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Advances in Applied Zoo Animal Welfare Science

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ABSTRACT
Nonhuman animal welfare science is the scientific study of the welfare state of animals that attempts to make inferences about how animals *feel* from their behavior, endocrine function, and/or signs of physical health. These welfare measurements are applicable within zoos yet inherently more complex than in farms and laboratories. This complexity is due to the vast number of species housed, lack of fundamental biological information, and relatively lower sample sizes and levels of experimental control. This article summarizes the invited presentations on the topic of "Advances in Applied Animal Welfare Science," given at the Fourth Global Animal Welfare Congress held jointly by the Detroit Zoological Society and the World Association of Zoos and Aquariums in 2017. The article focuses on current trends in research on zoo animal welfare under the following themes: (a) human–animal interactions and relationships, (b) anticipatory behavior, (c) cognitive enrichment, (d) behavioral biology, and (e) reproductive and population management. It highlights areas in which further advancements in zoo animal welfare science are needed and the challenges that may be faced in doing so.

KEYWORDS
Research; behavior; human–animal interaction; cognitive enrichment; management

Introduction

Nonhuman animal welfare refers to the state of the animal as perceived by the animal himself or herself with regards to their ability to cope (Bracke, Spruijt, & Metz, 1999; Broom, 1996). Definitions increasingly include reference to an animal's mind, body, and nature (Appleby, Hughes, Mench, & Olsson, 2011). The distinction between animal welfare and animal care is imperative; the best intentions of animal staff and good standards of care do not automatically translate to good animal welfare (Grandin, 2015).

"Animal welfare science" is the scientific study of the welfare state of animals that attempts to make inferences about how animals *feel*. It is based on a number of available welfare indicators (behavior, endocrine function, physical health, and so on) with the purpose of providing objective data. It also includes the study of cause and effect—in other words, which factors contribute to a reduced or enhanced welfare state. Animal welfare science and ethics are inextricably linked, and for brevity, we use the term animal welfare science to also include ethics. Strictly speaking, welfare science focuses on "*what is*," whereas ethics focuses on "*what ought to be*" (Kreger & Hutchins, 2010; White, 1981), but animal welfare scientists and animal ethicists have many overlapping goals. Ultimately, both disciplines are interested in advancing our understanding and articulation of the human relationship with other animals (Fraser, 1999).

The most substantial transformation of all animal industries within our lifetimes has arguably been the zoo industry. Traditionally, animals were kept in zoos for the purpose of human

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entertainment, and there was little commitment to animal welfare standards (Tribe & Booth, 2003). As public attitudes toward the use of animals have changed, many zoos have responded by moving away from entertainment and toward conservation (Carr & Cohen, 2011). Alongside this transformation came an increased focus on animal welfare. This focus has resulted in an intensification of zoo-based science dedicated to (a) evaluating the success of conservation aims (Ballantyne, Packer, Hughes, & Dierking, 2007) and (b) the impact of the zoo environment on animal behavior and welfare (Hosey, 2005). This focus on empirical operating philosophies for zoos (Maple & Perdue, 2013) has led to the development of zoo animal welfare science as a specialization within the broader field of welfare science.

Significant progress has been made in advancing our understanding of the welfare of animals in zoos; less than a decade ago, Melfi (2009) highlighted gaps in our fundamental knowledge of nondomesticated zoo animal welfare. Furthermore, Melfi highlighted that the gaps were due to a focus on measuring negative welfare indicators rather than positive ones, a lack of research on housing and husbandry requirements and human impacts, and a strong taxa bias toward mammals. Fortunately, since then, we have witnessed an increase in the publication of zoo welfare research (peer-reviewed and non-peer-reviewed), which highlights the increased research output of zoos and affiliated research institutes worldwide. Welfare research within zoos now covers a far wider sphere of topics (Maple & Bloomsmith, 2017). For example, numerous recent publications have outlined the link between housing and husbandry factors and welfare for many taxa (e.g., Fuller et al., 2016; Greco, Meehan, Heinsius, & Mench, 2017; Hulbert, Hunt, & Rose, 2017; Rowden & Rose, 2016), and they have focused on human impacts on animal welfare (Alba, Leighty, Pittman Courte, Grand, & Bettinger, 2017; Hosey, 2013; Krebs, Torres, Chesney, Moon, & Watters, 2017; Vasconcellos Da Silva et al., 2016; Ward & Melfi, 2015).

