Review

Applied Behavior Analysis and the Zoo: Forthman and Ogden (1992) Thirty Years Later

Eduardo J. Fernandez[1] and Allison L. Martin[2]

[1]School of Animal and Veterinary Sciences, The University of Adelaide
[2]Department of Psychological Science, Kennesaw State University
* Correspondence: edjfern@gmail.com

Abstract
The field of applied behavior analysis has been directly involved in both research and applications of behavioral principles to improve the lives of captive zoo animals. Thirty years ago, Forthman and Ogden (1992) wrote one of the first papers documenting some of these efforts. Since that time, considerable work has been done using behavioral principles and procedures to guide zoo welfare efforts. The current paper re-examines and updates Forthman and Ogden's original points, with attention to the five categories they detailed: (1) promotion of species-typical behavior, (2) reintroduction and repatriation of endangered species, (3) animal handling, (4) pest control, and (5) animal performances. In addition, we outline three current and future directions for behavior analytic endeavors: (i) experimental analyses of behavior and the zoo, (ii) applied behavior analysis and the zoo, and (iii) within-subject methodology and the zoo. The goal is to provide a framework that can guide future behavioral research in zoos, as well as create applications based on these empirical evaluations.

Keywords: animal welfare; animal training; applied animal behavior; behavior analysis; behavioral engineering; environmental enrichment; zoos

1. Introduction

Thirty years ago, Forthman and Ogden (1992) published one of the first papers to review the contributions of applied behavior analysis to zoos. Both authors were associated with the TECHLab (later, Georgia Tech Center for Conservation and Behavior), a partnership between Zoo Atlanta and the Georgia Institute of Technology led by Dr. Terry Maple (Maple, 2017). Dr. Maple pioneered, developed, and championed the concept of the "empirical zoo," recognizing the potential of university-zoo collaborations to impact basic and applied research, animal management and welfare practices, and education (Fernandez, 2017; Lukas et al., 1998; Maple, 2007; Maple, 2008; Maple, 2017; Perdue & Maple, 2013). Dr. Maple, along with distinguished behavior analytic scholar Dr. M. Jackson (Jack) Marr, trained many researchers who went on to advance the application of behavior analytic principles in zoo settings (Maple, 2016; Maple, 2017; Maple, 2021; Maple & Segura, 2015).

At the time, within-subject methodology to examine the effects of environmental enrichment was becoming an important cornerstone of zoo behavioral welfare research (Carlstead et al., 1993; Carlstead & Seidensticker, 1993; Newberry, 1995; Shepherdson et al., 1993; see later section on the use of within-subject methodology in zoos). The concept of enrichment itself was largely derived from Dr. Hal Markowitz's work on using operant conditioning to create desired behavioral changes in zoo animals, which was the focus of many of his publications in the late 1970s and 1980s (Markowitz, 1978; Markowitz, 1982; Markowitz et al., 1978; Markowitz & LaForse, 1987; for a review, see Fernandez & Martin, 2021). Thus, Markowitz's behavioral engineering practices, along with Forthman and Ogden's (1992) paper and the work of Dr. Terry

Maple and the TECHLab, would help pave the way for this past 30 years of applied behavior analytic endeavors into behavioral welfare efforts in zoos.

The current review re-examines the topics introduced by Forthman and Ogden (1992) as ways in which applied behavior analysis can promote the conservation, education, entertainment, and welfare goals of modern zoos. Below, we address the five topics they discussed (i.e., promotion of species-typical behavior, reintroduction and repatriation of endangered species, animal handling, pest control, and animal performances). The major focus of each section is to provide updated examples of applied behavior analytic research and efforts that have occurred in each area since Forthman and Ogden's original publication. In addition, the review concludes with behavior analytic areas of interest that are ongoing efforts and emphasize current and future zoo-based studies, including (1) experimental analyses of behavior and the zoo, (2) applied behavior analysis and the zoo, and (3) within-subject methodology and the zoo. The primary goal is to provide both a historical and theoretical foundation to guide the future of applied behavior analytic work in zoos.

2. Literature Review Criteria, Variables Coded, and Reliability

At its core, behavior analysis examines the relationship between the environment and behavior. Thus, almost all zoo-based behavioral studies can be viewed through a behavior analytic lens. Given the breadth of this topic, our goal was not to write a systematic review but instead was to further the discussion begun by Forthman and Ogden (1992) about what the science of behavior analysis can contribute to the zoo. Nonetheless, to assist the reader in understanding our review process, we have provided additional information about our publication selection criteria. Our inclusion of literature was based largely on knowledge of publications within the field by both authors, including articles included in past literature reviews (Fernandez, 2022; Fernandez & Martin, 2021; Forthman & Ogden, 1992; Martin, 2017; 98 total papers) as well as literature familiar to us through the typical ways in which scholars stay current in their field (e.g., reading journals, conducting literature searches for past studies, citation alerts; 122 total papers). In addition, we conducted a supplemental Google Scholar™ search (July, 2022) and then additional searches via PsycINFO™, PubMed™, and Web of Science™ (September, 2022) based on the following criteria: "zoo" AND "animal" AND "applied behavior analysis" OR "applied behaviour analysis". The Google Scholar™ search produced 885 results, and the other search engines produced 8 results which all overlapped with Google Scholar™. Based on titles and abstracts, we selected articles according to the following criteria: (1) must be a peer-reviewed research study, (2) involved nonhuman animals as some component of the research, and (3) were conducted at a zoo or similar facility that housed exotic animals. Based on these eligibility criteria, the search yielded 34 results. Articles were also removed if they were already included in our preliminary review (18 papers removed). This exclusion criteria left 16 results. We then assessed the full text of articles to determine relevance for our review. We excluded papers if they were (a) not of an applied nature (observation-only or otherwise not directly aimed at improving welfare; 7 papers removed), and (b) limited to a traditional enrichment-focused manipulation (not assessed for potential function; see Physical Variables section; 3 papers removed). This inclusion criteria yielded 6 results which were added to the review. Figure 1 details the results of our literature search.

