurred between 5 and – June 16 2017, with observations occurring between 08:30 and 17:30. Each individual was observed thrice daily between 08:30–10:30, 12:00–14:00 and 15:30–17:30. During each observational period for each rhino, 5 min of QBA was carried out followed by 5 min of quantitative behavioral assessment (ETG), with behaviors determined using an ethogram.

A single observer recorded rhino behavior throughout the study. QBA scoring terms were determined through a pilot study designed to assess the applicability of different behavioral descriptors for black rhinos. During this pilot phase, various behavioral expressions were observed and evaluated for their relevance in welfare assessment. The following QBA descriptors were identified as useful: Active, Alert, Angry, Anxious, Bold, Calm, Comfortable, Content, Dominant, Excited, Grumpy, Happy, Inquisitive, Interested, Lively, Nervous, Niggling, Relaxed, Resigned, Scared, Sociable, and Startled.

Each of these terms was assigned a 12.5 cm visual analogue scale (VAS), with endpoints representing the "minimum" and "maximum" intensity of the behavior. In the main study, following each 5-minute behavioral observation, the observer placed a single mark on the VAS to indicate the degree to which the behavior was expressed. The distance from the minimum marker was measured

Table 1. Ethogram and QBA utilized. Ethogram details adapted from Owen-Smith (1973) and the works of Cinková and Bičík (2013), Mueller et al. (2013) and Metrione et al. (2007). Social behaviors grouped as Agonistic/Cohesive/Playful to enhance cross-contrast interpretation. Solitary behaviors are distinguishable from each other.

Behaviour	Abbreviation	Description
Solitary Behaviours		
Browsing	BRW	Ingestion of food from either trees or bushes
Defecation	DEF	Up-curled tail with elimination of feces from the body
Digging	DIG	Horn, feet, or nose are used to manipulate substrate
Drinking	DRK	Ingestion of water
Environmental Investigation	EIV	Manipulation of the natural environment with horn, feet, or nose
Flehmen	FLM	Prehensile lip is curled dorsally with head raised
Foot Scrape	FTS	Alternating flicking of hind legs to scatter dung
Grazing	GRZ	Ingestion of food either in the form of hay, pellets, or grass
Lying Down	LDN	Animal asleep or maintaining body position with thorax in direct contact with the ground
Object Investigation	OIV	Manipulation of enrichment items with horn, feet, or nose
Recumbency	REC	Process of lying down
Rising	RIS	Animal raises body from the ground to standing position
Rubbing	RUB	Body or horn repeatedly rubbed against an object in the environment
Running	RUN	Fast locomotion, usually occurs after alarm
Scent Marking	SCM	A spray or burst of urine
Standing	STD	Animal remains stationary for 5 seconds or longer
Stereotypic Pacing	STP	Repetitive locomotion along the same route for 10 seconds or longer
Swaying	SWY	Weight is repeatedly transferred between forelimbs while hindlimbs remain stationary for 5 seconds or longer
Urination	URI	Up-curled tail with elimination of urine from the body
Walking	WLK	Steady locomotion from one place to another
Wallowing	WAL	Body is fully or partially submerged in mud
Social Behaviours		
Advancing Steps	AST	Agonistic; Rapid locomotion toward another animal over a short distance
Charging	CHA	Agonistic; One animal quickly advances toward another with the intent to intimidate
Ears Pinned Back	EPB	Agonistic; Ears flat against the back of the head, head thrust forward
Following	FOL	Cohesive; One animal follows in the direction of travel of another
Head Flings	HFL	Playful; Head is swung rapidly upwards and downwards
Horn Clash	HCL	Agonistic; Horn hit against the side of another animal
Naso-nasal Greeting	NAS	Cohesive; Slow movements resulting in the touching of noses
Pant	PAN	Cohesive; High-pitched, chesty exhalation
Play Horn Wrestling	PHW	Playful; Horns used in play with another animal
Side Presenting	SPR	Cohesive; Side turned toward another animal, head held low – to appease another
Snort	SNT	Agonistic; Sharp exhalation from nose
Submission	SUB	Cohesive; Animal slowly backs away from another animal
Suckling	SUC	Cohesive; Infant feeding from mother
Tactile Contact	TCO	Cohesive contact between two or more animals
QBA Behaviours		
Active	ACT	Exhibiting high levels of movement or engagement with surroundings
Alert	ALT	Focused awareness of the environment, often with raised head and ears forward
Angry	ANG	Displaying frustration or agitation, often with tense posture
Anxious	ANX	Showing signs of unease, often characterized by vigilance or avoidance behavior
Bold	BLD	Confident and exploratory interactions with the environment
Calm	CLM	Relaxed and at ease with surroundings
Comfortable	CFT	Displaying physical contentment and lack of distress such as a relaxed posture, stretching, or calmly engaging with surroundings
Content	CNT	Appearing emotionally satisfied and at ease in the environment such as steady engagement in routine activities, lack of agitation, and an overall demeanor of ease
Dominant	DOM	Assertive interactions with conspecifics, often taking priority in access to resources
Excited	EXC	Heightened energy, often accompanied by rapid movements or increased social interactions
Grumpy	GRM	Displaying mild irritation or reluctance to engage
Happy	HAP	Positive engagement with surroundings, often with relaxed posture and interactive behavior
Inquisitive	INQ	Curious and exploratory behavior directed toward the environment or conspecifics
Interested	INT	Focused engagement with objects, environment, or social partners
Lively	LIV	High-energy movements or behaviors

(*Continued*)

Table 1. (Continued).

Behaviour	Abbreviation	Description
Nervous	NRV	Signs of apprehension, including frequent scanning or withdrawal behaviors
Niggling	NIG	Minor irritation or discomfort expressed through subtle movements or vocalisations
Relaxed	RLX	Low-tension posture and absence of stress indicators
Resigned	RSG	Passive, withdrawn behavior, often appearing indifferent to surroundings
Scared	SCR	Displaying fear responses such as freezing, retreating, or startle reactions
Sociable	SOC	Engaging in positive social interactions with conspecifics
Startled	STL	Sudden reaction to an unexpected stimulus, often accompanied by a brief freeze or jump

Table 2. Breakdown of time spent conducting data collection for each rhino. Discrepancies in observational times were primarily due to the rhino being out of sight, either inside (for those with indoor housing) or in an area of the enclosure with no clear visibility. For such instances, data collection was omitted.

Rhino	Total number of QBA observation slots	Total time spent for QBA data collection (mins)	Total number of ETG observation slots	Total time spent for ETG data collection (mins)	Total number of observation slots for both QBA and ETG	Total observation time (mins)
Arusha	23	115	23	115	46	230
Kisima	35	175	35	175	70	350
Nyasa	33	165	34	170	67	335
Nyota	36	180	36	180	72	360
Ruaha	36	180	36	180	72	360
Rukuru	32	165	34	170	66	335
Sammy	36	180	36	180	72	360
Solio	35	175	35	175	70	350
Vuyu	36	180	36	180	72	360
Zuri	36	180	36	180	72	360
Total	338	1695	341	1705	670	3400

in millimeters to generate a quantitative score for each behavior. This approach allowed for a direct comparison of QBA scores with ethogram-based (ETG) behavioral data.