The current article summarizes a series of invited presentations on the topic of “Advances in Applied Animal Welfare Science,” given at the Fourth Global Animal Welfare Congress. This congress was hosted by the Detroit Zoological Society Center for Zoo Animal Welfare (CZAW) in May 2017. This article focuses specifically on the five themes within this topic covered by invited speakers: (a) human–animal interactions and relationships, (b) anticipatory behavior, (c) cognitive enrichment, (d) behavioral biology, and (e) reproductive and population management. Other articles within this special issue discuss other aspects of the World Association of Zoos and Aquariums (WAZA)-CZAW congress; these aspects include more fundamental ethical debates on the role(s) of modern zoos, public perceptions of zoos, and growing interest in welfare-based zoo accreditation.

Here, we review how welfare problems have recently been identified, assessed, evaluated, and mitigated in a zoo setting relating to the five themes (a–e) listed in the previous paragraph. We focus on evidence-based welfare science and cite examples of how zoo research has contributed to our growing understanding of animal welfare in the main (across all captive settings), as well as how research has been initiated to tackle specific zoo animal welfare problems. Crucially, we recognize areas for future focus within zoos. We hope that this article will act as a concise summary of a broad and rapidly expanding research area within zoos. We signpost the most representative or influential peer-reviewed papers and gray literature for readers seeking more detailed information on the topics covered.

Current trends in zoo animal welfare science

Human–animal interactions and relationships

Humans’ relationships with animals have long been of interest from an ethical perspective (DeMello, 2012) and more recently from an animal welfare perspective. The term human–animal interaction (HAI) refers to how animals in captivity interact with humans within their environment; in the case of zoos, these humans may be keepers and other staff and visitors (Hosey, 2008). Interactions can broadly be categorized as positive, neutral, or negative (Hemsworth & Boivin, 2011). The majority of research on HAIs thus far has been undertaken on domestic animals (Hemsworth & Coleman, 2011), but there has been a recent trend for investigating HAIs in zoo animals (Hosey & Melfi, 2014, 2015). Human–animal interaction research involving zoo visitors ("unfamiliar" humans) has identified that visitors can be perceived as a negative (Sherwen, Harvey et al., 2015; Sherwen, Magrath, Butler, & Hemsworth, 2015) or positive (Bloomfield, Gillespie, Kerswell, Butler, & Hemsworth, 2015) stimulus.

Repeated HAIs lead to the formation of human–animal relationships (HARs), which have been widely described in animals on farms and only comparatively recently for zoo animals (Hemsworth & Boivin, 2011; Hosey, 2008). Ward and Melfi (2013), based on a model proposed by Hosey (2008), found that positive interactions between zoo ungulates or primates and their keepers (perceived as "familiar" humans) led to positive animal responses indicative of enhanced welfare (the "zoo stockmanship cycle"). Interestingly, Ward and Melfi (2015) found that the animal rather than the human dictated the valence of HAIs and subsequently HARs in the zoo.

A particular area of focus for HAI/HAR research in zoos has been between animal care staff and primates. These relationships are not only important for an animal's direct short-term welfare; but they also have important implications for primates being rehabilitated and reintroduced to the wild from zoos or zoo sanctuaries and thus their longer-term, "unforeseen" welfare state (Russon, Smith & Adams, 2016). Bonds between great apes and their caregivers are known to be strong and persistent; recent research has demonstrated more negative relationships can exist between great apes (orangutans [*Pongo abelii*] and gorillas [*Gorilla gorilla*]) and unfamiliar humans, and more positive relationships can exist between apes and familiar humans (Smith, 2014). Interestingly, husbandry performed by orangutan keepers was found to be dependent on keepers' perceptions of an orangutan's mood (Palmer, Malone, & Park, 2016), indicating that staff may react to perceived welfare status without any formal (i.e., scientific) assessment.

