Journal of
Zoological and
Botanical Gardens

MDPI

Review

The Evolution of Zoos as Conservation Institutions: A Summary of the Transition from Menageries to Zoological Gardens and Parallel Improvement of Mammalian Welfare Management

Haley N. Beer, Trenton C. Shrader, Ty B. Schmidt and Dustin T. Yates *

Department of Animal Science, University of Nebraska-Lincoln, Lincoln, NE 68588, USA
* Correspondence: dustin.yates@unl.edu

Abstract: Zoological institutions, which were once exclusively for entertainment, are now leaders of wildlife conservation. This centuries-long transition was punctuated by key milestones that reformed wild animal exploitation into a mission of protection. Modern zoos perform ex situ activities to preserve natural resources, which are enabled by the housing of wild species. Zoo-managed animals facilitate new scientific knowledge, public education, and strategic breeding to maintain genetic diversity. Prioritizing animal welfare management is a key advancement for modern zoos, as it lessens stress and improves quality of life. Environments enriched with sensory stimuli promote naturalistic behaviors and provide opportunities for instinctual activities like foraging and hunting. This increases resiliency by reducing stress and boredom. However, such approaches only benefit welfare when appropriately matched to the animal. Behavioral responses to environmental cues reflect how animals experience their environment, and properly documenting them informs management decisions. Other modern advancements include enclosure designs, research initiatives, public education programs, species-specific staff training, and collaborative population management among zoos. This review chronicles the milestones that shaped the role of modern zoological institutions in species and habitat preservation. It also discusses opportunities for the continued evolution of welfare management practices, which is fundamental information for zoo employees and stakeholders.

Keywords: behavior; environmental enrichment; husbandry; species preservation conservation; zoo stress

Citation: Beer, H.N.; Shrader, T.C.; Schmidt, T.B.; Yates, D.T. The Evolution of Zoos as Conservation Institutions: A Summary of the Transition from Menageries to Zoological Gardens and Parallel Improvement of Mammalian Welfare Management. *J. Zool. Bot. Gard.* **2023**, *4*, 648–664. https://doi.org/10.3390/jzbg4040046

Academic Editors: Lance Miller and Weronika Maślanko

Received: 12 June 2023
Revised: 28 August 2023
Accepted: 12 September 2023
Published: 22 September 2023

1. Introduction

The role of zoos in society has expanded beyond entertainment and leisure, as present day institutions are expected to fulfill missions of conservation and public education in addition to recreation [1,2]. Because of this, modern zoos have become leaders in species preservation, a role aided by regional, national, and global conservation organizations like the *Association of Zoos and Aquariums* (AZA) and the *World Association of Zoos and Aquariums* (WAZA) [3]. Success in this role requires continuous efforts toward better welfare for animals in human-controlled environments. Initial progress has included strategies that provide opportunities for animals to express healthy naturalistic behaviors, as well as better and more standardized evaluations of these efforts [4–6]. The dynamic expression of behavioral repertoires, or high behavioral diversity, is generally good evidence that an animal's behavioral needs are being met [3,5,7–9]. Behavioral responses to environmental cues result from the degree of valence (i.e., the hedonic attraction/aversion) elicited by the stimulus and by the animals' state of arousal or activation [10]. Environments must provide opportunities for choices about engagement and activity expenditure, and enhancing the environmental complexity is an effective approach to supporting these behavioral flexibilities [5]. Although there is a considerable gap in the information about enriching reptile, amphibian, fish, and other non-mammalian species, far more research-backed environmental enrichment techniques have emerged for mammals and birds. These techniques broaden valence ranges and increase arousal, which, in turn, motivate species-appropriate behavioral responses that improve welfare [4,8,11–13]. The development of enrichment strategies has coincided with advancements in other components of animal welfare management and in the overall approach to species conservation. This review provides a historical look at the evolution of these factors, which have shaped modern zoological institutions. It highlights important milestones throughout this progression that have elevated the efforts toward animal welfare and species conservation to the forefront of the zoo mission. It also describes new information regarding staff-level approaches to welfare management, and it outlines opportunities for continued improvements. Due to the comprehensive nature of the topic, we focused our literature review via four main criteria:

i. Relevance: Information was included from scholarly articles, books, and reputable online sources that provided insight on the long transformation of the role that zoos fulfill in species conservation. We were particularly interested in the emergence of science-backed approaches to animal welfare management and their contribution to the ex situ components of conservation.
ii. Credibility: The scientific information described in this review is from studies that utilized sound methodology, were produced by experts in the field, and were available via reputable publishers and associations.
iii. Timeliness: For discussions of modern components, the most up-to-date information from the latest research was incorporated, along with seminal work and historical information, to capture the evolution of the zoo mission and welfare management.
iv. Diversity: The sources included represent diverse perspectives and interpretations of the subjects. This includes information produced from widely differing geographical regions, time periods, and cultures, as well as information produced across species and captive environments.

2. Historical Evolution of Zoos

2.1. Pre-Modern Animal Collections

The relationship between humans and nondomestic captive animals has continuously evolved over time. This has coincided with a shift in attitudes from early civilizations, which maintained captive animals for food, work, and entertainment [14]. The origins of animal collections are not well documented, but the first successful attempts to capture and keep native wild animals likely occurred around $10{,}000_{\mathrm{B.C.}}$ [2]. Early collections were typically utilitarian and, in fact, began the process of domestication for many species. Yet, some captured animals curiously remained untamed and became early precursors for entertainment-oriented wild animal collections [2]. Between $3000_{\mathrm{B.C.}}$ and $1456_{\mathrm{A.D.}}$, civilizations in Egypt, Mesopotamia, China, and India began commonly capturing wild animals for their extraneous collections [15,16]. The difficulty in capturing and showcasing live animals increased their desirability among rulers and other exclusive classes, and wild animal collections began replacing ornamental plant collections in popularity. The practice soon spread throughout regions of Asia, Europe, and the Americas [2]. Moreover, the explosive expansion of intercontinental trade throughout the 15th and 16th centuries resulted in a greater influx of non-native captured animals to these regions. These unfamiliar animals became known as *exotique*, a French term for objects from distant lands, and were popular trade items [17]. In Europe, large exotic animal collections of monarchs and nobles became known as *menageries* or *seraglios* [18]. These exclusive collections were often maintained as proof of the owners' wealth, power, and access to global trade [17]. Rare animals from these collections made popular gifts among affluent members of Renaissance era societies, which gave rise to a robust trade industry [2,19]. In the Ottoman Empire, smaller groups of well-trained animals were used in traveling menageries, which became the predecessors to circuses [20]. These traveling shows were still exclusive, and opportunities for members of lower classes to witness these animals was typically limited to those in transit, either for trade or as part of a traveling menagerie [18].

2.2. The Rise of the Modern Zoo

The modernization of zoos can be attributed to the combination of better-informed societal attitudes towards animals and advancements in zoo design and management practices [21]. Over time, the purpose of wild animal collections expanded beyond entertainment and status symbols [22]. Collections became platforms to educate the public and advocate for natural resources, ethical human–animal interactions, and healthy wild animal populations [19]. The European Age of Enlightenment throughout the 17th and 18th centuries brought new perspectives regarding interactions with animals in the wild and in collections [2]. Scholars studying the natural world began to better understand the behavioral and anatomical attributes of different classifications of wild animals. Their scientific curiosity led to the realization that *zoological gardens* were ideal for studying wild animal species, as they could be safely observed, studied, and appreciated for their unique characteristics. The resulting surge of new information sparked a shift in societal attitudes regarding the purpose of animal collections [2]. Slowly, zoological gardens began to combine the entertainment value of menageries with new scientific and educational objectives. Accessibility for commoners increased during the 18th century as admission became more affordable, often costing only the donation of a food item for the animals [23,24]. Traveling menageries brought animals to new locations and new audiences, which further piqued public interest [2]. The slow but revolutionary transition from the recreational spirit of menageries to the science of zoological gardens, or zoos, was reflected in several practices at the earliest institutions [2]. For example, menageries typically displayed animals in long rows of barred cages, which was typically not ideal for animal comfort but best facilitated the logistics of group entertainment [2,25–28]. Modern zoos instead began to design naturalistic exhibits based on species-specific ecology, which increased animal comfort and allowed study within a more natural setting [2,25–28]. Staff began receiving training to increase their relevant knowledge, and programs for education, research, and conservation became commonplace [29]. A noteworthy turning point occurred when Empress Maria Theresa marked her succession of Emperor Francis I by transforming Vienna's once-exclusive *Imperial Menagerie* into the *Tiergarten Schönbrunn* (*Schönbrunn Zoo*). This transformation, which was completed in 1752, opened the doors of the formerly private establishment to the public [17,30]. The *Tiergarten Schönbrunn*, now recognized as the world's oldest operating public zoo, became a template for additional public zoos, including Madrid's *Retiro Parque de Buen Retiro* (*Park of the Pleasant Retreat* or *Royal Park*) and Paris' *Menagerie du Jardin des Plantes* (*Menagerie of the Garden of Plants*) near the end of the 18th century [16,24]. By the early 19th century, science, public education, and animal advocacy had become central objectives for many public zoos. The *London Zoo in Regent's Park* was perhaps the first to fully embody this paradigm. It was founded in 1828 by the *Zoological Society of London* to promote the global conservation of animals and their habitats [17,31]. The *London Zoo's* innovative model and design influenced subsequent institutions, including New York's *Central Park Zoo* (1860) and the *Philadelphia Zoo* (1874) in the US [2].

