JZAR www.jzar.org JOURNAL OF ZOO AND AQUARIUM RESEARCH

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JZAR Review article

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Research article

The use of Qualitative Behavioural Assessment in zoo welfare measurement and animal husbandry change.

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Keywords: animal welfare; environmental enrichment; evidence-based husbandry; positive challenge; qualitative behavioural assessment.

Article history:
Received: 12 Oct 2018
Accepted: 25 Jun 2019
Published online: 31 Oct 2019

Abstract

Zoological institutions have come a long way over the past 20 years in their measurement and evaluation of animal behaviour and welfare. Environments that enable the performance of biologically relevant activity patterns, which increase behavioural diversity and ensure appetitive behaviours can be completed in full, are commonplace in zoos globally. The use of species-specific environmental enrichment (EE) techniques, where the effect of EE is evaluated and refined, further enhance the opportunities for species to experience positive welfare in zoos. What is still required is evaluation of the lasting effect of such husbandry and housing changes that provide meaningful long-term welfare improvements. To provide evidence for best practice management, benchmarks at a species-specific level are required that are comparable across husbandry and management regimes, as well as across environmental conditions in which captive populations occur. One such method for addressing individual-level welfare state is Qualitative Behavioural Assessment (QBA), an approach increasingly used in domestic animal industries to measure the individual's perception of the situation it finds itself within. This paper provides an outline of the relevance of QBA to those working in the field of zoo animal husbandry to show how valid and objective measurements of welfare state can be taken of individuals living in zoos in a range of different situations. An evaluation of the current literature shows the depth and breadth of QBA application and the paper provides suggestions for future areas of research investigation and a practical usage in the zoo. It is shown how QBA can be used to target the application of EE to meet specific husbandry needs or promote key welfare-positive behaviour. The paper evaluates the relevance of positive challenge "eustress" to captive species and identifies areas for the wider application of QBA across captive population and institutions to further support the key aims of the modern zoo. The paper provides coverage of literature on QBA in the domestic animal field and attempts to apply these methods to a zoo-based example. The paper concludes by evaluating why zoos need to consider the results of qualitative, multi-institution studies and how the results of this can be utilised to improve husbandry and animal experiences in the zoo.

Measuring quality of life in captivity

Whilst much work has been published on the welfare impacts of captivity (Clubb and Mason 2003) and the issues with species or individual animals being predisposed to the performance of stereotypic or Abnormal Repetitive Behaviours, ARBs (Mason et al. 2007; Mellor et al. 2018; Rose et al. 2017a, b), it is important to consider the wider application of such research to evidence change in zoo husbandry and management. The study of behaviour in zoos is one of the best ways of ensuring animals experience a good quality of life (Shepherdson et al. 2004). It is necessary to continue to investigate occurrences of ARBs to show where more research evidence is needed to guide the development of husbandry practice into the future (Rose et al. 2017b). Such research is a way of identifying an issue and then altering management regimes and using directed environmental enrichment (EE) approaches to enable animals to perform more naturalistic behaviour patterns for that species.

Species-wide ARB performed the same way in multiple individuals is identified in the literature (Mason 2010), suggesting that species cope differently with living in a human-created, human-controlled environment. Likewise, developmental differences between species lead to differences in behavioural flexibility when these species are housed in a captive environment (Mason et al. 2013). One such response variable might be the reaction to a stressor, and therefore

Figure 1. Determining the causes of ARBs, in this case feather plucking in a red-fronted macaw (*Ara rubrogenys*). Why are some individuals affected by ARB performance and yet other individuals of the same species do not show such outward negative indicators of their welfare state?

coping (hence welfare state) will be dependent upon this flexible approach to captive care. Within a species, individuals can exhibit different outward responses to the captive environment (Figure 1), further supporting the need for an individual approach to welfare measurement to ensure positive welfare is underpinned by husbandry provision. This example of feather-damaging behaviour in a specific species of parrot (Figure 1) is useful to consider in relation to Quality of Life (QoL), as feather plucking is a multifactorial condition that is expressed differently between individuals both within and between species based on their responses to a range of causalities (Garner et al. 2003; Lumeij and Hommers 2008; Meehan et al. 2004; Meehan et al. 2016). A non-invasive approach that compares the responses and coping mechanisms of individual parrots (of this species) in different housing and husbandry systems would identify husbandry and/ or environmental variables that may trigger feather plucking in individuals within a species. Individuals with increased behavioural flexibility, and are thus able to use a wider range of coping strategies, may fare better in a managed environment. As zoo-housed populations can be vital resources for field-based conservation, it is important that such behavioural flexibility (and ways of coping) does not change the behavioural phenotype of the population which would limit the success of future reintroductions or augmentation of wild population work.

The importance of behavioural plasticity is highlighted by Mason et al. (2013) who states that animals raised in captivity, even when first generation from wild founders, can show captivity-benefitting phenotypic changes (such as a reduced behavioural flexibility or a reduced stress response). It is clearly important to ensure captive animals experience positive affective states (Rose et al. 2017b; Whitham and Wielebnowski 2013). At the same time, however, experience of beneficial stressors, "eustress" (Meehan and Mench 2007), should be incorporated into husbandry regimes or enrichment programmes, based on the needs of the specific species. Such beneficial stressors could be increased cognitive challenge (Hopper et al. 2016; Meehan and Mench 2007), interactions that arise from multi-species exhibits (Little and Sommer 2002) or providing an appropriate outlet for a behaviour with a high internal motivation, such as contrafreeloading (the act of preferring to work for a reward even when the reward is present without effort) (de Jonge et al. 2008). Prediction and control over a stressor, reviewed in research on a mixed-species langur and bear enclosure (Little and Sommer 2002) is important to QoL in zoos. In this example, providing langurs with an acute biologically relevant challenging situation (the presence of a potential predator) reduced the likelihood of chronic boredom in this managed setting. This is because key components of stress physiology (the hypothalamic-pituitary adrenal system) are activated and direct the langurs away to other parts of the enclosure where they can use different resources. It is important to remember, however, that there is not necessarily evidence for all environmental stressors that are physiologically and psychologically beneficial for the animals in captivity (Little and Sommer 2002). Providing eustress may clearly have important, positive consequences to behavioural diversity in zoo individuals (i.e. by stimulating behaviours that would be common in the wild, such as- vigilance or predator avoidance, which may not be elicited during daily husbandry regimes), but how and when it is used, and in what context, is an area of animal welfare science worthy of future investigation.

