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New directions for zoo animal welfare science

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ABSTRACT

In recent years, zoos and aquaria have intensified efforts to develop approaches and tools for assessing the welfare of populations and individual animals in their care. Advances made by welfare scientists conducting studies on exotic, farm, laboratory, and companion animals have led to the emergence of a new perspective on welfare assessment in zoos. This perspective: (1) emphasizes the importance of supplementing resource-based assessments with animal-based approaches that require measures of the behavioral and/or physical state of individual animals, (2) focuses on the subjective experiences of individual animals, and (3) considers positive affective states. We propose that the zoo community also should increase efforts to integrate measures of positive affect into both population-level studies and tools for monitoring individual well-being. For years, zoo welfare researchers have conducted trans-disciplinary, multi-institutional studies to identify risk factors associated with poor welfare. In the future, large-scale research projects, as well as epidemiological studies specifically designed to examine the patterns of welfare issues within populations, should integrate behavioral, physiological, and biological measures of good well-being (e.g. play, exploratory behaviors, measures of immunological function). While the results of population-level studies can be used to refine animal care guidelines, individual animals should be monitored to ensure that their needs are being met. Furthermore, after determining how to elicit positive affective states in individual animals, the zoo community should attempt to promote these states by offering positive experiences. We describe two strategies that zoos can currently pursue to facilitate the occurrence of positive affective states: (1) provide animals with stimulating opportunities to overcome challenges, make choices, and have some level of control over their environments, and (2) promote appropriate and beneficial keeper–animal relationships. Ultimately, we hope that as welfare researchers gain a better understanding of how to assess and promote good well-being, zoos and aquaria can apply these findings to actively strive toward achieving the best possible welfare for all animals in their care.

1. Introduction

In recent years, zoos and aquaria (hereafter *zoos*) have responded to growing public concern about animal welfare, more stringent legislation, and an industry-wide call for higher internal standards by intensifying efforts to identify approaches and methods for welfare assessment. While societal attitudes toward animals vary greatly across the globe, an "ethical movement" is emerging that focuses the public's attention on improving welfare rather than simply preventing animal cruelty (Knierim et al., 2011; Rollin, 2004). The modern animal welfare science movement was sparked in the mid-1900s when popular press books such as *Animal Machines* (Harrison, 1964) generated heightened concern about livestock farmed in intensive husbandry

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systems. In the United Kingdom, this led to the formation of an expert panel, the Brambell Committee, which investigated production systems and called for additional research to be conducted in fields such as veterinary medicine, animal science, and animal behavior (Brambell, 1965). In its report, the Committee also delineated basic freedoms that should be granted to animals. These key principles of animal welfare ultimately evolved into the Five Freedoms (e.g. freedom from discomfort) (Farm Animal Welfare Council, 1992) that now underlie the legislation and standards guiding not only farm and laboratory operations, but also zoological institutions (Barber et al., 2010; Kagan and Veasey, 2010; Knierim et al., 2011).

Today, public pressure continues to influence animal welfare legislation and to drive many aspects of welfare science research. For example, in 2010, New Zealand's Agriculture Minister announced plans to develop a new national animal welfare strategy to reflect shifting attitudes and ensured that this process would include a public consultation phase (New Zealand's Ministry for Primary Industries, 2012). In a survey conducted by the European Commission regarding the attitudes of European Union citizens toward farmed animals, over one-third of respondents reported that animal welfare, "is of the highest possible importance" (i.e. provided a score of 10 out of 10) (European Commission, 2007). In fact, the Commission's previous report led to a multi-national, community-funded research project, Welfare Quality® (2012), for developing robust welfare monitoring and information systems (European Commission, 2005).

In response to increasing public awareness and an ethical demand for higher welfare standards within the zoo industry, the World Association of Zoos and Aquariums encourages its member institutions to adopt policies and procedures that exceed the minimum legal standards set at national and regional levels (WAZA, 2005). Indeed, zoo associations, such as the British and Irish Association of Zoos and Aquariums (BIAZA), the European Association of Zoos and Aquaria (EAZA), and the Association of Zoos and Aquariums (AZA), have boosted efforts to proactively identify and address welfare issues (Barber, 2009; Barber et al., 2010; Hill and Broom, 2009; Hosey et al., 2009). For example, AZA's Accreditation Standards (AZA, 2012a) now require institutions to develop Institutional Animal Welfare Processes to investigate welfare concerns raised by staff. The commitment to promoting excellence in animal care also has been embraced by institutional leadership across AZA, as evidenced by the creation of centers that focus on welfare policy and/or science, such as the Smithsonian Conservation Biology Institute's Center for Animal Care Sciences (CACS), Detroit Zoo's Center for Zoo Animal Welfare (CZAW), and the Chicago Zoological Society's Center for the Science of Animal Welfare (CSAW). In fact, the AZA's 2012 Directors' Policy Conference, attended by 120 zoo directors, included a special session on "Trends in Animal Welfare" that highlighted future directions for zoo welfare science.

There is consensus within the industry that one of these future directions must be to identify effective tools for systematically assessing and monitoring animal welfare in zoological collections (Barber, 2009; Barber et al., 2010; Butterworth et al., 2011; Hosey et al., 2009). Currently, the most common approach to zoo animal welfare assessment is resource-based, which refers to an indirect approach that focuses on what institutions provide to the animals by considering measures of the environment (e.g. space, shelter) and management practices (Whay, 2007; Whay et al., 2003a). For example, aside from its Accreditation Standards, AZA is in the process of developing 160 taxon-specific Animal Care Manuals that provide husbandry templates and outline detailed care guidelines (Barber, 2009). While considering the biological and physical needs of a taxon increases the potential for achieving good welfare, focusing solely on such factors does not ensure that individual animals will experience good well-being (Barber et al., 2010; Butterworth et al., 2011). Moreover, these recommendations typically are based on current best practices and not necessarily supported by scientific data (e.g. Melfi, 2009). To address these gaps in knowledge and resources, the current mission of AZA's Animal Welfare Committee (AWC) includes, "encouraging the development of research projects and assessment tools to advance and monitor animal welfare" (AZA, 2012b).

In the following section, we describe recent shifts in the zoo community's approach to welfare science. Zoos have adopted a new perspective based on research being conducted not only on exotic species, but also on farm, laboratory, and companion animals – a perspective that increasingly emphasizes the use of direct, animal-based approaches that include measures of an animal's behavioral or physical state (Whay, 2007; Whay et al., 2003a), considers the experiences of individual animals, and recognizes the importance of promoting positive affective states. Recent breakthroughs, both theoretical and applied, have paved the way for the development of tools that allow for regular monitoring of physical, emotional, and mental well-being. In addition, we will discuss some emerging topics and approaches that are expected to shape the future of zoo welfare science.