Following QBA data collection, ETG data was recorded for an additional 5 minutes by focal continuous sampling. The duration of each observed behavior was measured in seconds, allowing for precise quantification. When multiple behaviors occurred simultaneously (e.g., SNT and CHA), each was recorded independently. Observations were conducted in 2-hour time slots, with a 20-minute allowance for movement between paddocks. The order in which individual rhinos were observed was systematically rotated to ensure a representative cross section of behavioral data across each 2-hour period. This procedure was repeated for all three daily observation time slots. For each time slot, environmental variables including temperature, wind speed, and weather condition were recorded prior to observations. The observation schedule is detailed in Table 2. These systematic methods were designed to ensure that the collected data would be robust and reflective of the rhinos' behavioral variation under different conditions.

Data analysis

Generalized Linear Latent Variable Models (gllvm) in the package gllvm (Niku, Brooks, Herliansyah, Hui, Taskinen, & Warton, 2019) were used to contrast response differences between QBA and ETG behavioral scoring for individual rhinos. gllvm extend basic generalized linear models on multi-variate data using a factor analytic approach by incorporating latent variables to combine values with factor loadings that model correlation between responses. These latent variables have a natural interpretation as ordination axes and can predict new values, control for known variables, and assist model selection (Hui et al., 2015, 2017).

The rhino multivariate behavior dataset herein was constructed as a matrix with n rows (individual rhinos) and m columns of behavior responses (QBA/ETG) for each behavior observation session. The gllvm regressed the mean behavior μij against individual rhinos as variables and a vector of $d<md<m$ latent variables, $\boldsymbol{ui} = (u_{i1},\ldots,u_{id})'$;

$$g(\mu ij) = \eta ij = \alpha i + \beta 0j + \mathbf{x}\prime i\,\beta j + \mathbf{u}\prime i\,\theta j,$$

where $g(.)$ is a known link function, $\boldsymbol{u'i}$ are d-variate latent variables $(d<md<m)$ with d representing the number of latent dimensional spaces based on AIC fit, md representing intermediate dimensions applied to covariates and m total number of behavioral observations, αi is an optional row effect at behavior i that can be either fixed or a random effect, $\beta 0j$ is an intercept term for an individual rhino j, and $\boldsymbol{\beta j}$ and $\boldsymbol{\theta j}$ are column-specific coefficients related to covariates and latent variables, respectively.

Models were fitted to both Poisson and Negative Binomial families, implemented using package TMB (Kristensen et al., 2016), and applied to variational approximation (Hui et al., 2017). Package gllvm deploys factor analysis on Dunn-Smyth residuals to obtain starting values close to an anticipated solution. Dunn-Smyth residuals and quantile (Q–Q) plots were used to inspect model fit for both families. Best model fit was also assessed using BIC and AIC, and then used BIC selection with a for-loop iteration to identify the most suitable number of latent variables to be used for the models. gllvm fit can be sensitive to choice of initial latent variable values as they are unobserved. This limitation was overcome by integrating values and maximizing approximation to the log-likelihood. Models were cycled multiple times with a best of five run routines and the highest log-likelihood value selected out for different distribution families (Niku, Brooks, Herliansyah, Hui, Taskinen, Warton, & Li, 2019).

Latent variables induce correlation across response variables and provide estimation of correlation patterns, and the extent to which these are explainable by variables. In gllvm correlations are stored as factor loadings. The getResidualCor function was used to estimate correlation of the linear predictors across behaviors and visualized using package corrplot (Wei & Simko, 2017). The getResidualCov function in gllvm was utilized to quantify (co)variation by individual rhinos. Specifically, trace of the residual covariance matrix was used as a measure of such unexplained variation in the model. The ratio of the trace suggested the percentage of (co)variation across behaviors.

A strong residual covariance/correlation between factors can be interpreted as evidence of autocorrelation in a model, however, appreciable levels have been recognized as indicative of an interaction/association (Pollock et al., 2014). The residual precision matrix in gllvm can be used to directly identify association between factors (e.g., in our case rhino behaviors) (Ovaskainen et al., 2016). Two factors exhibiting a zero result in such plots may remain correlated, indicating they do not directly interact, but can also remain correlated because they co-occurred. Residual precision matrix results preferably should not exhibit elements equal to exactly 1 or −1 (suggesting strong autocorrelation). Nevertheless, relatively large values between these limits of precision imply a useful indication of a correlated relationship between two factors. Consequently, residual correlations in gllvm are expressed combined with latent variables and are effectively a “fuller” picture of natural correlation between variables in the model.

Application of analyses

In this study, relationships between response factors and predictors were interpreted from combined components derived from the model; correlation of latent variable factors between response variables, ordination clustering of response factors, and coefficients of response factors and their predictor interactions. The ordination cluster plots were created using the ordiplot function in package gllvm whilst the estimated coefficients for predictors, and their confidence intervals, were plotted using the coefplot function to reveal the nature of the two behavioral scoring methods (QBA/ ETG) and variation of these results for, and between, each rhino studied.

Results

Behavioural observation

A total of 338 observation sessions were completed during this study (Table 2), totaling 1,695 minutes of QBA and 1,705 minutes of ETG data collection. From this, 22 QBA descriptors and 35 ETG behaviors were analyzed.

Model fitting

The data comprised both QBA and ETG for ten individual rhinos ($N = 10$). Two types of model (model 1 and 2) fitted successfully. The first (1) was an unconstrained ordination of the behavior variables fitted with two latent variables and no predictors. The second fitted model (2) included individual rhinos as predictor variables in the model, in order to study their effects on behaviors, and patterns of behavioral co-occurrence after controlling for individuals.

Both models were fitted using Poisson first and then Negative Binomial (NB) families. Inspecting the plots of residuals against fitted values revealed some evidence for over-dispersion in both Poisson models evidenced by typical fan-shaped plot. NB was visually a better fit and reduced over-dispersion (Supplementary Material; Figs. S1a/b). BIC and AIC values confirmed NB was a better fit (Supplementary Material; Table S1). The for-loop iteration utilized BIC values and recommended $N = 2$ latent variables as appropriate (Supplementary Material; Fig. S2). We elected to proceed using NB family as Dunn-Smyth residuals presented a more robust picture of the data being approximately normal.

Model correlation

Proceeding with NB, we then used the getResidualCor function in gllvm to plot a full matrix correlation of all QBA and ETG variables for both NB models (1/2). We inspected correlation using the adjust= command in gllvm and found adjust = 2 to reduce correlation greatest across the model compared with adjust = 1 (Figure 1). Tracing the residual covariance matrix in model 2 revealed individual rhinos were responsible for ~35% of (co)variation in the model.

Ordination plotting

Models 1 and 2 were plotted in NB using ordiplot, reducing the alpha option to 0.01 in the plot to avoid overcrowding of nameplates. We plotted latent variables in a separate ordination to show their related spread through each model Figure 2(a,b). Ordinations indicated clustering of some behaviors with a spread of division between QBA and ETG that mostly reflected behaviors that naturally contrasted.