Linking behavioural diversity to animal welfare

If eustress can help provide challenges in the zoo environment and improve the behavioural flexibility of individuals of a species, its long-term effects must be measured and quantified. Methods used in the ecological sciences to determine species richness and diversity within a habitat (Heip and Engels 1974) can be applied to the analysis of behavioural data collected on captive species (Rose et al. 2018a; Van Metter et al. 2008). Both Shannon's Diversity Index (Shannon 1948) and the 1-Simpson's Index (Simpson 1949) are appropriate ways of evaluating the time expended on different forms of activity by different species or populations, and therefore allow for comparison of overall diversity of time-activity budgets (Rose et al. 2018a). Calculation of Behavioural Diversity Indices (BDI) has been relevant to the study of impacts of environmental enrichment on captive animal behavioural repertoires (Van Metter et al. 2008), as well as to research into the influence of different husbandry practices on behaviour patterns and stress responses (Miller et al. 2016). Van Metter et al. (2008) and Miller et al. (2016) emphasise the importance of collecting data on behavioural diversity to validate its use in determining positive welfare states across different captive species. Identification of when BDI may be markedly different from normal (e.g. a decline during a time of year when a species is normally very active) allows for evaluation of potential causes, such as weather patterns, climatic changes or differences in management practices that have occurred.

As an example, use of focal animal sampling (Martin and Bateson 2007) to calculate individual BDIs provides an attribute to input into social network analysis, which could explain the position and influence of one animal amongst its group. Individuals expressing higher BDIs, which may be more active, may have a wider range of social partners and therefore connect with different subsections of their group. It is possible to make ecological interpretations of captive activity patterns if data on wild time-activity budgets are available. This would encompass seasonal and physiological changes in behavioural repertoires, which provide a biological reason for displaying higher (e.g. courtship displaying) or lower (e.g. moulting) activity levels, and subsequently natural changes in social position or influence over their group. Whilst it is not possible to measure positive welfare states solely on the performance of complete natural behaviour patterns in captivity (Stamp Dawkins 2017; Veasey 2017), zoos must continue their efforts to integrate wild ecology into captive management protocols (Melfi 2009; Melfi and Hosey 2011). Changing enclosure design to make a zoo environment more naturalistic provides measurable welfare improvements (Little and Sommer 2002) and "functional substitution" (Robinson 1998), that is, replacing key habitat features with similar resources in the zoo to promote species-appropriate behaviour. As such, the use and evaluation of behavioural data from the wild alongside data from captivity is necessary to assess whether an enclosure is enabling behaviours associated with positive welfare outcomes (Rose et al. 2014b; Rose and Robert 2013). To further enhance the validity of comparative wild vs captive approaches, Howell and Cheyne (2018) suggest using multiple animal- and environmental-based metrics, using data collected via standardised methods across both conditions (wild and captive) to account for the complexity of translating wild time-activity patterns into a captive setting.

Objectively assessing zoo animal welfare to develop husbandry outcomes

As QoL can be determined by the responses of an individual to its environment, and standardised data collection methods are available to measure changes in behavioural repertoires over time, zoos can use such data to inform the effects of management regimes. Ideally, zoos should have a zero-tolerance approach to ARBs (Mason et al. 2007), but one needs to consider the influence on the animal that may cause deviations from natural or normal activity patterns. Maternal deprivation or early-life experiences are known to influence the QoL of adult animals (Harlow 1964; Rose et al. 2017b; Siciliano-Martina and Martina 2018), and such individuals may display ARBs even when housed in ecologically relevant, enriched environments. For example, monkeys hand-reared in isolation show reduced interactions and social behaviours when adult (Harlow 1964); maternally deprived giraffe are more reactive to external stimuli compared to parent-reared animals (Siciliano-Martina and Martina 2018) and a review of ARBs in mammals by Rose et al. (2017b) shows increased likelihood to perform ARB if an individual is not parent reared. As such, animal-based, individualistic welfare assessment needs to be considered if ARB is present, rather than broadly labelling zoo environments as poor or impoverished.

To conduct this individual approach, zoo researchers need to utilise data taken at various points through the life of an animal. The scientific literature surrounding farm animal behaviour and welfare research offers some useful descriptions of how to measure long-term QoL, and therefore provides a framework for conducting such types of investigation in zoos.

The integration of relatively new fields of animal behaviour science (such as social network theory) used alongside more traditional behavioural observation methods can provide a fuller picture of how an animal responds to a managed environment (Beisner and McCowan 2015). For example, social network methods allow consistency of dyadic relationships to be mapped across time (Rose and Croft 2018). This can provide evidence for how change in social composition (which can happen naturally or due to animal transfers between institutions for breeding purposes) influences the quality and patterning of associations or interactions experienced by each individual. By collecting and evaluating data that show how, where and when animals can exert choice over what they do, enabling them to experience autonomy (control over a situation), it might be possible to improve the outcomes of a species in a zoo (e.g. for conservation breeding or for educational initiatives).

When designing captive animal husbandry, it is important to consider the fitness consequences associated with the performance of a specific behaviour or set of behaviours (Pruitt and Riechert 2011; Silk et al. 2009). If the performance of an intrinsically important behaviour is thwarted, animals will not be satiated (Hughes and Duncan 1988; Jensen and Toates 1993). Both appetitive (searching / doing actions) and consummatory (end result) behaviours are important to the fulfilment of an animal's motivational needs (de Jonge et al. 2008; Hinde 1953) and restricting these can lead to frustration and disrupted behaviour patterns. Key elements of positive welfare in captivity arise from enabling captive animals to experience choice and control when housed in managed situations (Ross 2006; Whitham and Wielebnowski 2013). Ecologically relevant food provision and placement within an enclosure can promote contrafreeloading (Inglis et al. 1997; Osborne 1977), an important highly-motivated behaviour seen in many bear (Ursidae) species (Wagman et al. 2018).