2. Evolving concepts in zoo animal welfare science

2.1. From resource-based to animal-based assessments

Within the past several years, the zoo community has experienced a shift in thought regarding its approach to institutional welfare assessments. While the zoo industry traditionally has focused on delineating appropriate husbandry practices and environmental requirements for accreditation, zoo researchers have called for this resource-based approach to be supplemented with animal-based measures (Barber, 2009; Butterworth et al., 2011; see Rushen and dePassillé, 2009, for a more critical discussion of resource-based versus animal-based measures). Support for including animal-based measures, sometimes also termed evidence-based assessments, is growing in many countries and industries (e.g. Barber, 2009; Blokhuis et al., 2003; Hewson, 2003; Main et al., 2007; Webster, 2009; Whay, 2007; Whay et al., 2003a). For instance, farm animal welfare researchers at the University of Bristol have developed animal-based protocols comprised of items with high content validity that can be measured reliably by

trained observers. Whay et al. applied the Delphi technique (Linstone and Turoff, 1975), a process that involves consulting with expert panelists to achieve a consensus of opinion regarding subjective judgments, to identify the most appropriate animal-based measures for dairy cattle, pigs, and hens (Whay et al., 2003a; see also Anonymous, 2001). Even though these protocols include measures that are intended to reflect the mental state of cattle (Whay et al., 2003b) or the attitude of laying hens (Whay et al., 2007), there is evidence that high levels of inter-observer agreement can be reached and that such measures are valid. Zoo animal welfare researchers can gain valuable insight from the farm animal welfare community as they continue to develop animal-based assessment tools and techniques. In fact, an increase in information exchange and collaboration would benefit both fields of welfare research. Conferences such as the International Workshop on the Assessment of Animal Welfare at Farm and Group Level (WAFL) provide a forum for discussing animal-based assessment and promote collaboration between researchers working in zoo, farm, and even laboratory settings (Widowski et al., 2011).

2.2. Considering the perspective of individual animals

While the zoo industry traditionally has focused on outlining the appropriate management practices and environmental requirements for a taxon, members of the same species often have unique perspectives, preferences, and needs due to differences in factors such as genetic makeup, early experience, environmental conditions, and temperament (Barber, 2009; Boissy et al., 2007; Hosey et al., 2009). As a result, welfare, or quality of life (QoL), must be assessed at the level of the individual (Broom, 2007; Barber et al., 2010; Butterworth et al., 2011; Fraser, 2008; McMillan, 2000, 2003; Mench, 1998; Morton, 2007). Research on QoL in humans, which aims to collect data directly from individuals, has demonstrated that there may be discrepancies between assessments based on objective indicators (e.g. living conditions) and those based on measures of subjective life satisfaction (e.g. Li et al., 1998). Such studies not only provide further support for supplementing resource-based assessments with those that are animal-based, but also suggest that these tools should include measures that attempt to capture the individual's subjective experience. In fact, some might argue that tools should be comprised primarily of such measures, as several researchers have suggested that welfare is mostly, or even entirely, dependent upon an individual's perceptions and affective subjective states (Dawkins, 1990; Duncan, 1996, 2006; Duncan and Dawkins, 1983; McMillan, 2000, 2003).

Ideally, researchers gather information about an individual's perspective or subjective experience by collecting data directly from the subject. However, when humans, for example, cannot communicate care preferences directly, assessments can be made using proxy informants such as parents, spouses, and caregivers. In fact, sufficient agreement can be found when comparing self-reports of QoL to assessments made by caregivers (Addington-Hall and Kalra, 2001). In recent years, welfare researchers and veterinarians have argued that animal caretakers should serve as proxy informants and that the person most familiar with an individual's temperament, needs, preferences, and behavior should be his/her "voice" (McMillan, 2000, 2003; Meagher, 2009; Morton, 2000, 2007; Wiseman-Orr et al., 2006). It has become increasingly common to use keeper assessments to gain insight into the behavior, temperament, personality, perspectives, and/or affective states of individual animals (Carlstead et al., 1999; Carlstead and Brown, 2005; Gold and Maple, 1994; King and Landau, 2003; Kuhar et al., 2006; Less et al., 2012; Meagher, 2009; Weiss et al., 2006; Whitham and Wielebnowski, 2009; Wielebnowski, 1999; Wielebnowski et al., 2002). Efforts to integrate caretaker input into assessments of individual well-being will be described in more detail in the next section.

In addition to considering an individual's welfare at a given point in time, it is also of key importance to take into account an individual's lifetime experience from "cradle to grave". This concept, which recently has been described by Yeates as a "life worth living" (LWL), provides, "a holistic idea of an animal's welfare over its whole life. . ." (Yeates, 2011, p. 397). While researchers may focus on overall welfare at a particular point of time, or QoL over an extended period, the LWL approach considers the balance of an animal's experiences over its lifetime. According to this concept, it is quality not quantity that is relevant, and careful thought should be given to whether the opportunity for pleasant experiences outweighs the negative experiences the animal is expected to face (Yeates, 2011). In the zoo industry, management decisions related to hand-rearing practices, euthanasia and cross-institutional breeding loans should all be viewed through the LWL lens.

3. Current methods and approaches for assessing zoo animal welfare

3.1. Common measures

To date, zoo researchers have applied a medley of methods for assessing animal welfare. Traditionally, the focus has been on identifying physiological indicators (e.g. hypothalamic–pituitary–adrenal axis, or HPA, activation), behavioral indicators (e.g. self-injurious or stereotypic behaviors), and health indicators (e.g. prevalence of disease) (Hill and Broom, 2009; Melfi, 2009). While some studies have used only one type of indicator, there is general consensus that it is not sufficient to focus on just one metric when conducting welfare assessments (Barber, 2009; Broom, 1991; Swaisgood, 2007). Although there has been extensive work examining how various physiological indicators are associated with the occurrence of abnormal behaviors, these studies mostly have been conducted on laboratory and farm animals (e.g. Fraser, 2008; Mason, 1991; Moberg and Mench, 2000). There are limitations when applying some physiological measures to zoo animals. Typically, zoo researchers are not able to obtain measures that require invasive sampling (e.g. blood samples, biopsies), invasive experimentation and/or animal handling on a consistent basis. Even if invasive measures can be collected for some individuals, only a small subset of

an already small study population will be sampled, making it difficult to obtain statistically significant results.

