Journal of Applied Animal Welfare Science

ISSN: (Print) (Online) Journal homepage: www.tandfonline.com/journals/haaw20

Key Concepts for Enhancing Zoo Animal Welfare: Coping, Comfort, Choice, Control, Challenge, and Compassion

Paul E. Rose & Jack Lewton

To cite this article: Paul E. Rose & Jack Lewton (30 Dec 2024): Key Concepts for Enhancing Zoo Animal Welfare: Coping, Comfort, Choice, Control, Challenge, and Compassion, Journal of Applied Animal Welfare Science, DOI: 10.1080/10888705.2024.2440891

To link to this article: https://doi.org/10.1080/10888705.2024.2440891

Published online: 30 Dec 2024.

JOURNAL OF APPLIED ANIMAL WELFARE SCIENCE
https://doi.org/10.1080/10888705.2024.2440891

Routledge
Taylor & Francis Group

RESEARCH ARTICLE

OPEN ACCESS Check for updates

Key Concepts for Enhancing Zoo Animal Welfare: Coping, Comfort, Choice, Control, Challenge, and Compassion

Paul E. Rose[a,b] and Jack Lewton[c#]

[a]Centre for Research in Animal Behaviour, University of Exeter, Exeter, UK; [b]Wildfowl & Wetlands Trust, WWT Slimbridge, Gloucestershire, UK; [c]Department of Life Sciences, Imperial College London, Ascot, UK

ABSTRACT

Zoo animal welfare is subject to increasing scrutiny by many audiences. Although zoo husbandry and management techniques have progressed, common welfare issues are still apparent. To encourage further improvements, converting theoretical welfare definition into practical application is key. This paper evaluates a familiar definition to form a baseline for practical welfare assessment that benefits animals and zoo operations. If we consider coping and comfort as measurable indicators, plus choice and control to cement autonomy for the animal, achieving positive welfare is more likely. Providing positive cognitive challenge results in improvements to behavioral diversity. When husbandry is ecologically relevant, this welfare-friendly approach evolves into husbandry-based evidence, further justifying approaches to animal care. The human element of husbandry (e.g., development and training of personnel) impacts on welfare, necessitating a compassionate approach to daily operations. Compassion – for animal and human wellbeing – ultimately embeds welfare as a core zoo goal. The unique environment of the zoo, with its mix of wild species, human workforce and visitors, coupled with the amount we still must learn about species' husbandry needs emphasizes continual development of welfare approaches.

ARTICLE HISTORY
Received 19 August 2022
Accepted 5 December 2024

KEYWORDS
Zoo animal welfare; well being; evidence-based husbandry; zoo animal behavior

Introduction

Across different animal populations, defining welfare is a complex undertaking, with many theories being debated and reviewed (Devlin & Ogle, 2022; Grethe, 2017; Veasey, 2017). This is challenging for zoos and aquariums (hereafter "zoo/s") as these organizations are under pressure to ensure they house animals to a high standard of welfare. It is therefore important that animal welfare is defined and explained in a practical and logistically possible way that ultimately translates into metrics for assessment. Agricultural systems face similar pressures, but it could be argued that defining and measuring welfare for zoo animals is even more of a complication (Ward & Hosey, 2020) due to their species variety, enhanced animal longevity, captivity-associated stressors that change over time (Brando & Buchanan-Smith, 2018; Brando & Coe, 2022), and the zoo's differing roles (e.g., conservation outcomes, educational messaging, research requirements) that such species fulfil in their zoo. Despite these differences, baselines from agricultural research can provide fundamental support for deeper consideration of how to evaluate welfare across zoo housed species. For example, the UK's originally-for-agriculture "Five Freedoms" are written into zoo animal husbandry standards as the Five Welfare Needs (Defra, 2012) and help raise welfare

CONTACT Paul E. Rose p.rose@exeter.ac.uk Centre for Research in Animal Behaviour, Psychology, University of Exeter, Perry Road, Exeter, Devon EX4 4QG, UK

[#]Present affiliation for Jack Lewton is School of Animal, Rural and Environmental Sciences, Nottingham Trent University, UK. ack.lewton2024@my.ntu.ac.uk

standards as well as being presented in format that enables for review during licensing and inspection.

Practical measurement of animal welfare is important (S. P. Hill & Broom, 2009), and this must include physical, behavioral, and psychological states (Blackett et al., 2017; Broom, 1991) that are expressed across the course of a 24-hr cycle. Focus on inputs (e.g., resources and environmental conditions that the animal responds to) and outputs (e.g., fitness, feelings, and emotions that make up these responses) may enhance validation of welfare measures (Rushen et al., 2011), to provide the completest possible picture of welfare at a specific time or within a specific situation (Bousfield & Brown, 2010; Veasey, 2017; J. Webster, 2005).

One of the most cited definitions of animal welfare is "the state of the individual as it attempts to cope with its environment" (Broom, 1986). Coping describes an animal being able to maintain and regulate the stability of its body and mind, including tolerance and responses to a range of stimuli (Broom & Fraser, 2007; S. P. Hill & Broom, 2009); therefore, this baseline is useful for considering what to measure and what the results from such measurement may mean. Examples of identifiers to measure coping include performance of repetitive abnormal behavior, indicators of lethargy/boredom, uneven enclosure usage, and uncharacteristic social behavior. These coping identifiers are not straightforward to measure and can be subject to inconsistency/subjectivity biases. For example, when does an animal tip from coping into failing to cope? And what if two measures of coping (e.g., behavioral and physiological) are observed which contradict? Successful welfare assessment using welfare identifiers such as coping is dependent on robust species-specific definition and methods. Meaningful measures of animal welfare that are relevant to the species, their ecological needs, and how they engage with inputs from their environment are key (Rose, 2023; Veasey, 2017).

Broom (1986)'s definition considers an animal's state within their current environment, based on their responses to this environment; as well as whether the environment and/or the animal's responses are suitable; and it considers how such responses are manifested, so they can be observed and measured. This definition helpfully acknowledges that animal welfare is a broad term, it considers measurable and meaningful aspects of welfare, it suggests that welfare ranges from positive to negative, and has capacity for evaluating feelings, physical health, and psychological health (S. P. Hill & Broom, 2009). This definition, which is centered around how an animal "copes," can be expanded to include the additional aspects that animal welfare assessment should consider. For example, by identifying examples of "comfort" (when an animal experiences positive states that make it comfortable as well as when it inhabits a physically comfortable environment); providing opportunities for 'choice and control'; evaluating the effects of positive "challenge" (i.e., a solvable problem that increases behavioral outcomes); and ensuring zoo operations are "compassionate." Therefore, this paper evaluates how a baseline for practical welfare assessment using the six Cs of Coping, Comfort, Choice, and Control, Challenge, and Compassion can be useful for understanding what species need in captivity, and how it can be better provided to enhance animal welfare (and the well being of their human carers too). Human well being relates to "fully rounded humanity" (Taylor, 2011), which is easier to measure in human animals due to abilities in self-reporting emotional states. These core concepts (the six Cs) are defined in Table 1.

This paper describes zoo animal welfare as consisting of how the individual animal copes with their current environment, and how coping is balanced against comfort; how choice and control over the animal's immediate situation in the short-, mid-, and long term builds resilience and diversity to behavior patterns that can provide coping mechanisms that lead to comfort in the future. Finally, it considers how the human element of animal husbandry in the zoo should also be included based around the quality of care provided and how to continually uphold relevant animal husbandry for all species being housed. The overall objective of this paper is to suggest a holistic view of how the animal's responses to the zoo, plus the involvement of zoo personnel, would identify where welfare state is influenced. Encouraging practical welfare assessment using coping, comfort, choice, control, challenge, and compassion would yield evidence for the improvement of zoo operations to further promote zoo welfare and staff well being.

Table 1. Definition and description of the concepts of Coping, Comfort, Choice, Control, Challenge, and Compassion in the context of positive welfare states. General measurable identifiers are included in the table as examples for further consideration.

Concept	Definition	Examples of measurable identifiers	Example references
Coping	Animal is performing adaptive behaviours and maintaining homeostasis.	Lack of performance of abnormal behaviour. Indicators of lethargy, apathy, and perceived boredom. Performance of negative self-directed and/or displacement activities. Measures to contextualise any biased or uneven enclosure usage. Over-use of resources or sudden change in social dynamic.	Manteca et al. (2016); Meagher (2019); Rose et al. (2017); S. R. Ross et al. (2009)
Comfort	Animal is experiencing positive psychological, physical, and behavioural states as well as a physically comfortable environment	Quantifying time spent on biologically relevant behaviour patterns, for example the performance of time-activity budgets that demonstrate completion of highly motivated behaviour and therefore the animal can be said as being satiated. Performance of "luxury" activities, e.g., play, if relevant to the species in question. Categorisation of species-appropriate responses to husbandry.	Held and Špinka (2011)
Choice and Control	Animal is demonstrating independent and diverse biologically relevant behaviours that lead to feelings of autonomy.	Defining positive diversity of biologically relevant behaviours. Measuring flexibility of behaviour patterns. Scoring the choices an individual has (i.e., different zones or access to enrichment devices) within their environment. Identifying preferences for aspects of husbandry or management regime (i.e., favoured resting areas or access to housing). Analysis of individual social networks and patterning of associations to contextualise social relationships.	Decker et al. (2023); Miller et al. (2020); Rose and Croft (2015)
Challenge	Animal is experiencing positive challenge that facilitates behavioural resilience and promotes ecologically relevant behavioural diversity and flexibility.	Beneficial complexity of enrichment (i.e., defining when complex becomes too problematic). Problem solving abilities or latent effect of enrichment on behaviour (i.e., how long the positive influence of the enrichment lasts once it has been provided to the animal).	Meehan and Mench (2007)
Compassion (animals)	Relevant husbandry sympathetic to a species' needs, provided by trained animal care staff that feel supported and values in their work.	Integration of best practice guidelines (where relevant) into a zoo's management protocols for a species. Staff knowledge and understanding of current, accepted best practice husbandry approaches for species they are responsible for.	Learmonth (2020)
Compassion (humans)	Adequate training, provision of a suitable and well-resourced work environment, and opportunities for development to ensure animal management staff can provide appropriate husbandry to uphold good welfare.	Determining how well animal care staff feel equipped to deliver positive welfare and evidence-based husbandry. Promoting feelings of value in animal care staff and obtaining feedback on a sense of value. Measuring how much knowledge animal care staff have of the needs and requirements of the specific species within their responsibilities. Evaluating how the job demands of animal care staff are balanced against the relevant tools available to resource how to complete their work. Quantifying how staff feel valued/supported/resourced to ensure they can effectively deliver welfare-positive husbandry to the animals they are responsible for.	Cole and Fraser (2018)

The examples of measurable identifiers in Table 1 are not an exhaustive list, but reflect what could be practical, easy-to-implement measures of determining different influencers of animal welfare states. Consideration also needs to be given to individual animal differences (e.g., personality, past experiences, preferences) that will modify how each animal responds to what is considered optimum care for that species overall.