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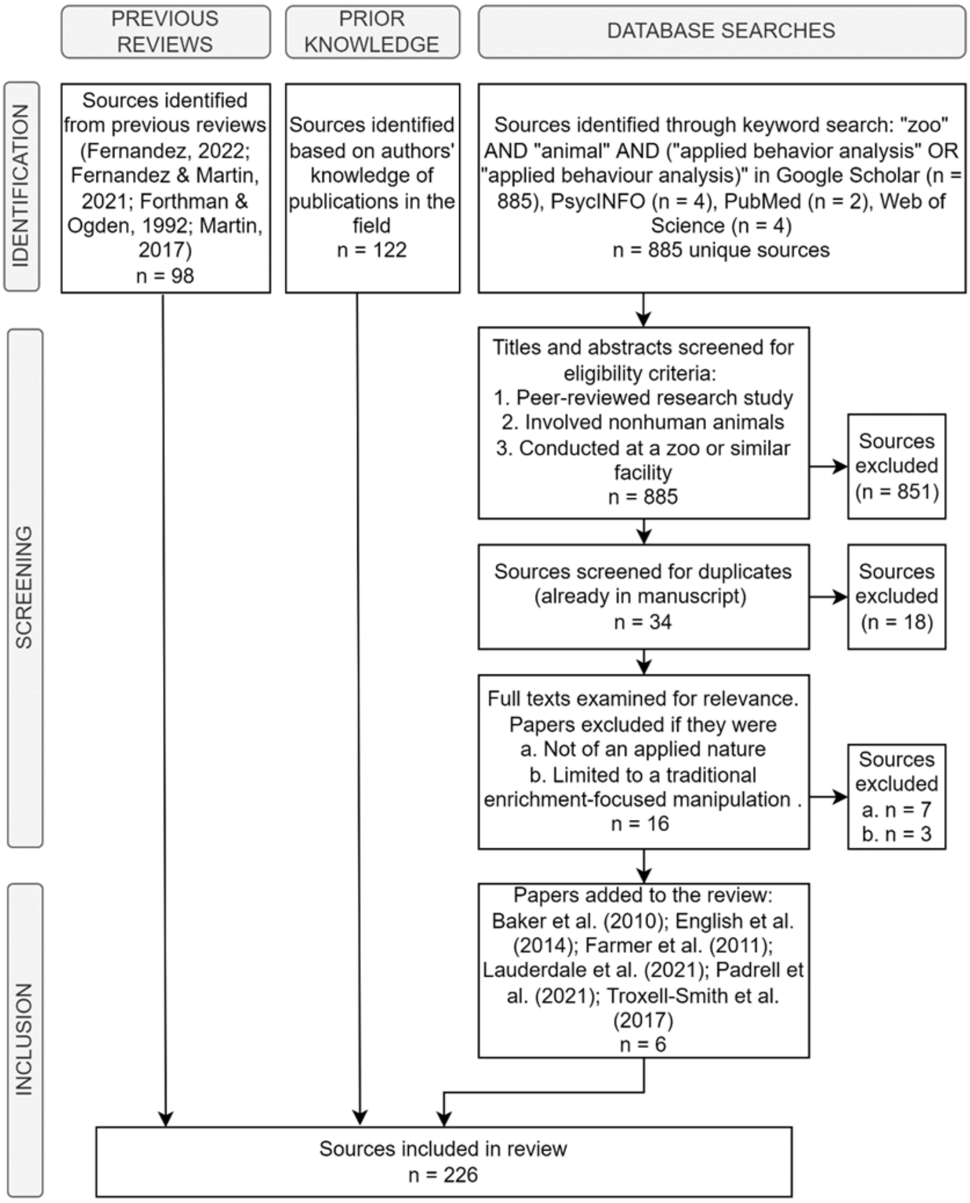

Figure 1. Flowchart of Literature Search.

Finally, given the large number of papers published in two emerging areas of research (functional analysis and preference assessments), we summarized these studies in tables (see Applied Behavior Analysis and the Zoo section later in the paper). This table-based summary required the categorization of articles on several dimensions. As a measure of inter-coder reliability, both authors independently coded exact agreement for 40% of the functional analysis articles for author and year (100% agreement), species (100% agreement), target behavior (100% agreement), experimental design (100% agreement), and primary function identified (100% agreement). Both authors also independently coded exact agreement for 32% of the preference assessment articles on author and year (100% agreement), species (100% agreement), type of stimuli used in each study (food, non-food, symbols, or mixed/multiple; 90% agreement), and whether the study presented stimuli singly, in pairs, in arrays with three or more stimuli, or in mixed/multiple ways (90% agreement).

3. Forthman and Ogden Revisited

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3.1. Promotion of Species-Typical Behavior

For the better part of a century, zoos and zoo-like facilities have been concerned with getting animals to behave similarly to their wild counterparts (Hediger, 1950; 1955; Morris, 1964; Yerkes, 1925). Early applied behavior analytic endeavors in zoos, such as the work of Markowitz and colleagues noted above, achieved some of these goals by developing simple operational definitions of the desired responses and using mechanical devices installed in exhibits to reinforce these contrived behaviors. However, these efforts were met with criticism, particularly how they related to non-natural behaviors and non-naturalistic environments (Hancocks, 1980; Hutchins et al., 1984). The eventual resolution would be an integrative approach that used both learning principles and species-typical understandings of behaviors and settings to guide welfare-based activities, such as environmental enrichment (Forthman-Quick, 1984). Modern examples include using wild-like enrichment activities and devices to encourage species-typical foraging behaviors, such as foraging patches with Parma wallabies (*Macropus parma*) and Patagonian cavies (*Dolichotus patagonum*; Troxell-Smith et al., 2017), as well as the use of artificial termite mounds with chimpanzees (*Pan troglodytes*; Padrell et al., 2021).

While a detailed historical examination of the convergence of learning and evolution to understand behavior is beyond the scope of this paper, it is worth noting that Forthman and Ogden's (1992) interest in species-typical behavior from a learning perspective echo concerns raised by Keller and Marian Breland (1961), as well as Dr. Richard Herrnstein (1977), when addressing the importance of attending to the evolutionary history of the organisms that are learning. Likewise, Skinner himself would make similar points about the importance of understanding the phylogeny of behavior to better understand how any response is selected (Morris et al., 2004; Skinner, 1966a; Skinner, 1984). In addition, behavior systems researchers emphasized non-learned, biological components of behavior that would influence an organism's ability to learn (Domjan, 1983; Shettleworth, 1993; Timberlake, 1993; Timberlake & Lucas, 1989), and more recently, behavior analysts such as Dr. William Baum (2012) have echoed the importance of Phylogenetically Important Events (PIEs) on learned behavior. Finally, the extent to which researchers use species-typical or "natural" behavior as an animal welfare metric across a variety of settings has been discussed and debated (Browning, 2019; Fraser, 2008; Hutchins, 2006). Nonetheless, species-typical behavior serves as an important assessment and improvement welfare measure, particularly for the diversity of wild animals typically displayed in zoos.