Nevertheless, due to the successful development of non-invasive glucocorticoid ("stress hormone") monitoring techniques over the past decade (e.g. Wielebnowski and Watters, 2007), it has become increasingly common for zoos to monitor HPA activity by measuring glucocorticoid metabolite concentrations in feces or urine (e.g. Brown et al., 2001; Carlstead and Brown, 2005; Menargues et al., 2008; Shepherdson et al., 2004; Wielebnowski et al., 2002). However, intense and repeated adrenal responses may occur in situations that generally are regarded as beneficial and that do not appear to compromise welfare over the long-term (e.g. during breeding season and mating introductions). Thus, it can be difficult to distinguish between normal, adaptive stress responses and detrimental, chronic stress responses. Furthermore, not all stressors lead to an increase in glucocorticoid concentrations, and concentrations may decline because of factors unrelated to the removal of a stressor (Wielebnowski, 2003). Therefore, hormone monitoring must be used in combination with other physiological and biological measures, as well as other types of assessments (e.g. behavioral monitoring), to allow for the hormonal data to be interpreted correctly.

Similarly, behavioral measures, when used alone, can be limited in their usefulness. For many exotic species, it is not adaptive to display signs of weakness or pain. As a result, many individuals do not overtly express behavioral indicators of poor welfare (Broom, 2007). Even when behavioral indicators are expressed, individuals of the same species may possess different coping styles, and therefore, perform different behaviors after experiencing a shift in welfare status (Wielebnowski, 2003). In fact, even though stereotypic behaviors often are considered indicators of poor welfare, there is evidence that engaging in these behaviors may help some individuals cope with stressors (Mason, 1991; Meagher and Mason, 2012; Rushen, 1993). Furthermore, Mason and Latham argue that the relationship between stereotypy and welfare is complicated by several processes (Mason and Latham, 2004). Specifically, while stereotypies that serve as a substitute for natural behaviors ("do-it-yourself enrichment") or that have calming effects may improve welfare in sub-optimal environments, other stereotypies (e.g. habit-like stereotypies) may not be reliable indicators of current welfare status. Therefore, while stereotypies may reflect potential welfare issues, one also must consider the behavior's motivational underpinnings and origins. Finally, while systematic behavioral data collection can be used to determine how an individual spends its day, some shifts in welfare status may not be reflected in the animal's activity budget (Hill and Broom, 2009). For example, an animal with a high parasite load may spend the same proportion of its day locomoting as when it is physically healthy but may do so at a slower pace, with a hunched posture and pained expressions. In other words, before a shift in welfare status can be captured by changes in an animal's activity budget, there may be observable changes in "how" the animal looks or behaves.

Fortunately, it may be possible to capture these subtle shifts in individual well-being as they occur. Experienced caretakers are capable of perceiving and integrating numerous details such as very minor changes in behavior, attitude, posture, and movement that usually are not captured by systematic behavioral data collection performed by "outside" observers. Experienced caretakers, therefore, may be able to detect shifts in welfare status that otherwise may go undetected (Block, 1977; Carlstead et al., 1999; Gosling, 2001; Wemelsfelder, 1997, 2007; Wemelsfelder and Lawrence, 2001; Wemelsfelder et al., 2000, 2001; Wielebnowski, 1999). For example, Wemelsfelder and co-workers (e.g. Wemelsfelder and Lawrence, 2001; Wemelsfelder et al., 2000, 2001) use qualitative assessments to integrate subtle bits of information that capture how an animal behaves and interacts with its environment (i.e. its behavioral expression or body language). These researchers promote the use of free choice profiling (FCP), a methodology that assumes that, ". . .human observers naturally integrate perceived details of behaviour into qualitative judgements," (Wemelsfelder and Lawrence, 2001, p. 24). FCP allows observers to generate their own descriptive terminologies to score subjects, and data are analyzed using a multivariate statistical technique (generalized Procrustes analysis) that calculates observer agreement independent of fixed variables (i.e. terms). There is evidence that high levels of inter-rater reliability can be reached, even when observers have no previous experience with the species being assessed (Wemelsfelder and Lawrence, 2001; Wemelsfelder et al., 2000, 2001). Moreover, these "whole animal" assessments have been validated using quantitative behavioral data (Minero et al., 2009; Napolitano et al., 2008; Rousing and Wemelsfelder, 2006) as well as biological and physiological indicators of health (e.g. Phythian et al., 2011).

Many keepers spend decades working not only with particular species but also with particular individuals. Furthermore, they have the ability to observe individuals across a variety of contexts. Not surprisingly, there is ample evidence that keepers can reach high levels of inter-rater reliability when rating traits and behaviors that may reflect individual well-being (e.g. Carlstead et al., 1999; King and Landau, 2003; Less et al., 2012; Weiss et al., 2006; Wielebnowski, 1999; reviewed in Gosling, 2001; Meagher, 2009; Whitham and Wielebnowski, 2009).

Keeper assessments have been validated by correlating ratings of traits and behaviors with other welfare indicators commonly measured in zoo settings. For instance, Wielebnowski et al. (2002) found that clouded leopards (*Neofelis nebulosa*) that were reported to exhibit self-injuring behaviors had higher mean overall, baseline, and peak concentrations of fecal glucocorticoid metabolites than individuals that did not perform these behaviors. Similarly, clouded leopards that were rated highly on behaviors such as "tense" and "stereotypic pacing" had higher mean overall, baseline, and peak fecal glucocorticoid metabolite concentrations than individuals that received low scores for these items. Keeper assessments of traits related to individual well-being also have been associated with quantitative behavioral measures. Wielebnowski (1999) found that cheetahs (*Acinonyx jubatus*) that received high scores on items such as "tense" took more time to approach a novel object than individuals rated highly on items such as "calm", "curious", and "self-assured". Likewise, Carlstead

et al. (1999) found that black rhinoceros (*Diceros bicornis*) with high "fear" scores were less likely to interact with a novel object and approach a novel scent than less fearful individuals. For a more thorough review of the reliability and validity of observer and caretaker assessments, see Gosling (2001), Meagher (2009), and Whitham and Wielebnowski (2009).