Coefficient interpretation

Coefficient plots were derived from NB model 2 and included the intercept utilized for one of the rhinos. Plots show clearly the different behaviors expressed significantly both positively and negatively for each rhino Figure 3(a,b); Supplementary Material; Figure. S5c-j). Rhinos exhibited some behaviors common across individuals, for example BRW, RIS and FOL, while others were more specific to individual animals, for example Alert for Nyasa and NAS for Kisima. Some rhinos shared behavioral traits such as Happy for Zuri and Rukuru. These findings set the stage for a deeper discussion on the implications of QBA as a welfare

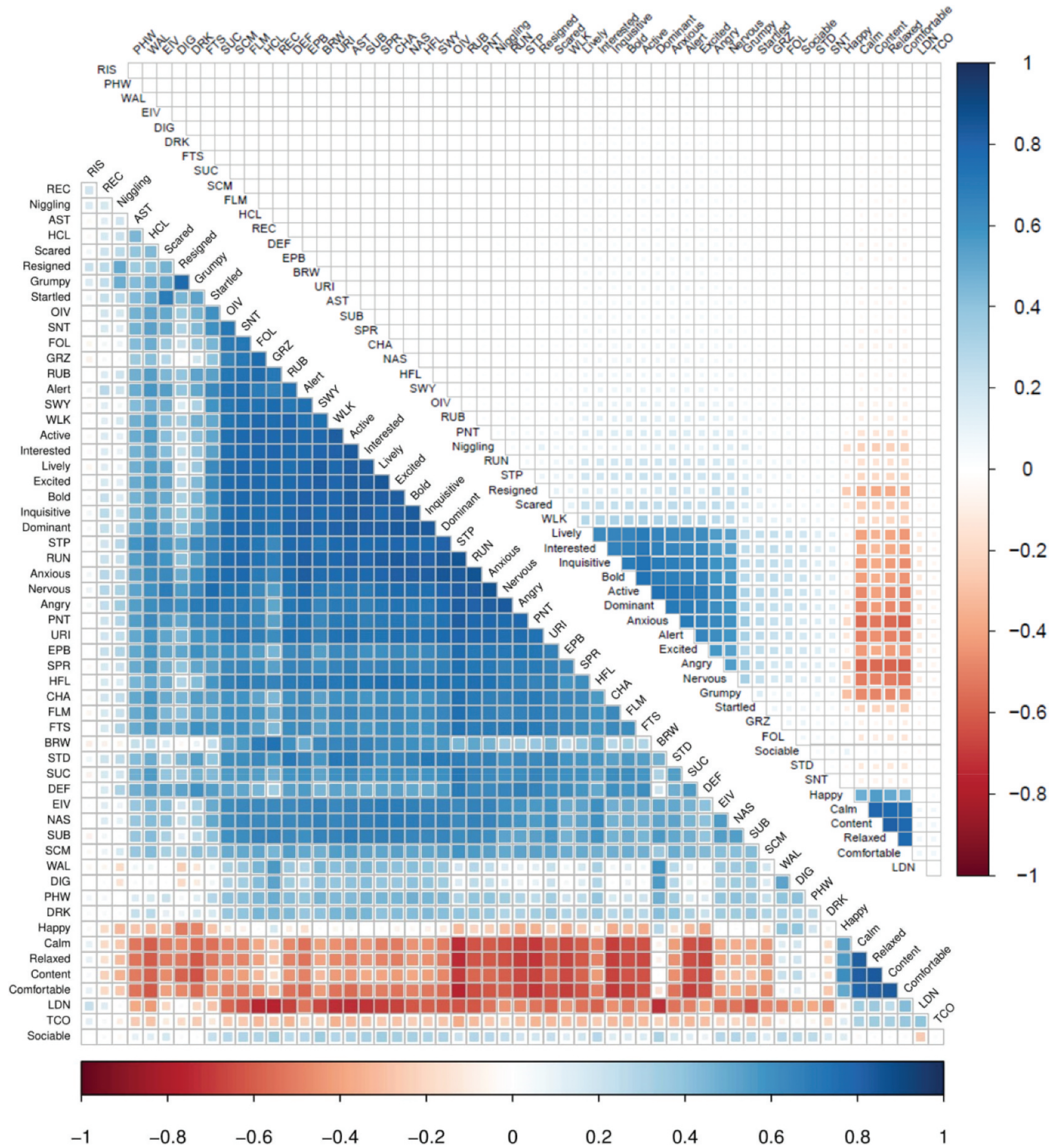

Figure 1. Residual correlation plots; ordination model 1 with adjust = 1 method (lower triangle) and adjust = 2 (upper triangle). Regions colored blue in correlation plot indicate clusters of behaviors positively correlated. Red indicates negative correlation between paired behaviors. Abbreviated labels represent ETG, while fully spelled-out names correspond to QBA behaviors.

assessment tool. The observed correlations such as Happy, Calm, and Relaxed negatively correlating with behaviors like Scared, Grumpy, and Resigned across the rhino group, combined with individual-specific behaviors, raise important questions about the utility and applicability of QBA in different captive environments.

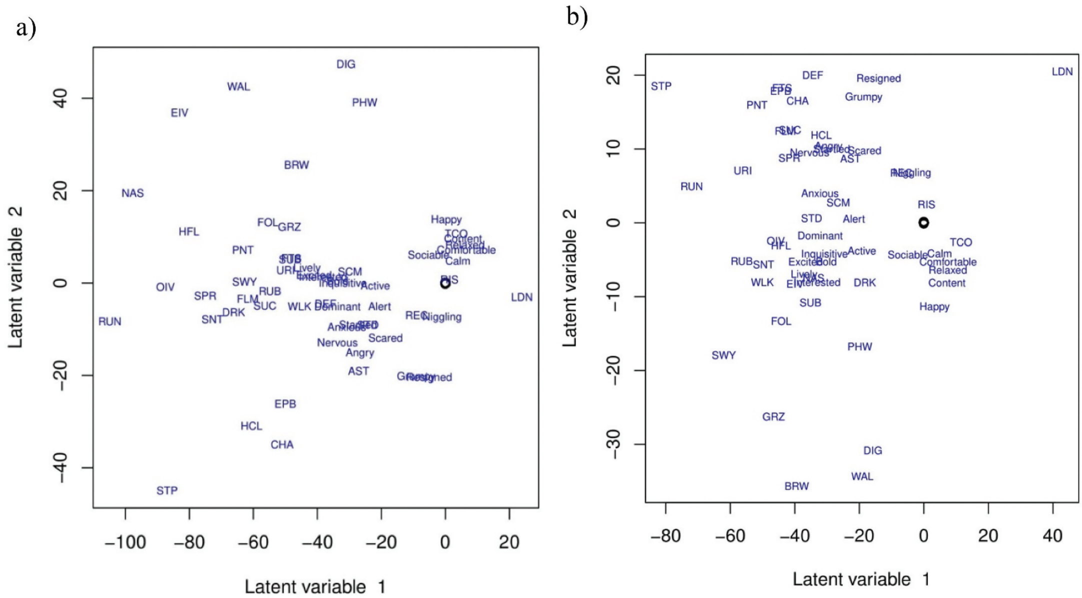

Figure 2. a/b. Ordination plot for rhino behaviour from ordination model 1a and model 2b (adjust =2). Abbreviated labels represent ETG, while fully spelled-out names correspond to QBA behaviours. Clustering of similar behaviours is evident across both QBA and Ethogram.