Below, we consider two sub-categories of promoting species-typical behavior that Forthman and Ogden (1992) originally outlined: (1) physical variables, such as exhibit space, feeding schedules, and potential enrichment items, and (2) social variables, such as the way zoo animals are housed with other animals. For both sub-categories, we focus on more recent behavioral advancements published after Forthman and Ogden's publication as well as how related research has been used in application to benefit the lives of zoo animals.

3.1.1. Physical Variables

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Applied behavior analysis as a field is certainly familiar with understanding the importance of the environment on behavior, particularly as it relates to antecedents (e.g., discriminative stimuli and setting events), and consequences. One of the key physical variables studied in zoos and noted by Forthman and Ogden (1992) is environmental enrichment. Since the time of their original publication, hundreds of studies on enrichment in zoos have been published. Thus, an extensive examination of each of these studies is not possible within this review (see Shyne, 2006; Swaisgood & Shepherdson, 2005; Zhang et al., 2021 for a selection of meta-analyses conducted on aspects of enrichment involving zoos or aquariums). However, a few noteworthy studies include examinations that have used common applied behavior analytic procedures to assess and enhance the welfare benefit of enrichment practices, such as the use of preference assessments to determine both the type and effectiveness of potential enrichment (Clayton & Shrock, 2020; Dorey et al., 2015; Fernandez et al., 2004; 2019b; Mehrkam & Dorey, 2014; Mehrkam & Dorey, 2015) as well as the use of feeding schedules, including fixed- and variable-time schedules, predictable vs. unpredictable feeding schedules, and live prey feeding events as forms of enrichment (Andrews & Ha, 2014; Bloomsmith & Lambeth, 1995; Fernandez, 2020; Fernandez, Myers, & Hawkes, 2021; Wagman et al., 2018). In all the above, a core element, as stressed by Forthman and Ogden, is a *functional* evaluation of the physical variables of interest. This necessarily means using experimental manipulations, ideally those that include within-subject manipulations such as reversals and/or multiple-baseline designs (Alligood et al., 2017; Fernandez & Timberlake, 2008; Maple & Segura, 2015).

Another set of physical variables important for promoting desired species-typical behaviors in zoo animals are the exhibits themselves. Following Forthman and Ogden's (1992) publication, a few zoo researchers and personnel have emphasized the importance of understanding how exhibit design influences the behavior and welfare of zoo animals, including using rotating exhibits (Coe, 2004), the effects of exhibit space use and choice (Owen et al., 2005; Ritzler et al., 2021), the effects of different exhibit structures and changes to exhibits (Carlstead et al., 1993; Fernandez et al., 2020), and the use of computer technology to modify exhibit interactions (Coe & Hoy, 2020; Carter et al., 2021). Again, like environmental enrichment, the emphasis here is on understanding the *function* of the physical exhibit variable on the behavior of the exhibited animal and for applied purposes. From a behavior analytic perspective, this is most readily accomplished through experimental, within-subject designs (see 'Within-Subject Methodology and the Zoo' section below).

3.1.2. Social Variables

Forthman and Ogden (1992) stressed the importance of understanding social factors, including how animals in zoos are exhibited with other animals. Nonetheless, only a few studies have directly examined how changes in social structures, specifically changes in the number of individuals housed together, benefits the behavior of zoo animals. For example, several studies have explored changes in the number of elephants housed together on the behaviors of those elephants (Lasky et al., 2021; Schmid et al., 2001). Other researchers have examined differences in the social housing of black and gold howler monkeys (*Alouatta caraya*), including the reproductive success of monkeys under different social housing conditions (Farmer et al., 2011). Likewise, researchers have investigated the social dynamic of giraffes (*Giraffa camelopardalis*) under different management and housing conditions (Bashaw et al., 2007; Bashaw, 2011), including maternally raised or deprived giraffes (Siciliano-Martina & Martina, 2018). One difficulty with these studies is that the conditions observed are not directly experimentally manipulated. Zoos rarely have the luxury of engaging in such manipulations, because they are both cost prohibitive and potentially detrimental to the welfare of their animals. However, a couple studies have experimentally examined changes in the social housing of zoo animals. Rowden (2001) studied social interactions in Bulwer's wattled pheasants (*Lophura bulweri*) by changing the number of individuals housed together, either in pairs or larger groups. Similarly, Fernandez and Harvey (2021) used quasi-experimental reversals to examine how changes in the social housing of African wild dogs (*Lycaon pictus*) impacted enclosure use. In both studies, these experimental manipulations allowed for greater prediction and control of the social variables of interest, which itself could allow for greater specificity in the social housing and management of zoo animals.

It is also worth noting that social variables can include the Human-Animal Interactions (HAIs) observed in zoos, a concept often described as Animal-Visitor Interactions (AVIs; Davey, 2007; Fernandez et al., 2009; Hosey, 2000; Sherwen & Hemsworth, 2019). Historically, AVIs were seen as problematic for the conservation education of visitors, as well as generally having a negative impact on the welfare of zoo animals (Kreger & Mench, 1995). However, in the past two-plus decades, greater emphasis has been placed on the positive impacts that visitors can have on zoo animals (i.e., visitor effects; Hosey, 2000), and the impact of zoo animals and the zoo itself on visitors (i.e., visitor experiences; Godinez & Fernandez, 2019; Learmonth et al., 2021). In addition, others have discussed HAIs in zoos that do not involve visitors, including keepers or staff (Hosey et al., 2018; Ward & Melfi, 2015). The relevant factor is that behavior analysis offers a unique perspective for understanding all HAIs observed in zoos, particularly as they relate to the directly observable behaviors offered by both animals and visitors. In addition, the use of experimental manipulations is necessary for distinguishing between visitor effects and visitor experiences. The assumption is often that changes observed in animal activity are the result of visitor presence, but without proper experimental control, researchers cannot assume that visitors cause changes in animal activity or vice versa, or whether they are even causally related (Fernandez & Chiew, 2021).