2.3. Contemporary Innovations in Zoo Strategies

The early 20th century brought about infrastructural advancements that helped transform and standardize zoo approaches to better align with modern ideals. In 1907, German wildlife merchant Carl Hagenbeck revolutionized zoo architecture by designing a bar-free facility in Hamburg [24]. Zoos began housing large terrestrial mammals in moat-confined enclosures, a design that better emulated natural habitats and created a more comfortable space between animals and visitors [24]. Traditional cage-style enclosures were used for smaller arboreal species, where appropriate propping could be more easily utilized to simulate natural environments [24]. By 1935, naturalistic enclosures had evolved into wildlife parks, where animals roamed over expansive areas of land and could be observed by visitors in safari-like encounters [32]. Architectural advancements coincided with the establishment of organizations that provided oversight, facilitated information sharing, and offered uniform guidance for captive animal care. In 1924, the role of US zoos and public aquariums in species conservation, publication education, and science was formalized with the founding of the *Association of Zoos and Aquariums* (AZA) [33]. AZA is a nonprofit organization that collects and disseminates information regarding animal care, population genetics, and species expertise. It also performs inspections and offers an institutional accreditation program in animal care and welfare. Organizations like the *European Association of Zoos and Aquaria* (EAZA), the *Zoo and Aquarium Association* (ZAA; Australia), and the *South East Asian Zoos Association* (SEAZA) fulfill comparable roles in other regions of the globe. The *World Association of Zoos and Aquariums* (WAZA), which has existed under several names since 1935, is a global alliance of regional and national entities (including the AZA, EAZA, ZAA, and SEAZA) with similar objectives applied on a worldwide scale [34]. In 1948, the *International Union for Conservation of Nature* (IUCN) was created to gather information regarding the impact of human activity on nature [34]. Although not directly involved in conservation initiatives, the analyses provided by the IUCN help to direct the efforts of relevant organizations. Notably, the IUCN maintains the Red List of Threatened Species, which determines and reports species conservation statuses and global extinction risks [35]. These organizations have been impactful, as new zoos have been designed and existing ones modified to embody the standards they have established and communicated.

Despite the growing interest in zoo animal welfare, some aspects have progressed slowly [26]. Although prioritized by modern zoos, animal welfare is not singularly defined. It is generally agreed, however, that welfare considerations include the range of physical, behavioral, and psychological components that constitute an animal's life experiences and impact how it perceives and interacts with its environment [8,11,36]. When welfare is managed properly, the animal is healthy, well nourished, able to express innate behaviors, and experiences more positive than negative affective states [11]. Productive welfare management can require extensive efforts and investments like new construction or the transfer of animals to new locations. It may also be as simple as providing an animal with the option to move further away from zoo visitors or to choose the terrain on which to rest (Figure 1). Behavioral outcomes related to welfare management were first described by Swiss Zoo Director Heini Hediger in the early 1950s when he began studying how enclosure designs could best accommodate variable factors like flight zones [37]. Among his seminal findings was that perceived safety was the primary concern for most wildlife and far exceeded their interests in pursuing mates or even food. This type of new information allowed enclosures to be designed for more efficient space utilization [26]. Hediger was also among the first to combine elements of psychology, ecology, and pathology in his research in an approach later designated as *zoo biology* [38]. As zoo animal research has expanded, regulatory oversight has adjusted in kind. The Laboratory Animal Welfare Act (1966) was expanded in 1970 to include warm-blooded animals used for exhibit, which covered essentially all mammals, marsupials, and birds housed in zoos [26]. In 1971, the AZA appointed a standing committee to determine the best practices for the care of zoo species. By 1974, the first institutions were accredited by the AZA through a voluntary process that later became mandatory for AZA membership [33]. Today, AZA accreditation helps to communicate expectations for welfare management and holds member institutions accountable when expectations are not met. Importantly, it also provides an avenue for zoos to formally demonstrate accountability to the community and other stakeholders [26,39].

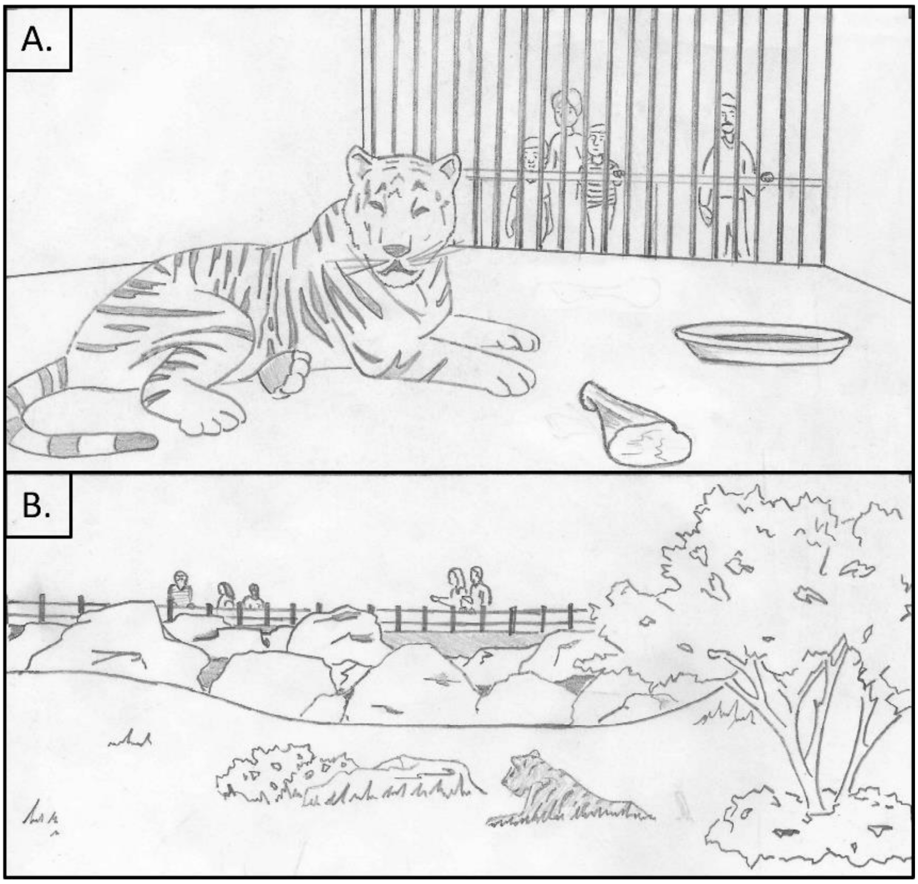

Figure 1. The evolution of terrestrial mammal enclosures includes changing from barred menagerie cages (**A**) to more spacious and naturalistic exhibits that are tailored to the ecology of the species (**B**). This provides more opportunities to engage in rewarding behaviors. It also fosters a sense of control or agency, as large dynamic enclosures offer choices regarding time allocation in different locations. Affording such choices is known to improve welfare by cultivating positive affective states [12]. Artwork by TJ Yates, Abilene Zoological Gardens.

3. The Mission of Modern Zoos

The four main components of the modern zoo mission are generally considered to be conservation, education, research, and recreation [40]. Recent arguments have been made to include welfare as an additional component [41], which illustrates its essential facilitative role in the other four components. Each of these elements has unique importance in understanding and protecting species around the globe, as described below.

3.1. Species Conservation

Stable population density and health status over time is a primary indicator of successful conservation in wild animal populations and their habitats [42]. For threatened species, population recovery (i.e., increased animal numbers within a region) may be a necessary step before focusing conservation efforts on population stability. To characterize this need, species are classified into nine explicitly-defined risk categories of the *Red List of Threatened Species* based on a comprehensive conservation status [43]:

Not Evaluated	Data Deficient	Least Concern
Near Threatened	Vulnerable	Endangered
Critically Endangered	Extinct in the Wild	Extinct

Management initiatives to restore the status of threatened species are outlined in individual species recovery plans prepared by the *Species Survival Commission* of the IUCN, and similar mandates were part of the US Endangered Species Act (1973) [44]. Robust genetic diversity is necessary to conserve healthy populations in the wild [45], as it increases fitness and adaptability to changing environments [46]. As such, a primary practice for zoos is to utilize captive populations to help maintain or recover genetic heterogeny in wild populations [44,46,47]. This requires identifying and pairing breeding animals with optimal genetic value for the species within global captive populations. Organizations like the AZA sponsor interinstitutional programs that facilitate this approach, particularly for threatened species [48]. These programs provide records and information that allow zoos to strategically coordinate breeding at the global level by moving animals, semen, or embryos among institutions. The ex situ breeding and release of offspring with specific genetic traits into wild populations has directly improved the Red List status of at least 9 threatened mammalian species, 6 avian species, and 16 total species as of this writing [45].