Coping

To extend the descriptions presented in Table 1, coping describes how the animal adapts to their environment and maintains homeostasis. Broom (1986) describes coping across a range of experiences: when an animal has coped at little expenditure of resources, this indicates satisfactory welfare, whereas if the individual fails to cope, this indicates poor welfare. Changes to behavior patterns or markers of stress hormone responses can indicate attempts at coping. For example, abnormal repetitive behaviors such as stereotypic pacing in leopards, *Panthera pardus* (Mallapur & Chellam, 2002), and repetitive licking in giraffes, *Giraffa camelopardalis* (Bashaw et al., 2001) that manifest due to a restrictive environment and/or inappropriate husbandry within the zoo. Behaviors can be observed, and these resulting data can be transformed into metrics that give an indicator of that behavior's performance. Thus, observing and scoring the performance of abnormal behaviors may be used as performance indicators of coping. Validation of such behavior alongside of species-specific endocrine measures (e.g., validated glucocorticoid profiles that illustrate normal functioning, acute stress, excitement, chronic stress, and learned helplessness) further support welfare inferences from behavioral observation.

Comfort

Comfort is used to describe the positive states that an animal can experience, as well as a physically comfortable environment (e.g., correct temperature, humidity, lighting, use of furnishings) and the performance of behaviors that leave the animal feeling comfortable. Comfort should also include positive psychological states resulting from lack of chronic stress and anxiety (Gonyou, 1986; Mellor, 2016). Comfort is a welfare influencer, similar to and an extension from coping (Tennessen, 1989; Veissier et al., 2012), and a welfare outcome in its own right. For comfort to be achieved, a prerequisite of coping must be met, and the animal feels at ease to perform behaviors indicative of relaxation or comfort. Consequently, if an animal is coping extremely well, then it is likely to be comfortable and has therefore moved from simply surviving in their environment to thriving (Melfi, 2009). For example, zoo-housed flamingo (Phoenicopteriformes) flocks demonstrate comfort within their enclosure by spreading widely across different enclosure areas, whereas an uncomfortable flock will clump in one location (Rose et al., 2014), something seen in wild birds when they are disturbed (Yosef, 2000). Knowledge of a species' flight distance (from a perceived or actual threat) has long been understood as an important piece of evidence to use when deciding the location of important resources within an enclosure (Hediger, 1950); animals will be more comfortable (physically and psychological) if they can choose where and when to access resources rather than being forced into uncomfortable situations that are beyond their control.

Comfort can be balanced between an animal's attempt at coping against measurement of their comfort. Attempts of coping can be measured by monitoring physiological indicators, such as markers of stress hormone responses (Mormède et al., 2007), and changes to behavior patterns under certain types of husbandry regimes. Measurement of comfort can be based on "luxury" behaviors (Held & Špinka, 2011), such as time spent playing for some species. Promoting daily bouts of rumination in ruminant herbivores (Baxter & Plowman, 2001), regular consumption of low-quality forage that ensures correct gut motility and promotes caecotrophy in lagomorphs (I. Sayers, 2010), maintaining strong and stable associates within primate troops (Kanngiesser et al., 2011; Silk et al., 2013) or thermoregulating across a range of ecologically relevant gradients for reptiles and amphibians

(Warwick et al., 2013) are all examples of behavioral indicators of comfort that could be developed into species-specific and potentially individual-specific welfare assessment tools.

Consideration of an affective states approach to animal welfare (Fraser, 2009) is also useful to include, especially when evaluating if an individual animal is comfortable with their current situation. Using methods such as Qualitative Behavioural Assessment (QBA) where behavioral expression ("body language) is documented to report on an animal's internal psychological states and feelings (Wemelsfelder, 2007), aspects of husbandry that promote comfort can be identified. The relevance of the "tripartite relationship" of how the animal's feelings, functions, and their natural behavior patterns interconnect to influence welfare state (Fraser et al., 1997) should not be ignored. Measuring fitness and feelings, e.g., via QBA, would provide further evidence for comfortable states and degree of coping in a managed environment.

Reviewing the evidence used for welfare-friendly husbandry practice, such as the design and application of environmental enrichment (Brereton & Rose, 2022; Foster-Turley & Markowitz, 1982; Markowitz et al., 1995) can identify areas of evidence-based husbandry and for which specific species this is used for, compared to areas of anecdote or unsupported practice where welfare benefits are not being fully realized. Further use of Delphi method, as per Whittaker et al. (2021)'s survey of animal-based welfare indicators for captive reptiles, across taxa would help gather quality evidence for how to infer welfare states that indicate comfort. Determining how to measure comfort could be based on approaches taken from the agricultural industry, where resting and activity budgets of dairy cattle are the outputs for a "cow comfort index" used to determine the suitability of on-farm cow management regimes (Haley et al., 2000). Similarly, cow comfort indices can be used to provide evidence for welfare-friendly bedding materials that improve animal health and well being (Van Gastelen et al., 2011) – assessing indicators of health (e.g., gait scoring) against the type of bedding to identify those that enhance normal locomotion. For the zoo, comfort scores could relate to the performance of adaptive behaviors, the use of space and time spent interacting with conspecifics. Research outputs do suggest that zoos take animal comfort seriously (Wark et al., 2020) and thus the outcomes of such studies should be used to inform best practice husbandry guidelines to support optimal welfare for specific taxa. However, zoos should consider asking research questions that relate to comfort across a wider range of species, especially those that are not charismatic large mammals.

Figure 1 provides an example of how well-used indicators of cow comfort – rumination and resting, time spent lying, and movement and joint mobility (Endres, 2017), plus body condition and nutrition (Vasseur et al., 2015) – could be adapted and used to determine the comfort of zoo housed elephants (Elephantidae). Elephants gain welfare benefits from positive social associations that they have choice over (Harvey et al., 2018); their foot and joint health is linked to appropriate substrate (Lewis et al., 2010); substrate improves sleeping and rest (Williams et al., 2015); and correct nutrition promotes foraging activity as well as regulating good body condition (Morfeld et al., 2016). In the same way as is noted for cows, these parameters can be measures of elephant comfort that welfare scientists and elephant keepers can use to help identify signs of positive well being and a good quality of life in their animals across life stages.

Choice and control

Choice and Control is a well-known term for improving welfare (Englund & Cronin, 2023; Greggor et al., 2018; Kagan et al., 2015; S. R. Ross, 2006; Whitham & Wielebnowski, 2013) that, when provided in a meaningful way (i.e., ecologically relevant, variable, species-specific, based on evidence) facilitate autonomy – an inherent right of an individual to self-govern (A. J. F. Webster, 2001) – and therefore experience self-control over actions, behaviors, and decision-making. Husbandry regimes and enclosure configurations that enable control and choice empower the animals within them (Allard & Bashaw, 2019) and therefore can improve the well being of zoo staff who benefit from seeing more comfortable animals.

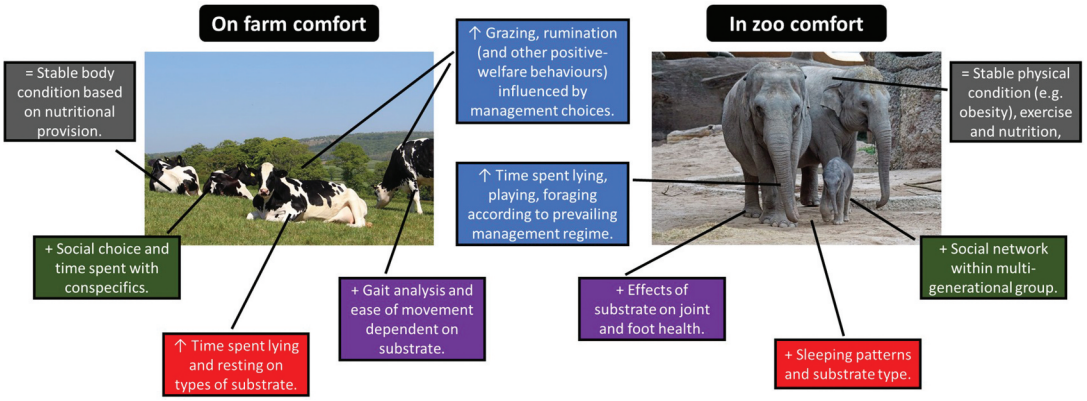

Figure 1. An example of how comfort indices from on-farm welfare assessment could translate into the zoo for other species. Boxes of the same color match the comfort measure on the farm to the zoo. Up arrow (↑) denotes an increase in a behavior or trait equates to improved welfare. A plus sign (+) means behavior has a positive connotation and hence improves welfare. An equal sign (=) states that a characteristic is maintained within certain optimum parameters. In this example, comfort indicators for dairy cattle (*Bos taurus*) are applied to elephants (Elephantidae) but this approach has potential across a wide range of taxonomic groups.