3.2. The usefulness of trans-disciplinary and multi-institutional studies

Studies that combine multiple measures and integrate approaches from various disciplines (e.g. animal behavior, ecology, physiology, veterinary medicine) are the most successful at identifying risk factors associated with poor welfare (e.g. Carlstead and Brown, 2005; Shepherdson et al., 2004; Wielebnowski et al., 2002). Indeed, a comprehensive dataset that considers an animal's behavior, nutrition, physiological state, and health status allows for a more systematic analysis of how the animal interacts with its environment than a study that considers only activity budgets, diet, glucocorticoid profiles, or veterinary interventions. Zoo welfare researchers conduct these overarching studies to evaluate how particular management practices, husbandry routines, and enclosure features influence measurable welfare indicators. For instance, Carlstead and Brown discovered that black rhino breeding pairs housed separately and introduced for breeding when the female was in estrous, exhibited lower variability in fecal glucocorticoid metabolite concentrations and less fighting (according to keeper ratings) than pairs regularly housed together (Carlstead and Brown, 2005). Furthermore, black rhinos living in enclosures with a high degree of public exposure had higher mean glucocorticoid metabolite concentrations than those with less public exposure. Similarly, in a large multi-institutional study, Wielebnowski et al. found that clouded leopards housed on public display had significantly higher mean fecal glucocorticoid metabolite concentrations than cats living off exhibit, and that the cats with higher glucocorticoid metabolite concentrations were more likely to pace, hide, and show self-injurious behavior (Wielebnowski et al., 2002). In a follow-up study, it was discovered that by adding hiding spaces to clouded leopard enclosures, fecal glucocorticoid metabolite concentrations decreased significantly, suggesting that adjustments to the environment may have improved welfare (Shepherdson et al., 2004). Carlstead et al. also evaluated the effects of providing concealment to felids and found that leopard cats (*Felis bengalensis*) experienced a reduction in pacing and urinary glucocorticoid metabolite concentrations after the addition of hiding places (Carlstead et al., 1993). The results of studies such as these can inform decisions about space requirements, as well as recommendations for exhibit design. For example, even though western lowland gorillas (*Gorilla gorilla gorilla*) traditionally are characterized as terrestrial, Ross and co-workers revealed that the gorillas at the Lincoln Park Zoo spent over half of their time above ground level, and thus recommended that zoos provide climbing opportunities for this species (Ross et al., 2011).

Other studies have combined measures to investigate how particular events and features of the environment influence welfare indicators. As described in Shepherdson et al. (2004), Carlstead tested the effects of unusual or unpredictable noises on Hawaiian honeycreepers (*Drepanididae* spp.) and found that on days following outdoor concerts and machinery noises, birds had significantly higher mean fecal glucocorticoid metabolite concentrations than on "normal" days. The birds also exhibited a decrease in activity levels (e.g. hopping, flying) and/or foraging the day after these disturbances occurred. Similarly, Owen et al. discovered that for giant pandas (*Ailuropoda melanoleuca*), behavioral indicators of stress (e.g. scratching) and/or urinary glucocorticoid metabolite concentrations increased on "loud" days (Owen et al., 2004; see also Powell et al., 2006).

Trans-disciplinary and multi-institutional research projects can substantially inform husbandry procedures and captive animal management. In some cases, the results of such studies already have been used to refine animal care guidelines and husbandry manuals. In fact, zoo welfare scientists are beginning to initiate large-scale, epidemiological studies specifically to address pressing welfare questions for species of high concern.

3.3. Welfare epidemiology

In 2009, Millman et al. discussed how epidemiological studies can be conducted to address concerns about animal welfare (Millman et al., 2009; see also Duffield et al., 2009; Garner et al., 2006; Rushen, 2003; see Woodward, 1999, for a thorough explanation of epidemiological studies). An epidemiological approach now is being applied in the zoo community to examine patterns of welfare issues and the prevalence of factors (positive and negative) that may influence welfare indicators in elephants. Carlstead et al. describe a multi-institutional, inter-disciplinary study that has been designed to investigate the environmental and husbandry factors impacting the welfare of elephants living in AZA-accredited zoos (the sample includes nearly the entire population: 166 African elephants and 125 Asian elephants housed across 72 institutions) (Carlstead et al., in press). This project, now underway, aims to assess welfare using a variety of animal-based measures (e.g. physiological measures, body condition scores, health indicators, behavioral measures) and to evaluate how these measures are influenced by factors such as enclosure design, exercise, training programs, and climate. The results from this study will allow zoos to benchmark against other AZA-accredited institutions and to prioritize plans for modifying the environment and/or routine to enhance welfare.

There is great potential for applying an epidemiological approach in the zoo community due to the fact that zoos have been cooperatively managing many taxa for decades to promote healthy, genetically diverse, and ultimately, sustainable captive populations. In 1981, AZA created the Species Survival Plan (SSP) Program to collaboratively manage animals across member institutions by identifying population management goals, making breeding recommendations, and coordinating initiatives related to research, husbandry, and management (see Allard et al.,

2010 for a description of programs in other regions). Each SSP program is managed by a Taxon Advisory Group (TAG), comprised of species-specialists such as curators, keepers, and other zoo staff.

Barber suggests that zoos could work with the TAGs to identify appropriate species-specific welfare indicators, to measure these indicators, and to identify patterns of welfare issues within a population (Barber, 2009). The Delphi technique (described in Section 2.1) could be used to identify which negative indicators (i.e. red flags) and positive indicators (i.e. green flags) should be tracked for a particular species (e.g. Anonymous, 2001; Whay et al., 2003a, 2003b). Whitham and Wielebnowski applied the Delphi technique to create species-specific welfare surveys for 12 species of mammals, birds, and reptiles (Whitham and Wielebnowski, 2009). Even though these surveys were designed to monitor the well-being of individual animals over time using the WelfareTrak® web application, the indicators identified by the expert panelists could be applied to an epidemiological approach for welfare monitoring. For instance, Goeldi's monkey (*Callimico goeldii*) experts agreed that the self-injurious behavior "self-biting" is an indicator of poor welfare, so this clearly would be considered a "red flag" for the species. After determining baseline levels for a particular indicator, the prevalence of flags could be monitored over time to identify potential risk factors and to evaluate whether welfare concerns are being addressed effectively. Furthermore, epidemiological data could be used to develop hypothesis-driven studies designed to identify causal factors for particular welfare issues. Results from such studies would help the industry revise current practices, animal care recommendations, and environmental requirements (Barber, 2009). Ideally, however, population-level assessments, and the changes that result from epidemiological studies, should be followed-up by individual-level assessments whenever possible.

3.4. A potential tool for monitoring the welfare status of individual animals

While the aforementioned studies can produce results that influence industry-wide animal care guidelines and environmental requirements, and therefore help raise overall welfare standards for a given taxon, there is no guarantee that higher standards will result in individuals actually experiencing good well-being. In fact, it may be necessary to modify the husbandry routine and/or environment to satisfy the changing needs and preferences of an individual over its lifetime. As mentioned earlier, keepers may be able to express the unique perspectives of animals under their care by serving as proxy informants, allowing zoos to monitor the welfare status of individuals on an ongoing basis.