As such, observation of normal or naturalistic behaviour patterns provides an insight into physical and psychological welfare enabling an evaluation of the appropriateness and relevance of current husbandry and management regimes. Extending this approach to additional institutions will enable the generation of large-scale, long-term datasets and a QBA approach is a useful method to achieve this.

Qualitative Behavioural Assessment

Development of animal-based welfare indicators are useful for capturing an individual's perception of its situation. An animal's emotional state, which ultimately reflects its current welfare experience, varies on a scale of positive and negative valence (the attractiveness or aversiveness of a situation) and arousal (the individual's level of activation) (Mendl et al. 2010). In a zoo, behaviours that can reflect high arousal and positive valence include courtship display (Rose 2018), whereas behaviours reflecting low arousal and negative valence include apathy or lethargy caused by a lack of stimulation or enrichment (Mason and Veasey 2010). Understanding the response of individuals of a species to their environment helps design husbandry practices that enhance positive valence/high or low arousal situations and reduce experiences of negative valence/high or low arousal. One method of assessing animal behaviour to inform on emotional and welfare states is through Qualitative Behavioural Assessment (QBA). QBA is a whole-animal method to assess the expressive qualities of animal demeanour, and describes the animal's response to its situation or environment using a set of behavioural descriptors, i.e. "anxious", "content" or "relaxed" (Wemelsfelder 2007; Wemelsfelder and Lawrence 2001). Fixed lists of descriptors

Table 1. Farm animal research papers that have used QBA as a means of determining an individual's welfare state and its response (behaviourally and emotionally) to current environmental conditions.

Author	Journal	Species	Output and evaluation.
Wemelsfelder et al. (2000)	Applied Animal Behaviour Science	Pig	Qualitative assessment of behaviour can provide empirical access to behavioural expression that links to welfare state. Dynamic details of the behaviour, and differences between individual animals can be scored accurately using the same descriptor because of the holistic manner of measuring behavioural expression and not the mechanics of the action.
Wemelsfelder and Lawrence (2001)	Acta Agriculturae Scandanavica	Multiple farm	QBA is reliable and repeatable under controlled experimental conditions and can be developed for on-site welfare assessment. Free Choice Profiling is adaptable to practical situations as observers would not need lengthen training in behavioural recording to make qualitative judgements based on the expression of demeanours they see.
Wemelsfelder (2007)	Animal Welfare	Multiple farm	Qualitative approaches can make an important contribution to our understanding of animal quality of life at a "whole animal" level. As animal care staff are well placed to "know" their animals well and judge their comfort and welfare state on a daily basis, determining QoL for an individual, based on QBA from its care-givers is a reliable way of collecting data quickly and repeatedly.
Temple et al. (2011)	Applied Animal Behaviour Science	Pig	QBA better at distinguishing negative welfare indicators rather than explaining differences in positive behaviours but it has a role is differentiating effects of farm on pig welfare. Therefore, even for "difficult to categorise" expressions (such as social behaviour), multi-institutional studies of welfare are possible.
Napolitano et al. (2012)	Applied Animal Behaviour Science	Water buffalo	Meaningful associations between quantitative and qualitative results show that both can be used to assess an animal's welfare state. Therefore, results on the emotional construct of behaviour are supported by observation based on what the animal is "doing" meaning a complete picture of the individual's behavioural repertoire can be evaluated against its emotional state.
Rutherford et al. (2012)	Applied Animal Behaviour Science	Pig	QBA can be a reliable method for informing on an animal's emotional state when judging behavioural characteristics of individuals in drugs trials. Therefore, QBA is a relevant approach for measuring welfare under changed husbandry or management regimes where more work or attention may be needed to ensure positive affective states are experienced by the animals at that time.
Phythian et al. (2013)	Applied Animal Behaviour Science	Sheep	High interobserver reliability when using QBA to look at behavioural expression in sheep and therefore scope to use for determining individual animal welfare state; but it is important to remember that using video footage of behaviour when training observers does not always prepare them fully for the reactions and orientation of animals when data collection is conducted in the field.
Grosso et al. (2016)	Applied Animal Behaviour Science	Goat	Housing system significantly affects goat behavioural expression and whilst QBA is useful for measuring welfare state, more work is needed to improve interobserver reliability. Specifically, whilst more expensive and time-consuming, on-location training of observers with live animals yields more reliable and valid results from QBA in the longer term.
Minero et al. (2016)	Applied Animal Behaviour Science	Donkey	QBA is a relevant tool for assessing donkey welfare and fixed descriptors can be used alongside of animal welfare indicators reliably by a range of assessors. QBA was particularly good at picking out positive aspects of a donkey's life on farm, which would be highly relevant for disseminating areas of management or husbandry practice to other institutions to promote these positive emotional states.
Phythian et al. (2016)	Applied Animal Behaviour Science	Sheep	QBA can be used to identify physical and health impacts on sheep welfare with lameness and fleece soiling correlating with poorer emotional and behavioural responses. Therefore, evidence for veterinary intervention is available to improve QoL by treating the health problem and thus improving the animal's emotional situation.
Hintze et al. (2017)	Applied Animal Behaviour Science	Horse	QBA is a relevant tool for assessing horse-human interactions when an immediate assessment of the horse's emotional state is needed. The animal's response to the human-animal bond can therefore be used as a quick and reliable way of determining its emotional state when it has contact with its owner.
Muri and Stubsjøen (2017)	Animal Welfare	Sheep	Reliable QBA difficult in on-farm situations, potentially because of differences between farm conditions, but was achieved when sheep behavioural traits were scored from videos. The practicalities of field-based data collection need to be considered as observer drift and limited between-institution variation can influence the reliability and thus wide-spread application of QBA results.
Battini et al. (2018)	Animals	Goat	QBA can identify differences in individual goat's emotions but only a few correlations with animal-based and resource-based welfare indicators were noted. QBA may be useful holistically but more research is needed to further validate this. Whilst background research on potentially related species may be relevant to developing QBA methodologies, species-specific field tests need to be run to ensure that emotional states can be described reliably.
de Boyer des Roches et al. (2018)	Applied Animal Behaviour Science	Cow	QBA is sensitive to changes in cow's emotional states during mastitis episodes and after treatment, potentially lending itself as a tool for mastitis detection. For repeated measures on the same animals, such links between animal health and emotion may allow differences in an individual's QBA scores (when used over time) to highlight circumstances for veterinary intervention.
Minero et al. (2018)	Applied Animal Behaviour Science	Horse	QBA is sensitive to the quality of human contact that a horse experiences, and therefore show that high-quality human relationships promote good horse welfare. When using QBA across institutions, the relationship with caregivers can be a factor to consider when evaluating changes in individual animal emotional states and welfare assessment.
Napolitano et al. (2018)	PLoS One	Goat	Continuous QBA may be a tool to use for assessment of welfare in a changing environment when animal's behavioural expression is also varied. Significant influences of social situation on descriptors of behavioural expression are noted, therefore evaluation of individual emotion against quantitative behaviour patterns and specific environmental predictors can help show how animal's cope and adapt to novelty around them.