3.2. Reintroduction and Repatriation of Endangered Species

The conservation of species via reintroduction of animals born and reared in zoos has been a major goal of the modern zoo (Fa et al., 2011; Fernandez & Timberlake, 2008). Although many reintroduction efforts are carefully assessed, the assessments often do not involve quantitative data. Forthman and Ogden (1992) note one species, the golden lion tamarin (*Leontopithecus rosalia*), where empirical efforts have been used to evaluate the effects of introducing captive-bred zoo animals into the wild (Kleiman et al., 1986). Since the time of Forthman and Ogden's publication, these efforts have continued, including comparisons of wild-born and captive-born tamarins, examinations of semi-free-ranging populations in captivity, and the use of different types of environmental enrichment in captivity and in relation to species-typical behaviors necessary for wild tamarins (Bryan et al., 2017; Castro et al., 1998; Price et al., 2012; Ruiz-Miranda et al., 2019; Sanders & Fernandez, 2020; Stoinski et al., 1997; Stoinski et al., 2003). Other notable species examples include examinations of wild-like captive conditions for the endangered black-footed ferret (*Mustela nigripes*; Miller et al., 1998), the effects of releasing oldfield mice (*Peromyscus polionotus subgriseus*) into testing settings meant to mimic the wild (McPhee, 2003), and examinations of captive breeding and rearing practices of Key

Largo woodrats (*Neotoma floridana smalli*) to improve their successful reintroductions (Alligood et al., 2008; Alligood et al., 2011; Wheaton et al., 2013). These empirical studies that focus on how the arrangement of environmental contingencies impact behavior and, as a result, the success of reintroductions, offer glimpses at how applied behavior analytic research efforts that focus on quantitative, experimental methodology could help assess and improve reintroduction efforts for a variety of species found in zoos.

3.3. Animal Handling

Forthman and Ogden (1992) detailed the importance of applied behavior analysis in improving the husbandry practices that are commonplace within zoos. As they noted, using behavioral principles, zoos have been able to move away from chemical or physical immobilization practices to conduct the routine veterinary care necessary for their animals. This in large part was a result of the work of Keller and Marian Breland, who effectively demonstrated the use of positive reinforcement to increase voluntary participation of a wide variety of animal species in many diverse settings (for a review, see Fernandez & Martin, 2021).

While the use of positive reinforcement to improve animal handling practices in zoos and similar exotic animal settings is now commonplace, only a handful of publications have empirically examined its effects. Denver Zoo trained nyala (*Tragelaphus angasi)* and bongo (*Tragelaphus eurycerus*) to voluntarily enter crates for blood draws and other veterinary procedures (Grandin et al., 1995; Phillips et al., 1998). Bloomsmith et al. (1998) and Veeder et al. (2009) successfully used reward-based methods to train large groups of chimpanzees (*Pan troglodytes)* and mangabeys *(Cercocebus atys atys)* to move (i.e., "shift") to different areas within their enclosures. Savastone et al. (2003) detailed reward-based procedures to train a variety of behaviors in a dozen different zoo-housed new world monkey species. Cheyenne Mountain Zoo trained giraffe (*Giraffa camelopardalis reticulata*) to participate in radiographs and hoof care (Dadone et al., 2016). Researchers have also examined the potential enriching or behavioral welfare effects of training Asian elephants (*Elephas maximus*) to paint, as well as training rhesus macaques (*Macaca mulatta*) for various body part presentations or similar responses (Baker et al., 2010). Finally, Zoo Atlanta researchers documented the changes in both trainer and elephant (*Loxodonta africana africana*) behaviors during a transition to a positive reinforcement-based management system (Wilson et al., 2015).

All the above studies involved before/after comparisons of various reinforcement-based procedures to increase targeted behaviors. More recently, several studies have been published that directly examined the shaping process to train petting zoo sheep (*Ovis aries*), a petting zoo goat (*Capra hircus*), and an African crested porcupine (*Hystrix cristata*) for different desired behaviors (Fernandez, 2020; Fernandez & Dorey, 2021; Fernandez & Rosales-Ruiz, 2021). In addition, Lauderdale et al. (2021) examined various features of training sessions on bottlenose dolphin (*Tursiops truncatus*) beaching/shifting responses, including number of sessions and trials, average trials per session, time between session, and criteria changes between trials, attempt and success rates, and magnitude of reinforcers delivered. Shaping research focused on continuous learning achievements, rather than pre-/post-test training results, should facilitate our understanding of the conditions that are more likely to improve zoo animal handling practices. Regardless, the idea is simple: Positive reinforcement-based animal handling and training practices can increase the likelihood of better physiological welfare for zoo animals, in addition to potentially functioning as behavioral enrichment (Fernandez, 2022).

3.4. Pest Control

Forthman and Ogden (1992) proposed that applied behavior analytic techniques could be useful in managing free ranging "pest" species such as rodents and birds that enter zoo exhibits and pose potential for disease transmission and other hazards. While this area has not seen a large growth in behavior analytic research, the potential remains. Any form of pest-management must take behavior into account, and applied behavior analysis could offer guidance in this area. Most pest control techniques focus on antecedents that attract or repel animals, and preference assessments can be useful in determining traps an animal is likely to enter (Carey et al., 1997) or baits an animal is likely to consume (Allsop et al., 2017; Morgan, 1990). In addition, if a potentially harmful bait will be used in a zoo enclosure, preference assessments and/or conditioned taste aversion can help to ensure that the bait is unlikely to be consumed by non-target animals (Clapperton et al., 2013; Clapperton et al., 2015). Taking a more natural approach, antecedent manipulations could be used to attract natural predators that can help to reduce pest populations (Antkowiak & Hayes, 2004).

3.5. Animal Performances

The training of marine mammals for shows played a key role in the promotion of regular husbandry training procedures in zoos, which has been essential as an application for improving zoo animal lives. As noted earlier, this was due in large part to the influence of Keller and Marian Breland in bringing behavior analytic principles to a variety of settings, which included show animals located in dolphinariums. Since then, the use of positive reinforcement to promote voluntary involvement in husbandry practices and improve behavioral welfare has been a hallmark for show animals (Brando, 2012; Eskelinen et al., 2015). Nonetheless, in recent years greater concern has been placed on the use of animals for shows or performance, including whether animals such as cetaceans (whales and dolphins) should exist in any form of captivity (Rose & Parsons, 2019). It is also worth noting that modern zoos have updated their focus on animal performances to include educational efforts that promote the conservation and welfare of the individuals and species involved in such shows (D'Cruze et al., 2019). In the past 30 years, the public and the zoos themselves have had a dramatic change in the perceptions of the purpose of animal performances, including the outcomes of these activities on the well-being of those animals.