Discussion

This study applied qualitative behavioral assessment (QBA) to captive black rhinoceros (*Diceros bicornis*) to evaluate its effectiveness as a behavioral welfare assessment technique for the species. We compared QBA with ethogram (ETG) data collected from ten rhinos at Port Lympne Reserve, using a joint latent variable model. Clustering of QBA and ETG variables in the ordination plots Figure 2 (a,b) revealed structural similarities and overlap between the two behavioral methodologies. Multivariate analysis further identified significant correlations, supporting the use of QBA as a reliable welfare indicator for captive rhinos. The use of multivariate latent variable models in organismal and behavioral research is gaining traction due to their ability to identify underlying patterns and relationships in complex datasets (Jenner & Lewis, 2023; Lewis et al., 2021; Rice et al., 2022). By integrating QBA and ETG data within a single framework, this approach allows for a more comprehensive assessment of behavioral expression, making it a promising tool for refining welfare evaluations in captive animal management.”

Behavioural interactions

Our results showed clustering between similar variables within a single behavioral technique, showing relatedness between variables. For example, the QBA variables, Calm, Content, Comfortable, Sociable and Relaxed are closely grouped, suggesting commonality in the occurrence of these behaviors Figure 2(a,b). There was also clear overlap between QBA descriptors, for example, Grumpy and Resigned; this overlap identified such behaviors as often occurring concurrently and were scored with similar weighting by the observer Figure 2(a). Grouping can also be seen between ETG behavior types (descriptions of each behavior in Table 1). Ears pinned back (EPB), horn clash (HCL) and charging are all clustered, which given that they are all agonistic behaviors is expected. However, overlap between contrasting behavior types Figure 2(b) such as pant (PNT) and charge (CHA) may stem from the varying husbandry conditions of the rhino observed. Mothers with calves were more likely to exhibit territorial behavior but also more likely to show cohesive behavior to offspring, with PNT rarely being seen under solitary husbandry conditions.

QBA and ETG equivalence

The QBA data overlapped meaningfully with the ETG data. For example, QBA behaviors Lively/ Interested are grouped with ETG behavior types naso-nasal greeting (NAS)/environmental investigation (EIV), whilst QBA behaviors Angry/Scared/Startled/Nervous were all closely grouped with ETG behaviors advancing steps (AST)/horn clash (HCL)/side presenting (SPR) (Figure 2(b)). Overlap between such QBA descriptors and behaviors was largely unsurprising with agonistic or submissive behaviors grouped with descriptions such as Angry and playful/cohesive behaviors linked with descriptors such as Lively. This supports previous studies in which the use of both behavioral methods can strengthen the data collected in animal behavioral research (Minero et al., 2009; Rutherford et al., 2012; Walker et al., 2016).

Correlations between QBA and ETG data have previously been used to determine usefulness of QBA as a welfare indicator in species (Arena et al., 2019; Rutherford et al., 2012; Walker et al., 2016; Yon et al., 2019). The use of QBA to date has primarily occurred in domesticated species (Napolitano et al., 2008; Carreras et al., 2016; Ellingsen et al., 2014; Grosso et al., 2016; Walker et al., 2016), with its use for rhino previously being undocumented. However, Figure 1 shows clear positive and negative correlation across and between both behavioral assessment techniques, which further supports the overlap highlighted through clustering in the ordination plots. QBA behaviors previously identified as clustering/overlapping in Figure 2a/b were also found to have strong correlations (e.g., positive correlations between Calm/Comfortable/Relaxed and negative correlations between Resigned/Startled/Grumpy). Angry had a strong positive correlation to advancing steps (AST)/horn clash (HCL), whilst naso-nasal greeting (NAS)/environmental investigation (EIV) were positively correlated to Active/Lively/Interested. Strong negative correlations between stereotypic pacing (STP) and Calm/Relaxed/Content and a weak negative correlation between wallowing (WAL)/digging (DIG) with Resigned can also be seen. Within Figure 3(a) there are also unexpected correlations between ETG and QBA data. For example, head fling (HFL) and Anxious, or suckling (SUC) and Dominant. Many of these unexpected correlations were removed with the change in adjustment used to generate Figure 1, however weak correlations are still present between objectively impassive factors such as grazing (GRZ)/walking (WLK) with Dominant/Bold. Overall, there is overlap between agonistic behavior types with "negative" QBA descriptors and between cohesive/ play behavior types with "positive" QBA descriptors, supporting the use of QBA as a rapid welfare assessment technique for captive wild animal species, as is routinely used in the agricultural industry (Napolitano et al., 2012; Fleming et al., 2016; Grosso et al., 2016).

Individual rhino differences

Clear differences in the behavior displayed between individual rhino can be seen in Figure 3(a,b) and Figures S5c-j. Whilst this may be due to the differing husbandry conditions of the animals in the study, this may also be due to individual variation within each rhino. Figures S5c-j represent the behavior displayed by the two calves, which exhibited behaviors specific to their age group (e.g., suckling (SUC)). However, they also exhibited increased cohesive behaviors compared to adult individuals. For individuals kept solitarily such behaviors were unable to be displayed due to the need of a counterpart. Individuals kept in smaller enclosures, as seen in Figures S5-d, S5-e and S5-i, significantly displayed negative behaviors such as stereotypic pacing (STP) and swaying (SWY). There are similarities in both significant positive and negative behaviors displayed within the individuals of the female only herd (Figure 3(a) and S5c/g). Much of the significant behavior identified is social, and a mix of both agonistic and cohesive behavior. Agonistic behavior, such as