To address the need for tracking the welfare status of individuals, the Chicago Zoological Society recently developed the WelfareTrak® system, a tool that uses caretaker assessments to monitor the well-being of individual animals over time (Whitham and Wielebnowski, 2009). The WelfareTrak® website, which will become publically accessible in 2013, allows caretakers to complete brief, species-specific welfare surveys on a weekly basis. Surveys are comprised of 10–15 indicators that reflect both physical well-being (e.g. coat condition) and emotional/mental well-being (e.g. attitude). The site's built-in web application tracks the raters' responses and generates reports that flag shifts in well-being scores. By reviewing reports, animal care staff can proactively identify potential welfare issues, respond swiftly and efficiently when shifts in welfare status occur, and evaluate the success of attempts to improve individual well-being. It is important to note that many species' surveys include some measures of good well-being (e.g. calm-relaxed, content vocalizations) in addition to indicators of poor well-being (e.g. self-mutilating behaviors). The system has been designed to flag not only cases of deteriorating scores but also cases of improving scores. Therefore, once fully operational, this tool can help zoos gain insight into which conditions, events, and practices may be preferable to an individual, bringing attention to positive as well as negative aspects of welfare.

4. Future directions

4.1. Considering positive affective states

Recently, zoo welfare researchers have increased efforts to measure positive affective states by using indicators of good or great well-being. Many researchers believe that positive affective states and experiences are crucial elements of good welfare that must be measured if at all possible (Boissy et al., 2007; Broom, 1988; Dawkins, 2001; Duncan, 1996, 2006; Fraser, 1993, 1995; Knierim et al., 2001; Mench, 1998; Morton, 2007; Spruijt et al., 2001; Yeates, 2011; Yeates and Main, 2008). In fact, it has been argued that experiencing positive events may, at times, offset the impact of negative events (Duncan, 2006; McMillan, 2003; Yeates, 2011) and that the presence of positive affective states may be more relevant to assessments of well-being than the absence of negative affective states (Boissy et al., 2007). Indeed, Boissy et al. point out that the absence of positive affect or pleasure, in itself, may indicate that the animal is experiencing a negative affective state (e.g. discomfort) and note that, "repeated or steady positive emotional experiences commonly lead to, and are often referred to, as a global state of "happiness" (Boissy et al., 2007, p. 390). Ultimately, zoos should attempt to measure/monitor both negative and positive affective states, and when aiming to improve individual well-being, should try to provide pleasant experiences to outweigh any known or potential negative experiences.

4.2. Measuring and promoting positive affective states

A critical new direction for zoo welfare science will be to identify measures indicative of positive affect. Once integrated into welfare monitoring and assessment tools, such measures can help zoos determine how to present opportunities that will result in persistent states of good well-being for individual animals and encourage animal care professionals to attain the highest possible levels of welfare for animals in their care. Below, we briefly describe some physiological and biological markers, as well as behaviors, that

can be measured to examine whether animals may be experiencing positive affective states. For the most part, the methods and technology required for measuring physiological and biological markers in a zoo setting have yet to be developed. Behaviors, in some cases as subtle as changes in facial expressions, can be easy-to-use, non-invasive indicators of positive affect once they have been cross-validated with other welfare indicators for each species. Ultimately, regularly obtainable physiological and biological markers (e.g. fecal consistency, measures of heart rate), as well as behavioral measures, should be used jointly and integrated into monitoring tools.

While we focus on presenting markers and behaviors that have a strong potential for integration into tools that allow for frequent and continuous tracking of individual well-being, we also would like to mention the work of Mendl and co-workers (Mendl et al., 2009) who investigate how cognitive tests may be used to measure positive affective states. Studies of cognitive bias (i.e. studies that examine how cognitive processes are influenced by affective state), and specifically studies of judgment bias, have shown that animals in a negative emotional state may be more likely to categorize an ambiguous cue as indicating a negative event than control animals (Harding et al., 2004). Mendl et al. review studies that employed this experimental paradigm for a variety of species and argue that judgment bias can be used as an indicator of affective state (Mendl et al., 2009). While the theoretical framework underlying cognitive bias research is applicable to zoo animals, its practical application for daily animal management and regular welfare monitoring may be difficult.

4.2.1. Measuring positive affective states: physiological and biological markers

There is great potential for using physiological and biological markers to gain insight into positive affective states. The emerging field of affective neuroscience specifically seeks to investigate the brain mechanisms associated with motivation, affect, and emotion (Berridge and Kringelbach, 2008; Burgdorf and Panksepp, 2006; Panksepp, 2011). While much could be learned about the neurobiology of positive affective states by including measurements of endorphins, oxytocin, and serotonin (reviewed in Berridge and Kringelbach, 2008; Boissy et al., 2007; Burgdorf and Panksepp, 2006; Yeates and Main, 2008), current techniques for collecting these data from animals are either invasive or cannot feasibly be applied in a zoo setting on a regular basis (e.g. collection of blood or cerebrospinal fluid, neuroimaging). Below, we describe two types of markers that already have been used to measure positive affect (in humans and/or animals) and have been measured non-invasively in animals.

4.2.1.1. Immunological markers. In humans, there is evidence that positive affective states may boost immunity and improve physical health (reviewed in Barak, 2006; Pressman and Cohen, 2005; Salovey et al., 2000). Pressman and Cohen review the ways in which positive affect may impact immunity, such as influencing the production of specific cytokines, reducing allergic reactions, increasing peripheral white blood cell populations, and increasing secretory immunoglobulin-A (IgA) concentrations (Pressman and Cohen, 2005). IgA, an antibody that can be measured non-invasively and provides an indicator of immune function, increases after experiencing a positive emotional state or a pleasant stimulus. For example, an increase in salivary IgA concentrations has been induced by pleasant linguistic stimuli (i.e. comical story-telling) (Watanuki and Kim, 2005), viewing humorous videotapes (Dillon et al., 1985), and experiencing self-induced positive emotional states (McCraty et al., 1996). Salivary and fecal IgA already have been used as markers of stress in rats (salivary IgA: Guhad and Hau, 1996; fecal IgA: Eriksson et al., 2004). In dogs, salivary IgA was found to be negatively correlated with salivary cortisol and also associated with behavioral assessments. Specifically, low levels of IgA were associated with low behavioral scores (i.e. scores indicative of "a dog exhibiting stress") and high levels of IgA were found for dogs with high behavioral scores (i.e. dogs considered "calm", "confident", etc.) (Skandakumar et al., 1995). For zoos, the most promising candidates for regular welfare monitoring would be markers such as IgA, which can be sampled non-invasively.