Anticipatory behavior

Most zoo animals live in highly predictable environments: Provisions of resources are highly scheduled, and cues such as keeper presence at certain times of the day reliably signal their arrival. Predictable conditions promote the development of anticipatory behavior (i.e., behavior occurring in response to a cue that signals the arrival of the resource). In his review, Watters (2014) therefore proposed anticipatory behavior as a practical indicator of zoo animal welfare and argued that it may signal the animal's own appraisal of how rewarding their environment is, which fits the framework toward assessing more positive welfare states and asking animals what they "want" (Dawkins, 2017). However, the interpretation of anticipatory behavior must be undertaken with caution. In brief, anticipatory behavior can be an indicator of positive welfare; it is associated with the release of dopamine, which signals that the animal is expecting the arrival of a reward (Spruijt, Van Den Bos, & Pijlman, 2001). However, animals may develop extreme anticipatory behaviors in very predictable environments and spend significant parts of the day performing them at the expense of seeking or dealing with novel situations (reviewed by Watters, 2014).

The link between anticipatory behavior and welfare is a relatively new avenue of study in zoo animals and mainly consists of a few small studies thus far. For example, Krebs et al. (2017) found that one gorilla and one red panda (*Ailurus fulgens*) exhibited anticipatory behavior prior to HAIs, suggesting animals had a positive appraisal of these interactions. In bottlenose dolphins (*Tursiops truncatus*), anticipatory behavior in the form of increased vigilance and activity has been found to peak before training sessions and shows (Clegg et al., 2017; Jensen, Delfour, & Carter, 2013), but the link between welfare and these increased behaviors, at the expense of synchronized social swimming, is not entirely clear. Stereotypic pacing in large zoo carnivores has long been documented as a welfare concern, but the link between the expression of stereotypical behaviors and the current welfare state in zoo animals is still not fully understood (Rose, Nash, & Riley, 2017). Cless and Lukas (2017) reported that 3 out of 10 zoo-housed polar bears across seven zoos performed pacing behavior in anticipation of a positive husbandry event such as food or enrichment. Nine of the 10 bears in this study paced along exhibit edges—in other words, at the boundaries of their environments.

Cognitive enrichment

"Cognitive enrichment" for zoo animals has rapidly gained popularity during the past decade. Cognitive enrichment was borne from increased interest in the link between environmental challenge and welfare (Meehan & Mench, 2007; Špinka & Wemelsfelder, 2011) and initial research on farm animals and animals in the laboratory (Langbein, Siebert, & Nürnberg, 2009; Meyer, Puppe, & Langbein, 2009; Milgram, Siwak-Tapp, Araujo, & Head, 2006). In brief, "cognitive enrichment (1) engages cognitive skills by providing opportunities to solve problems and control some aspect of the environment, and (2) is correlated to one or more validated measures of wellbeing" (Clark, 2011, p. 6).

Most attempts at cognitive enrichment thus far have aimed to stimulate physical cognitive skills such as problem solving, memory, and learning (Clark, 2017). Recently, chimpanzees (*Pan troglodytes*) and bottlenose dolphins were provided with vertical gridlike or pipe mazes containing reward items (Clark, Davies, Madigan, Warner, & Kuczaj, 2013; Clark & Smith, 2013). Chimpanzees and dolphins were highly motivated by food and nonfood rewards, and they used a variety of novel techniques to solve the problems.