While Forthman and Ogden (1992) noted their opinion that animal performances improve the physiological and psychological welfare of animals, it is only more recently that studies have investigated the behavioral effects of animal performances or similar performance-like interactions on the welfare of those animals. For instance, Kyngdon et al. (2003) found that short-beaked common dolphin (*Delphinus delphis*) trained to engage in a 'Swim-with-Dolphins' program increased their surfacing and use of outside areas during programs, but otherwise showed few behavioral changes before, during, or after the interactions (thus suggesting little to no negative welfare impact from such programs). Similarly, Trone et al. (2005) found few behavioral differences in bottlenose dolphins (*Tursiops truncatus*) in the times before or after interaction programs. They additionally noted an increase in play behaviors following interactions, which may have indicated potential positive welfare effects of the interactions. Finally, Fernandez, Upchurch, and Hawkes

(2021) examined the effects of a visitor feeding program on the activity of the exhibited elephants. They successfully demonstrated that the feeding programs increased overall activity and decreased undesired behaviors, such as stereotypies. Thus, as the purpose of animal performances in zoos has changed, this should require greater understanding of the impact of such shows on the animals. Future applied behavioral research in zoos could focus more directly on some of these direct welfare impacts, as well as what visitors learn from such shows.

4. Current and Future Directions

Below, we consider additional areas of focus that are of mutual interest to both the field of behavior analysis and zoos. These three foci include (1) experimental analyses of behavior and the zoo, (2) applied behavior analysis and the zoo, and (3) within-subject methodology and the zoo. We consider each of these areas because basic and applied research have been traditional distinctions for the field of behavior analysis, and each focus has benefits they could bring to future zoo research and application through some of their areas of interest. Likewise, within-subject methodology has been a staple of behavior analytic research and practice, and greater use of such methodology could directly benefit the welfare of zoo animals.

4.1. Experimental Analyses of Behavior and the Zoo

While a detailed examination of all the experimental analyses of behavior's potential contributions to zoo research exceeds the purpose of this review, it is worth pointing out several areas of overlap that are of mutual interest to both zoos and basic research in behavior analysis. These three areas include studies that involve (1) contrafreeloading, (2) autoshaping, and (3) conditioned reinforcement. Below we focus on how experimental studies of these topics could simultaneously improve our scientific understanding of behavior while contributing to behavioral welfare improvements or other applications meant to improve the lives of zoo animals.

4.1.1. Contrafreeloading

Contrafreeloading describes the phenomenon where animals will choose to work for food (e.g., press a lever or operate similar operandum) over freely available food (Jensen, 1963; Neuringer, 1969). While the concept of contrafreeloading has been investigated across multiple species and settings (see Inglis et al., 1997 for a review), only a few studies have examined contrafreeloading in zoos. For instance, McGowan et al. (2010) were able to demonstrate that captive grizzly bears (*Ursus arctos horribilis*) would spend at least a portion of their time retrieving food from ice blocks or enrichment boxes over free food alone. Vasconcellos et al. (2012) showed that captive maned wolves (*Chrysocyon brachyurus*) would spend more time searching for food scattered across vegetation, as well as consume half their diet from scattered feedings when compared to food delivered on a tray in one section of their enclosures. Sasson-Yenor and Powell (2019) demonstrated that several zoo-housed giraffes (*Giraffa camelopardalis*) were more likely to contrafreeload when presented simultaneously with easily accessed or more time-consuming enrichment foraging devices.

The topic of contrafreeloading itself raises interesting theoretical questions about the interplay between learning and evolved foraging patterns (Killeen, 2019; Timberlake, 1984). In addition, contrafreeloading should be of great interest to zoos, since many of the problem behaviors observed in exhibited animals (e.g., stereotypies) have been associated with species-typical foraging patterns (Fernandez, 2021; Fernandez & Timberlake, 2019a). It could be argued that all food-based enrichment deliveries elicit behavior like that observed in contrafreeloading procedures, and therefore should equally be of interest for testing behavioral theories of contrafreeloading while benefiting exhibited animals by increasing species-typical foraging patterns and increasing overall activity.

4.1.2. Autoshaping

Autoshaping describes a phenomenon in which voluntary behavior, such as key pecking, is respondently conditioned (Brown & Jenkins, 1968; Williams & Williams, 1969). Since the time of its discovery, it has been the focus of intense theoretical scrutiny, including the extent to which operant contingencies alone can successfully describe the behaviors observed under standard laboratory conditions (Timberlake, 2004; Timberlake & Lucas, 2019). The concept of autoshaping itself should be of interest to both basic researchers and practitioners when examining their effects on zoo animals. For example, researchers have been able to use respondent conditioning procedures to increase the reproductive success of animals (Domjan et al., 1998; Gaalema, 2013; Hollis et al., 1997). Given that reproductive behavior is both voluntary activity and of great applied interest for zoo animals on Species Survival Plans (SSP; AZA, 2022), behavior analysts would do well to help foster empirical studies done on autoshaping and reproduction in zoos. Likewise, autoshaping has been used as a training procedure to increase time spent contacting a pool-based enrichment feeding device, and therefore time spent swimming, in zoo penguins (Fernandez et al., 2019). Again, like efforts using autoshaping to increase reproductive efforts, autoshaping could be studied across a plethora of different species in zoos, while simultaneously increasing enrichment device interactions, and thus have applied welfare benefits in the process of conducting such theoretical examinations.

4.1.3. Conditioned Reinforcement

Conditioned reinforcement, whereby a secondary stimulus associated with a primary reinforcer comes to maintain operant behavior, has been an important concept for the experimental analysis of behavior (Lattal & Fernandez, 2022; Pierce & Cheney, 2013). As early as 1938, Skinner described the ability of a clicking sound paired with food to reinforce lever pressing in the absence of food deliveries. Both Skinner and Keller and Marian Breland would later describe the importance of using conditioned reinforcement to train animals outside of the lab (Breland & Breland, 1951; Skinner, 1951). The idea was popularized by Karen Pryor as a form of "clicker training" that could be used to train dogs, as well as other animals, for a variety of applied purposes (Pryor, 1984). In the lab, the concept would become a focal point for understanding operant procedures (for reviews, see Fantino & Romanovich, 2007; Kelleher & Gollub, 1962). Similarly, the use of conditioned reinforcement for applied purposes has been examined, including whether conditioned reinforcement successfully improves some dimension of responding, such as speed of acquisition (Chiandetti et al., 2016; Dorey et al., 2020; Dorey & Cox, 2018; Gilchrist et al., 2021; Pfaller-Sadovsky et al., 2020).