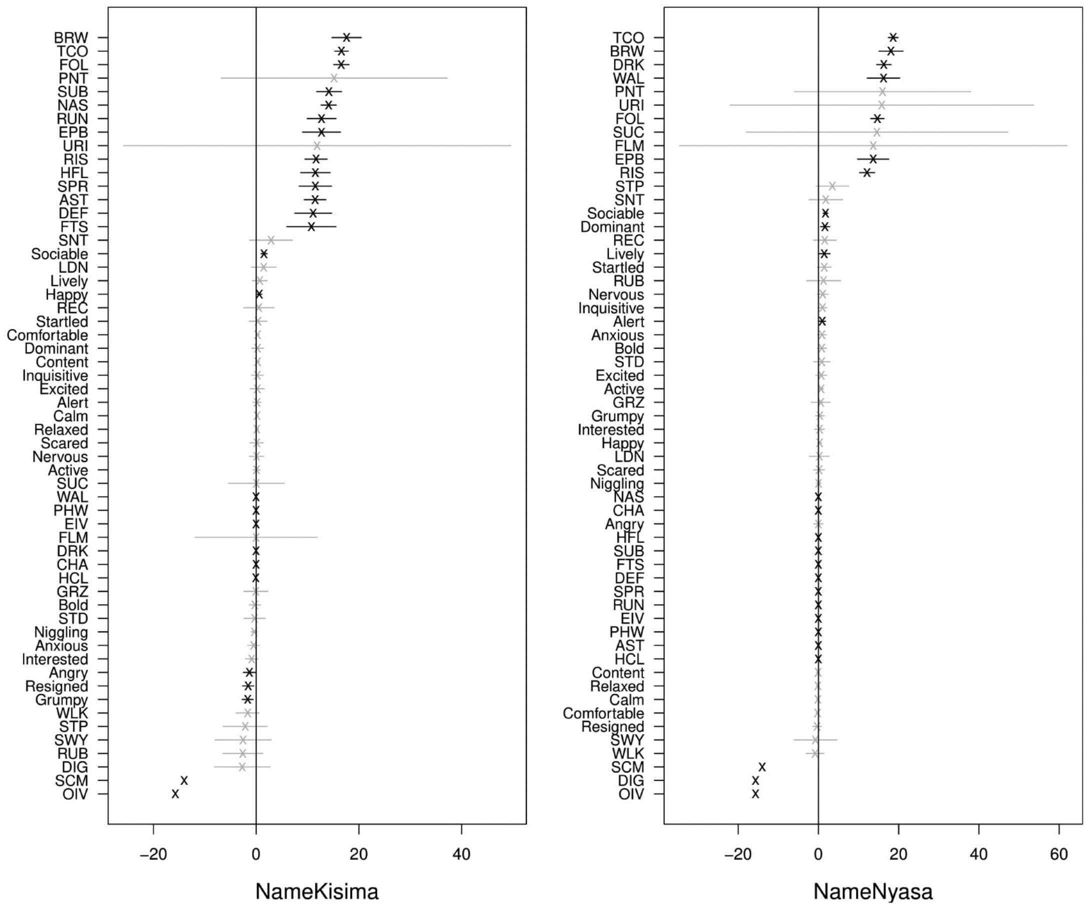

Figure 3. A/B. Coefficient plots from predictor model 2 for 2 × individual rhino behavior (QBA + ETG). The coefplot comprises point estimates (crosses/ticks) for coefficients of variables and their 95% confidence intervals (lines). Those colored gray denote intervals passing zero-crossing (not significant), and those black as non-zero crossing (significant) either positively (right of the 0 crossing) signaling a positive association, or negatively (left of the 0 crossing) for a negative association. Abbreviated labels represent ETG, while fully spelled-out names correspond to QBA behaviors. For further coefficient plots for individual rhino see supplementary material.

charging (CHA) and ears pinned back (EPB), and territorial behaviors such as foot scrape (FTS), were significant behaviors for the only male in this study (Fig. S5-f). Whilst this may signify a difference in the behavior displayed between the sexes, the husbandry changes that occurred during the study period, with the male being mixed with a cheetah for a single day, may have biased the degree to which such behaviors are usually prevalent. Furthermore, some of these behaviors were significantly exhibited by both the male and female calves, which again may dissuade the possibility that these behaviors are significantly different between the sexes. The behaviors displayed by both calves were more varied than the adults and may be representative of the calves exploring new behaviors. Overall, individual rhinos were responsible for ~35% of (co)variation in the model with many ambiguous behaviors such as grazing (GRZ)/standing (STD)/walking (WLK)/following (FOL) and QBA descriptors such as Calm/Relaxed/Niggling/Interested largely being insignificant across all individuals. However, coefficient plots were derived from the adjusted model, minimizing the degree of correlation. Whilst this allows for the key significant variables to be identified, allowing for easier interpretation, the coefficient plots generated may under different unadjusted modeling present an even “fuller picture” using the present data.

Limitations

The overlap between the two methodologies may have been strengthened if the data collection for the two techniques occurred during exactly the same observation window. Previous studies, across a range of species, have used filming to allow for review of behaviors displayed for both ETG and QBA collection (Arena et al., 2019; Patel et al., 2019; Rutherford et al., 2012; Walker et al., 2016; Yon et al., 2019). In this study, 5 minutes of QBA observation data collection followed by 5 minutes of ETG observation data collection was used. Whilst the collection of QBA data prior to that of ETG helped minimize bias for QBA scoring, the staggered data collection may have weakened the overlap between the two behavioral techniques. Furthermore, only a single observer was used to collect data, with no visual recording to allow for subsequent viewing by secondary observers. Whilst this ensured consistent interpretation of scoring of all rhinos, it meant that QBA descriptors were dependent on a single observer whereas usually a pool of observers may be used. Similarly, the data collection was limited by the accessibility of study animals which did not allow for a control group or standardized environment. Resultantly an unequal number of observations both between animals and in the number of QBA vs ETG observations for the same animal were obtained due to some animals being out of sight at allocated observation times.

Evaluating QBA and ETG

Overall, there is overlap between agonistic ETG behavior types with "negative" QBA descriptors and between cohesive/play behavior types with "positive" QBA descriptors, supporting the use of QBA as a welfare assessment technique for captive rhino, as is routinely used in the agricultural industry (Fleming et al., 2016; Grosso et al., 2016; Napolitano et al., 2012; Wemelsfeder and Lawrence, 2010). QBA data have the potential to be collected in frequent, short observation windows, allowing for quick assessment of welfare without the need for large data sets and time-consuming data analysis that is often inherent with ETG data collection (Williams et al., 2012). QBA also allows for comparison across husbandry conditions, given that different behaviors are likely to be seen dependent upon whether an animal is kept solitarily or in a herd/crash. Furthermore, given that the use of QBA has been previously documented for captive giraffe (Patel et al., 2019) and for captive and wild elephants (Wemelsfeder et al., 2010; Yon et al., 2019) it has the potential to be applied in other captive species where welfare may be a concern. There is also the potential that QBA could be used to assist in the rapid welfare assessment of translocated rhino, both during the translocation process, and after release, reducing the need for more invasive physiological techniques.

Furthermore, this study did not apply Free-Choice Profiling (FCP), as data collection was conducted by a single observer. However, conceptually, latent variables in GLLVMs induce unobserved variables that reflect shared variation among response variables, as demonstrated by Jenner and Lewis (2023). These latent variables can function similarly to the input from multiple observers in FCP, providing an independent and systematic interpretation of relationships within the data. This parallel suggests that model frameworks such as GLLVM or Bayesian equivalents might reduce or even eliminate the need for multiple human observers in FCP-like assessments. Consequently, future studies using model-based multivariate approaches with latent variables, as demonstrated here, could offer an alternative pathway for nuanced behavioral interpretations.