A fundamental step in species conservation is identifying populations that would benefit the most from intervention efforts. Throughout the 1970s and 1980s, comprehensive biodiversity threats were documented for many wildlife species, particularly high-profile mammals [48,49]. In 1981, the AZA began *Species Survival Plans* (SSP), which formalized record-keeping and communication mechanisms to help manage the collective breeding efforts of threatened species [50]. SSP allow institutions to share genetic, reproductive, and health information for animals under their respective care to inform breeding matches. They also facilitate the rapid spread of knowledge regarding breeding strategies, veterinary care, behavioral assessments, and demography in zoos [44]. As of this writing, SSP have been established for about 300 species [33]. Each SSP is advised by a *Taxon Advisory Group* (TAG) comprised of AZA-appointed experts with species-specific knowledge and experience. TAG-compiled information allows zoo-housed animals across the US to be managed more like a single population. For example, *studbooks* are maintained to coordinate pedigree and demographic data for breeding recommendations and research initiatives [45,46]. These efforts were further streamlined in 1974 by the foundation of Species360 (formerly the International Species Information System), which centralized information into the web-based *Zoological Information Management System* (ZIMS) portal [51]. The ZIMS archives comprehensive details of individual zoo animals, including place of origin, birth and death dates, parentage, and progeny for animals in over 1300 institutions and more than 100 countries [45,46].

Experts estimate that ex situ breeding programs should utilize enough animals to retain 90% of the initial genetic diversity over a period of 100 years in order to be effective [25,48]. For most participating zoos, the greatest challenge is the space, labor, and resources needed to house and breed animals [46,48]. These and other ex situ activities must be balanced with the institution's in situ efforts to form some combination of public education, training, research, species preservation, and habitat preservation [44,45,52,53]. Common in situ efforts focus on population monitoring, threat mitigation, and habitat restoration [44]. Ideally, ex situ projects complement in situ efforts by leveraging captive animals to support healthy wild populations [42,44]. In addition to strategic breeding, ex situ conservation activities may include rescue, rehabilitation, or relocation. Many zoos also perform applied research on husbandry, visitor experiences, and the effectiveness of education programs [46,52]. Some with more extensive research programs may study basic biology, diet and nutrition, ethology, ecology, health, or other scientific areas [46,52]. Zoos are ideal centers for recruiting and training new conservationists, and they help organize collaborations with governments, academic institutions, and nongovernmental organizations [42,44]. Their high-visibility ex situ efforts also help engage public interest, which, in turn, aids fundraising and sponsorships for all conservation activities [42]. The collective conservation efforts of zoos have led to their recognition by the IUCN as primary allies in the recovery of threatened species [45].

3.2. Leveraging Recreation to Facilitate Education

Effectively educating the public about animals, habitats, and species preservation helps to sustain the community support needed for conservation success. Zoos are dynamic educational institutions that leverage natural wonderment to connect diverse audiences with the planet's biodiversity [45,54]. This allows zoos to inspire action from a more informed and environmentally responsible society [45,54]. The educational opportunities that zoos provide are often interwoven within the recreational aspects that attract visitors. The practice of informing a highly entertained public of conservation needs as part of the zoo experience helps to cultivate an understanding of ecological issues and human responsibilities toward the environment [1,55]. Community outreach, youth programs, and the hosting of special events are some of the popular strategies that zoos implement to raise awareness and support for wildlife and ecosystems' conservation [25]. Yet, in-person visits are still the greatest attribute to facilitate public education. Properly designed enclosures effectively serve as dioramas of the natural world, and zoo-housed animals are ambassadors for their wild counterparts [45,54]. The constant flux of cultural and economic influences, both local and global, makes it essential for zoos to persistently invest time and resources into public education and, in turn, inspiration and awareness [42,46]. By exhibiting the biology and ecology of wild species, zoos can facilitate a better understanding of nature and highlight solutions for threatened species [45,48]. Moreover, they can do so in a uniquely entertaining way, as encounters with wildlife strongly influence visitor perspectives. This help zoos overcome misinformation and residual distrust from the days of menageries. Studies show that dynamic approaches to communication best resonate with visitors [45,49]. Creative signage, live presentations, digital technologies, social media campaigns, and research dissemination reinforce pro-conservation messaging [45,46]. Zoos may also incorporate details of the actions and goals of their conservation efforts (e.g., locations and time elements) to reduce the abstractness [45,56]. The effectiveness of these efforts is apparent, as data collected from zoos around the world indicate that guests have come to value and even expect educational opportunities as part of their visit [1]. Studies also show that visitors are most receptive to staff interactions, and conversing with experts about animal welfare and husbandry are particularly effective for connecting with stakeholders [1]. When zoo staffers share knowledge through demonstrations, highlight conservation campaigns, and show respect for animals, surveyed visitors were more likely to indicate support for conservation efforts and for zoos in general [45,54].

3.3. Performing Research to Enable Education

Research performed in zoos and in the wild by zoo experts generates the scientific knowledge that makes educational programs possible. It provides fundamental information for diverse learning topics like animal behavior, reproduction, health, genetics, nutrition, ecology, and technology. Zoo personnel involvement in research provides a two-way avenue for insight into species conservation. Caretakers and other experts help identify research needs, and research findings contribute to the improvement of animal welfare within zoos. Zoo research also contributes to broader scientific efforts to protect biodiversity and address global environmental challenges by offering opportunities to collect diverse biological data from the same individuals over extended periods [36]. One emerging area of research that has been driven, in large part, by increased attention from public stakeholders is animal welfare management [36]. Scientific research on species-specific housing, dietary requirements, and the best individualized husbandry practices has manifested in more effective welfare management practices [45]. In concert, scientific journals such as *Zoo Biology* (1982), *Animal Welfare* (1992), *Journal of Applied Animal Welfare Science* (1998), and *Journal of Zoological and Botanical Gardens* (2020) have been established to bring research-derived information and ideas to broader audiences. Over time, many welfare management practices that were originally developed based on livestock and companion animal data have been revised to accommodate unique behavioral, physiological, and social considerations of the species [26].

3.4. Research Leading to Better Welfare

Multidisciplinary research evaluations of animals show that the conditions that adversely impact well-being and even survival are often unique to individual animals, even when group-housed [36]. This illustrates the importance of science-based staff training in identifying and correcting physical and psychological issues for the individuals under their care. Investigating and applying welfare management to individuals within zoo populations also provides an informative template for employing conservation management on individuals within wild populations, an approach known as conservation welfare [5,6,13,27,57,58]. The priority placed on the welfare status of captive and wild animals is part of a paradigm shift that expands upon the generalized *Five Freedoms* framework. In particular, the newer approach discourages the one-size-fits-all mindset by recognizing the animal-to-animal variations for many factors that influence their affective states and, ultimately, quality of life [39,59]. Research allows zoos to understand the barriers to sustainable welfare and why they may differ among animals in similar environments or even the same animal over time [50]. Collaborative approaches build information across broad categories, such as activity budgets, social patterns, and biological stress indicators, to comprehensively understand how animals cope with environmental elements. As one example, black rhino (*Diceros bicornis*) housing recommendations were recently updated after researchers documented reduced concentrations of glucocorticoid metabolites and less aggressive behaviors when rhinos were separated until breeding and housed in less-exposed enclosures [60]. Studies on adjusting capacity indicate that effective welfare management starts with providing more frequent positive than negative experiences [8,27,45]. Strategically maintaining a positive experience balance has been shown in several mammalian species to manifest in greater natural behaviors and fewer negative affective states [4,11,45,59,61].

