Zoos as Conservation Institutions

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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.

Keywords: behavior ; environmental enrichment ; husbandry ; zoo stress

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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][5][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][8][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][12][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.

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$_{\text{B.C.}}$ [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$_{\text{B.C.}}$ and 1456$_{\text{A.D.}}$, 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][26][27][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][26][27][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.

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][35]. 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 [36]. 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* [37]. 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][38].

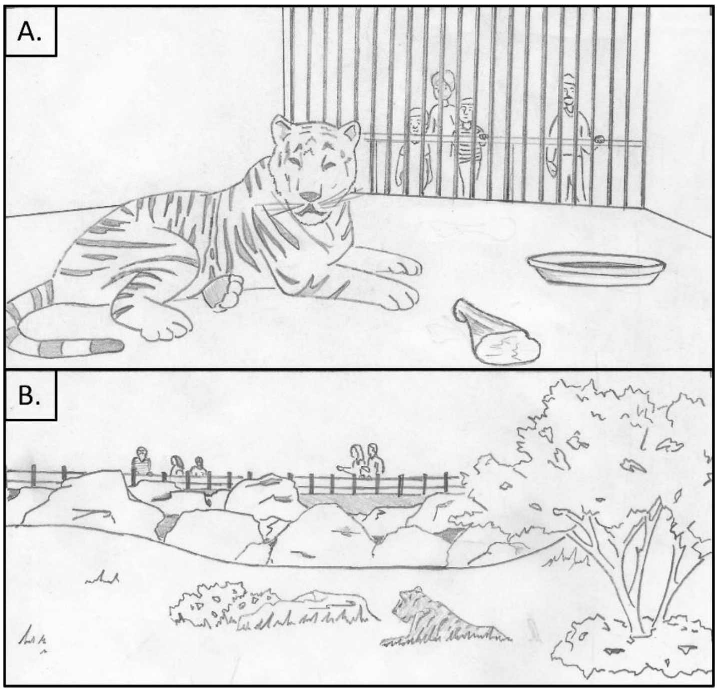

Figure 1. The evolution of terrestrial mammal enclosures includes changing from barred menagerie cages (**A**) to more spacious and naturalistic exhibits that are tailored to the ecology of the species (**B**). This provides more opportunities to engage in rewarding behaviors. It also fosters a sense 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. Artwork by TJ Yates, Abilene Zoological Gardens.

3. Advancements in Zoo Animal Welfare

3.1. 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 [39][40]. 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 [39][41]. Initially, the *Five Freedoms* framework for food animal production was adopted as a guide for managing zoo animal welfare [42]. 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 [42][43]. 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][44]. 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 [35]. 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 [35][45].

3.2. 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 [46][47].

3.3. Environmental Enrichment

3.3.1. The Impact of Enriched Environments on Zoo Animal Welfare

In 2002, the AZA convened a committee on animal welfare priorities among its accredited institutions [41], 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][48][49][50]. Dynamic enclosures increase interactivity and encourage exercise, exploration, planning, and problem-solving [40][49][50][51], which, in turn, reduce the impetus for stereotypies and other ARB [52][53][54][55]. 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][40][50][56][57][58].

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.

3.3.2. Effective Environmental Enrichment Approaches

Tactile, sensory, and social enhancements may emulate the species' natural environment or may elicit natural behaviors through artificial features [5][50][55][58]. 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 [50][53][59]. *Extrinsic* exploration fulfills primal impulses such as escaping danger or obtaining food, whereas *intrinsic* exploration is motivated by curiosity [54][59]. Not surprisingly, preferences for specific enrichment devices and strategies can differ markedly among individual animals, even within the same group [5][52]. 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 [60][61]. 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 [62]. 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][52]. 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.

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 [63]. 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 [64]. 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 [65][66][67]. 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][49][50][53][56][58][62][68][69]. **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 [70]. 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 [55][71].

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.

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