Comfortable animals are those individuals that may experience more choice and control over what they can do, where it can be done, and for social species who it can be done with; and this is a suitable avenue for future research to investigate. Individual differences are important to measure as differing personality traits of zoo-housed species will impact on how they cope with their environment, and therefore if they are comfortable (Vaz et al., 2022). As environmental enrichment is a common way of providing choice and control (Buchanan-Smith, 2011), bespoke enrichment for individuals of a species within a specific zoo may be required to ensure interaction with the enrichment provides positive experiences for each animal.

Access to specific enclosure areas and providing freedom of movement leads to noticeable improvements in behavior patterns (S. R. Ross, 2006) and use of ecologically relevant substrate and opportunities for resting should be investigated to further understand improving welfare by making animals more comfortable (Takagi et al., 2019). In addition, the abilities to form social bonds of their own choosing (Rose & Croft, 2015), mate choice within their breeding programs (Martin-Wintle et al., 2019) are all ways of integrating choice and control into the lives of zoo-housed species. Enriching opportunities such as reproduction and raising young or foraging across an ecologically relevant temporal and seasonal schedules improves positive behavioral diversity and can provide outlets for highly motivated behaviors that satiate the individual animal. This is not to say that breeding itself will enhance the welfare of individuals (Cronin et al., 2016), rather it is the voluntary engagement in reproductive activities that will.

Contrafreeloading – where an animal chooses to work for food even though it is freely available without effort (McGowan et al., 2010) – is indicative of choice and control over the immediate environment (Hughes & Duncan, 1988) and has been noted in several species including ecological specialists like maned wolves, *Chrysocyon brachyurus* (Vasconcellos et al., 2012) to more general foragers such as brown bears, *Ursus arctos* (McGowan et al., 2010), and potentially in parrots (Psittaciformes) too (Coulton et al., 1997). Further research into contrafreeloading should explore this phenomenon in a wider range of species to help build choice and control into feeding regimes and daily husbandry practices as well as to create opportunities for it in the fundamental nature of the animal's enclosure. Preference testing using zoo animals to see if they prefer to work for a specific reward, or access to a part of their enclosure, or usage of an enrichment device would enable the animal to participate in their own care (Learmonth et al., 2021; Wolfensohn et al., 2018), and thus have more control over their daily lives. Use of such preference testing (providing the

preferences on offer were valuable, ecologically sound, and actually beneficial to the animal) would go part way to understanding a key component of animal welfare, which is do animals have what they want (Dawkins, 2004).

Similarly, creativity in enclosure design to incorporate novel technologies, such as computer-based enrichment (Coe & Hoy, 2020) could further enhance choice and control if they provided a specific outlet for key behaviors that are linked to feelings of autonomy. Embedding enrichment directly into enclosure design features is likely the most helpful for promotion of longer-term positive welfare (Coe, 2017); a diverse environment of the animal's enclosure provides multiple opportunities to perform a wide array of biologically relevant behaviors and enables different levels of engagement with stimulating and relaxing areas suitable for varying degrees of appropriate cognitive challenge.

Challenge

Providing a problem to solve that is not overwhelming but which motivates an individual to work for something it currently does not have but which it desires (C. A. Smith, 1991) is beneficial for the development of behavioral plasticity and abilities at problem solving (Villalba & Manteca, 2019). Cognitive challenge improves an animal's feelings of control over their current situation and provides an outlet for evolved traits that may otherwise be restricted in performance (Clark, 2011). These ideas form the basis of positive challenges for the improvement of zoo animal husbandry and, ultimately, welfare.

Building relevant diversity into behavioral repertoires (i.e., promoting a wider range of positive valence natural behaviors) (Miller et al., 2020) and enabling animals to develop resilience in how they respond to their environment – for example, by allowing control over aspects of their daily lives (Colditz & Hine, 2016; Owen et al., 2005) – can be facilitated by opportunities for positive challenge (Meehan & Mench, 2007).

As an animal's resilience is aligned with coping (Arndt et al., 2022), and as we need to ensure that animals can cope with their care in the zoo, providing stimuli that promote behavioral adaptation to different environmental conditions enables resilience. Different forms of challenge (e.g., variation in enrichment regimes, a dynamic and changeable environment that offers a range of physical and sensory stimuli, and unpredictable husbandry practices) can go beyond building resilience to generate robustness (Colditz & Tilbrook, 2023).

Positive challenge, which arise from the zoo's enclosure design or use of environmental enrichment, enables feelings of eustress. Eustress, or positive stress, is an adaptive response to stress that is ultimately beneficial to the individual (Villalba & Manteca, 2019); it is the opposite of distress (Moberg, 1999) and is suggestive of an individual able to cope with environmental challenges. Positive challenges can be important for developing a sense of agency in the animals that live in a specific environment (Špinka & Wemelsfelder, 2018). In this case, Špinka and Wemelsfelder (2018) define agency as an animal's inclination to actively engage with their environment, gaining novel information and knowledge, and thus enhancing skills for future application. Positive challenge that builds this sense of agency can reduce feelings of boredom or apathy, and maintain long-term positive outputs, to improve an individual's quality of life.

Developing behavioral resilience in zoo-housed species is essential for training plans that form part of reintroduction plans (Shepherdson, 1994), and to the conservation of adaptive behaviors and culture (Riley, 2018), as well as for long-term attainment of positive welfare states (M. Ross et al., 2020). Behavioral resilience allows animals to cope with changeable, heterogeneous environments and can utilize functional traits to gain advantages from the behaviors they perform (Reading et al., 2013; Tetzlaff et al., 2019). Exposing individuals to eustress that can be rectified by positive emotion or state and behavioral flexibility, via the application of appropriate environmental enrichment or alterations to enclosure design can promote advantageous behavioral

diversity (Jacobson et al., 2019; Little & Sommer, 2002; S. R. Ross et al., 2010). This enables animals to develop a wide range of biologically relevant behavioral traits that lead to problem solving abilities (Salvanes et al., 2013).

As mentioned previously, opportunities for contrafreeloading that promote choice and control, also allow the animal a chance to experience positive challenge (Maple & Perdue, 2013). As contrafreeloading can form the basis for environmental enrichment (Coulton et al., 1997; Vasconcellos et al., 2012), as well as how daily care is provided, i.e., daily diet provided in a "work for reward" situation (G. E. Smith et al., 2021), it is possible to provide opportunities for positive challenges within different parts of an animal's enclosure, at different times of the day and at different levels of complexity, to promote naturalistic activity patterns. Targeted and species-specific environmental enrichment that creates an acute, beneficial, stressor which can be overcome by the animal is the goal (Rose & Riley, 2019). It is essential that the beneficial effects of the challenge, i.e., the novel behaviors that can result and the use of cognitive processes, are overriding any frustration caused by the problem an animal is provided with (Meehan & Mench, 2007). Therefore, monitoring and evaluation of any added challenge needs to be undertaken to ensure that chronic stress does not result if the animal cannot resolve the challenge it is facing. Differences in the responses of individual animals to cognitive challenges should be considered based on the animal's background, development, and experiences (Rosenberger et al., 2022) as generalized conclusions around the responses of animals to a stressor are tempered by individual variation.

Compassion

Facilitating positive choice and control, and challenge would be the responsibility of animal care staff, involved in the daily husbandry of captive wild species. Therefore, human influences over zoo animal welfare also need further consideration (Cole & Fraser, 2018; Rault et al., 2020) and this dimension could be labeled as compassion – how much do zoo professionals give to the animals they look after and how is their own mental health and well being accounted for too (Yam et al., 2022)? Is the zoo's management structure compassionate to its animal care staff, promoting their own well being in a caring and supportive manner (White et al., 2021)?

Compassion for animals

Compassion for animals in zoos should be embedded into daily husbandry and care activities. Animal care staff following appropriate husbandry guidelines and keeping up-to-date with developments to species management is part of a compassionate approach – active participation in evidence-based husbandry by applying the correct care for that species. Ultimately, such an approach can lead to animals experiencing good welfare (Kagan et al., 2015).

Compassion is an important emotion when considering the ethical treatment of individual animals, for example geriatric individuals or those that may require a quality-of-life assessment. Being compassionate also means giving animals the best possible opportunities to "do well" in their environment. For example, individuals that are part of conservation breeding programs, destined for wild release, will need different ethical and compassionate considerations (e.g., what behaviors for survival need to be trained? What challenges do these individuals need to experience? What aversive stimuli need to be presented and how?) compared to animals within captive breeding programs for long term in-zoo population sustainability. Providing animals with challenging stimuli and aversive situations that they must solve and rectify hones survival skills and therefore it would not be compassionate to deny animals in reintroduction (or similar conservation) schemes the chance to further develop behaviors that are essential to a life in the wild.

Given that life in the zoo enhances longevity for many species (Föllmi et al., 2007; Tidière et al., 2016), compassionate approaches to care across all life stages, especially for stages of life, and associated health and welfare challenges, that a free-living individual would be unlikely to face, are crucial. Zoo staff must be considerate of an individual animal's needs; how they access resources, how social choices may change with age, and how cognitive capacity may alter over time, to maintain a living space perceived as safe and comfortable, and be prepared to consider veterinary treatment essential to reducing suffering and maintaining a good quality of life for aged individuals.

Compassion for humans

Zookeepers and zoo managers are under more pressure to provide the most appropriate living conditions for their animals against a backdrop of increasing public scrutiny, from zoo visitors, activists, and animal welfare commentators (Maynard, 2018; Mkono & Holder, 2019; J. Sayers, 2020; Sherwen & Hemsworth, 2019; Ward & Sherwen, 2018). Human well being is important alongside animal welfare to ensure that zoo personnel feel capable of providing for their animals, which are well supported by management and have the tools they need to enact appropriate husbandry standards that beneficially influence welfare states (Brando et al., 2023; McDonald et al., 2024; Rose & Riley, 2022). This compassionate approach adds a societal value to the zoo by encouraging others to care about welfare in the same way as they would experience when visiting a zoo with a compassionate ethos (Greenwell et al., 2023).