4. Advancements in Zoo Animal Welfare

4.1. Accurately Assessing Welfare Status

Evaluating the welfare status of zoo animals is complex due to the diversity among individuals and the knowledge gaps regarding the needs for many species [8]. AZA-accredited institutions are required to develop transparent processes for evaluating nutrition, exercise, enrichment, training, and other components of welfare management [50,62]. Considerations may include resource adequacy, health records, and the effectiveness of environmental designs [4,27]. Animal metrics such as physical condition, physiological indicators of stress and disease, and behavioral changes are also valuable assessment tools [50,63]. Initially, the *Five Freedoms* framework for food animal production was adopted as a guide for managing zoo animal welfare [64]. A primary emphasis of this framework was to avoid or minimize negative affect states. More recently, the *Five Domains Model* has emerged to include positive and negative affect states, which provides a more holistic assessment [61,64]. This model includes the four discreet categories of nutritional status, environment, health status, and behavioral patterns. The fifth category of assessment is the general mental state, which is innately influenced by the components of the other categories. The most current approaches to welfare evaluation include templates for dietary intake, daily time budgets, and even cognitive bias testing that are modified to fit the individual characteristics of each animal. Similar to the variations in affective states, studies show that variations in coping mechanisms exist among individuals within the same group [5,27,65]. As one example, stress hormones that have traditionally been used to indicate poor welfare may actually be transiently elevated from positive encounters like hunting or mating in some animals [36]. In this case, contextual factors unique to the animal like the pattern of activity and duration of the event would be necessary for an accurate interpretation. Even objective indicators like body temperature and water consumption vary markedly among animals and ambient circumstances. Consequently, welfare assessments based on biomarkers and behavioral patterns are the most effective when customized for each animal within the group over time. Behavioral responses to modifications of the animal's environment or routine (e.g., changes in staff, neighboring animals, or feeding regimen) are particularly indicative of long-term health and well-being. They can distinguish between stress from unfavorable (e.g., adverse climate) or advantageous (e.g., escaping a predator) conditions [36,66].

When environmental conditions impede an animal's behavioral flexibility, its tolerance of social, environmental, or nutritional challenges can be limited [66]. This, in turn, increases health risks by aggravating otherwise benign conditions and impeding normal behaviors such as eating, resting, or mating [67,68]. Such states are often characterized by maladaptive behaviors not fitting the normal patterns, frequency, or context for the species and not previously observed in the individual. In zoos, these behaviors commonly result from ill-suited housing components such as insufficient space, improper ambient temperatures, isolation or overcrowding, and excessive or unfamiliar noise [27]. If sustained, they can lead to cognitive and physiological degeneration that manifests in repetitive, self-injurious, or apathetic behaviors [8]. Abnormal repetitive behaviors (ARB), or stereotypies, occur in essentially all mammals. In zoos, stereotypies are highly conspicuous, leading to negative perceptions among visitors [4,8,69]. Stereotypies may reflect displays of frustration or repeated efforts to acclimate to the environment, but they may also be the result of central nervous system dysfunctions [8]. The specific neuropathologies responsible for motor stereotypies and other ARB are unknown. In humans, however, prolonged exposure of the brain to the stress hormone cortisol causes hippocampus degeneration, which is associated with obsessive–compulsive disorder and schizophrenia [4,28,70]. The research consensus is that stereotypies are products of essential environmental elements going unfulfilled [5,71,72]. The repetitive behaviors result from the failure of satiety mechanisms to be engaged, which would provide negative feedback under normal conditions. Instead, positive sensory feedback from alternative coping behaviors progressively sensitizes the frequently activated neural pathways, resulting in the more frequent and less-inhibited performance of these rituals [73]. Predicting ARB responses can be challenging and requires specific knowledge of the individual and familiarity with the species. For example, feather plucking is a hallmark ARB in most bird species, making it a reliable stress indicator. In parrots, however, the practice is common even under optimal conditions and, thus, is a poor basis for welfare management decisions in these birds [5]. This highlights the importance of context when considering stereotypies as a measure of welfare [5,11]. In fact, their presence is often reflective of the historical experiences of the animal rather than their current welfare status. This is referred to as behavioral scarring [8,69,70]. Nevertheless, zoo animals provided dynamic opportunities to engage in natural coping strategies have been shown to handle new environmental challenges more successfully [5,27].

4.2. The Role of Zoo Staff in Welfare Management

Zookeepers maintain an integral role in animal welfare by managing habitats, nutrition, enrichment activities, and veterinary support [25]. Their frequent interactions and regular observation of individual animals positions them to discern nuanced details in their attitude, posture, and movements indicative of their underlying welfare status [8,11]. As information regarding welfare management emerged, staff training in animal handling became a necessary component of effective strategies. Proper animal handling yields interactions that are safer and cause lower stress for humans and animals. These are built upon proper handler demeanor, knowledge, and experience with the animals under their care [4]. For example, a zookeeper that is properly trained and experienced with hoof stock may understand that gentle flight zone pressure is appropriate when moving sheep or deer species to keep the group from separating. They would also understand that this approach might be ineffective for a hand-reared individual due to its different prior experiences with humans. Likewise, a keeper's familiarity and experience with an imposing species like bison would likely reduce their timidity around the animals, which would allow calmer and safer interactions. Staff are major environmental components for every zoo animal, making quality keeper–animal relationships essential for good welfare [74,75]. Data from human–animal relationship assessments show that routine interactions create an ability for each to anticipate the other's behavior, which reduces stress [63,75]. Of course, the relationship is strengthened by the quality of interactions as well [75]. Keepers and trainers learn to recognize individual temperaments and personalities, which help staff identify subtle shifts in behavior that might otherwise go undetected [50]. For example, an animal at the back of the feeding line may catch an experienced zookeeper's attention if they know this animal has historically been at the top of the social order.

Training animals for voluntary cooperation is an emerging component of welfare management, as it expands behavioral repertoires and makes routine husbandry safer and more manageable. It also enables biological sample collection, veterinary procedures, and transportation to be performed without the acute medical risks associated with tranquilization [66,75,76]. Most zoo training strategies are based on B.F. Skinner's operant conditioning principles [76,77]. These techniques promote desired behaviors by offering or removing stimuli in response to the animal's behavioral decisions [62,78]. Rewarding the correct execution of a requested behavior (positive reinforcement training) is preferred in zoos, because it establishes comfort and trust between the trainer and animal [66,75]. Progressive operant conditioning, or *shaping*, is utilized to reach desired behaviors unlikely to occur spontaneously, such as opening the mouth on cue for a dental exam. This technique rewards increasingly accurate approximations of the targeted behavior by using clickers or other conditioning techniques [79]. When an animal chooses behavior further from the target, desirable stimuli are taken away. This can be as simple as briefly ignoring the animal. Operant conditioning is effective, because it allows animals to maintain control over their behavior, which research shows benefits their psychological well-being, reduces stereotypies, and improves breeding and reintroduction success [4,54,66,76,79].

4.3. Environmental Enrichment

4.3.1. The Impact of Enriched Environments on Zoo Animal Welfare

In 2002, the AZA convened a committee on animal welfare priorities among its accredited institutions [63], and strategic environmental enrichment for all animals emerged as a core directive. The AZA began developing standards for environmental enrichment and other welfare management practices that would be expected of prospective and member institutions [33]. Consequently, enrichment programs are evaluated as part of the accreditation and renewal processes [33]. Environmental enrichment is the strategic addition of permanent or interchangeable elements to the animal's surroundings that engage healthy intrinsic behaviors [4,76,80,81]. Dynamic enclosures increase interactivity and encourage exercise, exploration, planning, and problem-solving [62,80–82], which, in turn, reduce the impetus for stereotypies and other ARB [70,83–85]. In addition to human and animal safety, primary considerations for enrichment include the relevance to the preferences of the species and individual and the cognitive complexity that it adds [5]. Enrichment is most effective when designed to elicit prospectively identified desirable behaviors by posing a meaningful mental or physical challenge [4]. For example, food may be hidden, scattered, or placed within puzzle feeders to stimulate foraging behaviors observed in the wild. This is illustrated in Figure 2, which depicts a parrot with its meal inside a paper cylinder that must be peeled away like the skin of the fruits it might encounter in the jungle. Studies across many species have found that good enrichment programs reduce stress biomarkers and prevent or eliminate up to 66% of ARB [13,62,71,81,86,87].

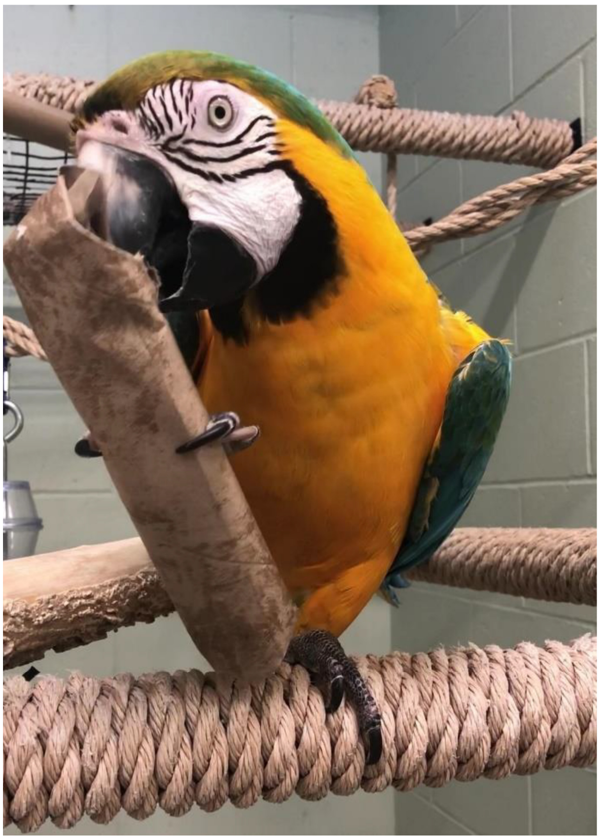

Figure 2. Environmental enrichment is most effective when designed to elicit the species' natural behaviors. Here, a parrot is offered food inside a paper tube, which replicates a natural foraging behavior (i.e., peeling fruit) while also ensuring that essential nutritional needs are met.