While the importance of understanding conditioned reinforcement for both basic and applied research purposes continue, a divide still exists between information obtained from the lab and the field. For instance, early confusion existed on delivering conditioned reinforcers in the absence of following primary reinforcers, an idea originally thought of as a form of "variable reinforcement" (Fernandez, 2001). Likewise, laboratory research on the importance of delay-reduction and information hypotheses of conditioned reinforcement have rarely been acknowledged outside of the lab, or only loosely identified or contrasted to marking/bridging hypotheses as they might apply in and outside of the lab (Dorey & Cox, 2018; Egger & Miller, 1962; Fantino, 1969; Williams, 1994). Zoos could provide a testing ground for translational research that experimentally examined the theoretical underpinnings of conditioned reinforcement, while providing a better connection between lab and field studies of conditioned reinforcement and improving the training procedures vital to the welfare of zoo animals.

4.2. Applied Behavior Analysis and the Zoo

In addition to using behavioral science to optimize existing animal management practices such as environmental enrichment, researchers and zoo personnel have also borrowed specific techniques and protocols from applied behavior analytic clinical practices and modified them for use in applied animal settings. This represents a unique reverse-translational cycle (Dixon et al., 2016; Edwards & Poling, 2011; Gray & Diller, 2016), where 1) basic principles from animal laboratory studies are used to 2) develop effective behavioral assessments and treatments in human clinical settings, and then 3) these human clinical protocols are used to improve captive animal care and welfare. As pointed out by others (Bloomsmith et al., 2007; Gray & Diller, 2016; Maple & Segura, 2015; Martin, 2017), the research and clinical approaches of behavior analysts have commonalities with the needs of zoos that make the transfer of behavioral technologies between the two settings beneficial. These commonalities include treatments developed for and evaluated at the individual level (Alligood et al., 2017; DeRosa et al., 2021; Fisher, Groff et al., 2021; Saudargas & Drummer, 1996) and a focus on both building skills (Fisher, Piazza et al., 2021) (or, in zoos, promoting species-typical behaviors) and decreasing behavioral excesses, including some of the same topographies of problem behavior seen in both settings (Bloomsmith et al., 2007).

4.2.1. Functional Analysis

One example of this reverse translational research is the functional analysis technique. Drawing from his work with laboratory animals, Skinner (1953) developed the conceptual foundation for the functional analysis, emphasizing the impact of environmental events on behavior. Iwata and colleagues (1994) then formalized a behavioral protocol that identified the existing environmental contingencies that reinforce and maintain problem behaviors. Over the past four decades, behavior analysts have successfully used function-based treatments in human clinical settings to reduce behaviors including self-injury, aggression, disruptiveness, and food refusal (Beavers et al., 2013; Hanley et al., 2003). More recently, researchers have used this same approach to successfully assess and treat problem behaviors in captive animals, including in zoo-housed species. Functional analysis methodology has been used to assess and treat self-directed behaviors as well as disruptive or aggressive behaviors in nonhuman primates and in birds (Table 1). In all cases, a function-based treatment consisting of some combination of extinction, differential reinforcement, and/or the application of non-contingent reinforcement successfully reduced these problem behaviors (Dorey et al., 2009; Farmer-Dougan, 2014; Franklin et al., 2021; Martin et al., 2011; Morris & Slocum, 2019).

This functional approach to reducing abnormal behaviors in animals has many benefits, but it also has some limitations. While most of the functional analyses conducted with zoo-housed species have involved primates (Table 1), the inclusion of a vulture (Morris & Slocum, 2019) as well as the success of this approach in companion dogs (*Canis lupus familiaris*) and cats (*Felis catus*) (Dorey et al., 2012; Hall et al., 2015; Mehrkam et al., 2020; Pfaller-Sadovsky et al., 2019; Salmeron et al., 2021; Winslow et al., 2018) suggests that it can be useful across a range of species. However, these assessments are time and labor-intensive, and they can only be used to assess antecedents and consequences that can be systematically presented and withdrawn. Indeed, most functional analyses of zoo-housed species identified either social attention (i.e., attention function) and/or human-delivered food items (i.e., tangible function) as the reinforcer for the problem behaviors (Table 1). Thus, in zoo settings, this approach seems especially useful to assess problem behaviors that may be maintained by interactions with zookeepers or visitors. However, many abnormal behaviors in zoo-housed animals are likely to be maintained by consequences from other animals or by non-social (or "automatic") reinforcers such as sensory stimulation or a decrease in arousal. These behaviors are more challenging to assess and treat, although the behavior analytic literature can offer some guidance in these areas as well, including possibilities like antecedent assessments, non-contingent reinforcement, sensory extinction, or sensory-matched enrichment (see Martin, 2017).

4.2.2. Preference Assessments

Another behavioral protocol developed in human clinical settings that has been of use in zoos is the stimulus or reinforcer preference assessment. In applied behavior analytic work with children, empirical preference assessments are conducted in educational settings and treatment clinics to determine items or activities that are likely to serve as positive reinforcers for desired behaviors (Saini et al., 2021). Protocols include those in which items are presented one at a time (Pace et al., 1985), in pairs (Fisher et al., 1992), or in an array with multiple stimuli (DeLeon & Iwata, 1996), and items ranked higher in preference using these methods have been found to function as more effective reinforcers for various desired behaviors than lower preference items (e.g., Carr et al., 2000; Lee et al., 2010; Pace et al., 1985; Piazza et al., 1996). Given the wide use of positive reinforcement training in zoos (Fernandez & Martin, 2021), researchers and zoo personnel recognize the importance of using highly preferred items to make training as efficient as possible. In addition, foods chosen by human or animal caregivers have been found to have low correlation with preferences determined empirically (e.g., Cote et al., 2007; Gaalema et al., 2011; Green et al., 1988; Mehrkam & Dorey, 2015), emphasizing the need for empirical assessments.

The three decades since Forthman and Ogden's (1992) paper have seen a surge in the use of empirical preference assessments in zoo-houses species. As summarized in Table 2, researchers have empirically determined preferences in a wide variety of species, from invertebrates to apes. Most preference assessments have involved food items, but some have involved other stimuli, including enrichment items, scents, and activities. Most studies have used some variation of free-operant or forced-choice paired presentations, but methodologies involving single-item presentations and arrays with three or more stimuli were also used. Additionally, some researchers have further extended methodologies by using symbolic representations of items (e.g., images, tokens) to facilitate choice or by adapting the methodologies by presenting stimuli to groups rather than individuals (Table 2).