Considerations of well being extend beyond the resilience of the animal population to cope with a human-created environment. Compassion fatigue is noted as a cause of mental health difficulties in those working with wildlife (Mobo et al., 2010; Yeung et al., 2017) and can lead to feelings of occupational stress, burnout, and dissatisfaction with self and career (Figley & Roop, 2006; E. M. Hill et al., 2020; Rohlf, 2018). Job demands (e.g., the need to deal with emotionally challenging situations) are noted as a key predictor of compassion fatigue (Monaghan et al., 2020) and the effects of such demands on individual well being can be moderated by the resources that are provided – especially those resources that enable animal care workers to complete their tasks successfully and enable them to feel empowered by and engaged in what they do (Demerouti et al., 2001). It is also likely that limited salaries and employee welfare may cause compassion fatigue. Human-animal relationships in zoos can be enriching for the animals (Claxton, 2011) and improve the animal's responses to their environment (Wolfensohn et al., 2018); reduced job satisfaction or high staff turnover in the zoo may reduce the time caregivers spend with their animals which can remove a welfare-positive aspect of the animal's environment.

Compassion for zoo personnel can be embedded by improving access to best practice husbandry, supporting zoo staff in how they deliver care, and ensuring the availability of information and tools for enhancing animal welfare (DeSmet & Ogle, 2022). It is essential that husbandry is provided to a consistently high standard by enfranchised, motivated staff, as this is the foundation for long-term, positive welfare for the animals within the zoo. As such, compassion (both for the animals themselves and how zoo workers experience compassion) should be included within animal welfare approaches as it influences how animal care may be provided as well as how the standard of such care is perceived by those executing it.

Bringing these welfare-specific key words together

Figure 2 illustrates how a spectrum from coping to comfort can represent an animal's states and responses related to managing (and experiencing) emotions and stress. This spectrum is influenced by factors of choice and control, challenge, and compassion. The animal's behaviors, and physical and psychological conditions (states) are measurable and provide an objective assessment of welfare. These states can be evaluated against influences from the environment and perceived levels of coping and comfort. Providing outlets for comfort-focused activities can assist animals to feel that they are

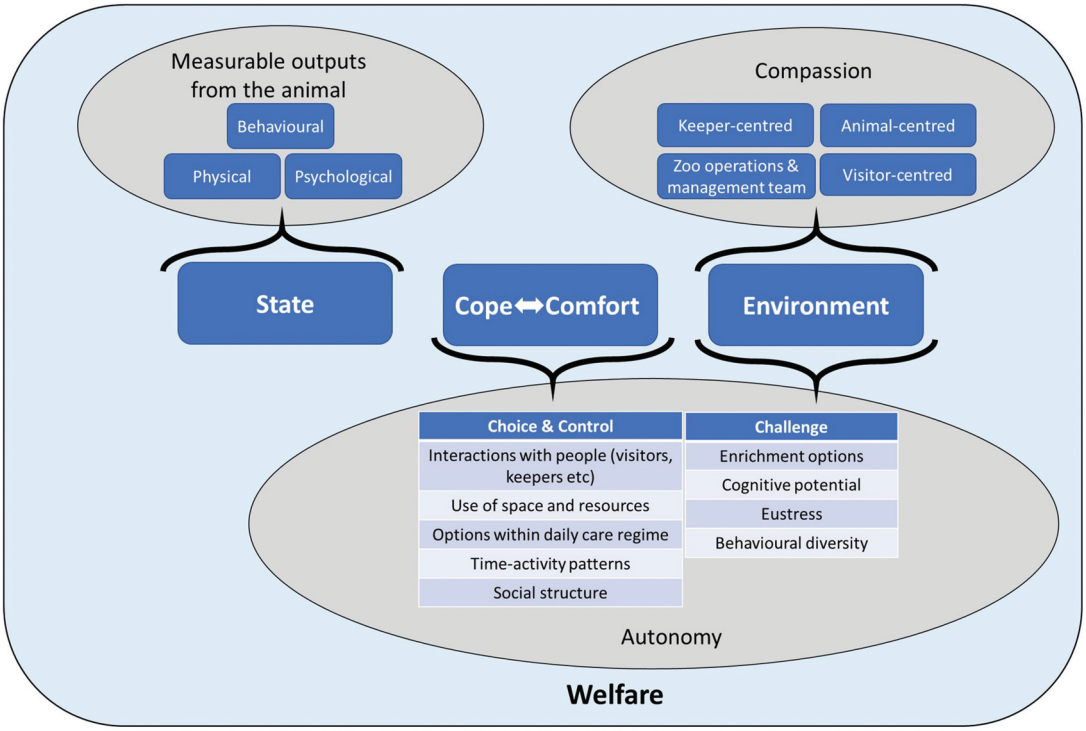

Figure 2. Taking key elements from Broom's (1986) definition of welfare (state, cope, and environment), this figure expands on how to create a complete set of welfare assessment options in the zoo. States are measurable entities where data can be quantitative (time spent on behavior) or qualitative (description of behavioral expression) to providing inferences on the animal's fitness and feelings. Coping (negative connotations if a species appears to be failing, or positive connotations if a species appears to the thriving) can be balanced against the degree of comfort experienced (from positive elements of husbandry and care). These welfare outputs will be influenced by the degree of choice and control that the animal has over their immediate situation, and thus the agency they have over their life. The environment that the animal lives within is under the influence of the zoo and is a balance of needs- the animal's, the zoo's visitors, the keeping staff, and the will of the zoo's management. A compassionate management approach enhances human well being and animal welfare. Challenge, which builds in behavioral resilience can be integrated into the animal's environment and together with choice and control lead to feelings of autonomy. Therefore, extension of state, coping and environment by including in comfort, choice, control, challenge, and compassion provide a complete picture of prevailing welfare state that could be used to refine, define, and support welfare assessment tools and approaches.

coping with their environment and therefore move the animal away from simply surviving to thriving (Melfi, 2009). Exercising choice and control over their current situation and facing beneficial challenges emphasizes feelings of autonomy. Finally, positive welfare is enhanced by the addition of compassion; to consider the human element of welfare and upholding staff mental health and well being that is impactful to effective day-to-day husbandry. Animal-centered, keeper-centered, and visitor-centered aspects of the environment should be designed in a manner sympathetic to the needs of all, but ultimately reducing or eliminating any stressors that may be beyond the animal's ability to cope and hence reduce comfort within the environment.

Promoting welfare by turning evidence-based husbandry into husbandry-based evidence

Providing valid, empirical evidence that supports husbandry and management decisions is essential to upholding good welfare in the zoo and ensuring that animals can fulfill their role within the zoo's living collection. Gaps in our knowledge of what constitutes species-appropriate husbandry can exist for poorly researched taxa (Melfi, 2009) and research bias can be apparent across many years of

research output (Binding et al., 2020; Rose et al., 2019). It is essential that evidence on natural history, ecology, behavior, and sociality, alongside multi-institutional surveys of what zoos are doing with regard to captive care (Brereton & Rose, 2022; Clubb & Mason, 2003; Mason & Clubb, 2004; Melfi, 2009; Rose & Roffe, 2013) be used to refine and review husbandry practice to turn husbandry guidelines into specific best practice standards. Scientific evidence that shows how prevailing husbandry practices promote positive welfare should be disseminated across all holders of a species so that stakeholders are confident in the quality and reliability of evidence used to support zoo animal care.

When the evidence basis for species' care in the zoo or aquarium is sound and the uptake of such care is widespread across facilities, benchmarks for the appropriateness of the husbandry and housing (e.g., good welfare states, improved health and body condition, reduced abnormal behaviors, improved reproductive success and viability of offspring, marked changes in longevity compared to previous records) can become evidence in their own right – therefore creating husbandry-based evidence for why such practice is the ideal. A method for this evolution of what evidence is and where it comes from is provided in Table 2, and such an approach can be used for species-level assessment as well as evaluation of individual animal responses.

For species with a substantial history of in-zoo care, records across institutions can be used to identify markers of good care (e.g., number of viable offspring that survive to breed, or low rates of environmentally caused pathologies) and therefore analyze any relationship between the prevalence of such potential welfare markers alongside evolving husbandry (Roller et al., 2021; Tidière et al., 2016). Questions can then be asked to unpick aspects of husbandry that can be translated across species to help improve welfare for other animals within a taxonomic group.

Multi-institutional research – multiple institutions collecting data on how species are being kept to identify areas of ecologically relevant husbandry (Melfi, 2009) – can form the basis of best practice guidelines for specific species (Table 2). Evaluation of husbandry regimes for species that possess specific functional traits that convey advantages within the wild habitat may form the strongest support for future animal management programs. A global survey of lechwe (*Kobus leche* & *K. megaceros*) by Rose and Rowden (2020) identified areas of relevant practice as well as areas for improvement within a sample of 33 lechwe herds. Lechwe are wetland-dwelling antelopes (IUCN

Table 2. A proposed step-by-step approach to creating Husbandry-based Evidence from Evidence-based Husbandry that ultimately promotes good zoo animal welfare.

Methodological step
A: Research into what zoos provide for a species alongside of review of natural history and ecological data (e.g., social structure, home range size, habitat preferences, time-activity patterns).
B: Review of existing enclosures for this species across zoological collections to determine the biological relevance of these human-created environments evaluated against information already collected in step A. Such a review needs to consider all areas of housing, not just those that are viewed by zoo visitors.
C: Identification of best practice and implementation across holders of the species based on outputs from steps A and B (e.g., number of viable young produced, longevity alongside of good health, highest performance of species-typical behavioural diversity). Positive engagement with husbandry (inputs provided) can be a proxy for the attainment of positive emotional welfare states.
D: Undertake a global survey of holders of that species that have used such updated, best practice information to determine improvements to animal welfare and population goals (e.g., improved breeding output, survival of offspring to maturity). Results of such a survey would provide (current) evidence on what are best practice inputs to support positive welfare outputs.
E: Continual, periodical review of in-zoo practice against new information on ecology or natural history, e.g., against new research findings on habitat usage or social structure, and against systematic observation of animal responses to husbandry to identify relevant aspects of management that promote welfare inputs and outputs.
F: Continual refinement of evidence used to support optimal husbandry standards (e.g., zoos achieving improved body condition and/or welfare scores when providing sex-specific social groupings and access to resources/space at certain times of the year based on a species' population dynamics and seasonal changes to behavior).
End result: As evidence-based husbandry improves welfare, population sustainability and animal care, it becomes husbandry-based evidence that shows to others what form of management is best for a specific species and why that style of management regime should be implemented.