Conclusion

Comparison of QBA and ETG data collection identified meaningful overlap between the two behavioral collection techniques, suggesting there is good potential for the use of QBA as a behavioral/welfare assessment technique for the species. Usefulness of this technique would need confirmation through further comparison and modeled contrast with ETG data, and potentially combined with physiological indicators to identify whether QBA can be used to determine stress in the species. Clear correlations (for example, negative correlation between Calm and stereotypic pacing (STP) and positive correlation between Interested and environmental investigation (EIV) further highlight overlap between the two behavioral techniques. Such overlaps in the results of both methods suggest that QBA has the potential to be a useful alternative approach for future welfare studies of captive black rhino and its use in other species within zoos should be further explored. Given the observed overlap between QBA and ethogram data, QBA could be particularly valuable in settings where rapid welfare assessment is needed. However, further studies are necessary to refine QBA methodologies, validate its use across various species, and possibly integrate physiological measures to enhance its accuracy and reliability.

Acknowledgments

We thank Port Lympne Reserve, The Aspinall Foundation and University of Bristol for supporting this study. We especially thank Paul Beer for his help and guidance during the collection of behavioral data. We are grateful to David Warton and Jenny Niku for creating, introducing, and answering our enquiries about generalized linear latent variable modeling. We also thank Rowland Griffin at Zoológico La Aurora, Guatemala for thoughts on the modeling design. Finally, we thank Oliver Hooker at PR Statistics https://www.prstatistics.com, for connecting us all.

Disclosure statement

No potential conflict of interest was reported by the author(s).

Funding

The author(s) received no financial support for the field research for this article. Support for time and publication was given by the Port Lympne Reserve, The Aspinall Foundation, University of Bristol, Durrell Institute of Conservation and Ecology and the University of the West of England.

Author contribution

EH conceived the ideas, designed the methodology, completed the fieldwork, performed data analysis and led writing of the manuscript; TK contributed to writing of the manuscript; TRL performed data analysis and contributed to writing of the manuscript. All authors contributed critically to the drafts and gave their final approval for publication.

Data availability statement

Data and R Code are available open access at: https://doi.org/10.5281/zenodo.13753981

Ethics approval statement

All rhinos in this study were observed from a safe working distance and were undisturbed from their normal captive care routine. The study was conducted in accordance with the ethical standards at Port Lympne Reserve and University of Bristol and followed all relevant guidelines for the care and use of animals.

Significance statement

Black rhinos are critically endangered, and their successful management in captivity is vital for conservation efforts. However, limited reproductive success and high stress levels in captive environments present significant challenges. This study provides the first application of Qualitative Behavioral Assessment (QBA) alongside traditional ethogram techniques for black rhinos, offering a novel approach to welfare assessment in this species. By identifying clear correlations between these behavioral assessment methods, this work highlights the potential of QBA to enhance welfare monitoring, support husbandry decisions, and improve the overall well-being of captive rhinos. These findings could serve as a model for other captive species, contributing to more effective conservation strategies.

ORCID

Emily J. Hughes http://orcid.org/0000-0002-5349-0686
Tony King http://orcid.org/0000-0003-4597-0134
Todd R. Lewis http://orcid.org/0000-0001-5433-8777

References

Alroy, J. (2015). Limits to captive breeding of mammals in zoos. *Conservation Biology*, *29*(3), 926–931. https://doi.org/10.1111/cobi.12471

Arena, L., Wemelsfelder, F., Messori, S., Ferri, M., & Barnard, S. (2019). Development of a fixed list of terms for the qualitative behavioural assessment of shelter dogs. *PLOS ONE*, *14*(10), e0212652. https://doi.org/10.1371/journal.pone.0212652

Binding, S., Farmer, H., Krusin, L., & Cronin, K. (2020). Status of animal welfare research in zoos and aquariums: Where are we, where to next? *Journal of Zoo and Aquarium Research*, *8*, 166–174. https://doi.org/10.19227/jzar.v8i3.505

Brichieri-Colombi, T. A., Lloyd, N. A., McPherson, J. M., & Moehrenschlager, A. (2019). Limited contributions of released animals from zoos to North American conservation translocations. *Conservation Biology*, *33*(1), 33–39. https://doi.org/10.1111/cobi.13160

Carlstead, K., & Brown, J. L. (2005). Relationships between patterns of fecal corticoid excretion and behavior, reproduction, and environmental factors in captive black (*Diceros bicornis*) and white (*Ceratotherium simum*) rhinoceros. *Zoo Biology*, *24*(3), 215–232. https://doi.org/10.1002/zoo.20050

Carr, N., & Cohen, S. (2011). The public face of zoos: Images of entertainment, education and conservation. *Anthrozoös*, *24*(2), 175–189. https://doi.org/10.2752/175303711X12998632257620

Carreras, R., Mainauab, E., Arroyo, L., Molesa, X., González, J., Bassols, A., Dalmau, A., Faucitano, L., Manteca, X., & Velarde, A. (2016). Housing conditions do not alter cognitive bias but affect serum cortisol, qualitative behaviour assessment and wounds on the carcass in pigs. *Applied Animal Behaviour Science*, *185*, 39–44. https://doi.org/10.1016/j.applanim.2016.09.006

Cinková, I., & Bičík, V. (2013). Social and reproductive behaviour of critically endangered northern white rhinoceros in a zoological garden. *Mammalian Biology*, *78*(1), 50–54. https://doi.org/10.1016/j.mambio.2012.09.007

Conde, D. A., Colchero, F., Gusset, M., Pearcekelly, P., Byers, O., Flesness, N., Browne, R. K., & Jones, O. R. (2013). Zoos through the lens of the IUCN red list: A global metapopulation approach to support conservation breeding programs. *PLoS One*, *8*(12), e80311. https://doi.org/10.1371/journal.pone.0080311

Dawkins, M. S. (2004). Using behaviour to assess animal welfare. *Animal Welfare*, *13*(S1), S3–S7. https://doi.org/10.1017/S0962728600014317

EAZA Executive Office. (2013). *The modern zoo: Foundations for management and development*.

Edwards, K. L., Walker, S. L., Dunham, A. E., Pilgrim, M., Okita-Ouma, B., & Shultz, S. (2015). Low birth rates and reproductive skew limit the viability of Europe's captive Eastern black rhinoceros, *Diceros bicornis michaeli*. *Biodiversity and Conservation*, *24*(11), 2831–2852. https://doi.org/10.1007/s10531-015-0976-7

Ellingsen, K., Coleman, G. J., Lunda, V., & Mejdella, C. M. (2014). Using qualitative behaviour assessment to explore the link between stockperson behaviour and dairy calf behaviour. *Applied Animal Behaviour Science*, *153*, 10–17. https://doi.org/10.1016/j.applanim.2014.01.011

Fitzjohn, T. (2013). Progress report on three eastern black rhinoceroses translocated from Port Lympne, UK, to mkomazi rhino sanctuary, Tanzania. *Wild Cons*, *1*(2), 66–68. http://www.rhinoresourcecenter.com/index.php?s=1&act=pdfviewer&id=1571162951&folder=157