4.2.1.2. Measures of heart rate. For years, measures of heart rate have been used to examine how various stressors affect the autonomic nervous system (ANS) of various farm animal species (e.g. Baldock and Sibly, 1990; Marchant et al., 1995). Recently, heart rate variability (HRV), which can be monitored non-invasively, has been used to investigate how changes in sympathovagal balance are related to disease, management practices, and behavioral problems (reviewed in von Borell et al., 2007). Studies on human subjects have shown that ANS activity, including HRV, may be impacted by positive affective states specifically (reviewed in Pressman and Cohen, 2005; Kreibig, 2010). For instance, McCraty et al. found that HRV was altered after subjects experienced self-induced positive emotional states (McCraty et al., 1995). Basic emotions may even be associated with distinctive patterns of ANS activity in humans, so that while both anger and happiness are associated with an increase in heart rate, only the latter results in a change in HRV (Rainville et al., 2006). von Borell et al. provide a description of the portable equipment available for recording cardiac activity in farm, laboratory, and companion animals (von Borell et al., 2007). While it would not be possible to use some of these devices (e.g. electrode chest belts) on many zoo-housed species, some zoos are now investing time and money into developing automatic devices for exotic animals (e.g. "cuffs" designed to monitor blood pressure in gorillas – T. Meehan, personal communication; implantable heart monitors to record active heart rates in chimpanzees – S. Ross, personal communication).

4.2.2. Measuring positive affective states: behavioral measures

In this section, we provide a description of some behavioral measures that could be integrated into welfare monitoring and assessment tools to capture aspects of good well-being. This list is by no means exhaustive (see Boissy et al., 2007 and Yeates and Main, 2008 for a review). Indeed, while we discuss some behaviors (e.g. play,

inquisitive exploration) that are expressed in "opportunity situations" after basic needs have been met and costs are sufficiently low (Duncan, 2006; Fraser and Duncan, 1998), many species perform other behaviors in these situations that they likely derive pleasure from, such as hoarding and territorial marking (Fraser, 2008). We emphasize again that each measure would have to be cross-validated with other measures for each species prior to establishing it as an acceptable welfare indicator.

4.2.2.1. Affiliative behaviors. For social species, the expression of affiliative behaviors, such as allo-grooming and allo-preening, may, "...play a major role in achieving a positive mood in animals" (Boissy et al., 2007, p. 388; see also Carlstead, 2009). Allo-grooming reduces tension amongst group members and promotes the maintenance of social bonds (e.g. Schino et al., 1988) and even has calming effects on individual animals. For instance, in macaques (*Macaca* spp.), there is evidence that individuals experience a deceleration in heart rate while receiving grooming (Aureli et al., 1999; Boccia et al., 1989) and that "groomers" perform fewer behavioral indicators of anxiety and aggression following a grooming session (Aureli and Yates, 2010). Engaging in allo-grooming even stimulates the release of endorphins (Keverne et al., 1989). Fortunately, zoo researchers regularly include measures of affiliative behaviors in their ethograms, and these behaviors are relatively easy for inexperienced observers to monitor. However, it is important to note that there are circumstances in which increased levels of affiliation may not be associated with positive affective states (Boissy et al., 2007).

4.2.2.2. Sleep. Although rife with challenges, it may be possible to monitor sleep patterns to determine if animals are experiencing positive affective states. In humans, self-reported positive affect was found to be associated with fewer sleep problems (e.g. number of times waking up, trouble falling asleep), independently of medical factors and psychological distress (Steptoe et al., 2008). Langford and Cockram suggest that measures of sleep can be integrated into animal welfare studies to investigate how individuals respond to stressors, how they are impacted by management procedures, and whether they are comfortable (Langford and Cockram, 2010). While previous studies have focused on how sleep is associated with pain (cats: Moldofsky, 2001; rats: Onen et al., 2001) and various stressors (reviewed in Pawlyk et al., 2008 for rodents), long sleeping bouts characterized by few disturbances may reflect positive waking experiences. While there are difficulties to monitoring sleep outside of a laboratory setting, Langford and Cockram suggest that there are unique features and behaviors associated with sleep (Langford and Cockram, 2010). For instance, animals may sleep in locations that are not used for resting, adopt certain postures, or twitch once asleep (Langford and Cockram, 2010; Tobler, 1995). However, because the sleep patterns of zoo-housed animals are influenced by the husbandry routine, proximity to the public, and environmental features, this behavior should be incorporated into tools designed to monitor individual animals over time rather than to compare animals across institutions. Also, very little information is currently available on natural or "healthy" sleep patterns for most exotic species, but this may be an important area for future investigation.

4.2.2.3. Play. The expression of play behaviors also may be indicative of positive affective states (Boissy et al., 2007; Burgdorf and Panksepp, 2006; Held and Špinka, 2011; Špinka, 2006; Špinka and Wemelsfelder, 2011; Špinka et al., 2001). Play can be considered a "luxury" (Špinka, 2006), as it does not serve an immediate goal and occurs in "opportunity situations" after basic needs have been met (Burghardt, 2005; Duncan, 2006; Fraser and Duncan, 1998). Indeed, play is suppressed when fitness is compromised, such as when experiencing unfavorable environmental conditions (e.g. food shortages) or negative states (e.g. pain) (Burghardt, 2005; Fagen, 1981; Martin and Caro, 1985). Špinka et al. suggest that "having fun" is the underlying emotion of play, and that play, "is emotionally exciting... and rewarding, maybe even pleasurable, while at the same time being relaxed" (Špinka et al., 2001, p. 144). There is good evidence that play is indeed rewarding (Burgdorf and Panksepp, 2006; Martin and Caro, 1985; Špinka et al., 2001; Špinka and Wemelsfelder, 2011). Aside from the fact that animals seek out opportunities to engage in play (Fagen, 1981), studies have shown that administering opioid agonists promotes social play while opioid antagonists suppress it (Normansell and Panksepp, 1990), and that engaging in social play results in an increase in opioidergic activity (Vanderschuren et al., 1995).

Held and Špinka caution that although play is a promising candidate as a welfare indicator, there are limitations and challenges to using play behaviors to assess positive states (Held and Špinka, 2011). For instance, play may be accompanied by negative affective states. Palagi et al. discovered that captive bonobos (*Pan paniscus*) engage in play to prevent social tension (Palagi et al., 2006). Therefore, while play behaviors may be beneficial as far as preventing aggression and promoting social cohesion over the long-term, the affective states being experienced while expressing play behaviors may not be entirely positive. Furthermore, there is evidence that poor conditions may reduce not only the quantity of play but also the quality, as high-energy forms of play may be replaced by low-energy behaviors (Barrett et al., 1992). Therefore, before play behaviors can be fully integrated into welfare science research, it will be crucial to validate species-specific behaviors and signals (Boissy et al., 2007; Held and Špinka, 2011; Petrů et al., 2009), to identify the contexts in which an increase in play would be considered an indicator of good welfare, and to evaluate whether qualitative assessments of play may be necessary.