SSC Antelope Specialist Group, 2017a, 2017b) and although the different species appear similar, they differ in their social, breeding, and foraging activities (Nefdt & Thirgood, 1997; Williamson, 1990, 1994). It is clear that the old adage *"If it looks like a duck, swims like a duck, and quacks like a duck, then it probably is a duck"* is unhelpful when fine tuning zoo animal care regimes even for closely related species. The family resemblance between different species of lechwe does not mean that all behavioral and ecological traits will be the same and therefore in-zoo husbandry protocols for one species may not be the best fit for another species. Therefore, a "common sense" approach to zoo animal husbandry, which is based on fundamental information regarding a specific species' ecology, helps implement care regimes and management practices that are likely to be most suitable for the species being housed. For example, if a species is called a tree snake, due to the arboreal nature of the species in the wild, providing opportunities for climbing, and this arboreal life in the zoo would be the surest starting point that such a species is eventually able to experience positive welfare.

The relationship between evidence-based husbandry (science that supports appropriate care) and husbandry-based evidence (the outcomes from husbandry in the zoo are evidence for what works well) provides enhanced opportunities for choice and control, comfort, and compassion. This relationship will reduce an animal's reliance on coping strategies that may be unhelpful or unwanted (e.g., stereotypic behavior). When husbandry is supported by evidence (wild ecology and cross-facility data on exemplary practice) animals can feel more comfortable. For example, the provision of wetlands for captive lechwe creates opportunities for behavioral diversity that has been recorded in other swamp-dwelling antelopes in zoos, such as sitatunga, *Tragelaphus spekii* (Rose & Robert, 2013). The heterogeneous nature of an ecologically relevant environment gives more chances of choice and control over behavior patterns, space occupancy, and use of resources (Glaeser et al., 2021; Krishnan et al., 2022; Spain et al., 2020). As animal care is improved and becomes easier, the compassionate nature of welfare-friendly husbandry provides benefits to human well being too (e.g., increasing job satisfaction and reducing compassion fatigue). Husbandry-based evidence can be taken from the zoo into the wild, to enhance the welfare of wild animals – for example, nest boxes designed for zoo-housed hornbills (Bucerotidae) being installed in situ to enhance habitat quality and resource access for free-living birds (Beilby, 2022).

As zoos continue to develop welfare assessment frameworks, we believe it is important to consider what identifiers are available, and what can be practically and meaningfully measured. The Five Domains model is commonly advocated for as a welfare assessment framework with zoos and aquariums (Harley & Clark, 2019; Mellor et al., 2015); however, the utility of this approach has been questioned (Hampton et al., 2023). Animal welfare theory is useful from a fundamental science perspective but may be less helpful for busy zoo professionals that may need quick but valid snapshots of their animal's welfare. Caring for a multitude of species can be pressured, especially when such species may be of high conservation value, and keepers feel a strong sense of obligation to ensure that the animals they have ultimate responsibility for remain healthy, safe, and well. Zoo welfare scientists should publish their methods and approaches to evaluating inputs and determining outputs, so that validated and reliable means of consistent welfare scoring are available at the species-specific level across taxa.

Conclusions

Using the "Six Cs," this paper provides key concepts of animal welfare and identifies measurable indicators of behavioral, physical, and psychological states. Whilst species-specific or even individual-specific welfare assessment is important, this general framework highlights important concepts that influence the welfare for a broad range of animals. Furthermore, having a common framework can help ensure that welfare assessments are comparable across zoos, facilitating benchmarking and collaborative research.

When the evidence basis for zoo animal care is robust, and it is implemented across facilities, welfare improvements are likely to occur more rapidly and significantly. As more zoos adopt this

evidence-based approach, the husbandry practices themselves become evidence for good care (Table 2). Therefore, the evidence-based approach needs to continue in earnest, both for species with no current husbandry guidelines and for species where guidelines are written to ensure they are reviewed to remain current.

Overall, the zoo has a duty to enable appropriate husbandry to be developed and implemented and to the well being of animal care staff to ensure they are supported in their efforts to uphold good animal welfare. By building on an existing, well-used, and familiar definition of animal welfare to include metrics that could identify a wider range of behaviors that are linked to improved or positive welfare (comfort and choice and control) as well as by considering human aspects of well being, zoos, and aquariums can collect and analyze the effect of inputs (resources and environment) on outputs (behavior, personality, emotions) of their animals to quantify and assess welfare states (Figure 2). We hope that this approach of review and reflection will encourage the development of husbandry-based evidence for all zoo-housed taxa.

Disclosure statement

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

Funding

The author(s) reported that there is no funding associated with the work featured in this article.

References

Allard, S. M., & Bashaw, M. J. (2019). Empowering zoo animals. In A. B. Kaufman, M. J. Bashaw, & T. L. Maple (Eds.), *Scientific foundations of zoos and aquariums: Their role in conservation and research* (pp. 241–273). Cambridge University Press. https://doi.org/10.1017/9781108183147.010

Arndt, S. S., Goerlich, V. C., & van der Staay, F. J. (2022). A dynamic concept of animal welfare: The role of appetitive and adverse internal and external factors and the animal's ability to adapt to them. *Frontiers in Animal Science*, 3. https://doi.org/10.3389/fanim.2022.908513

Bashaw, M. J., Tarou, L. R., Maki, T. S., & Maple, T. L. (2001). A survey assessment of variables related to stereotypy in captive giraffe and okapi. *Applied Animal Behaviour Science*, *73*(3), 235–247. https://doi.org/10.1016/S0168-1591(01)00137-X

Baxter, E., & Plowman, A. B. (2001). The effect of increasing dietary fibre on feeding, rumination and oral stereotypies in captive giraffes (Giraffa camelopardalis). *Animal Welfare*, *10*(3), 281–290. https://doi.org/10.1017/S0962728600024052

Beilby, J. (2022). The behavioural biology of hornbills, toucans, and kingfishers. In P. E. Rose (Ed.), *The behavioural biology of zoo animals* (pp. 185–196). CRC Press.

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*(3), 166–174.

Blackett, T. A., McKenna, C., Kavanagh, L., & Morgan, D. R. (2017). The welfare of wild animals in zoological institutions: Are we meeting our duty of care? *International Zoo Yearbook*, *51*(1), 187–202. https://doi.org/10.1111/izy.12143

Bousfield, B., & Brown, R. (2010). Animal welfare. *The Veterinary Bulletin*, *1*(4), 1–12.

Brando, S., & Buchanan-Smith, H. M. (2018). The 24/7 approach to promoting optimal welfare for captive wild animals. *Behavioural Processes*, *156*, 83–95. https://doi.org/10.1016/j.beproc.2017.09.010

Brando, S., & Coe, J. (2022). Confronting back-of-house traditions: Primates as a case study. *Journal of Zoological and Botanical Gardens*, *3*(3), 366–397. https://doi.org/10.3390/jzbg3030029

Brando, S., Rachinas-Lopes, P., Goulart, V. D. L. R., & Hart, L. A. (2023). Understanding job satisfaction and occupational stressors of distinctive roles in zoos and aquariums. *Animals*, *13*(12), 2018. https://doi.org/10.3390/ani13122018

Brereton, J., & Rose, P. E. (2022). An evaluation of the role of 'biological evidence' in zoo and aquarium enrichment practices. *Animal Welfare*, *31*(1), 13–26. https://doi.org/10.7120/09627286.31.1.002

Broom, D. M. (1986). Indicators of poor welfare. *The British Veterinary Journal*, *142*(6), 524–526. https://doi.org/10.1016/0007-1935(86)90109-0