In most of these animal preference studies, some measure of choice (e.g., approach, consumption) was the main dependent variable. However, some studies took the additional step to see if preference translated to actual reinforcer effectiveness. Just as in the human literature, most studies have shown that high preference items served as more effective reinforcers than lower preference items, resulting in more lever presses (Dixon et al., 2016), more touchscreen touches (Hopper et al., 2019), more touches to training targets (Martin et al., 2018), more enrichment use (Fay & Miller, 2015; Fernandez & Timberlake, 2019; Mehrkam & Dorey, 2014; Woods et al., 2020), higher engagement in husbandry training (Martin et al., 2018), or swimming against stronger currents (Sullivan et al., 2016). However, one study (Schwartz et al., 2016) showed no difference in amount of work capuchin monkeys (*Cebus apella*) were willing to perform (as measured by weight lifted) based on preference as assessed through pair-wise presentation. Preference assessments have also been used to investigate concepts such as preference for novelty (Addessi et al., 2005), variety (Addessi et al., 2008; Addessi et al., 2010), work/contrafreeloading (Sasson-Yenor & Powell, 2018), or choice (Perdue et al., 2014). Preference stability across time has also been investigated (Addessi et al., 2010; Clay et al., 2009; Hopper et al. ,2019; Martin et al., 2018; Vonk et al., 2022). All these findings can be used to guide animal management practices to optimize welfare (see Broom & Johnson, 2019). These protocols also offer zoo animals choice, which is increasingly considered an important component of animal welfare (Melfi & Ward, 2020; Patterson-Kane et al., 2008; Wickens-Drazilova, 2006).

4.2.3. Future Use of Applied Behavior Analysis Protocols

While we have highlighted two behavioral protocols that were developed in human treatment clinics and adapted for use in the zoo (functional analysis and preference assessments), there are many other behavioral protocols that could be useful in zoo settings. For example, a veterinarian having difficulty getting an animal to consume oral medications to animals could borrow from the applied behavior analytic literature related to blending (Mueller et al., 2004) or the use of chasers (Vaz et al., 2016; see Daly et al., 2019) to increase food consumption. A zookeeper working to train a long duration behavior could model their training after similar protocols with children that used percentile schedules (e.g., Athens & Vollmer, 2013; Galbicka, 1994; Hall et al., 2013). Further sharing of protocols between human and non-human settings has great potential. However, realizing the full potential of applied behavior analysis in zoo settings will require the training of more individuals who are both well-versed in the fundamentals of behavior analysis and who have experience in animal management so that new behavioral protocols can be developed and implemented to maximize animal welfare (Fernandez & Timberlake, 2008; Friedman et al., 2021; Gray & Diller, 2017; Maple & Perdue, 2013; Maple & Segura, 2015; Martin, 2017).

4.3. Within-Subject Methodology and the Zoo

A final note worth making is the importance of within-subject methodology in the study and improvement of the behavioral welfare of zoo animals. Skinner (1957; 1966b) defined the experimental analysis of behavior as any manipulation of an independent variable (IV) that included a contingency, which Skinner identified as reinforcement, with a measured dependent variable (DV) of some dimension of behavior, which Skinner presumed would be rate. While the components of either the IV or DV need not necessarily be either reinforcement or rate, respectively, the importance of using within-subject methodology to analyze behavior was clearly emphasized in Skinner's operational definition of the experimental analysis of behavior, and therefore behavior analysis.

Likewise, the zoo environment has a strong need for such methodological designs, given the limited number of individuals often exhibited in any one enclosure, as well as the demand for understanding the function of any event, such as environmental enrichment, on the individual behaviors of those zoo-housed animals (Alligood et al., 2017; Fernandez, 2022; Fernandez & Timberlake, 2008; Maple & Segura, 2015). While the incongruence in larger group, between-subject methodology and the small number of individuals often housed in any one zoo exhibit is clear, a common misunderstanding is that therefore the only options left are case studies or observation-only designs. However, as noted in the paragraph above and by the title of this section, within-subject methodology offers quantitative, empirical solutions to optimally understand zoo animal behavior. Some of the many benefits of within-subject methodology (over between-subject methodology) include (a) a focus on many data points from a few individuals (as opposed to few data points from many individuals), (b) an emphasis on inductive data collection that modifies procedures based on real-time results (as opposed to a priori hypothesis testing), and (c) the ability to assess an individual's learning repeatedly and over time (as opposed to pre- versus post-test analyses) (Bailey & Burch, 2017; DeRosa et al., 2021; Johnston & Pennypacker, 2010). In short, all research efforts aimed at improving the lives of individual animals are studies of (n) = 1. Even if it were possible to produce enough subjects to run a standard between-subject study on some welfare advancement (generally not the case, given the limitations of exhibit space size and/or species numbers within zoos), providing individualized welfare plans based on differences between the *average* of some group is of limited use if the animal in question does not respond in the average way. Single-case designs allow for the empirical examination of each individual animal's important behavior contingencies to best promote welfare.

5. Conclusions

Forthman and Odgen (1992) saw the great potential for applied behavior analysis and zoo collaborations. In the three decades since their publication, applied behavior analysis has provided the scientific basis for many empirical studies that have both advanced applied science and have improved the welfare of zoo animals. Behavior analytic methodologies and their focus on the overt behaviors of individuals is ideally suited for improving the lives of zoo animals, and it is our hope that this updated review of applied behavior analysis in zoos provides a proper framework for both past efforts and future endeavors to continue making such research possible.

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Author Note

Eduardo J. Fernandez: https://orcid.org/0000-0001-5444-6604

Allison L. Martin https://orcid.org/0000-0003-2868-0899

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Correspondence concerning this publication should be addressed to Eduardo J. Fernandez, Ph.D., School of Animal and Veterinary Sciences, University of Adelaide, Adelaide 5005, AUSTRALIA; Email: edjfern@gmail.com

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Table 1

Summary of Functional Analysis Studies involving Zoo-Housed Species, Including Species, Target Behavior(s), Experimental Design, and the Function Identified as Having the Highest Levels of Behavior (Primary Function).