4.2.2.4. Anticipatory behavior. One novel approach to identifying positive affect involves observing the behaviors that an animal exhibits while anticipating a reward (Boissy et al., 2007; Dawkins, 2012; Spruijt et al., 2001; Van der Harst and Spruijt, 2007; Van der Harst et al., 2003a, 2003b). Anticipatory behaviors are linked to the motivational state of "wanting" and associated with increased dopaminergic activity (Berridge, 1996; Spruijt et al., 2001). In a study of laboratory rats, Van der Harst et al. found that when

animals were anticipating a reward (transfer to an enriched cage or a sexual encounter) they exhibited significantly higher levels of activity, as measured by the total frequency of behavioral elements, than when a neutral stimulus (transfer to a standard cage) or aversive stimulus (forced swimming) was signaled (Van der Harst et al., 2003b). Furthermore, certain behavioral elements such as locomotion, exploration, and arousal appeared to be associated with the rats' anticipatory response and related to the type of event signaled.

In zoos, animals have many opportunities to anticipate rewards, due to relatively predictable husbandry routines and keeper activity. However, it is important to note that the animal's response may be influenced by its current needs (Boissy et al., 2007). Animals living in standard housing conditions may be more sensitive to signaled rewards than those living in enriched environments (Van der Harst et al., 2003a), and animals that are fully satisfied may not respond at all. Therefore, while an animal is not necessarily experiencing great well-being just because it is performing anticipatory behaviors, much can be learned about what an individual finds rewarding – i.e. what it "wants" and looks forward to in its day – by observing animals that are preparing to receive a signaled reward.

4.2.2.5. Vocalizations. Vocalizations that express positive affective states also could be useful as behavioral indicators of good or great welfare (Boissy et al., 2007; Fraser, 2008; Yeates and Main, 2008). Indeed, Fraser suggests that just as animals have evolved systems to signal alarm, distress, or hunger, it may be advantageous for animals to produce signals of positive affect (Fraser, 2008). He suggests that we should listen in on calls that animals produce when "all's well" such as the "singing" of hens and "snuffly" sounds produced by pigs. Similarly, Panksepp and Burgdorf argue that the ultrasonic "chirps" of adolescent rats, elicited in contexts such as play and while receiving "tickling" from handlers, are similar to primitive human laughter (Panksepp and Burgdorf, 2003). The value of tracking vocalizations already has been recognized by the zoo community. Indeed, the expert panel recruited to develop the WelfareTrak® welfare survey for western lowland gorillas agreed that the item "produces content grumbles" was necessary for monitoring individual well-being (Whitham and Wielebnowski, unpublished). Finally, in a recent study, Soltis et al. found that African elephants (*Loxodonta africana*) express the intensity of affect in their "rumble" vocalizations and suggested that additional research be conducted to determine whether, "...the unique combination of acoustic features observed in the positive social context may constitute a 'vocal signature' of positive affect..." (Soltis et al., 2011, p. 1064).

4.2.2.6. Exploratory behaviors. It also may be possible to measure levels of exploration or interest in the environment to gain insight into an individual's welfare status. Before doing so, it is important to recognize that animals may engage in two types of exploration. While inspective exploration occurs when an animal is responding to a change in the environment, inquisitive exploration occurs when the animal is actively seeking change or novel stimuli (Berlyne, 1960; Boissy et al., 2007; Špinka and Wemelsfelder, 2011). Therefore, the latter is performed when basic needs have been satisfied and is assumed to be a pleasurable activity in itself (Boissy et al., 2007). Evidence does exist for exploration being self-rewarding, as piglets will choose to spend time in pens with novel objects over pens with familiar objects, even if none of the objects has value (Wood-Gush and Vestergaard, 1991). Exploratory behavior is seen as a vital indicator of individual well-being in the zoo setting, as nearly all of the species-specific welfare surveys (e.g. aardvark, fennec fox, red-tailed hawk, okapi) created by expert panelists for the WelfareTrak® project include the item "interest in the environment/enrichment-curious" (Whitham and Wielebnowski, unpublished).

4.2.3. Promoting positive affective states: choice and control

To encourage animals to explore and interact with their surroundings, modern zoos are increasing efforts to provide complex, challenging environments. Several researchers have discussed the benefits (e.g. reduction in stereotypic behaviors, decrease in HPA activity) of presenting animals with opportunities to overcome challenges, make choices, and control the environment (Bassett and Buchanan-Smith, 2007; Carlstead and Shepherdson, 2000; Markowitz, 1982; Meehan and Mench, 2007; Mellen and MacPhee, 2001; Sambrook and Buchanan-Smith, 1997; Shepherdson et al., 1998; Špinka and Wemelsfelder, 2011). Although challenging environments may elicit some short-term stress and frustration, an "appropriate challenge" (Meehan and Mench, 2007) stimulates activity and enhances welfare over the long-term by allowing the animal to build competencies (e.g. skills, strategies) to deal with future challenges (Špinka and Wemelsfelder, 2011). Therefore, we emphasize that it is not necessary to eliminate all negative affective states, but to recognize that such states may be expected to occur when an animal attempts to overcome a challenge and ultimately can be offset by very positive outcomes. Indeed, animals that are given the opportunity to make choices in their daily lives and to experience contingencies between their actions and particular outcomes may experience positive affective states (Boissy et al., 2007; Fraser, 2008; Špinka and Wemelsfelder, 2011).

Zoo researchers have shown that making minor modifications to the environment and routine can promote behaviors indicative of good welfare. For instance, Ross found that giving polar bears (*Ursus maritimus*) the option of accessing their indoor dens resulted in an increase in social play (Ross, 2006). For most zoos, it has become part of the daily routine to offer environmental enrichment to improve individual well-being (reviewed in Shepherdson, 2010). Many studies have shown that providing enrichment not only results in fewer stereotypic behaviors, an increase in activity levels, and greater behavioral diversity (Shepherdson et al., 1993; Swaisgood et al., 2001), but also elicits behavioral indicators associated with positive affective states (e.g. play, exploration). For example, Carlstead et al. were able to increase investigatory activity and promote natural behaviors in sloth bears (*Melursus ursinus*) by

providing honey-filled logs (Carlstead et al., 1991; see also Watters et al., 2011 for fennec foxes).

Understandably, zoos' attempts to modify environments and routines generally are prompted by animals exhibiting abnormal behaviors, low activity levels, and/or a limited range of natural behaviors. However, an animal that encounters novel enrichment may show an increase in activity levels and begin to perform more natural foraging behaviors without experiencing great well-being. We suggest that zoos continue to "push the envelope" by introducing challenges specifically aimed at promoting positive affective states, even when no welfare concerns exist. Fortunately, it is becoming increasingly common for zoos to design enclosures with built-in "enrichment features" and opportunities for controlling the environment (e.g. motion detectors to activate fans, food dispensers) (Coe and Dykstra, 2010). However, as Watters notes, it is important to consider the "dose of certainty of reward" for all enrichment and intended challenges, as animals given complete control over a predictable environment may not be challenged or stimulated at all (Watters, 2009). Furthermore, because a challenging environment may elicit some negative affective states over the short-term, behavioral and/or physiological data collection should extend well past the introduction of any changes.