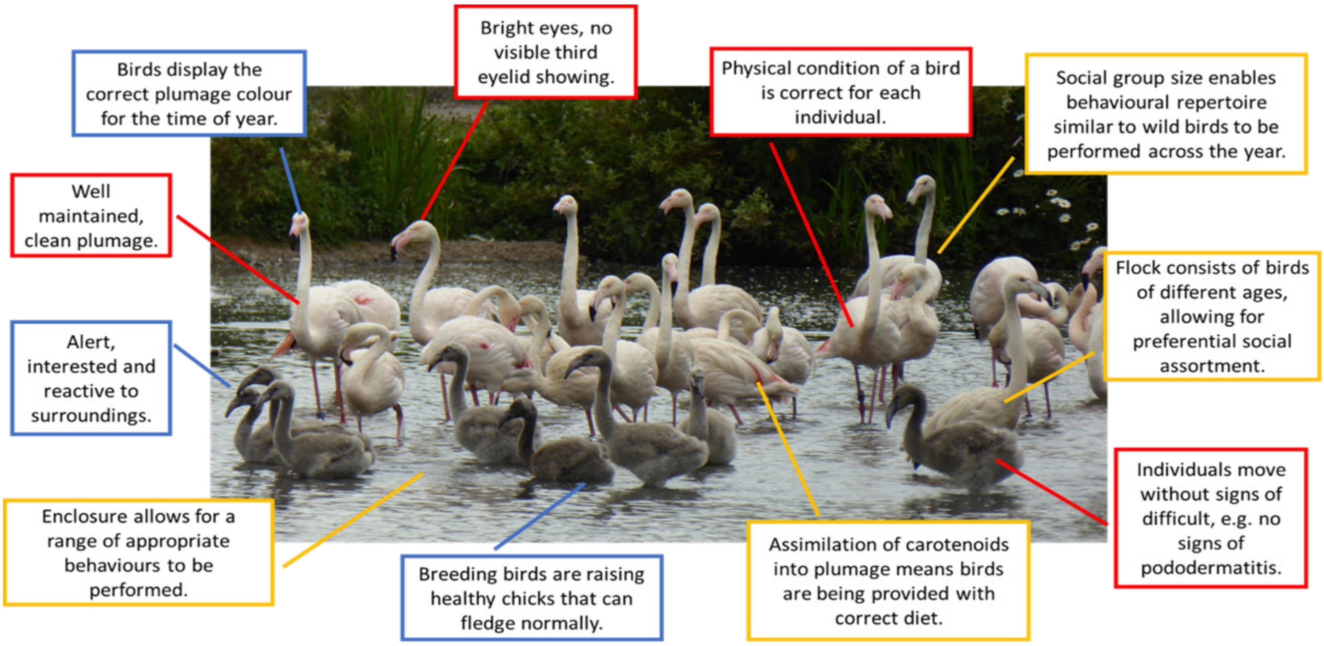

Figure 2. An example of how animal (physical and behavioural) and environmental measures could be defined for use across institutions and populations to objectively measure captive flamingo welfare. Blue boxes define a behavioural measure of good welfare, red boxes a physical measure of good welfare and yellow boxes an environmental or management variable that influences good welfare states.

can be used (Clarke et al. 2016), or additional behavioural descriptors can be created by observers ("Free Choice Profiling") to enable the fullest expression of behaviour to be captured in that current condition (Wemelsfelder and Lawrence 2001). As a holistic measure of welfare, QBA puts an individual's behavioural response in the context of the whole animal and therefore provides insight into the individual's psychology and its current state of being at that time and place (Wemelsfelder 2007). It is this description of behavioural expression, not the mechanics of the behaviour, that explains the animal's underlying psychology and physiology (Wemelsfelder et al. 2000).

QBA has been successful in identifying behavioural measures of internal states that provide an understanding of the observer's perception of the animal's current welfare trajectory (Minero et al. 2016; Wemelsfelder and Lawrence 2001). Minero et al. (2016) explain a range of movements and descriptions of conditions that could be observed and recorded as individual animal-based measures, as well as behavioural scores from a standardised ethogram, that support the descriptions from each animal. The prevalence of a specific score across individuals within a study population points to the most common forms of welfare compromise in that species (i.e. consistency in response between individuals that may indicate a negative valence due to X husbandry situation or environmental effect). The individual animal's environment, housing and husbandry can then be evaluated against prevalence of poor welfare indicators to determine which variables are likely to influence an individual's chances of experiencing a more positive valency.

Table 1 outlines the range of situations in which QBA has been used to provide objective, individual measurements of welfare in a domestic setting. Many of the outputs are directly transferable to the zoo environment. Empirical evidence of changes in welfare state and the use of a standardised recording system can quantify the likelihood that individuals will have positive welfare experiences in a given environment and under a specific husbandry regime. These examples also show that animal/individual-based welfare experiences are easier to compile in some species, such as horses (Hintze et al. 2017; Minero et al. 2018), but can be more challenging in others, such as goats (Battini et al. 2018; Grosso et al. 2016; Napolitano et al. 2018). Such challenges may be due to human perceptions of animal behaviour, that is, the familiarity of the observers with a given species' way of expressing emotion

Box 1. QBA descriptors that could be applied to individual birds in a flock based on their behavioural expressions in a given situation.