Fleming, P. A., Clarke, T., Wickham, S. L., Stockman, C. A., Barnes, A. L., Collins, T. A., & Miller, D. W. (2016). The contribution of qualitative behavioural assessment to appraisal of livestock welfare. *Animal Production Science*, *56*(10), 1569. https://doi.org/10.1071/AN15101

Fyumagwa, R. D., & Nyahongo, J. W. (2010). Black rhino conservation in Tanzania: Translocation efforts and further challenges. *Pachyderm*, *47*, 59–65. https://doi.org/10.69649/pachyderm.v47i.212

Grosso, L., Battinia, M., Wemelsfelder, F., Barbieri, S., Minero, M., Costa, D., & Mattiello, S. (2016). On-farm qualitative behaviour assessment of dairy goats in different housing conditions. *Applied Animal Behaviour Science*, *180*, 51–57. https://doi.org/10.1016/j.applanim.2016.04.013

Hosey, G. (2005). How does the zoo environment affect the behaviour of captive primates? *Applied Animal Behaviour Science*, *90*(2), 107–129. https://doi.org/10.1016/j.applanim.2004.08.015

Hui, F. K. C., Taskinen, S., Pledger, S., Foster, S. D., & Warton, D. I. (2015). Model-based approaches to unconstrained ordination. *Methods in Ecology and Evolution*, *6*(4), 399–411. https://doi.org/10.1111/2041-210X.12236

Hui, F. K. C., Warton, D., Ormerod, J., Haapaniemi, V., & Taskinen, S. (2017). Variational approximations for generalized linear latent variable models. *Journal of Computational and Graphical Statistics*, *26*(1), 35–43. https://doi.org/10.1080/10618600.2016.1164708

Jenner, B. M., & Lewis, T. R. (2023). Environmental conditions and vehicle disturbance influence stress behaviors in a working Harris's hawk (*Parabuteo unicinctus*). *Journal of Applied Animal Welfare Science*, *27*(2), 373–385. https://doi.org/10.1080/10888705.2023.2253143

King, T., & Beer, P. (2018). Rhinos, elephants and the Aspinall foundation: Over 30 years of captive-breeding, reintroduction and conservation. *Pachyderm*, *59*, 127–131. https://doi.org/10.69649/pachyderm.v59i.96

Kristensen, K., Nielsen, A., Berg, C. W., Skaug, H., & Bell, B. M. (2016). TMB: Automatic differentiation and Laplace approximation. *Journal of Statistical Software*, *70*(5), 1–21. https://doi.org/10.18637/jss.v070.i05

Laméris, D. W., Salas, M., Eens, M., Gillespie, L., Staes, N., Torfs, J. R., Verspeek, J., Vervaecke, H., Ward, S. J., & Stevens, J. M. (2024). Qualitative behavioural assessment of bonobo emotional expressivity across observer groups and zoo housing environments. *Animal Welfare*, *33*, e28. https://doi.org/10.1017/awf.2024.29

Lees, C. M., & Wilcken, J. (2009). Sustaining the Ark: The challenges faced by zoos in maintaining viable populations. *International Zoo Yearbook*, *43*(1), 6–18. https://doi.org/10.1111/j.1748-1090.2008.00066.x

le Roex, N., & Ferreira, S. M. (2020). Age structure changes indicate direct and indirect population impacts in illegally harvested black rhino. *PLOS ONE*, *15*(7), e0236790. https://doi.org/10.1371/journal.pone.0236790

Lewis, T. R., Griffin, R. K., Martin, I. M., Figueroa, A., Ray, J. M., Feltham, J., & Grant, P. B. C. (2021). Ecology and morphology of the dwarf bromeliad boa *ungaliophis panamensis* (Squamata, Boidae, Ungaliophiinae) in Costa Rica and Panama. *Neotropical Biology and Conservation*, *16*(2), 317–331. https://doi.org/10.3897/neotropical.16.e57872

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*(6), 574–588. https://doi.org/10.1002/zoo.20288

Metrione, L. C., Penfold, L. M., & Waring, G. H. (2007). Social and spatial relationships in captive southern white rhinoceros (*Ceratotherium simum simum*). *Zoo Biology*, *26*(6), 487–502. https://doi.org/10.1002/zoo.20143

Minero, M., Tosi, M. V., Canali, E., & Wemelsfelder, F. (2009). Quantitative and qualitative assessment of the response of foals to the presence of an unfamiliar human. *Applied Animal Behaviour Science*, *116*(1), 74–81. https://doi.org/10.1016/j.applanim.2008.07.001

Mueller, J. E., Dennis, P. M., Willis, M. A., Simone, E. A., & Lukas, K. E. (2013). Seasonal and diurnal variations in African elephant (*Loxodonta africana*) and black rhinoceros (*Diceros bicornis*) behavior in a northern climate zoo. *International Journal of Comparative Psychology*, *26*(4), 304–323. https://doi.org/10.46867/ijcp.2013.26.04.02

Napolitano, F., De Rosa, G., Braghieri, A., Grasso, F., Bordi, A., & Wemelsfelder, F. (2008). The qualitative assessment of responsiveness to environmental challenge in horses and ponies. *Applied Animal Behaviour Science*, *109*(2–4), 342–354. https://doi.org/10.1016/j.applanim.2007.03.009

Napolitano, F., De Rosa, G., Grasso, F., & Wemelsfelder, F. (2012). Qualitative behaviour assessment of dairy buffaloes (*Bubalus Bubalis*). *Applied Animal Behaviour Science*, *141*(3–4), 91–100. https://doi.org/10.1016/j.applanim.2012.08.002

Niku, J., Brooks, W., Herliansyah, R., Hui, F. K. C., Taskinen, S., & Warton, D. I. (2019). *R package "gllvm": Generalized linear latent variable models*. Version 1.1.2. https://doi.org/10.18637/jss.v070.i05

Niku, J., Brooks, W., Herliansyah, R., Hui, F. K. C., Taskinen, S., Warton, D. I., & Li, J. (2019). Efficient estimation of generalized linear latent variable models. *PLOS ONE*, *14*(5), e0216129. https://doi.org/10.1371/journal.pone.0216129

Oginah, S. A., Ang'ienda, P. O., & Onyango, P. O. (2020). Evaluation of habitat use and ecological carrying capacity for the reintroduced Eastern black rhinoceros (*Diceros bicornis michaeli*) in Ruma National Park, Kenya. *African Journal of Ecology*, *58*(1), 34–45. https://doi.org/10.1111/aje.12674

Otiende, M. Y., Kivata, M. W., Makumi, J. N., Mutinda, M. N., Okun, D., Kariuki, L., Obanda, V., Gakuya, F., Mijele, D., Soriguer, R. C., & Alasaad, S. (2015). Epidemiology of *theileria bicornis* among black and white rhinoceros metapopulation in Kenya. *BMC Veterinary Research*, *11*(1), 4. https://doi.org/10.1186/s12917-014-0316-2

Ovaskainen, O., Abrego, N., Halme, P., & Dunson, D. (2016). Using latent variable models to identify large networks of species-to-species associations at different spatial scales. *Methods in Ecology and Evolution*, *7*(5), 549–555. https://doi.org/10.1111/2041-210X.12501