Broom, D. M. (1991). Animal welfare: Concepts and measurement. *Journal of Animal Science*, *69*(10), 4167–4175. https://doi.org/10.2527/1991.69104167x
Broom, D. M., & Fraser, A. F. (2007). *Domestic animal behaviour and welfare* (4 ed.). CABI.
Buchanan-Smith, H. M. (2011). Environmental enrichment for primates in laboratories. *Advances in Science and Research*, *5*(1), 41–56. https://doi.org/10.5194/asr-5-41-2010
Clark, F. E. (2011). Great ape cognition and captive care: Can cognitive challenges enhance well-being? *Applied Animal Behaviour Science*, *135*(1), 1–12. https://doi.org/10.1016/j.applanim.2011.10.010
Claxton, A. M. (2011). The potential of the human–animal relationship as an environmental enrichment for the welfare of zoo-housed animals. *Applied Animal Behaviour Science*, *133*(1–2), 1–10. https://doi.org/10.1016/j.applanim.2011.03.002
Clubb, R., & Mason, G. J. (2003). Captivity effects on wide-ranging carnivores. *Nature*, *425*(6957), 473–474. https://doi.org/10.1038/425473a
Coe, J. (2017). *Embedding environmental enrichment into zoo animal facility design*. Proceedings of the Zoo Design 2017 Conference Wroclaw, Poland.
Coe, J., & Hoy, J. (2020). Choice, control and computers: Empowering wildlife in human care. *Multimodal Technologies and Interaction*, *4*(4), 92. https://doi.org/10.3390/mti4040092
Colditz, I. G., & Hine, B. C. (2016). Resilience in farm animals: Biology, management, breeding and implications for animal welfare. *Animal Production Science*, *56*(12), 1961–1983. https://doi.org/10.1071/AN15297
Colditz, I. G., & Tilbrook, A. (2023). A biological integrity framework for describing animal welfare and wellbeing. *Animal Production Science*, *63*(5), 423–440. https://doi.org/10.1071/AN22285
Cole, J., & Fraser, D. (2018). Zoo animal welfare: The human dimension. *Journal of Applied Animal Welfare Science*, *21* (sup1), 49–58. https://doi.org/10.1080/10888705.2018.1513839
Coulton, L. E., Waran, N. K., & Young, R. J. (1997). Effects of foraging enrichment on the behaviour of parrots. *Animal Welfare*, *6*(4), 357–364. https://doi.org/10.1017/S0962728600020066
Cronin, K. A., West, V., & Ross, S. R. (2016). Investigating the relationship between welfare and rearing young in captive chimpanzees (Pan troglodytes). *Applied Animal Behaviour Science*, *181*, 166–172.
Dawkins, M. S. (2004). Using behaviour to assess animal welfare. *Animal Welfare*, *13*(S1), S3–S7. https://doi.org/10.1017/S0962728600014317
Decker, S., Lavery, J. M., & Mason, G. J. (2023). Don't use it? Don't lose it! Why active use is not required for stimuli, resources or "enrichments" to have welfare value. *Zoo Biology*, *42*(4), 467–475. https://doi.org/10.1002/zoo.21756
Defra. (2012). *Secretary of States' standards for modern zoo practice*. Department for the Environment, Food & Rural Affairs.
Demerouti, E., Bakker, A. B., Nachreiner, F., & Schaufeli, W. B. (2001). The job demands-resources model of burnout. *Journal of Applied Psychology*, *86*(3), 499. https://doi.org/10.1037/0021-9010.86.3.499
DeSmet, A., & Ogle, B. (2022). The influence of welfare and bonds with animals on the job satisfaction of felid keepers in North America. *Zoo Biology*, *41*(3), 193–199. https://doi.org/10.1002/zoo.21667
Devlin, S., & Ogle, B. (2022). Examining how a general audience rates herptile welfare in zoos. *Journal of Zoo and Aquarium Research*, *10*(2), 101–106.
Endres, M. I. (2017). The relationship of cow comfort and flooring to lameness disorders in dairy cattle. *Veterinary Clinics: Food Animal Practice*, *33*(2), 227–233. https://doi.org/10.1016/j.cvfa.2017.02.007
Englund, M. D., & Cronin, K. A. (2023). Choice, control, and animal welfare: Definitions and essential inquiries to advance animal welfare science. *Frontiers in Veterinary Science*, *10*, 1250251. https://doi.org/10.3389/fvets.2023.1250251
Figley, C. R., & Roop, R. G. (2006). *Compassion fatigue in the animal-care community*. Humane Society Press.
Föllmi, J., Steiger, A., Walzer, C., Robert, N., Geissbühler, U., Doherr, M. G., & Wenker, C. (2007). A scoring system to evaluate physical condition and quality of life in geriatric zoo mammals. *Animal Welfare*, *16*(3), 309–318. https://doi.org/10.1017/S0962728600027123
Foster-Turley, P., & Markowitz, H. (1982). A captive behavioral enrichment study with Asian small-clawed river otters (Aonyx cinerea). *Zoo Biology*, *1*(1), 29–43. https://doi.org/10.1002/zoo.1430010104
Fraser, D. (2009). Animal behaviour, animal welfare and the scientific study of affect. *Applied Animal Behaviour Science*, *118*(3–4), 108–117. https://doi.org/10.1016/j.applanim.2009.02.020
Fraser, D., Weary, D. M., Pajor, E. A., & Milligan, B. N. (1997). A scientific conception of animal welfare that reflects ethical concerns. *Animal Welfare*, *6*(3), 187–205. https://doi.org/10.1017/S0962728600019795
Glaeser, S. S., Shepherdson, D., Lewis, K. D., Prado, N., Brown, J. L., Lee, B., & Wielebnowski, N. C. (2021). Supporting zoo Asian elephant (Elephas maximus) welfare and herd dynamics with a more complex and expanded habitat. *Animals*, *11*(9), 2566. https://doi.org/10.3390/ani11092566
Gonyou, H. W. (1986). Symposium on "Indices to Measure Animal Well-Being" assessment of comfort and well-being in farm animals. *Journal of Animal Science*, *62*(6), 1769–1775. https://doi.org/10.2527/jas1986.6261769x
Greenwell, P. J., Riley, L. M., Lemos de Figueiredo, R., Brereton, J. E., Mooney, A., & Rose, P. E. (2023). The societal value of the modern zoo: A commentary on how zoos can positively impact on human populations locally and globally. *Journal of Zoological and Botanical Gardens*, *4*(1), 53–69. https://doi.org/10.3390/jzbg4010006

Greggor, A. L., Vicino, G. A., Swaisgood, R. R., Fidgett, A., Brenner, D., Kinney, M. E., Farabaugh, S., Masuda, B., & Lamberski, N. (2018). Animal welfare in conservation breeding: Applications and challenges. *Frontiers in Veterinary Science*, *5*, 323. https://doi.org/10.3389/fvets.2018.00323

Grethe, H. (2017). The economics of farm animal welfare. *Annual Review of Resource Economics*, *9*(1), 75–94. https://doi.org/10.1146/annurev-resource-100516-053419

Haley, D. B., Rushen, J., & de Passillé, A. M. (2000). Behavioural indicators of cow comfort: Activity and resting behaviour of dairy cows in two types of housing. *Canadian Journal of Animal Science*, *80*(2), 257–263. https://doi.org/10.4141/A99-084

Hampton, J. O., Hemsworth, L. M., Hemsworth, P. H., Hyndman, T. H., & Sandøe, P. (2023). Rethinking the utility of the Five Domains model. *Animal Welfare*, *32*, e62.https://doi.org/10.1017/awf.2023.84

Harley, J., & Clark, F. E. (2019). *Animal welfare toolkit*. BIAZA.

Harvey, N. D., Daly, C., Clark, N., Ransford, E., Wallace, S., & Yon, L. (2018). Social interactions in two groups of zoo-housed adult female Asian elephants (Elephas maximus) that differ in relatedness. *Animals*, *8*(8), 132. https://doi.org/10.3390/ani8080132

Hediger, H. (1950). *Wild animals in captivity*. Butterworths Scientific Publications.

Held, S. D. E., & Špinka, M. (2011). Animal play and animal welfare. *Animal Behaviour*, *81*(5), 891–899. https://doi.org/10.1016/j.anbehav.2011.01.007

Hill, E. M., LaLonde, C. M., & Reese, L. A. (2020). Compassion fatigue in animal care workers. *Traumatology*, *26*(1), 96. https://doi.org/10.1037/trm0000218

Hill, S. P., & Broom, D. M. (2009). Measuring zoo animal welfare: Theory and practice. *Zoo Biology*, *28*(6), 531–544. https://doi.org/10.1002/zoo.20276

Hughes, B. O., & Duncan, I. J. H. (1988). The notion of ethological 'need', models of motivation and animal welfare. *Animal Behaviour*, *36*(6), 1696–1707. https://doi.org/10.1016/S0003-3472(88)80110-6

IUCN SSC Antelope Specialist Group. (2017a). *Kobus leche ssp. leche. The IUCN Red List of Threatened Species*. Gland, Switzerland: IUCN. https://www.iucnredlist.org/

IUCN SSC Antelope Specialist Group. (2017b). *Kobus megaceros the IUCN Red List of Threatened Species*. Gland, Switzerland: IUCN. https://www.iucnredlist.org/

Jacobson, S. L., Kwiatt, A. C., Ross, S. R., & Cronin, K. A. (2019). The effects of cognitive testing on the welfare of zoo-housed Japanese macaques (Macaca fuscata). *Applied Animal Behaviour Science*, *212*, 90–97. https://doi.org/10.1016/j.applanim.2018.12.014

Kagan, R., Carter, S., & Allard, S. (2015). A universal animal welfare framework for zoos. *Journal of Applied Animal Welfare Science*, *18*(sup1), S1–S10. https://doi.org/10.1080/10888705.2015.1075830

Kanngiesser, P., Sueur, C., Riedl, K., Grossmann, J., & Call, J. (2011). Grooming network cohesion and the role of individuals in a captive chimpanzee group. *American Journal of Primatology*, *73*(8), 758–767. https://doi.org/10.1002/ajp.20914

Krishnan, S., Klaphake, E., Rao, S., & Sadar, M. J. (2022). The effect of varied enrichment types on snake behavior. *Journal of Zoo and Wildlife Medicine*, *53*(2), 266–274. https://doi.org/10.1638/2020-0031

Learmonth, M. J. (2020). Human–animal interactions in zoos: What can compassionate conservation, conservation welfare and duty of care tell Us about the ethics of interacting, and avoiding unintended consequences? *Animals*, *10*(11), 2037. https://doi.org/10.3390/ani10112037

Learmonth, M. J., Sherwen, S. L., & Hemsworth, P. H. (2021). Assessing preferences of two zoo-housed Aldabran giant tortoises (Aldabrachelys gigantea) for three stimuli using a novel preference test. *Zoo Biology*, *40*(2), 98–106. https://doi.org/10.1002/zoo.21585

Lewis, K. D., Shepherdson, D. J., Owens, T. M., & Keele, M. (2010). A survey of elephant husbandry and foot health in North American zoos. *Zoo Biology*, *29*(2), 221–236. https://doi.org/10.1002/zoo.20291

Little, K. A., & Sommer, V. (2002). Change of enclosure in langur monkeys: Implications for the evaluation of environmental enrichment. *Zoo Biology*, *21*(6), 549–559. https://doi.org/10.1002/zoo.10058

Mallapur, A., & Chellam, R. (2002). Environmental influences on stereotypy and the activity budget of Indian leopards (Panthera pardus) in four zoos in Southern India. *Zoo biology*, *21*(6), 585–595.

Manteca, X., Amat, M., Salas, M., & Temple, D. (2016). Animal-based indicators to assess welfare in zoo animals. *CABI Reviews*, 1–10. https://doi.org/10.1079/PAVSNNR201611010

Maple, T. L., & Perdue, B. M. (2013). Environmental enrichment. In T. L. Maple & B. M. Perdue (Eds.), *Zoo animal welfare* (pp. 95–117). Springer.