Behavioural expression	
Positive valence	Negative valence
Bold outgoing, adventurous, exploratory	Angry starts fights, volatile, pushy
Calm relaxed, at ease, steady	Anxious unsure, lacking confidence, reticent
Confident self-assured, unconcerned	Flighty easy to spook, edgy, jumpy
Excited keen, eager, active	Fearful distressed, panicky, "fight or flight"
Interested engaged, receptive, aware	Withdrawn retiring, disinterested, apathetic

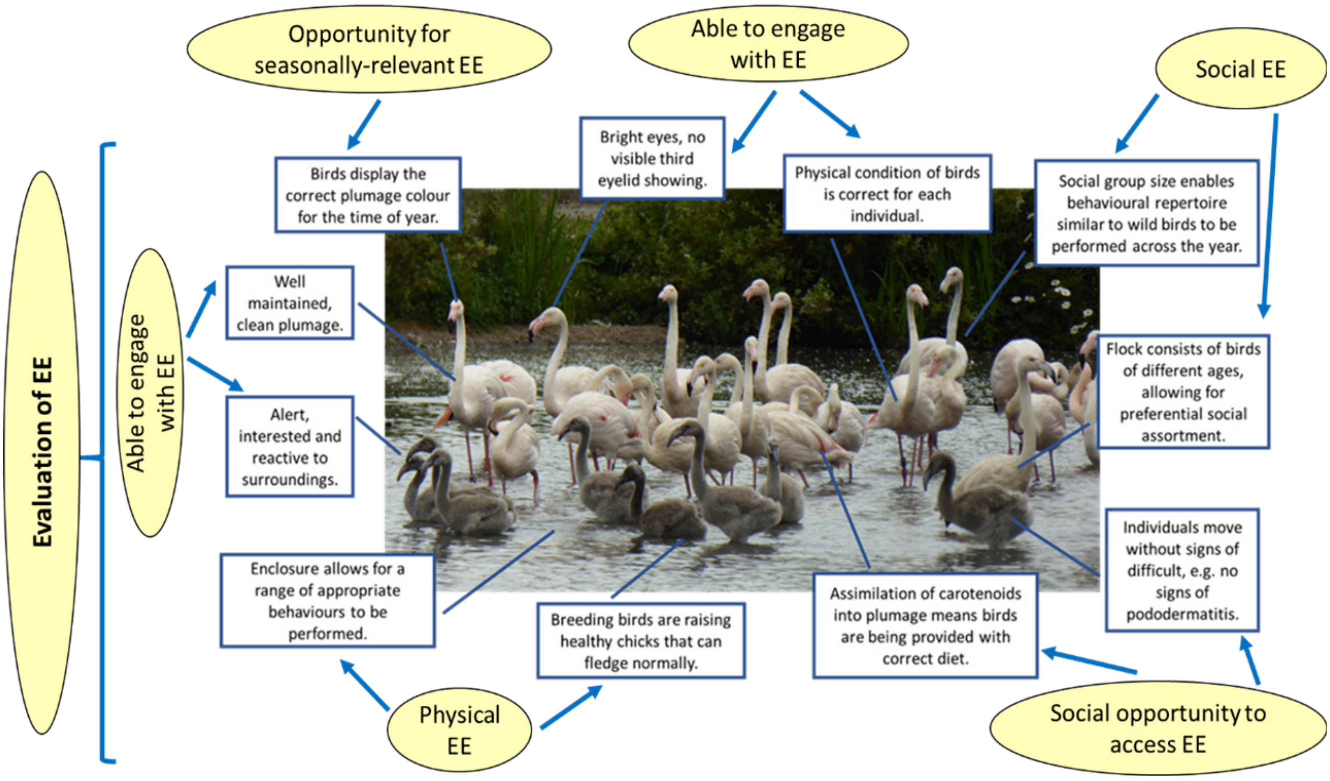

Figure 3. An example of how engagement with environmental enrichment could be used to determine the Quality of Life experienced by captive flamingos evidenced from different behavioural, physical and environmental welfare indicators.

(Darwin and Ekman 1998); how that species has evolved to visibly display emotions or their internal state to conspecifics (Hintze et al. 2016); or how, in a domestic setting, a species responds to the emotions of nearby humans (Smith et al. 2016). This is relevant information for those attempting QBA in non-domestic captive animals, as an understanding of how methods transfer between species is required to assess the validity of QBA's findings from individuals of a given species.

With properly constructed methods, applying QBA to zoo animal welfare can allow an epidemiological study design to be implemented at species-specific and population-specific levels. Such an epidemiological approach has been applied to zoo elephants in North America (Meehan et al. 2016) and has the potential to be used for a multitude of captive species. Health, welfare and fitness indicators that can be matched against husbandry conditions would provide evidence as to where best practice guidelines are needed to ensure standardised, optimum management of a species in all zoos involved in its care. As an example, behavioural and physiological indicators of elephant welfare in UK zoos have been designed based on a structured literature search; 37 elephant-specific welfare indicators were deduced from 30 peer-reviewed publications to give a valid and non-invasive method for determining elephant QoL, regardless of the zoo in which they are housed (Williams et al. 2018). Furthermore, a welfare assessment tool that enables changes to an individual elephant's welfare state to be tracked has been developed and implemented at 11 UK and Irish institutions (Yon et al. 2019). These studies conclude that such an approach has a relevant application across all zoo-housed taxa but can be specifically valuable where a rapid collection of welfare information may be required (if, for example policy or legislative change are to affect the future of such species in zoos).