The use of computer technology in zoos is rapidly increasing (Perdue, Clay, Gaalema, Maple, & Stoinski, 2012; Webber, Carter, Smith, & Vetere, 2017). Consequently, animals participating in computerized cognitive tasks (usually involving computer touchscreens or a computer screen paired with a joystick) have shown signs of increased welfare such as voluntary engagement, reduced abnormal behaviors, and signs of "satisfaction," but there is a crucial link between task complexity and welfare (reviewed by Clark, 2017). Tasks have been designed with the primary goal of enriching animals (e.g., Tarou, Kuhar, Adcock, Bloomsmith, & Maple, 2004) or the primary goal of testing animal cognition (reviewed by Hopper, 2017). A recent and novel approach has been to incorporate technology into a mobile task; Krebs and Watters (2017) developed a mobile feeding device for rhinoceroses (*Diceros bicornis michaeli*) which animal care staff could move remotely.

Behavioral biology

The assessment of zoo animal welfare can broadly be separated into three camps: the biological functioning of an animal, the feelings or affective state of an animal, and the naturalness of the environment in allowing the animal to express natural behaviors (Fraser, 2009). It is important to note that these three standpoints are not mutually exclusive. It is now well recognized that affective (mental) experiences are a component of biological functioning (Hemsworth & Coleman, 2011). In turn, biological functioning (inclusive of affective states) is influenced by the "naturalness" of the environment and the behavioral opportunities offered to an animal. The evolution of animals in their natural environment has resulted in each species having certain needs that must be provided for welfare to be good (Broom, 2011). Thus, understanding an animal's welfare and identifying strategies to improve it requires an in-depth understanding of the evolutionary history of the species, including behavioral biology and sensory perception (Mason, 2010).

In zoos, behavioral biology has been applied to determine which species are likely to fare well (i.e., have fewer welfare concerns) in captivity. Clubb and Mason (2003) highlighted that even in closely related species, there is large variation in how well different species cope in captivity. Since this first publication, researchers have considerably advanced our knowledge using phylogenetic comparative methodology to identify natural behavioral biology traits across several taxonomic groups that are deemed risk factors for poor performance in captivity (Clubb & Mason, 2007; Kroshko et al., 2016; McDonald Kinkaid, 2015; Müller et al., 2010; Pomerantz, Meiri, & Terkel, 2013). This information could have considerable value in deciding which species to exhibit in zoos as it could weigh up species' conservation value against potential "costs" such as the risk for welfare problems. However, it is not known to what extent curators rely on behavioral biology in this way when collection planning.

Once appropriate species have been highlighted based on the multidimensional criteria mentioned earlier, the next consideration should be how zoos can provide an environment that facilitates "*thriving*." Again, the principles of behavioral biology should inform this consideration. Progress continues to be made in this area, with the creation of "naturalistic" zoo enclosures (WAZA, 2016). Increasingly, captive environments are incorporating computer technology, which may at first seem counterintuitive but can be used to enhance naturalism by replicating or enhancing sounds, olfactory cues, and an animal's control over their environment (Carter, Webber, & Sherwen, 2015).

Reproduction and population management

Difficult reproductive management decisions are omnipresent in zoos; there is limited space to house animals and their offspring, movement of a species between zoos is restricted (see review by Princée, 2016), and reproduction is known to be affected by a number of captive factors such as stress and nutrition (Blache, Terlouw, & Maloney, 2011).

A clear advancement has been the inclusion of reproductive behavior as a welfare indicator. The old assumption has been that if an animal is healthy enough to reproduce, he or she has good welfare (Broom, 1991). However, the five domains model of welfare assessment (Mellor & Beausoleil, 2015), recently adopted by WAZA (Mellor, Hunt, & Gusset, 2015), suggests that the expression of reproductive (courtship, mating, parenting) behaviors are associated with positive mental (affective) states. An animal can therefore have good welfare without necessarily producing viable offspring.