Author(s) (Year)	Species	Target Behavior(s)	Experimental Design	Primary Function
Dorey et al. (2009)	Olive baboon (*Papio hamadryas anubis*)	Self-directed behavior (hair pulling, hand biting, foot biting)	Multi-element	Positive Reinforcement (attention from humans)
Farmer-Dougan (2014)	Black-and-white ruffed lemur (*Varecia variegate variegata*)	Disruptive/Aggressive Behavior (aggression toward humans)	Other/Unable to Determine	Other/Unable to Determine
Franklin et al. (2022)	Rhesus macaque (*Macaca mulatta*)	Disruptive/Aggressive Behavior (noise)	Multi-element	Positive Reinforcement (food)
Martin et al. (2011)	Chimpanzee (*Pan troglodytes*)	Disruptive/Aggressive Behavior (human-directed feces throwing, object throwing, and spitting; screaming, cage shaking)	Reversal	Positive Reinforcement (attention and juice from humans)
Morris & Slocum (2019)	Black vulture (*Coragyps atratus*)	Self-directed (feather-plucking)	Multi-element	Positive Reinforcement (attention from humans)

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Table 2

Summary of Preference Assessment Studies Involving Zoo-Housed Species, Including the Species, the Types of Stimuli Used, and Whether Stimuli Were Presented Singly, in Pairs, or as Arrays with Three or More Items Presented Simultaneously

Author(s) (Year)	Species	Stimuli	Presentation
Addessi (2008)	Capuchin monkeys (*Cebus apella*)	Food	Paired
Addessi et al. (2005)	Capuchin monkeys (*Cebus apella*)	Food	Paired
Addessi et al. (2010)	Capuchin monkeys (*Cebus apella*)	Mixed/Multiple (Food, Symbols/tokens representing foods)	Mixed/Multiple (Paired, Array)
Bloomfield et al. (2015)	Sumatran orangutans (*Pongo pygmaeus abelii*), Bornean (*Pongo pygmaeus pygmaeus)* and Sumatran orangutan hybrid	Non-food (views of humans)	Single
Brox et al. (2021)	Slender-tailed meerkats (*Suricata suricatta*)	Food	Paired (presented to groups)
Clay et al. (2009)	Sumatran organutans (*Pongo pygmaeus abelii*); Bornean orangutan (*Pongo pygmaeus pygmaeus*)	Food	Paired
Clayton & Shrock (2020)	Bengal tigers (*Panthera tigris tigris*); Siberian (*Panthera tigris altaica*) and Bengal tiger hybrid	Mixed/Multiple (Scents; Food-based enrichment; Non-food enrichment)	Mixed/Multiple (Paired, Array)
Cox et al. (1996)	California sea lion (*Zalophus californianus*)	Symbols (drawings representing foods)	Paired
Dixon et al. (2016)	Madagascar hissing cockroach (*Gromphordahina portentosa*)	Food	Array
Dorey et al. (2015)	Gray wolves (*Canis Lupus)* and Artic wolves *(Canis Lupus Arctos*)	Mixed/Multiple (Food-based enrichment; Symbols / items representing training activities)	Paired
Fay & Miller (2015)	Rothschild giraffes (*Giraffa camelopardalis rothschildi*)	Non-food (scents)	Paired
Fernandez & Timberlake (2019)	Ring-tailed lemurs (*Lemur catta*), red ruffed lemurs (*Varecia rubra*), collared lemurs (*Eulemur collairs*), and blue-eyed black lemurs (*Eulemur flavifrons*)	Food	Paired

Author(s) (Year)	Species	Stimuli	Presentation
Fernandez et al. (2004)	Cotton-top tamarins (*Saguinus oedipus*)	Food	Paired
Gaalema et al. (2011)	Giant pandas (*Ailuropoda melanoleuca*) and African elephants (*Loxodonta africana*)	Food	Paired
Hopper et al. (2019)	Gorilla (*Gorilla gorilla*)	Mixed/Multiple (Food, Symbol/images of food)	Paired
Huskisson et al. (2020)	Gorillas (*Gorilla gorilla*), chimpanzees (*Pan troglodytes*), Japanese macaques (*Macaca fuscata*)	Symbols (Images of food)	Paired
Huskisson et al. (2021)	Western lowland gorillas (*Gorilla gorilla*), chimpanzees (*Pan troglodytes*), Japanese macaques (*Macaca fuscata*)	Symbols (Images of food, computer icon representing a random food)	Paired
Martin et al. (2018)	Rhesus macaques (*Macaca mulatta*)	Food	Array
Mehrkam & Dorey (2014)	Galapagos tortoises (*Chelonoidis nigra*)	Mixed/Multiple (Non-food/enrichment, Symbol/items representing human interaction activities)	Paired
Mehrkam & Dorey (2015)	Squirrel monkeys (*Saimiri*); springbok (*Antidorcas marsupialis*), red-billed hornbirds (*Tockus erythrorhynchus*), Eastern indigo snake (*Drymarchon couperi*), American bullfrog (*Lithobates catesbeianus*), Mexican redknee tarantula (*Brachypelma*)	Mixed/Multiple (Non-food enrichment, Scents)	Mixed/Multiple (Paired, Single)
Ogura & Matsuzawa (2012)	Japanese macaques (*Macaca fuscata*)	Symbols (thumbnails of videos)	Array
Passos et al. (2014)	Tortoises (*Chelonoidis denticulata*)	Mixed/Multiple (Food-based enrichment, non-food enrichment)	Mixed/Multiple (Single, Array)
Perdue et al. (2014)	Capuchin monkeys (*Cebus*), rhesus macaques (*Macaca mulatta*)	Symbols (icons representing computer tasks)	Mixed/Multiple (Paired, Array)

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Author(s) (Year)	**Species**	**Stimuli**	**Presentation**
Remis (2002)	Western lowland gorillas (*Gorilla gorilla*), chimpanzees (*Pan troglodytes*)	Foods	Paired
Sasson-Yenor & Powell (2019)	Rothschild's giraffe (*Giraffa camelopardalis rothschildi)*	Mixed/Multiple (Food, Food-based enrichment)	Mixed/Multiple (Paired with duplication, presented to group)
Schwartz et al. (2016)	Capuchin monkeys (*Cebus apella*)	Food	Paired
Slocum & Morris (2020)	Black vultures (*Coragyps atratus*), turkey vulture (*Cathartes aura*)	Food	Paired
Sullivan et al. (2016)	Goldfish (*Carassius auratus*)	Non-food (plant enrichment)	Paired
Truax & Vonk (2021)	Western lowland gorillas (*Gorilla gorilla)*	Symbols (icons representing sounds)	Mixed/Multiple (Paired, Array)
Vonk et al. (2022)	Western lowland gorillas (*Gorilla gorilla)*	Mixed/Multiple (Foods, Symbols/images of foods)	Paired
Woods et al. (2020)	lions (*Panthera leo*)	Mixed/Multiple (Scents, non-food enrichment)	Paired