Markowitz, H., Aday, C., & Gavazzi, A. (1995). Effectiveness of acoustic "prey": Environmental enrichment for a captive African leopard (Panthera pardus). *Zoo Biology*, *14*(4), 371–379. https://doi.org/10.1002/zoo.1430140408

Martin-Wintle, M. S., Wintle, N. J. P., Díez-León, M., Swaisgood, R. R., & Asa, C. S. (2019). Improving the sustainability of ex situ populations with mate choice. *Zoo Biology*, *38*(1), 119–132. https://doi.org/10.1002/zoo.21450

Mason, G. J., & Clubb, R. (2004). Pacing polar bears and stoical sheep: Testing ecological and evolutionary hypotheses about animal welfare. *Animal Welfare*, *13*(S1), 33–40. https://doi.org/10.1017/S0962728600014354

Maynard, L. (2018). Media framing of zoos and aquaria: From conservation to animal rights. *Environmental Communication*, *12*(2), 177–190. https://doi.org/10.1080/17524032.2017.1310741

McDonald, S. E., Kogan, L. R., Nageotte, N. L., Currin McCulloch, J., & Dickler-Mann, R. (2024). Zoo professionals and volunteers in the U.S: Experiences and prevalence of burnout, mental health, and animal loss. *Frontiers in Psychiatry*, *15*. https://doi.org/10.3389/fpsyt.2024.1373525

McGowan, R. T. S., Robbins, C. T., Alldredge, J. R., & Newberry, R. C. (2010). Contrafreeloading in grizzly bears: Implications for captive foraging enrichment. *Zoo Biology*, *29*(4), 484–502. https://doi.org/10.1002/zoo.20282

Meagher, R. K. (2019). Is boredom an animal welfare concern? *Animal Welfare*, *28*(1), 21–32. https://doi.org/10.7120/09627286.28.1.021

Meehan, C. L., & Mench, J. A. (2007). The challenge of challenge: Can problem solving opportunities enhance animal welfare? *Applied Animal Behaviour Science*, *102*(3–4), 246–261. https://doi.org/10.1016/j.applanim.2006.05.031

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

Mellor, D. J. (2016). Updating animal welfare thinking: Moving beyond the "five freedoms" towards "a Life Worth Living". *Animals*, *6*(3), 21. https://doi.org/10.3390/ani6030021

Mellor, D. J., Hunt, S., & Gusset, M. (2015). *Caring for wildlife: The world zoo and aquarium animal welfare strategy*. WAZA Executive Office.

Miller, L. J., Vicino, G. A., Sheftel, J., & Lauderdale, L. K. (2020). Behavioral diversity as a potential indicator of positive animal welfare. *Animals*, *10*(7), 1211. https://doi.org/10.3390/ani10071211

Mkono, M., & Holder, A. (2019). The future of animals in tourism recreation: Social media as spaces of collective moral reflexivity. *Tourism Management Perspectives*, *29*, 1–8. https://doi.org/10.1016/j.tmp.2018.10.002

Moberg, G. P. (1999). When does stress become distress? *Lab Animal*, *28*, 422–426.

Mobo, B. H. P., Rabinowitz, P. M., Conti, L. A., & Taiwo, O. A. (2010). Occupational health of animal workers. In P. M. Rabinowitz & L. A. Conti (Eds.), *Human-Animal Medicine* (pp. 343–371). Saint Louis, USA: W.B. Saunders.

Monaghan, H., Rohlf, V. I., Scotney, R., & Bennett, P. (2020). Compassion fatigue in people who care for animals: An investigation of risk and protective factors. *Traumatology*, *30*(1), 77–85. https://doi.org/10.1037/trm0000246

Morfeld, K. A., Meehan, C. L., Hogan, J. N., Brown, J. L., & Ryan, S. J. (2016). Assessment of body condition in African (Loxodonta africana) and Asian (Elephas maximus) elephants in North American zoos and management practices associated with high body condition scores. *PLOS ONE*, *11*(7), e0155146. https://doi.org/10.1371/journal.pone.0155146

Mormède, P., Andanson, S., Aupérin, B., Beerda, B., Guémené, D., Malmkvist, J., Manteca, X., Manteuffel, G., Prunet, P., van Reenen, C. G., Richard, S., & Veissier, I. (2007). Exploration of the hypothalamic–pituitary–adrenal function as a tool to evaluate animal welfare. *Physiology & Behavior*, *92*(3), 317–339. https://doi.org/10.1016/j.physbeh.2006.12.003

Nefdt, R. J. C., & Thirgood, S. J. (1997). Lekking, resource defense, and harassment in two subspecies of lechwe antelope. *Behavioral Ecology*, *8*(1), 1–9. https://doi.org/10.1093/beheco/8.1.1

Owen, M. A., Swaisgood, R. R., Czekala, N. M., & Lindburg, D. G. (2005). Enclosure choice and well-being in giant pandas: Is it all about control? *Zoo Biology*, *24*(5), 475–481. https://doi.org/10.1002/zoo.20064

Rault, J.-L., Waiblinger, S., Boivin, X., & Hemsworth, P. H. (2020). The power of a positive human–animal relationship for animal welfare. *Frontiers in Veterinary Science*, *7*, 590867. https://doi.org/10.3389/fvets.2020.590867

Reading, R. P., Miller, B., & Shepherdson, D. (2013). The value of enrichment to reintroduction success. *Zoo Biology*, *32*(3), 332–341. https://doi.org/10.1002/zoo.21054

Riley, L. M. (2018). Conserving behaviour with cognitive enrichment: A new frontier for zoo conservation biology. In M. Berger & S. Corbett (Eds.), *Zoo animals: Husbandry, welfare and public interactions* (pp. 199–264). Nova Science Publishers.

Rohlf, V. I. (2018). Interventions for occupational stress and compassion fatigue in animal care professionals—A systematic review. *Traumatology*, *24*(3), 186–192. https://doi.org/10.1037/trm0000144

Roller, M., Müller, D. W. H., Bertelsen, M. F., Bingaman Lackey, L., Hatt, J. M., & Clauss, M. (2021). The historical development of juvenile mortality and adult longevity in zoo-kept carnivores. *Zoo Biology*, *40*(6), 588–595. https://doi.org/10.1002/zoo.21639

Rose, P. E. (2023). Identifying essential elements of good giraffe welfare—can we use knowledge of a species' fundamental needs to develop welfare-focussed husbandry? *Journal of Zoological and Botanical Gardens*, *4*(3), 549–566. https://doi.org/10.3390/jzbg4030039

Rose, P. E., Brereton, J. E., Rowden, L. J., Lemos de Figueiredo, R., & Riley, L. M. (2019). What's new from the zoo? An analysis of ten years of zoo-themed research output. *Palgrave Communications*, *5*(1), 1–10. https://doi.org/10.1057/s41599-019-0345-3

Rose, P. E., & Croft, D. P. (2015). The potential of Social Network Analysis as a tool for the management of zoo animals. *Animal Welfare*, *24*(2), 123–138. https://doi.org/10.7120/09627286.24.2.123

Rose, P. E., Croft, D. P., & Lee, R. (2014). A review of captive flamingo (Phoenicopteridae) welfare: A synthesis of current knowledge and future directions. *International Zoo Yearbook*, *48*(1), 139–155. https://doi.org/10.1111/izy.12051

Rose, P. E., Nash, S. M., & Riley, L. M. (2017). To pace or not to pace? A review of what abnormal repetitive behavior tells us about zoo animal management. *Journal of Veterinary Behavior*, *20*, 11–21. https://doi.org/10.1016/j.jveb.2017.02.007

Rose, P. E., & Riley, L. M. (2019). The use of Qualitative Behavioural Assessment to zoo welfare measurement and animal husbandry change. *Journal of Zoo and Aquarium Research*, *7*(4), 150–161.

Rose, P. E., & Riley, L. M. (2022). Expanding the role of the future zoo: Wellbeing should become the fifth aim for modern zoos. *Frontiers in Psychology*, *13*, 6649. https://doi.org/10.3389/fpsyg.2022.1018722

Rose, P. E., & Robert, R. (2013). Evaluating the activity patterns and enclosure usage of a little-studied zoo species, the sitatunga (Tragelaphus spekii). *Journal of Zoo and Aquarium Research*, *1*(1), 14–19.

Rose, P. E., & Roffe, S. M. (2013). A case study of Malayan tapir (Tapirus indicus) husbandry practice across 10 zoological collections. *Zoo Biology*, *32*(3), 347–356. https://doi.org/10.1002/zoo.21018

Rose, P. E., & Rowden, L. J. (2020). Specialised for the swamp, catered for in captivity? A cross-institutional evaluation of captive husbandry for two species of lechwe. *Animals*, *10*(10), 1874. https://doi.org/10.3390/ani10101874

Rosenberger, K., Simmler, M., Langbein, J., Nawroth, C., & Keil, N. (2022). Responsiveness of domesticated goats towards various stressors following long-term cognitive test exposure. *PeerJ*, *10*, e12893. https://doi.org/10.7717/peerj.12893

Ross, M., Rausch, Q., Vandenberg, B., & Mason, G. (2020). Hens with benefits: Can environmental enrichment make chickens more resilient to stress? *Physiology & Behavior*, *226*, 113077. https://doi.org/10.1016/j.physbeh.2020.113077

Ross, S. R. (2006). Issues of choice and control in the behaviour of a pair of captive polar bears (Ursus maritimus). *Behavioural Processes*, *73*(1), 117–120. https://doi.org/10.1016/j.beproc.2006.04.003

Ross, S. R., Schapiro, S. J., Hau, J., & Lukas, K. E. (2009). Space use as an indicator of enclosure appropriateness: A novel measure of captive animal welfare. *Applied Animal Behaviour Science*, *121*(1), 42–50. https://doi.org/10.1016/j.applanim.2009.08.007

Ross, S. R., Wagner, K. E., Schapiro, S. J., & Hau, J. (2010). Ape behavior in two alternating environments: Comparing exhibit and short-term holding areas. *American Journal of Primatology*, *72*(11), 951–959. https://doi.org/10.1002/ajp.20857

Rushen, J., Butterworth, A., & Swanson, J. C. (2011). Animal behavior and well-being symposium: Farm animal welfare assurance: Science and application. *Journal of Animal Science*, *89*(4), 1219–1228. https://doi.org/10.2527/jas.2010-3589

Salvanes, A. G. V., Moberg, O., Ebbesson, L. O. E., Nilsen, T. O., Jensen, K. H., & Braithwaite, V. A. (2013). Environmental enrichment promotes neural plasticity and cognitive ability in fish. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1767), 20131331. https://doi.org/10.1098/rspb.2013.1331

Sayers, I. (2010). Approach to preventive health care and welfare in rabbits. *In Practice*, *32*(5), 190–198. https://doi.org/10.1136/inp.c2228

Sayers, J. (2020). The influence of animal welfare accreditation programmes on zoo visitor perceptions of the welfare of zoo animals. *Journal of Zoo and Aquarium Research*, *8*(3), 188–193.