Another advancement is the promotion of early and frequent reproduction in female mammals to prevent loss of reproductive function, a phenomenon known as "*use it or lose it*" (Penfold, Powell, Traylor-Holzer, & Asa, 2014). "Lifetime reproductive planning," as championed by the St. Louis Zoo, involves using reproductive viability analysis to determine correlates of successful breeding based on animal characteristics such as age and rearing history (Asa, 2016).

Advancements in contraception and assisted reproductive technology have been reviewed elsewhere (see Comizzoli, 2015; Silber, Barbey, Lenahan, & Silber, 2013). These technological advances may indirectly enhance welfare by promoting natural reproductive behavior as discussed earlier, or conversely, they may negatively impact welfare through drug side effects, capture, restraint, transport, or invasive sampling. Fortunately, there have been many recent advances in noninvasive reproductive hormone monitoring in a range of mammals (e.g., Edwards et al., 2016; Flacke et al., 2017; Saunders, Harris, Traylor-Holzer, & Beck, 2014). Whitham and Miller (2016) reviewed novel technologies available to monitor zoo animal physiological states, including ingestible "pills" and thermo-imaging cameras.

Future trends in zoo animal welfare science

Human–animal interactions and relationships

Current research has highlighted that HAIs significantly affect the behavior of zoo animals, and they have the potential to develop into HARs. However, so far, we can only infer from the agricultural literature that these interactions and relationships could affect animal welfare, and so more research in this area is essential. With the number of keepers working with animals and/or relocations of zoo animals for breeding purposes, we do not yet know whether the development of HARs is indeed a good thing from the animals' perspective. There are also more methodological challenges faced with HAR research in a zoo compared with more controlled farm settings, and we lack a standardized methodology to measure welfare associated with relationships. An evaluation of current methods utilized in other animal industries as well as investigations into potential new methods, such as qualitative behavior analysis (Wemelsfelder & Lawrence, 2001), are needed to enable us to measure HARs in zoos and therefore their impact on animal welfare. In addition, with increasing opportunities for visitors to interact with a variety of species, in meet-and-greet scenarios or feeding sessions, research on the welfare of “ambassador animals” used in these encounters is vital to justify their continued operation.

Anticipatory behavior

The identification of what constitutes an anticipatory behavior for a zoo animal and what it tells us about their welfare is still a work in progress. However, increased interest in this area highlights the impacts we realize our human routines can have on the animals for whom we care in zoos. It can also be used as a method to understand what animals “want” or “value” within their captive environment (Dawkins, 2004). Currently, research has highlighted that anticipatory behaviors can be an indicator of positive or negative well being, and therefore, evaluation requires focused attention for different species or even individuals, rather than making broad assumptions. A continued focus on anticipatory behavior in pacing zoo carnivores is warranted, but anticipatory behavior could also be used as a novel indicator of the value that a wide range of species place on different enrichment items or other choices within their environment.

Cognitive enrichment

There is a future need for work on the concepts of “flow,” “competence,” and “agency,” which are positive welfare indicators upon which we have only briefly touched in the zoo setting (Appleby et al., 2011; Clark, 2017). From our experience, one of the main blockades to further research on cognitive enrichment is the negative perception of some zoo staff. It may be perceived as too complex, requiring a high level of technology, or creating an unnatural environment (in contrast to the positive views of visitors; see Perdue et al., 2012). This perception can certainly be altered, given time. Indeed, Hopper (2017) pointed out the irony in that importance is placed on public engagement with science (Mellor et al., 2015), yet little research has been undertaken on visitor perceptions of seeing animals engage in research.

Behavioral biology

To advance the application of behavioral biology principles in zoos, we need to scientifically evaluate current and new housing and husbandry programs using species-specific behavioral biology as a benchmark (Bashaw et al., 2016). Critical to the success of these evaluations is ensuring we select the most appropriate measure of success. In this regard, the assessment of behavioral diversity offers considerable potential value (Miller, Pisacane, & Vicino, 2016). Lastly, it should also be noted that there is likely to be significant value in collaboration between research on cognitive enrichment (mentioned earlier) and the field of behavioral biology because the provision of cognitive enrichment is likely to be an important behavioral opportunity for many species housed in zoos. As both areas of science advance, it will be exciting to see the mutually synergistic benefits to animal welfare.