4.2.4. Promoting positive affective states: keeper–animal relationships

We believe that it is vital to recognize that animal keepers are a central element of each zoo animal's environment and that the quality of a given keeper–animal relationship may influence an individual's well-being. The literature on human-animal interactions in farm animals is extensive and reveals that even domesticated species have a basic fear of humans and that poor relationships may lead to chronic stress (reviewed by Hemsworth, 2003; Waiblinger et al., 2006). However, this fear can be reduced, and positive human-animal relationships can develop, if the stockperson engages in positive interactions (e.g. petting, talking) with the animal (Boivin et al., 2003). In a study of small exotic felids (*Felis* spp.), Mellen found a significant relationship between the number of litters produced by the cats and husbandry style, with reproductive success being highest when keepers, "...spent a great deal of time with each cat, soliciting contact and talking to the cat" (Mellen, 1991, p. 99). In terms of keepers' impact on behavioral indicators of welfare, Mellen et al. determined that pacing was negatively correlated with the amount of keeper interaction in small felids (Mellen et al., 1998). For chimpanzees (*Pan troglodytes*), Baker found that when caretakers spent additional time engaging in positive interactions (e.g. playing, grooming, feeding treats, and talking) with animals, individuals performed higher levels of allogrooming, exhibited fewer abnormal behaviors, and were less reactive (Baker, 2004; but see Chelluri et al., 2013). The husbandry routine also may affect physiological indicators of welfare. For instance, Wielebnowski et al. discovered that for clouded leopards, fecal glucocorticoid metabolite concentrations were lower if keepers spent more time interacting with the animals and higher if a greater number of keepers worked at the facility (Wielebnowski et al., 2002). In sum, some species fare better when they are cared for by a handful of regular keepers who can invest time in interacting with and carefully observing the animals under their care.

Recently, zoo researchers have begun to investigate which elements of keeper–animal relationships (KARs) may influence individual well-being (see Waiblinger et al., 2006, for a more general discussion of HARs, or human-animal relationships). Carlstead distributed questionnaires to keepers working with black rhinos, cheetahs, and maned wolves (*Chrysocyon brachyurus*) and found that two main factors underlie KARs for these species – "Affinity to Keepers" and "Fear of People" – and that the latter may be associated with indicators of poor well-being (Carlstead, 2009). Indeed, for individual black rhinos, scores for "Fear of People" were positively correlated with fecal glucocorticoid metabolite concentrations. These findings are consistent with research on farm animals which has found that fear of humans is frequently associated with increases in basal cortisol concentrations and adrenal weight (reviewed by Hemsworth, 2003; Waiblinger et al., 2006). Carlstead also found that caretaking behaviors may influence affinity and fear scores, and thus, impact KARs (Carlstead, 2009). For example, by observing keepers as they called the animals (i.e. the keeper calling test), it was determined that some of the keepers' nonverbal behaviors (e.g. making noises with keys, hand-clapping) negatively impacted the behavior of cheetahs and maned wolves. Finally, Carlstead identified a negative relationship between "Fear of People" and keepers' "Job Satisfaction" scores, the latter of which may reflect an aspect of keepers' attitudes (Carlstead, 2009). Interestingly, studies on farm animals have revealed that the quality of human-animal interactions is influenced by the attitude, beliefs, and personality of the stockperson (reviewed by Boivin et al., 2003; Hemsworth, 2003; Waiblinger et al., 2006). Overall, careful consideration should be given to how individual animals are affected not only by specific caretaking behaviors but also by general management approaches applied across facilities and species (e.g. general hands-off versus hands-on management rules, acclimation practices). Welfare studies specifically designed to investigate which aspects of KARs are most beneficial to species and to individual animals are needed to ensure high-quality KARs in the future.

Improving KARs may enhance individual well-being numerous ways. For example, Hosey suggests that increasing the frequency of positive interactions may increase the positivity of relationships with humans in general, thereby moderating the effects of negative interactions with unfamiliar people (Hosey, 2008; see Waiblinger et al., 2006 for similar effects in farm animals). Melfi and Thomas found that when keepers employed positive reinforcement training when working with colobus monkeys (*Colobus guereza*), colobus-initiated interactions with the public declined and eventually ceased (Melfi and Thomas, 2005). Positive reinforcement training also improves keeper–animal rapport and communication (e.g. Savastano et al., 2003) and has been shown to reduce behavioral indicators of stress in laboratory animals (e.g. Bassett et al., 2003). In fact, some have suggested that keepers themselves may be a form of

environmental enrichment (Bloomsmith et al., 1999; Claxton, 2011; Laule et al., 2003).

However, it is important to note that certain types of keeper–animal interactions may impact behavior in ways that are unintended and unexpected. For instance, Chelluri et al. found that while unstructured, affiliative interactions with keepers were associated with behaviors that reflect positive welfare in chimpanzees (fewer self-directed behaviors) and gorillas (fewer self-directed behaviors and abnormal behaviors), both species also exhibited higher levels of agonism following observations that included these interactions (Chelluri et al., 2013). Future studies, therefore, must consider how different types of keeper–animal interactions (e.g. structured vs. unstructured affiliative interactions) affect particular species and even particular individuals.

5. Conclusion

Over the past few decades, enormous progress has been made in the field of zoo welfare science. The days of using primarily resource-based assessments to improve the welfare of populations of animals have passed, and zoos are now looking to supplement these with animal-based approaches that include measures of the physical, emotional, and mental well-being of individuals. Moreover, by attempting to integrate measures of positive affective states, the bar has been raised so that instead of simply trying to avoid negative states, zoos strive to attain great well-being for individual animals.

The future of zoo welfare science will involve: (1) conducting trans-disciplinary, multi-institutional studies and epidemiological approaches to examine patterns of welfare issues and to identify the factors that influence welfare indicators (both positively and negatively) within populations, and (2) performing individual-level assessments, and if possible, ongoing monitoring to ensure that each animal's needs and preferences are considered over the course of its lifetime. Both the large-scale, population-level studies and the tools designed for individual monitoring should include measures that capture positive affective states. In the future, as welfare scientists gain a better understanding of how to reliably measure and elicit positive affect, modern zoos will be challenged to provide opportunities that result in persistent states of good well-being for the species in their care.

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