Integrating welfare measurement, QBA and environmental enrichment in zoos

With an understanding of the important aspects of species biology and ecology, it is possible to judge the captive environment as appropriate (or not) for behavioural functioning and therefore any potential impact on welfare can be judged objectively. Linking such environmental measurements to individual animal BDI scores, for example, would also allow for cross-population welfare assessment at individual and group levels because changes in a behavioural state could be directly compared for all birds housed in zoos. Scoring features of the environment (including management features) and their potential impact on behaviour and the key characteristics of an animal's demeanour, enable QBA to be completed for all situations in which a species may be kept. Literature reviews are useful for identifying valid behavioural indicators of welfare (Williams et al. 2018; Yon et al. 2019), to compare with eventual QBA outputs. Qualitative assessment can then be performed holistically on an animal's overall condition in its current situation, based on a care-giver or zoo keeper's opinion, while considering how experienced they are likely to be in recognising the behaviour, mood and physical state of the animals they see daily (Whitham and Wielebnowski 2009). As an example of such an integrated approach, here it is illustrated how categories for welfare assessment could be used to identify variables that impact upon captive flamingo QoL (Figure 2) and

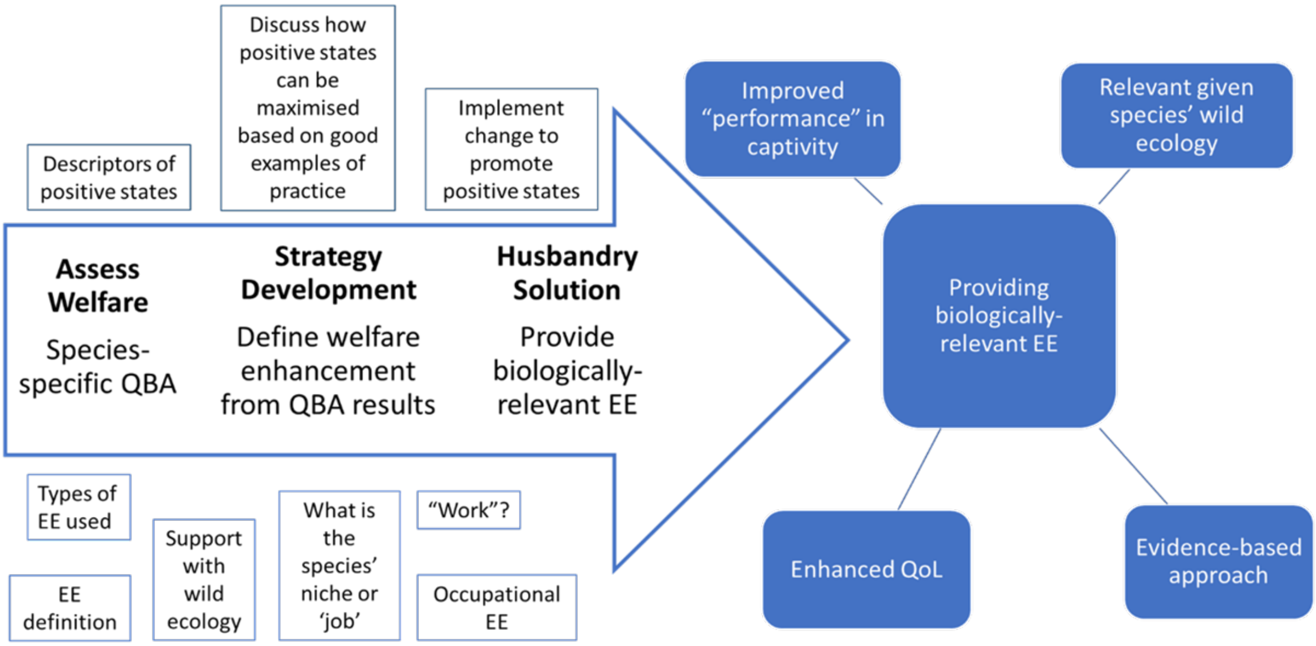

Figure 4. The interaction between the use of EE for improving in-zoo welfare and the outcomes from the presentation of species-appropriate EE. The arrow documents the process from QBA through to discussing husbandry change and then implementation. The boxes above the arrow show the use of QBA data to informed decision. The boxes below the arrow give an example of how occupational EE could be used to promote positive emotions and good animal welfare based on QBA from a cross-institution study. The blue boxes after the arrow explain what the animal will gain once the husbandry solution is implemented.

then to assess individual bird responses based on descriptors of their behavioural expression (Box 1).

Descriptors for individual bird QBA can also be extracted from the literature, which can tell us what flamingos "need " in captivity (Greene and King 2005), what factors influence optimum care (King 2008), how keepers can infer welfare state from management and provision (Rose et al. 2016) and what wild birds have evolved to do, and therefore what should they be able to do, in captivity (Rose et al. 2014a). Based on the behavioural ecology of these birds, Box 1 suggests biologically relevant descriptors to define behavioural expression for use in a multi-zoo QBA. A correct social environment will enable choice (of where to go and what to do) and control (who to do what with and when) by captive flamingos. Species-specific and context-appropriate physical and behavioural measures of welfare can be combined to infer the presence of positive or negative affective states. Having evaluated the condition of the animals and the quality of their environment, the demeanour of each individual within the flock can then be scored (Box 1) to provide more information on the individual's potential experiences at any given time.

Assessment of positive and negative affective states from behavioural and emotional inferences is well documented in farm animals (Boissy et al. 2011; Boissy et al. 2007; Millman 2013) but there is limited study in captive wild animals. It is known from laboratory animal research that the use of environmental enrichment promotes positive affective states and an optimistic outlook (Brydges et al. 2011). Therefore, the use of biologically relevant enrichment within the zoo can have the same effect and can enable captive wild animals to experience more positive welfare outcomes, evidenced by QBA scores that indicate favourable behavioural expression and positive valence. In the flamingo example, maintaining large, diverse social groups would be considered a beneficial form of enrichment. Social enrichment has been documented as having a positive impact on the well-being of captive species (Bloomsmith et al. 1991) and as such zoos should consider managing an individual's social environment to provide an output for specific behavioural needs or activity patterns.