4.3.2. Effective Environmental Enrichment Approaches

Tactile, sensory, and social enhancements may emulate the species' natural environment or may elicit natural behaviors through artificial features [5,81,85,87]. An effective approach to environmental modification is the encouragement of exploration through strategic design. Exploration is a highly conserved behavior that can be stimulated by directing attention and activity toward novel environmental elements [81,83,88]. *Extrinsic* exploration fulfills primal impulses such as escaping danger or obtaining food, whereas *intrinsic* exploration is motivated by curiosity [84,88]. Not surprisingly, preferences for specific enrichment devices and strategies can differ markedly among individual animals, even within the same group [5,70]. Thus, documenting the effectiveness of each strategy in achieving the targeted behaviors from each individual is important. Conventional assessments often begin with rudimentary biometrics and user-defined behavioral categories, such as the frequency of walking, lying, or grooming [89,90]. More recently, the *Qualitative Behavioral Assessment* framework was developed to produce a more comprehensive summary of behavioral and emotional patterns by including interpretive descriptions of an animal's demeanor [4,5]. Thorough and detailed observational repertoires, including those for enrichment, help guide plans to establish healthy behaviors [91]. Enrichment efficacy can be estimated from behavioral diversity indices. These provide context for behavioral responses by holistically considering the underlying psychology and cognition involved [4,5,70]. The optimal frequency at which specific enrichment items should be offered or replaced is based on several factors, including the age, background, and sentience of the animal. Thus, although general recommendations for mammals and birds include at least one enriching experience per day, individuals that belong to a species with known higher cognitive abilities or that are actively exhibiting ARB may require a greater enrichment frequency. Enrichment components from established categories (sensory, manipulation, foraging, social/behavioral, and structure/substrate) can be offered in rotations and rated for interactivity. When behavioral outcomes are properly documented over time, the animal's perception of its environment will become clearer to caretakers. This insight better equips staff to develop management practices that align with the distinctive characteristics and personality traits of the individual, including selecting enrichment that fosters optimal engagement and avoiding less effective enrichment devices [5].

Environmental enrichment strategies often leverage *contrafreeloading*, which is the innate attraction to challenges that require problem-solving and action to obtain a rewarding outcome, traditionally food, even when alternative sources are freely available [5]. Moreover, a study on macaques (*Macaca fuscata*) observed contrafreeloading-like behavior when the playing of a movie on a cage-adjacent screen was substituted for food as the rewarding outcome [92]. Another study on rats (*Rattus norvegicus*) indicated that contrafreeloading engages the dopamine system of the brain, meaning that the behaviors result in a neurological "rush" that is similar to the thrill of a hunt [93]. This helps to explain why enrichment strategies targeting hunting-oriented behaviors are quite successful in big cats, as they alleviate the boredom caused by the inability to hunt [94–96]. Such predation behaviors might be simulated by presenting food items in intentionally laborious orientations, perhaps hanging above ground level, hidden within objects, or buried. Activities like cheetah runs also leverage hunting and foraging tools, as do items that stimulate olfactory (e.g., spices), auditory (e.g., music and radio), visual (e.g., automated toys and movies), and tactile (e.g., substrate propping) sensations [13,57,71,72,80,81,83,87,91]. Figure 3 depicts cheetahs offered enrichment items designed to engage their natural hunting behaviors. In the top row of panels, the cheetahs are offered oblong plastic spheres that move erratically when batted like small prey animals. In the bottom row of panels, they are offered a woven firehose log that mimics the deadweight of a fresh kill. Importantly, individual cats differed in their enthusiasm for the respective items [97]. The majority of information regarding environmental enrichment has been produced from land mammal species that are ubiquitous in zoos across the globe. However, studies on marine mammals and even fish show that proper enrichment strategies can be effective for all human-managed animals [85,98].

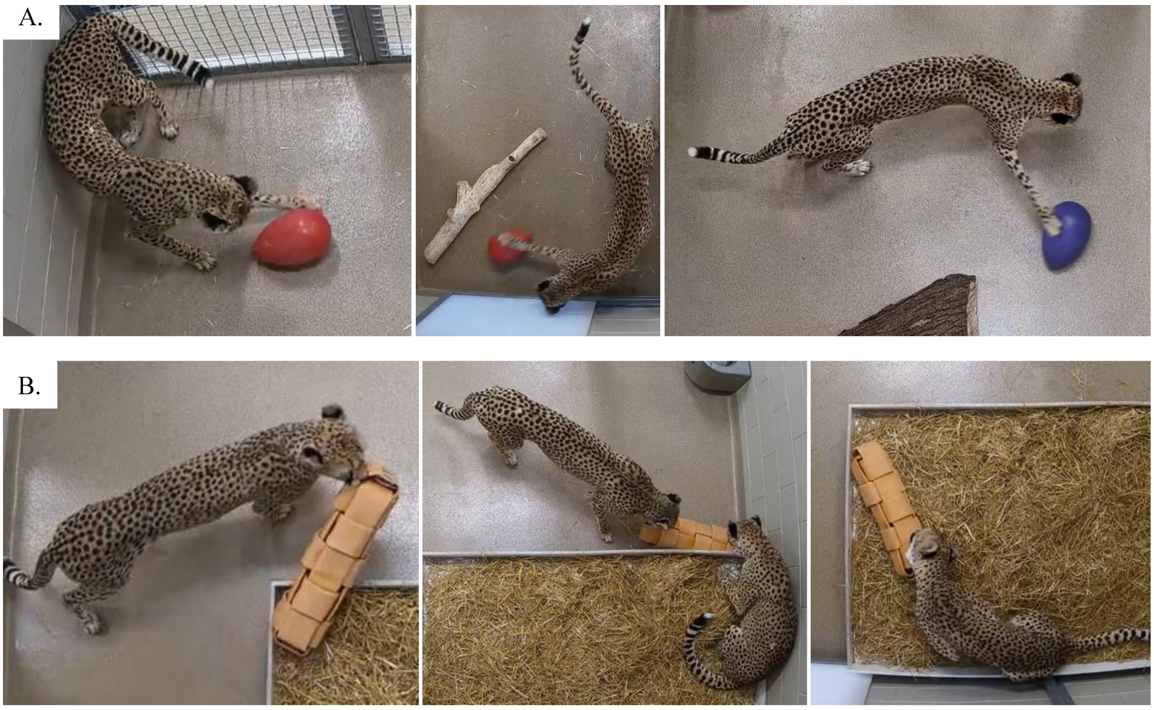

Figure 3. Instinctual behaviors can be elicited artificially by strategic environmental enrichment. In the top row (**A**), oblong plastic spheres (Jolly Eggs) mimic the erratic, nonlinear movement of small

prey animals when batted by the cheetah, which engages the cat's instinct to chase and pounce. In the bottom row (**B**), a log of weaved firehose mimics the size, texture, and deadweight of a captured prey, which engages the cat's instinct to drag the item to a resting area and methodically chew it.

5. Opportunities for Continued Improvements in Welfare Management

The benefits of documenting welfare management outcomes are clear, yet barriers exist that affect the accuracy and efficacy of welfare evaluation. One common obstacle is inadequate knowledgeability among staff regarding animal behavior [99]. Often, the responsibility of assessing behaviors falls by default to staff members with little or no formal training, although professional welfare and behavior experts are becoming more commonplace [39,100]. Another limitation is the subjective nature of user-based assessments, which can be influenced by individual bias or other factors that limit direct comparisons among records [89]. These observational records have merit when performed consistently, but they require extensive labor and time that is often limited in zoos. Choice frequencies and other course behavioral metrics are more objective but pose their own challenges. Untrained observers can easily detect obvious activity changes, but changes that are subtle, interrelated with other behaviors, or influenced by context may be overlooked or even intentionally excluded [89]. For example, early pathological indicators of chronic stress are quite challenging to identify due to most animals' evolutionary tendency to hide illness and injury [67,101]. The interpretation of observed behaviors can vary even among well-trained staff. Moreover, responses of animals within specific zoo populations may not be broadly representative due to differences in human interactions and the intermittent nature of in-person monitoring. A comprehensive assessment of true natural behaviors requires uninhibited and continuous observation without disruption by human presence, such as that achieved by video monitoring. Some early advancements in these areas have already demonstrated avenues for improving animal welfare management [8,36,39], and these efforts are ongoing. The widespread adoption of emerging evidence-based assessment tools will allow animal care personnel to better associate individual behaviors with specific needs for animals to thrive [61]. These endeavors will improve the quality of life for animals within zoo populations but will also play a fundamental role in conservation welfare.