Owen-Smith, R. N. (1973). *The behavioural ecology of the white rhinoceros* [Doctoral dissertation]. University of Wisconsin,

Palme, R. (2019). Non-invasive measurement of glucocorticoids: Advances and problems. *Physiology & Behavior*, *199*, 229–243. https://doi.org/10.1016/j.physbeh.2018.11.021

Patel, F., Wemelsfelder, F., & Ward, S. J. (2019). Using qualitative behaviour assessment to investigate human-animal relationships in zoo-housed giraffes (*Giraffa camelopardalis*). *Animals*, *9*(6), 381. https://doi.org/10.3390/ani9060381

Pollock, L. J., Tingley, R., Morris, W. K., Golding, N., O'Hara, R. B., Parris, K. M., Vesk, P. A., McCarthy, M. A., & McPherson, J. (2014). Understanding co-occurrence by modelling species simultaneously with a Joint Species Distribution Model (JSDM). *Methods in Ecology and Evolution*, *5*(5), 397–406. https://doi.org/10.1111/2041-210X.12180

Rice, E. A., Lewis, T. R., Griffin, R. K., & Grant, P. B. C. (2022). Heads nods and boat bobs: Behavior of *iguana iguana* is affected by environment and boat traffic in riparian tropical forest. *Biotropica*, *54*(4), 820–828. https://doi.org/10.1111/btp.13136

Ricketts, V., Dierenfeld, E. S., Sauer, C., & Whitehouse-Tedd, K. (2021). Feed intake and dietary composition of iron (fe), copper (cu), vitamin E, and tannic acid of five captive black rhinoceros (*Diceros bicornis*) in a UK collection. *Zoo Biology*, *40*(1), 52–58. https://doi.org/10.1002/zoo.21580

Rutherford, K. M. D., Donald, R. D., Lawrence, A. B., & Wemelsfelder, F. (2012). Qualitative behavioural assessment of emotionality in pigs. *Applied Animal Behaviour Science*, *139*(3–4), 218–224. https://doi.org/10.1016/j.applanim.2012.04.004

Skovlund, C. R., Kirchner, M. K., Contiero, B., Ellegaard, S., Manteca, X., Stelvig, M., Tallo-Parra, O., & Forkman, B. (2023). Qualitative behaviour assessment for zoo-housed polar bears (*Ursus maritimus*): Intra- and inter-day consistency and association to other indicators of welfare. *Applied Animal Behaviour Science*, *263*, 105942. https://doi.org/10.1016/j.applanim.2023.105942

Spooner, S. L., Farnworth, M. J., Ward, S. J., & Whitehouse-Tedd, K. M. (2021). Conservation education: Are zoo animals effective ambassadors and is there any cost to their welfare? *Journal of Zoological and Botanical Gardens*, *2*(1), 41–65. https://doi.org/10.3390/jzbg2010004

Stagni, E., Brscic, M., Contiero, B., Kirchner, M., Sequeira, S., & Hartmann, S. (2022). Development of a fixed list of terms for qualitative behavioural assessment of brown bear (*Ursus arctos*) in Sanctuaries. *Applied Animal Behaviour Science*, *246*, 105523. https://doi.org/10.1016/j.applanim.2021.105523

Stanbridge, D. (2020). *Genetic admixture of Kruger National Park black rhino (*Diceros bicornis minor*): Conservation implications* [MSc Thesis]. University of Cape Town. https://open.uct.ac.za/handle/11427/32994,

Temple, D., Manteca, X., Velarde, A., & Dalmau, A. (2011). Assessment of animal welfare through behavioural parameters in Iberian pigs in intensive and extensive conditions. *Applied Animal Behaviour Science*, *131*(1–2), 29–39. https://doi.org/10.1016/j.applanim.2011.01.013

van Coeverden de Groot, P. J., Putnam, A. S., Erb, P., Scott, C., Melnick, D., O'Ryan, C., & Boag, P. T. (2011). Conservation genetics of the black rhinoceros, *Diceros bicornis bicornis*, in Namibia. *Conservation Genetics*, *12*(3), 783–792. https://doi.org/10.1007/s10592-011-0185-1

Walker, J. K., Dale, A. R., D'Eath, R. B., & Wemelsfelder, F. (2016). Qualitative behaviour assessment of dogs in the shelter and home environment and relationship with quantitative behaviour assessment and physiological responses. *Applied Animal Behaviour Science*, *184*, 97–108. https://doi.org/10.1016/j.applanim.2016.08.012

Ward, S. J., Sherwen, S., & Clark, F. E. (2018). Advances in applied zoo animal welfare science. *Journal of Applied Animal Welfare Science*, *21*(sup1), 23–33. https://doi.org/10.1080/10888705.2018.1513842

Watters, J. V. (2014). Searching for behavioral indicators of welfare in zoos: Uncovering anticipatory behavior. *Zoo Biology*, *33*(4), 251–256. https://doi.org/10.1002/zoo.21144

Wei, T., & Simko, V. (2017). *R package "corrplot": Visualization of a correlation matrix. Version 0.84*. https://github.com/taiyun/corrplot

Wemelsfelder, F., Hunter, E. A., Mendl, M. T., & Lawrence, A. B. (2000). The spontaneous qualitative assessment of behavioural expressions in pigs: First explorations of a novel methodology for integrative animal welfare measurement. *Applied Animal Behaviour Science*, *67*(3), 193–215. https://doi.org/10.1016/S0168-1591(99)00093-3

Wemelsfelder, F., Hunter, E. A., Mendl, M. T., & Lawrence, A. B. (2001). Assessing the 'whole animal': A free choice profiling approach. *Animal Behaviour*, *62*(2), 209–220. https://doi.org/10.1006/anbe.2001.1741

Wemelsfelder, F., & Lawrence, A. B. (2001). Qualitative assessment of animal behaviour as an on-farm welfare-monitoring tool. *Acta Agriculturae Scandinavica, A*, *51*(2), 21–25. https://doi.org/10.1080/090647001316923018

Wemelsfelder, F., Njraini, N., & Cleaveland, S. (2010). *The application of qualitative behaviour assessment to wild African elephants*. Presentation for the Born Free Foundation.

Williams, R. L., Porter, S. K., Hart, A. G., & Goodenough, A. (2012). The accuracy of behavioural data collected by visitors in a zoo environment: Can visitors collect meaningful data? *International Journal of Zoology*, *2012*, 1–13. https://doi.org/10.1155/2012/724835

Wolfensohn, S., Shotton, J., Bowley, H., Davies, S., Thompson, S., & Justice, W. S. M. (2018). Assessment of welfare in zoo animals: Towards optimum quality of life. *Animals*, *8*(7), 110–116. https://doi.org/10.3390/ANI8070110

Yon, L., Williams, E., Harvey, N. D., Asher, L., & Cameron, E. Z. (2019). Development of a behavioural welfare assessment tool for routine use with captive elephants. *PLOS ONE*, *14*(2), e0210783. https://doi.org/10.1371/journal.pone.0210783