By assessing welfare against measures of valence and arousal, one can gain a better understanding of the emotional construct of the state of an animal (Mendl et al. 2010); an approach that occurs regularly in the literature on laboratory and domestic species (Désiré et al. 2002; Makowska and Weary 2013; Reefmann et al. 2009), but is only documented for a limited number of captive species, for example, some primates (Pomerantz et al. 2012). Flamingos perform a range of behaviours that fit this valence and arousal model. For example, in a social context, increasing levels of aggression may disrupt important bonds between individuals and a flock size that does not allow birds to express social choice may lead to poorer welfare states. Integrating QBA to assess bird expression, using BDI to determine overall variation in time-budgets and using social network analyses to quantify and define the organisation of flocks and an individual's place within it, can all provide evidence for husbandry change to target the promotion of positive welfare behaviours. Integrating QBA profiles as attributes into a network, factors that describe the individuals within the group (Croft et al. 2008), would help evaluate i) how social position and number of connections influences welfare state; and

Figure 5. An African harrier hawk (*Polyboroides typus*) using its doubled-jointed legs to extract a food reward from a fake weaver-bird nest. This instinctive hunting behaviour has been turned into enrichment to provide physical and occupational enrichment, which encourages natural hunting behaviour and increases zoo visitor interest in this species. As captive birds of prey may be viewed as sedentary and lacking in diverse behaviour patterns, this example clearly demonstrates the principle of Figure 4 in practice.

ii) whether birds with more positive QBA profiles have more or less of role within their flock, based on calculation or centrality scores (Rose and Croft 2015), for example.

Expanding on positive welfare states with targeted environmental enrichment

Targeted strategies of EE can therefore be appraised alongside indicators of welfare categories. Here it is shown how engagement with, opportunity for, and evaluation of, EE links to the measurements of welfare state (Figure 3). Using Bloomsmith et al.s (1991) five categories of enrichment, the role that EE can play in upholding positive affective states is emphasised, providing control and choice, and enabling positive challenges and therefore combating boredom or chronic stress in zoo populations. Opportunities for social and physical enrichment are shown by the birds themselves: flamingos that produce their characteristic pink colouration into the breeding season are being provided with the correct form of nutrition, and the production of healthy eggs and chicks signifies a flock provided with the correct environment for breeding. Flock cohesion and number of birds housed can affect breeding behaviours (Pickering et al. 1992; Stevens 1991); these factors can easily be counted across zoos. Discussions with flamingo keepers can lead to the sharing of good practice, whereby EE can be integrated into daily husbandry (Rose et al. 2016), providing further outlets for the birds to engage with EE at different times of the year. The social environment of the flock consists of strong and stable bonds between and within the sexes (Rose and Croft 2017) and these social bonds can differ between the breeding and non-breeding seasons (Rose and Croft 2018). Such information is useful to management as flocks could be split and brought back together (encouraging social enrichment), but with known partners being kept together (during bird moves or transfers between zoos) to ensure buffering against any stress from a change to the flamingo's social situation.

Finally, as more is understood about the full 24-hour cycle of animals within captive care, it is possible to use remote technology to monitor long-term behaviour patterns. Wild flamingos are known to be active overnight (Britton et al. 1986) and research into captive greater flamingos (*Phoenicopterus roseus*) has identified similar 24-hour time budgets to those documented in free-living birds (Rose et al. 2018b). As performed for captive elephant welfare assessment (Yon et al. 2019), collecting behavioural data overnight and during the day adds a new layer of understanding to individual animal welfare states, which is especially helpful if not all QBA terms cannot be fully validated to capture valence. Consequently, QBA assessment and provision of EE should not just occur in a human-centric timescale but should consider the circadian rhythm of the animal under study and how best to monitor the performance of positive and negative behaviours (and therefore associated welfare states).

Linking QBA to evidence-gathering for husbandry change

To fully integrate QBA assessment into evidence-based husbandry change, it is necessary to consider how zoos can develop strategies to tackle the performance of ARBs and to monitor how animals respond to their captive care. It is well known that EE is used as means of improving the lives of animals housed in zoos (Carlstead and Shepherdson 2000; Mason et al. 2007; Newberry 1995) and if animals are provided with stimulation and a diverse environment, the zoo is able to fulfil its conservation and education outcomes more successfully (Hosey 2005; McDougall et al. 2006; Meehan and Mench 2007; Shepherdson 1994). Given the overall relevance of QBA as a way of successfully measuring the emotional states of animals across situations (as noted in Table 1), there is an argument for it to be used in the zoo world to both provide support for and to subsequently evaluate how husbandry tools are used to enhance QoL. Therefore, Figure 4 provides a schematic for decision-making in zoos with the aim of fulfilling an outcome or goal of husbandry change, based on a prior QBA in a particular species or situation.

In this example, if EE use is firstly defined (i.e. what is enriching rather than routine husbandry?) and goal-orientated (i.e. to promote a specific behaviour or to encourage a key activity). This is evaluated based on the "job" (i.e. niche within a habitat) or role of a behaviour to the individual, as well as to the species' wider habitat. Subsequently, the use of EE will provide a fix to any husbandry issues or challenges regarding the particular species. In Figure 4, the EE is designed to be occupational and to encourage a species to work, thus providing a cognitive challenge and consequently beneficial eustress (an example of which is further provided in Figure 5). The outcome of this process, and what QBA can be measured against, is the usefulness of this biologically relevant EE together with the long-term improvement to species husbandry (as described in the blue boxes). Such a process can help unpick differences that exist in the behaviour patterns of individuals from wild habitats to those observed in captive-bred individuals. This is done by providing an outlet for behaviours that may have important fitness consequences (e.g. foraging actions, communication between conspecifics or ensuring group stability).

Table 2. How using information from multi-institution species-specific QBA could help underpin the four main roles of the modern zoo. What does the zoo aim to achieve and how can QBA output help reach this (in italics)?