6. Conclusions

This historical look at the evolution of zoo animal welfare management and the role it has played in the transformation of the modern zoo mission illustrates both the amount of progress made and the amount of work remaining. Recent and ongoing research efforts are building upon the fundamental information produced by the behavioral studies of early pioneers of zoological science. These efforts are continuing to expand and improve welfare assessments and management strategies. The next steps include the continued development of technology-based systems, which are objective and unblinking, to better observe and assess the behaviors of individual animals. Additional needs include new strategies and support mechanisms to translate the information produced in zoo populations to protect wild populations. Lastly, it is important that zoos continue to publicly highlight their conservation successes to their community stakeholders through social media campaigns and other media. Communicating honestly and transparently regarding the role of zoos in species and habitat conservation and their persistent pursuit of the optimal welfare for the animals they house helps to alleviate misconceptions and generates support for the preservation of global natural resources.

Author Contributions: Conceptualization, H.N.B., T.C.S., T.B.S. and D.T.Y.; writing—original draft preparation, H.N.B. and D.T.Y.; and writing—review and editing, H.N.B., T.C.S., T.B.S. and D.T.Y. All authors have read and agreed to the published version of the manuscript.

Funding: This research received no external funding.

Institutional Review Board Statement: Not applicable.

Data Availability Statement: No data are associated with this manuscript.

Acknowledgments: The authors gratefully acknowledge the supportive relationships with the staff of the Lincoln Children's Zoo and Omaha's Henry Doorly Zoo & Aquarium.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Roe, K.; McConney, A.; Mansfield, C.F. The Role of Zoos in Modern Society—A Comparison of Zoos' Reported Priorities and What Visitors Believe They Should Be. *Anthrozoös* **2015**, *27*, 529–541. [CrossRef]
2. Kisling, V.N.J. *Zoo and Aquarium History: Ancient Animal Collections to Zoological Gardens*; CRC Press: Boca Raton, FL, USA, 2000.
3. Barber, J.C. Programmatic approaches to assessing and improving animal welfare in zoos and aquariums. *Zoo Biol.* **2009**, *28*, 519–530. [CrossRef]
4. Bacon, H. Behaviour-Based Husbandry-A Holistic Approach to the Management of Abnormal Repetitive Behaviors. *Animals* **2018**, *8*, 103. [CrossRef] [PubMed]
5. Rose, P.; Riley, L. The use of Qualitative Behavioural Assessment in zoo welfare measurement and animal husbandry change. *J. Zoo Aquar. Res.* **2018**, *7*, 150–161. [CrossRef]
6. Diana, A.; Salas, M.; Pereboom, Z.; Mendl, M.; Norton, T. A Systematic Review of the Use of Technology to Monitor Welfare in Zoo Animals: Is There Space for Improvement? *Animals* **2021**, *11*, 3048. [CrossRef] [PubMed]
7. Miller, L.J.; Vicino, G.A.; Sheftel, J.; Lauderdale, L.K. Behavioral Diversity as a Potential Indicator of Positive Animal Welfare. *Animals* **2020**, *10*, 1211. [CrossRef]
8. Tallo-Parra, O.; Salas, M.; Manteca, X. Zoo Animal Welfare Assessment: Where Do We Stand? *Animals* **2023**, *13*, 1966. [CrossRef]
9. Jordan, B. Science-based assessment of animal welfare: Wild and captive animals. *Rev. Sci. Tech.* **2005**, *24*, 515–528. [CrossRef]
10. Mendl, M.; Burman, O.H.; Paul, E.S. An integrative and functional framework for the study of animal emotion and mood. *Proc. Biol. Sci.* **2010**, *277*, 2895–2904. [CrossRef]
11. Jones, N.; Sherwen, S.L.; Robbins, R.; McLelland, D.J.; Whittaker, A.L. Welfare Assessment Tools in Zoos: From Theory to Practice. *Vet. Sci.* **2022**, *9*, 170. [CrossRef]
12. Melfi, V.A. There are big gaps in our knowledge, and thus approach, to zoo animal welfare: A case for evidence-based zoo animal management. *Zoo Biol.* **2009**, *28*, 574–588. [CrossRef] [PubMed]
13. Quirke, T.; O'Riordan, R.M. The effect of a randomised enrichment treatment schedule on the behaviour of cheetahs (*Acinonyx jubatus*). *Appl. Anim. Behav. Sci.* **2011**, *135*, 103–109. [CrossRef]
14. Foster, K.P. The earliest zoos and gardens. *Sci. Am.* **1999**, *281*, 64–71. [CrossRef]
15. Bostock, S.S.C. *Zoos and Animal Rights: The Ethics of Keeping Animals*; Taylor & Francis Group: London, UK, 1993; p. 1789.
16. Hancocks, D. *A Different Nature: The Paradoxical World of Zoos and Their Uncertain Future*; University of California Press: Berkeley, CA, USA, 2001.
17. Baratay, E.; Hardouin-Fugier, E. *Zoo: A History of Zoological Gardens in the West*; Reaktion Books: London, UK, 2002; p. 400.
18. Parker, M. The genealogy of the zoo: Collection, park and carnival. *Organization* **2020**, *28*, 604–620. [CrossRef]
19. Kallipoliti, L. Evolution of the Zoo. An Overview of Significant Zoological Developments Spanning from Biblical Times through to Contemporary Proprosals. *Wordpress Terra Incogn.* **2014**, *6*, 1–26.
20. Dölek-Sever, D. Captive wild animals as visual commodities in the Ottoman Empire: A historical review. *Middle East. Stud.* **2023**, *59*, 1–17. [CrossRef]
21. Rabb, G.B. The evolution of zoos from menageries to centers of conservation and caring. *Curator Mus. J.* **2004**, *47*, 237–246. [CrossRef]
22. Coe, J.C. Towards a co-evolution of zoos, aquariums and natural history museums. In Proceedings of the Annual Conference Proceedings, American Association of Zoological Parks and Aquariums, Wheeling, WV, USA, 8–12 September 1985; pp. 366–376.
23. Ryan, S. *The Unorthodox Imagination in Late Medieval Britain*; Cambridge University Press: Cambridge, UK, 2011; Volume 62, pp. 818–819.
24. Graetz, M.J. The Role of Architectural Design in Promoting the Social Objectives of Zoos: A Study of Zoo Exhibit Design with Reference to Selected Exhibits in Singapore Zoological Gardens. Master's Thesis, National University of Singapore, Singapore, 1996.
25. Escobar-Ibarra, I.; Mota-Rojas, D.; Gual-Sill, F.; Sánchez, C.R.; Baschetto, F.; Alonso-Spilsbury, M. Conservation, animal behaviour, and human-animal relationship in zoos. Why is animal welfare so important? *J. Anim. Behav. Biometeorol.* **2021**, *9*, 2111. [CrossRef]
26. Powell, D.M.; Watters, J.V. The Evolution of the Animal Welfare Movement in U.S. Zoos and Aquariums. *Zool. Gart.* **2017**, *86*, 219–234. [CrossRef]
27. Hill, S.P.; Broom, D.M. Measuring zoo animal welfare: Theory and practice. *Zoo Biol.* **2009**, *28*, 531–544. [CrossRef]
28. Maulana, R.; Gawi, J.M.; Utomo, S.W. Architectural design assessment of Javan leopard rehabilitation facility regarding the occurrence of stereotypical pacing. *IOP Conf. Ser. Earth Environ. Sci. Bristol.* **2020**, *426*, 12075. [CrossRef]
29. Spooner, S.L.; Farnworth, M.J.; Ward, S.J.; Whitehouse-Tedd, K.M. Conservation education: Are zoo animals effective ambassadors and is there any cost to their welfare? *J. Zool. Bot. Gard.* **2021**, *2*, 41–65. [CrossRef]