Shepherdson, D. (1994). The role of environmental enrichment in the captive breeding and reintroduction of endangered species. In P. J. S. Olney, G. M. Mace, & A. T. C. Feistner (Eds.), *Creative conservation: Interactive management of wild and captive animals* (pp. 167–177). Springer.

Sherwen, S. L., & Hemsworth, P. H. (2019). The visitor effect on zoo animals: Implications and opportunities for zoo animal welfare. *Animals*, *9*(6), 366. https://doi.org/10.3390/ani9060366

Silk, J. B., Brosnan, S. F., Henrich, J., Lambeth, S. P., & Shapiro, S. (2013). Chimpanzees share food for many reasons: The role of kinship, reciprocity, social bonds and harassment on food transfers. *Animal Behaviour*, *85*(5), 941–947. https://doi.org/10.1016/j.anbehav.2013.02.014

Smith, C. A. (1991). The self, appraisal, and coping. In C. R. Snyder & D. R. Forsyth (Eds.), *Handbook of social and clinical psychology: The health perspective* (pp. 116–137). Pergamon Press.

Smith, G. E., Greene, D., Hartsfield, L. A., & Pepperberg, I. M. (2021). Initial evidence for eliciting contrafreeloading in grey parrots (Psittacus erithacus) via the opportunity for playful foraging. *Journal of Comparative Psychology*, *135*(4), 516–533. https://doi.org/10.1037/com0000295

Spain, M. S., Fuller, G., & Allard, S. M. (2020). Effects of habitat modifications on behavioral indicators of welfare for Madagascar giant hognose snakes (Leioheterodon madagascariensis). *Animal Behavior and Cognition*, *7*(1), 70–81. https://doi.org/10.26451/abc.07.01.06.2020

Špinka, M., & Wemelsfelder, F. (2018). Environmental challenge and animal agency. In M. C. Appleby, I. A. S. Olsson, & F. Galindo (Eds.), *Animal welfare* (3 ed. pp. 39–55). CABI.

Takagi, N., Saito, M., Ito, H., Tanaka, M., & Yamanashi, Y. (2019). Sleep-related behaviors in zoo-housed giraffes (Giraffa camelopardalis reticulata): Basic characteristics and effects of season and parturition. *Zoo Biology*, *38*(6), 490–497. https://doi.org/10.1002/zoo.21511

Taylor, D. (2011). Wellbeing and welfare: A psychosocial analysis of being well and doing well enough. *Journal of Social Policy*, *40*(4), 777–794. https://doi.org/10.1017/S0047279411000249

Tennessen, T. (1989). Coping with confinement — features of the environment that influence animals' ability to adapt. *Applied Animal Behaviour Science*, *22*(2), 139–149. https://doi.org/10.1016/0168-1591(89)90050-6

Tetzlaff, S. J., Sperry, J. H., & DeGregorio, B. A. (2019). Effects of antipredator training, environmental enrichment, and soft release on wildlife translocations: A review and meta-analysis. *Biological Conservation*, *236*, 324–331. https://doi.org/10.1016/j.biocon.2019.05.054

Tidière, M., Gaillard, J.-M., Berger, V., Müller, D. W. H., Bingaman Lackey, L., Gimenez, O., Clauss, M., & Lemaître, J.-F. (2016). Comparative analyses of longevity and senescence reveal variable survival benefits of living in zoos across mammals. *Scientific Reports*, *6*(1), 36361. https://doi.org/10.1038/srep36361

Van Gastelen, S., Westerlaan, B., Houwers, D. J., & Van Eerdenburg, F. J. C. M. (2011). A study on cow comfort and risk for lameness and mastitis in relation to different types of bedding materials. *Journal of Dairy Science*, *94*(10), 4878–4888. https://doi.org/10.3168/jds.2010-4019

Vasconcellos, A. D. S., Harumi Adania, C., & Ades, C. (2012). Contrafreeloading in maned wolves: Implications for their management and welfare. *Applied Animal Behaviour Science*, *140*(1–2), 85–91. https://doi.org/10.1016/j.applanim.2012.04.012

Vasseur, E., Gibbons, J., Rushen, J., Pellerin, D., Pajor, E. A., Lefebvre, D., & de Passillé, A. M. (2015). An assessment tool to help producers improve cow comfort on their farms. *Journal of Dairy Science*, *98*(1), 698–708. https://doi.org/10.3168/jds.2014-8224

Vaz, J., Bartley, A., & Hunt, J. (2022). Personality matters: Exploring the relationship between personality and stress physiology in captive African lions. *BMC Zoology*, *7*(1), 1–12. https://doi.org/10.1186/s40850-022-00126-9

Veasey, J. S. (2017). In pursuit of peak animal welfare; the need to prioritize the meaningful over the measurable. *Zoo Biology*, *36*(6), 413–425. https://doi.org/10.1002/zoo.21390

Veissier, I., Aubert, A., & Boissy, A. (2012). Animal welfare: A result of animal background and perception of its environment. *Animal Frontiers*, *2*(3), 7–15. https://doi.org/10.2527/af.2012-0043

Villalba, J. J., & Manteca, X. (2019). A case for eustress in grazing animals. *Frontiers in Veterinary Science*, *6*, 303. https://doi.org/10.3389/fvets.2019.00303

Ward, S. J., & Hosey, G. (2020). The need for a convergence of agricultural/laboratory and zoo-based approaches to animal welfare. *Journal of Applied Animal Welfare Science*, *23*(4), 484–492. https://doi.org/10.1080/10888705.2019.1678038

Ward, S. J., & Sherwen, S. L. (2018). Zoo animals. In G. Hosey & V. Melfi (Eds.), *Anthrozoology: Human-animal interactions in domesticated and wild animals* (pp. 81–103). Oxford University Press.

Wark, J. D., Wierzal, N. K., & Cronin, K. A. (2020). Mapping shade availability and use in zoo environments: A tool for evaluating thermal comfort. *Animals*, *10*(7), 1189. https://doi.org/10.3390/ani10071189

Warwick, C., Arena, P., Lindley, S., Jessop, M., & Steedman, C. (2013). Assessing reptile welfare using behavioural criteria. *Practice*, *35*(3), 123–131. https://doi.org/10.1136/inp.f1197

Webster, A. J. F. (2001). Farm animal welfare: The five freedoms and the free market. *The Veterinary Journal*, *161*(3), 229–237. https://doi.org/10.1053/tvjl.2000.0563

Webster, J. (2005). Evaluación y materialización del bienestar animal : de la teoría a la práctica. *Revue Scientifique Et Technique-Office International Des Epizooties*, *24*(2), 723–734. https://doi.org/10.20506/rst.24.2.1602

Wemelsfelder, F. (2007). How animals communicate quality of life: The qualitative assessment of behaviour. *Animal Welfare*, *16*(2), 25–31. https://doi.org/10.1017/S0962728600031699

White, B., Yeung, P., Chilvers, B. L., & O'Donoghue, K. (2021). Reducing the "cost of caring" in animal-care professionals: Social work contribution in a pilot education program to address burnout and compassion fatigue. *Journal of Human Behavior in the Social Environment*, *31*(7), 828–847. https://doi.org/10.1080/10911359.2020.1822249

Whitham, J. C., & Wielebnowski, N. C. (2013). New directions for zoo animal welfare science. *Applied Animal Behaviour Science*, *147*(3–4), 247–260. https://doi.org/10.1016/j.applanim.2013.02.004

Whittaker, A. L., Golder-Dewar, B., Triggs, J. L., Sherwen, S. L., & McLelland, D. J. (2021). Identification of animal-based welfare indicators in captive reptiles: A Delphi consultation survey. *Animals*, *11*(7), 2010. https://doi.org/10.3390/ani11072010

Williams, E., Bremner-Harrison, S., Harvey, N. D., Evison, E., & Yon, L. (2015). An investigation into resting behavior in Asian elephants in UK zoos. *Zoo Biology*, *34*(5), 406–417. https://doi.org/10.1002/zoo.21235

Williamson, D. T. (1990). Habitat selection by red lechwe (Kobus leche leche Gray, 1850). *African Journal of Ecology*, *28*(2), 89–101. https://doi.org/10.1111/j.1365-2028.1990.tb01141.x

Williamson, D. T. (1994). Social behaviour and organization of red lechwe in the Linyanti Swamp. *African Journal of Ecology*, *32*(2), 130–141. https://doi.org/10.1111/j.1365-2028.1994.tb00564.x

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. https://doi.org/10.3390/ani8070110

Yam, K. C., Tang, P. M., & Lam, C. (2022). Working with animals: Implications for employees' compassion, awe, prosocial behavior, and task performance. *Personnel Psychology*, *76*(1), 181–220. https://doi.org/10.1111/peps.12517

Yeung, P., White, B., & Chilvers, B. L. (2017). Exploring wellness of wildlife carers in New Zealand: A descriptive study. *Anthrozoös*, *30*(4), 549–563. https://doi.org/10.1080/08927936.2017.1370213

Yosef, R. (2000). Individual distances among greater flamingos as indicators of tourism pressure. *Waterbirds: The International Journal of Waterbird Biology*, *23*(1), 26–31. https://doi.org/10.2307/1522143