Conservation	Education	Research	Recreation
Improve population sustainability by reducing stress on an individual level. *Builds resilience in individuals used for conservation efforts by tweaking husbandry based on QBA results that identify negative husbandry affects, which can compromise breeding.*	Promote natural behaviour performance, which is more engaging for zoo visitors. *The function of the animal to inform and educate is greater if QBA has identified husbandry impacts on individual behaviour patterns, and such impacts rectified to reduce ARBs (for example).*	Scientific validity is improved if animals are better representatives of wild counterparts. Individual QBA results that can alter husbandry to improve outward signs of good welfare (i.e. normal behaviour) allows animals to be used for a wider-range of research projects.	Uphold zoo-positive experiences for visitors during their time at the zoo viewing the animals. *A zoo's animals will appear more contented and hold a greater appeal, thus increasing dwell time, if individual welfare assessment has taken place and results used to inform practice.*
Assess individual states at specific times of the year to improve propagation or breeding efforts. *Positive welfare & positive challenge has benefits to fertility and breeding output; using husbandry change or EE can enhance the performance of key reproductive behaviours.*	Appropriate ecological settings can be designed on evidence from across collections. *Habitat recreation and enclosure fixtures that promote naturalistic behaviours and positive affective states can be shared across zoos, thus enhancing visitor interest in the species and/or exhibit.*	Reduce stress and promote appetitive and consummatory behaviours improves data collection for research projects. *Identify releasers of high-motivation behavioural states from cross-zoo QBA and improve husbandry accordingly.*	Increase awareness of an animal's place in the world. *Better understanding of why animals are housed in captivity which helps bring visitors back to the zoo on multiple occasions and/or increases engagement with associated awareness or conservation projects.*
Use QBA regularly to provide data on when to provide healthcare and therefore enhance longevity. *Identifying husbandry variables that positively impact on key markers of good health reduces veterinary costs and promotes wild life spans.*	Improve the link between media, television and "real" animals. *Increased media coverage of wild animals and increased engagement with social media means that zoo animals need to be a better representation of their wild counterparts. QBA output allows identification of negative factors that some individual animals may not be coping with in captivity, and provides a way of reducing or eliminating this factor's influence.*	Larger sample populations of animals available that are experiencing positive welfare thus reducing variation during data collection. *QBA-informed husbandry applied across zoos reduces impacts of extraneous management variables on scientific research by integrating individual outputs into management regimes, thus reducing chronic or distressing stressors.*	Increase footfall and visitor engagement. *Return visits more likely when animals are displayed in a manner that enhances their wellbeing. Use of QBA over the course of an animal's can check that welfare is not compromised by a visitor effect (for example).*

Examples occur in the literature that highlight areas of zoo husbandry or population management where directed use of EE would promote wild-type traits to ensure behavioural phenotypes remain stable in captivity. Butterfly splitfins (Ameca splendens) are noted as developing more aggressive personality traits when aquarium-bred over multiple generations (Kelley et al. 2006) and captive-reared Otago skinks (*Oligosoma otagense*) are slower at sprinting than wild counterparts (Connolly and Cree 2008). Consideration of why fish may become more aggressive or why lizards may show a reduced acceleration can help redesign enclosures or re-structure social groups to promote a suite of behaviours more suitable for life in the wild. Assessing the welfare of such animals, comparing outward signs of fear or boldness, confidence or neophobia between individuals in groups, and developing ways of encouraging more positive behavioural expressions with use of relevant EE, could decrease unwanted aggression in fish and encourage lizards to be more active.

QBA can help identify areas of species' husbandry that need to be improved in some zoological collections (based on comparing QBA scores of animals across institutions), with evidence of good practice disseminated across the holders of a species. The evidence-based approach has been shown to be key to the advancement of excellent welfare states experienced by animals in the zoo (Melfi 2009) and a QBA approach can help zoo researchers to gather evidence on gaps in husbandry knowledge, for example the recent elephant husbandry and welfare indicators research (Williams et al. 2018; Yon et al. 2019). The development of best practice guidelines (BPG) as a replacement of general husbandry instructions (EAZA 2019) helps zoos follow and implement a husbandry regime that has been designed with positive welfare in mind. BPG indicate species-specific care in a more standardised format, providing evidence-based requirements compiled by experts in the field (EAZA 2019). Further evolution of such BPG by updating and reviewing standards against data from animal-specific responses to care (i.e. QBA findings) would help move zoo welfare assessment and measurement away from a heavily resource-based approach to one more aligned to individual animal-based responses. The role of the individual in the determination of what makes "good welfare" is key, as individual-specific differences will affect how well husbandry alterations equate to improvements in welfare state and QoL.

The well-known roles of the modern zoo are therefore better upheld, providing more resilience against criticism, if a species-focussed QBA is used to solve husbandry-related issues or welfare and behavioural challenges. By asking questions of the individual itself, describing how the individual is experiencing its environment from the animal's perspective, it is possible to adapt and change husbandry so that character and personality traits of all individuals are catered for. This will, therefore, provide further support for the roles of the modern zoo by underpinning excellent animal care that strengthens educational messages, increases the health and fitness of individuals in conservation programmes, builds resilience in individuals when on display to the public and improves the validity of science by ensuring that animals used for research projects can behave in a wild-type manner and be less prone to negative effects of stress in the managed environment.

This study provides examples of how QBA can be integrated into the roles of the modern zoo in Table 2, providing examples of what zoo populations need to achieve to cover each of the zoo's aims, and detailing the QBA output that supports each aim in turn. It is hoped that this table shows the scope of QBA across individuals and populations to pave the way for a change in animal management in a way that further enhancing the role animals play in helping the zoo to meet each of these four aims. As illustrated in Figure 5, targeted EE will improve behavioural repertoires and provide positive challenge that would be a favourable result from individual QBA; combining these results with the outcomes detailed in Table 2 can provide a wider application of welfare measurement and engage researchers to undertake multi-zoo QBA projects, as well as encouraging zoo personnel to consider the results of QBA more carefully when instigating changes to management practice.

Conclusions

The challenge of providing animals with meaningful choice and control in captive environments is something that zoo scientists are striving to address. This paper has shown that QBA has a role in the objective and systematic measurement of behavioural expression (and therefore of QoL) in the zoo. It is important to consider how to provide a meaningful assessment of welfare (based on a QoL approach) so that all individuals experience ecologically relevant challenges and positive welfare outcomes when housed in the zoo. Methods that assess welfare across conditions (e.g. different animal collections or husbandry regimes) can provide valuable information for the evolution of BPG. The evidence-based approach increases the application of a zoo's animals in helping the zoo meet its ultimate aims. Animals experiencing good welfare display better for the public as well as passing on relevant wild-type traits to future generations (that may be used in conservation work). This paper hopes to stimulate thought and discussion on the role of QBA across a wide range of captive species whose results can ultimately help improve and evolve husbandry practices to further reduce any signs of poor welfare or deviations from a species' natural behavioural repertoire.

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