30. Hosey, G.; Melfi, V.; Pankhurst, S. *Zoo Animals: Behaviour, Management, and Welfare*; Oxford University Press: Oxford, UK, 2009; Volume 1, p. 659.
31. Ito, T. *London Zoo and the Victorians, 1828–1859*, 2nd ed.; The Boydell Press: Woodbridge, UK, 2020; Volume 2, p. 216.
32. Taplin, R.H. Competitive importance-performance analysis of an Australian wildlife park. *Tour. Manag.* **2012**, *33*, 29–37. [CrossRef]
33. AZA. Association of Zoos & Aquariums. Available online: https://www.aza.org/ (accessed on 19 July 2022).
34. Dick, G. *WAZA History at a Glance*; World Association of Zoos and Aquariums: Gland, Switzerland, 2015; pp. 2–5.
35. Rodrigues, A.S.; Pilgrim, J.D.; Lamoreux, J.F.; Hoffmann, M.; Brooks, T.M. The value of the IUCN Red List for conservation. *Trends Ecol. Evol.* **2006**, *21*, 71–76. [CrossRef]
36. Beausoleil, N.J.; Mellor, D.J.; Baker, L.; Baker, S.E.; Bellio, M.; Clarke, A.S.; Dale, A.; Garlick, S.; Jones, B.; Harvey, A.; et al. "Feelings and Fitness" Not "Feelings or Fitness"—The Raison d'etre of Conservation Welfare, Which Aligns Conservation and Animal Welfare Objectives. *Front. Vet. Sci.* **2018**, *5*, 296. [CrossRef]
37. Hediger, H. *Studies of the Psychology and Behavior of Captive Animals in Zoos and Circuses*; Butterworths Scientific Publications: London, UK, 1955; p. 166.
38. Rübel, A. *Heini Hediger: Tierpsychologe, Tiergartenbiologe, Zoodirektor*; Gelehrte Gesellschaft: Zürich, Switzerland, 2009.
39. Miller, L.J.; Chinnadurai, S.K. Beyond the Five Freedoms: Animal Welfare at Modern Zoological Facilities. *Animals* **2023**, *13*, 1818. [CrossRef]
40. Greenwell, P.J.; Riley, L.M.; Lemos de Figueiredo, R.; Brereton, J.E.; Mooney, A.; Rose, P.E. The Societal Value of the Modern Zoo: A Commentary on How Zoos Can Positively Impact on Human Populations Locally and Globally. *J. Zool. Bot. Gard.* **2023**, *4*, 53–69. [CrossRef]
41. Rose, P.E.; Riley, L.M. Expanding the role of the future zoo: Wellbeing should become the fifth aim for modern zoos. *Front. Psychol.* **2022**, *13*, 1018722. [CrossRef]
42. Buckley, K.A.; Smith, L.D.G.; Crook, D.A.; Pillans, R.D.; Kyne, P.M. Conservation impact scores identify shortfalls in demonstrating the benefits of threatened wildlife displays in zoos and aquaria. *J. Sustain. Tour.* **2020**, *28*, 978–1002. [CrossRef]
43. Mace, G.M.; Collar, N.J.; Gaston, K.J.; Hilton-Taylor, C.; Akcakaya, H.R.; Leader-Williams, N.; Milner-Gulland, E.J.; Stuart, S.N. Quantification of extinction risk: IUCN's system for classifying threatened species. *Conserv. Biol.* **2008**, *22*, 1424–1442. [CrossRef]
44. Che-Castaldo, J.P.; Grow, S.A.; Faust, L.J. Evaluating the Contribution of North American Zoos and Aquariums to Endangered Species Recovery. *Sci. Rep.* **2018**, *8*, 9789. [CrossRef]
45. Barongi, R.; Fisken, F.; Parker, M.; Gusset, M. *Committing to Conservation: The World Zoo and Aquarium Conservation Strategy*; WAZA Executive Office: Gland, Switzerland, 2015; Volume 6.
46. WAZA. *Building a Future for Wildlife—The World Zoo and Aquarium Conservation Strategy*; WAZA Executive Office: Bern, Switzerland, 2005.
47. Ballou, J.D.; Foose, T.J. Demographic and genetic management of captive populations. In *Wild Mammals in Captivity*; DG, K., Ed.; The University of Chicago Press: Chicago, IL, USA, 1996; pp. 263–283.
48. Keulartz, J. Captivity for Conservation? Zoos at a Crossroads. *J. Agric. Environ. Ethics* **2015**, *28*, 335–351. [CrossRef]
49. Miller, B.; Conway, W.; Reading, R.P.; Wemmer, C.; Wildt, D.; Kleiman, D.; Monfort, S.; Rabinowitz, A.; Armstrong, B.; Hutchins, M. Evaluating the Conservation Mission of Zoos, Aquariums, Botanical Gardens, and Natural History Museums. *Conserv. Biol.* **2004**, *18*, 86–93. [CrossRef]
50. Whitham, J.C.; Wielebnowski, N. New directions for zoo animal welfare science. *Appl. Anim. Behav. Sci.* **2013**, *147*, 247–260. [CrossRef]
51. Flesness, N. International Species Information System (ISIS): Over 25 years of compiling global animal data to facilitate collection and population management. *Int. Zoo Yearb.* **2003**, *38*, 53–61. [CrossRef]
52. Mace, G.; Balmford, A.; Leader-Williams, N.; Manica, A.; Walter, O.; West, C.D.; Zimmerman, A. Measuring conservation success: Assessing zoos' contributions. In Proceedings of the Catalysts for Conservation: A Direction for Zoos in the 21st Century, London, UK, 19–20 February 2004; pp. 322–342.
53. Gusset, M.; Dick, G. 'Building a Future for Wildlife'? Evaluating the contribution of the world zoo and aquarium community to in situ conservation. *Int. Zoo Yearb.* **2010**, *44*, 183–191. [CrossRef]
54. Anderson, U.S.; Kelling, A.S.; Pressley-Keough, R.; Bloomsmith, M.A.; Maple, T.L. Enhancing the Zoo Visitor's Experience by Public Animal Training and Oral Interpretation at an Otter Exhibit. *Environ. Behav.* **2016**, *35*, 826–841. [CrossRef]
55. Brando, S.; Herrelko, E.S. Wild Animals in the City: Considering and Connecting with Animals in Zoos and Aquariums. In *Animals in Our Midst: The Challenges of Co-Existing with Animals in the Anthropocene*; The International Library of Environmental, Agricultural and Food Ethics; Springer International Publishing AG: Cham, Switzerland, 2021; Volume 33, pp. 341–360.
56. Curtin, P.; Papworth, S. Increased information and marketing to specific individuals could shift conservation support to less popular species. *Mar. Policy* **2018**, *88*, 101–107. [CrossRef]
57. Quirke, T.; O'Riordan, R.; Davenport, J. A comparative study of the speeds attained by captive cheetahs during the enrichment practice of the "cheetah run". *Zoo Biol.* **2013**, *32*, 490–496. [CrossRef]
58. Higgs, S.J.; Van Eck, E.; Heynis, K.; Braodberry, S.H. Humans as Enrichment: Human-Animal Interactions and the Perceived Benefit to the Cheetah (*Acinonyx jubatus*) Human and Zoological Establishment. *Int. J. Biol. Life Agric. Sci.* **2018**, *11*, 97–103. [CrossRef]