Reproductive and population management

Going forward, we believe that zoos will increase their participation in long-term reproductive planning by combining results from longitudinal records with endocrine profiles. It is unknown how zoos may choose to be more selective in their breeding; for example, there may be an increase in artificial selection for animals with fewer underlying risks of developing welfare problems (depression, neophobia) and/or inherited diseases that have been linked to chronic pain and suffering. An avenue for future research that may become more relevant to zoos in the coming decades is the welfare of aged animals whose life spans continue to exceed those of their counterparts in the wild.

Taxonomic bias

The other noteworthy gap in zoo animal welfare science that exists across all the themes covered in this review is species bias. Traditionally, the focus has been on studying mammals, particularly nonhuman primates, with comparatively little attention dedicated to advancing our understanding of welfare for birds, reptiles, amphibians, and fish. More research directed toward these taxonomic groups will provide significant improvements in welfare standards for these animals. To this end, it may be necessary to reach out to researchers in laboratories or even those working in the field.

Capacity building

We strongly encourage a more collaborative approach to applied animal welfare in zoos. Specifically, we champion the construction of a global database of animal welfare researchers based in universities, zoos, laboratories, and farms to enable collaborations between zoos and other industries, which would enable more rapid advances in animal welfare science. To date, the CZAW based at the Detroit Zoo provides an excellent online welfare resource to connect researchers. In the United Kingdom, the Animal Welfare Research Network (AWRN), which was established in 2016, aims "to bring together the UK animal welfare research community, researchers in related disciplines, and stakeholders with a professional interest in animal welfare issues, in order to enhance communication and collaboration, and promote high quality fundamental and applied animal welfare research and its implementation" (Animal Welfare Research Network, 2017). We also encourage zoos to employ dedicated animal welfare scientists where possible—staff who are able to respond quickly to early welfare issues detected by keepers and vets, instigate targeted welfare research, and forge collaborations with external experts when needed. These staff members would also be responsible for maintaining high baseline welfare standards through periodic internal welfare auditing.

Animal welfare assessment

The majority of zoos worldwide are in tune with the need to assess animal welfare on a continual basis. Currently, there is no methodical system in place to make it an easy process across taxa or species or on an individual level. As discussed in this article, research on identifying positive welfare states is under way; however, more work is needed to enable a larger scale and the opportunity for animal welfare assessments to occur. Some zoos already conduct welfare audits; however, these audits are mainly measures of housing and husbandry provisions, and as previously discussed, good husbandry and care do not always equate to good welfare. Research on how to conduct animal welfare assessments in zoos, including methods that will enable the most appropriate measures of welfare in this format, is essential.

Funding

Lastly, funding for zoo animal welfare research is difficult to obtain from external sources such as the UK Research Councils due to low sample sizes in zoos in comparison with other animal research systems (e.g., farm, laboratory, and companion animals) and a perceived loss of experimental control. We feel that external research funding for zoos should not always need to be tied to conservation outputs (e.g., to facilitate *ex situ* conservation of threatened species); investigations on welfare are important in their own right. As Maple and Bloomsmith (in press) highlighted, animal welfare should be given equal institutional priority to conservation, and zoos should pay homage to both. Organizational structure and funding allocation should reflect this prioritization.

Conclusion and animal welfare implications

This article highlights that animal welfare is a key, if not the primary, consideration of modern zoos. Zoo animal welfare science is flourishing, and science can help with many applied management problems, even with the variety of unique stakeholders involved with the operation of zoos. Difficulties unfortunately arise due to low financial investment; however, we hope that this article will help to showcase the good scientific work of zoos worldwide and will encourage further collaborations and funding.

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