59. Mellor, D.J. Updating Animal Welfare Thinking: Moving beyond the “Five Freedoms” towards “A Life Worth Living”. *Animals* **2016**, *6*, 21. [CrossRef] [PubMed]
60. Carlstead, K.; Brown, J.L. Relationships between patterns of fecal corticoid excretion and behavior, reproduction, and environmental factors in captive black (*Diceros bicornis*) and white (*Ceratotherium simum*) rhinoceros. *Zoo Biol. Publ. Affil. Am. Zoo Aquar. Assoc.* **2005**, *24*, 215–232. [CrossRef]
61. Mellor, D.J.; Beausoleil, N.J.; Littlewood, K.E.; McLean, A.N.; McGreevy, P.D.; Jones, B.; Wilkins, C. The 2020 Five Domains Model: Including Human-Animal Interactions in Assessments of Animal Welfare. *Animals* **2020**, *10*, 1870. [CrossRef] [PubMed]
62. Greco, B.J.; Meehan, C.L.; Miller, L.J.; Shepherdson, D.J.; Morfeld, K.A.; Andrews, J.; Baker, A.M.; Carlstead, K.; Mench, J.A. Elephant Management in North American Zoos: Environmental Enrichment, Feeding, Exercise, and Training. *PLoS ONE* **2016**, *11*, e0152490. [CrossRef]
63. Sherwen, S.L.; Hemsworth, L.M.; Beausoleil, N.J.; Embury, A.; Mellor, D.J. An Animal Welfare Risk Assessment Process for Zoos. *Animals* **2018**, *8*, 130. [CrossRef]
64. Mellor, D.J.; Beausoleil, N.J. Extending the ‘Five Domains’ model for animal welfare assessment to incorporate positive welfare states. *Anim. Welf.* **2023**, *24*, 241–253. [CrossRef]
65. Dickens, M.J.; Delehanty, D.J.; Michael Romero, L. Stress: An inevitable component of animal translocation. *Biol. Conserv.* **2010**, *143*, 1329–1341. [CrossRef]
66. Spiezio, C.; Vaglio, S.; Scala, C.; Regaiolli, B. Does positive reinforcement training affect the behaviour and welfare of zoo animals? The case of the ring-tailed lemur (*Lemur catta*). *Appl. Anim. Behav. Sci.* **2017**, *196*, 91–99. [CrossRef]
67. Edes, A.N.; Wolfe, B.A.; Crews, D.E. Evaluating Allostatic Load: A New Approach to Measuring Long-Term Stress in Wildlife. *J. Zoo Wildl. Med.* **2018**, *49*, 272–282. [CrossRef]
68. McEwen, B.S. Stress, adaptation, and disease. Allostasis and allostatic load. *Ann. N. Y. Acad Sci.* **1998**, *840*, 33–44. [CrossRef]
69. Quirke, T.; O’Riordan, R.M.; Zuur, A. Factors influencing the prevalence of stereotypical behaviour in captive cheetahs (*Acinonyx jubatus*). *Appl. Anim. Behav. Sci.* **2012**, *142*, 189–197. [CrossRef]
70. Furlong, E.; Gaskill, B.; Erasmus, M. *Exotic Feline Enrichment*; Purdue University: Purdue, IN, USA, 2021; pp. 1–5.
71. Skibiel, A.L.; Trevino, H.S.; Naugher, K. Comparison of several types of enrichment for captive felids. *Zoo Biol.* **2007**, *26*, 371–381. [CrossRef] [PubMed]
72. Sena, M.V.d.A.; Santos, G.d.S.; Oliveira, M.A.B.d. Strategies of Environmental Enrichment for ocelot Leopardus pardalis (Carnivora, Felidae) at Parque Estadual Dois Irmãos: A study case in Brazil. *Rev. Bras. Zoociências* **2018**, *19*, 35–46. [CrossRef]
73. Mason, G.; Rushen, J. *Stereotypic Animal Behaviour Fundamentals and Applications to Welfare*, 2nd ed.; CAB International: Wallingford, UK, 2006.
74. Coe, J.; Hoy, J. Choice, Control and Computers: Empowering Wildlife in Human Care. *Multimodal Technol. Interact.* **2020**, *4*, 92. [CrossRef]
75. Carlstead, K. A comparative approach to the study of Keeper-Animal Relationships in the zoo. *Zoo Biol.* **2009**, *28*, 589–608. [CrossRef]
76. Fernandez, E.J. Training as Enrichment: A Critical Review. *Anim. Welf.* **2022**, *31*, 1–12. [CrossRef]
77. Skinner, B.F. *The Behavior of Organisms*; D. Appleton-Century Company: New York, NY, USA, 1938.
78. Crowell-Davis, S.L. Use of operant conditioning to facilitate examination of zoo animals. *Compend. Contin. Educ. Vet.* **2008**, *30*, 218–219.
79. Daffin, L.W. *Principles of Learning and Behavior*, 2nd ed.; Washington State University: Pullman, WA, USA, 2021; p. 397.
80. Lithner, J. On the Hunt for Improvements-Possibilities of Increasing Welfare in Captive Cheetahs through Hunting Enrichment. Ph.D. Thesis, Sveriges lantbruksuniversitet (Swedish University of Agricultural Sciences), Uppsala, Sweden, 2014.
81. Damasceno, J.; Genaro, G.; Quirke, T.; McCarthy, S.; McKeown, S.; O’Riordan, R. The effects of intrinsic enrichment on captive felids. *Zoo Biol.* **2017**, *36*, 186–192. [CrossRef]
82. Hoy, J.M.; Murray, P.J.; Tribe, A. Thirty years later: Enrichment practices for captive mammals. *Zoo Biol.* **2010**, *29*, 303–316. [CrossRef]
83. Fischer Meinert, R.; Pitlovanciv, A.K.; Marenzi, R.C.; Silva Barreto, A. Behavioral Evaluation of Herpailurus yagouaroundi (E. Geoffroy Saint-Hilaire, 1803) in Response to Environmental Enrichment. *J. Appl. Anim. Welf. Sci.* **2021**, *24*, 149–158. [CrossRef]
84. Ellis, S.L. Environmental enrichment: Practical strategies for improving feline welfare. *J. Feline Med. Surg.* **2009**, *11*, 901–912. [CrossRef] [PubMed]
85. Makecha, R.N.; Highfill, L.E. Environmental Enrichment, Marine Mammals, and Animal Welfare: A Brief Review. *Aquat. Mamm.* **2018**, *44*, 221–230. [CrossRef]
86. Cannon, T.H.; Heistermann, M.; Hankison, S.J.; Hockings, K.J.; McLennan, M.R. Tailored Enrichment Strategies and Stereotypic Behavior in Captive Individually Housed Macaques (*Macaca* spp.). *J. Appl. Anim. Welf. Sci.* **2016**, *19*, 171–182. [CrossRef] [PubMed]
87. Regaiolli, B.; Rizzo, A.; Ottolini, G.; Miletto Petrazzini, M.E.; Spiezio, C.; Agrillo, C. Motion Illusions as Environmental Enrichment for Zoo Animals: A Preliminary Investigation on Lions (*Panthera leo*). *Front. Psychol.* **2019**, *10*, 2220. [CrossRef] [PubMed]
88. Machado, J.C.; Genaro, G. Influence of olfactory enrichment on the exploratory behaviour of captive-housed domestic cats. *Aust. Vet. J.* **2014**, *92*, 492–498. [CrossRef]

89. Berman, G.J.; Choi, D.M.; Bialek, W.; Shaevitz, J.W. Mapping the stereotyped behaviour of freely moving fruit flies. *J. R. Soc. Interface* **2014**, *11*, 20140672. [CrossRef]
90. Schmidt, T.B.; Lancaster, J.M.; Psota, E.; Mote, B.E.; Hulbert, L.E.; Holliday, A.; Woiwode, R.; Pérez, L.C. Evaluation of a novel computer vision-based livestock monitoring system to identify and track specific behaviors of individual nursery pigs within a group-housed environment. *Transl. Anim. Sci.* **2022**, *6*, txac082. [CrossRef]
91. Rangel, M.; Júnior, N.D.S. Environmental food and cognitive enrichment: A study of well-being for large captive felids at the Zoo of Goiânia. *Sci. Rep.* **2021**. [CrossRef]
92. Ogura, T. Contrafreeloading and the value of control over visual stimuli in Japanese macaques (*Macaca fuscata*). *Anim. Cogn.* **2011**, *14*, 427–431. [CrossRef]
93. Frederick, M.J.; Cocuzzo, S.E. Contrafreeloading in Rats Is Adaptive and Flexible: Support for an Animal Model of Compulsive Checking. *Evol. Psychol.* **2017**, *15*, 147470491773593. [CrossRef]
94. Markowitz, H.; LaForse, S. Artificial prey as behavioral enrichment devices for felines. *Appl. Anim. Behav. Sci.* **1987**, *18*, 31–43. [CrossRef]
95. Markowitz, H.; Aday, C.; Gavazzi, A. Effectiveness of acoustic “prey”: Environmental enrichment for a captive African leopard (*Panthera pardus*). *Zoo Biol.* **1995**, *14*, 371–379. [CrossRef]
96. Bashaw, M.J.; Bloomsmith, M.A.; Marr, M.; Maple, T.L. To hunt or not to hunt? A feeding enrichment experiment with captive large felids. *Zoo Biol. Publ. Affil. Am. Zoo Aquar. Assoc.* **2003**, *22*, 189–198. [CrossRef]
97. Beer, H.N. Continuous Video Monitoring of Zoo Cheetahs Demonstrates Differential Engagement Patterns for Six Different Types of Environmental Enrichment; Placental Insufficiency Indicators Improve in Intrauterine Growth-Restricted Fetal Sheep Receiving Daily ω-3 Polyunsaturated Fatty Acid Infusions; Investigation of Differentially Expressed Transcripts of the Adipose Tissue in Fetal and Neonatal IUGR Sheep. Ph.D. Thesis, The University of Nebraska-Lincoln, Lincoln, NE, USA, 2022.
98. Barcellos, H.H.A.; Koakoski, G.; Chaulet, F.; Kirsten, K.S.; Kreutz, L.C.; Kalueff, A.V.; Barcellos, L.J.G. The effects of auditory enrichment on zebrafish behavior and physiology. *PeerJ* **2018**, *6*, e5162. [CrossRef]
99. Maple, T.L.; Segura, V.D. Advancing Behavior Analysis in Zoos and Aquariums. *Behav. Anal.* **2015**, *38*, 77–91. [CrossRef] [PubMed]
100. Cole, J.; Fraser, D. Zoo Animal Welfare: The Human Dimension. *J. Appl. Anim. Welf. Sci.* **2018**, *21*, 49–58. [CrossRef] [PubMed]
101. Rodrigues, S.M.; LeDoux, J.E.; Sapolsky, R.M. The influence of stress hormones on fear circuitry. *Annu. Rev. Neurosci.* **2009**, *32*, 289–313. [CrossRef]