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Maximizing the effectiveness of environmental enrichment: Suggestions from the experimental analysis of behavior☆

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Abstract

Environmental enrichment programs provide benefits to both captive animals and the facilities that house them, but cost time and resources to design, implement, and maintain. As yet, there have been few theoretically based guidelines to assist animal care staff in establishing cost-efficient enrichment methods that both elicit the desired behavioral changes and maintain their success over time. We describe several well-studied principles from the field of experimental analysis of behavior, including intrinsic reinforcement, extrinsic reinforcement, habituation, extinction, and schedules of reinforcement that could be very useful for evaluating the short- and long-term effectiveness of enrichment. We use this theoretical framework to generate testable hypotheses and provide examples of enrichment studies relevant to our predictions. In particular, we suggest that enrichment devices that offer extrinsic reinforcement (food, social access, etc. as a result of performing behaviors) should produce greater and more prolonged changes in behavior than devices that rely on the behavior itself being reinforcing to the animal. For techniques that provide no extrinsic reinforcement, using stimuli that are novel, are more different from the environment, have been withheld or altered in some way, or are presented less frequently may help reduce habituation. For techniques that provide extrinsic reinforcement, making reinforcement more difficult to obtain and providing more or higher quality reinforcers may increase the long-term success of the enrichment program. In addition, enrichment may be more effective if animal care staff avoid continuously reinforcing behaviors after they are established, enriching immediately after feeding, and exposing animals to

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enrichment when reinforcement is no longer available. While the current enrichment literature supports the application of behavior analytic theory, empirical evaluation of many of our predictions is still needed.

Keywords: Environmental enrichment; Experimental analysis of behavior; Intrinsic and extrinsic reinforcement; Habituation

1. Introduction

The physical and psychological well-being of captive animals is of primary importance to facilities that house them and has been a topic of concern for many years. Environmental enrichment is ‘‘an animal husbandry principle that seeks to enhance the quality of captive animal care by providing the environmental stimuli necessary for optimal psychological and physiological well-being’’ (Shepherdson, 1998). Enrichment benefits both animals and facilities, but achieving these benefits can be costly. Animal care staff must decide on the best ways to provide enrichment considering their time, resource, and space limitations (Markowitz and Aday, 1998; Mellen et al., 1998; Mench, 1998; Sanz et al., 1999). Ineffective enrichment programs, or those that produce only short-term benefits, are not cost-effective and do little to improve animal well-being.

Many studies have been conducted to evaluate the efficacy of enrichment, and it is clear that some types of enrichment alter behavior more effectively than others. However, no single theoretical framework has been agreed upon to guide animal managers in designing and maintaining effective environmental enrichment programs. Research conducted in the experimental analysis of behavior (EAB), the scientific discipline that originated from B.F. Skinner’s philosophy of behaviorism and focuses on how behavior changes in response to the environment, is well suited to fill this role. Because basic research in EAB is typically performed in laboratory settings where potential confounds can be controlled, behavior analysts have been able to identify the specific effects of changing a variety of characteristics of environmental stimuli. The knowledge gained from this detailed experimentation provides an invaluable resource for situations in which less experimental control is possible, including enrichment research. Although many captive animal managers are familiar with the concepts of the experimental analysis of behavior, particularly operant conditioning techniques, from their use in training animals (Bloomsmith et al., 2007; Laule and Desmond, 1998), these concepts have only rarely been applied to describe changes in behavior that occur as a result of environmental enrichment (Markowitz and Aday, 1998). The objective of this manuscript is to describe several well-studied principles from the field of experimental analysis of behavior, including habituation, intrinsic reinforcement, extrinsic reinforcement, extinction, and schedules of reinforcement, that could be very useful for guiding the field of environmental enrichment. Rather than examining these principles in depth, we will discuss each briefly in relation to its potential usefulness for implementing effective enrichment programs. We will provide testable predictions for enrichment programs based on well-documented phenomena from basic science reported in the literature, and when possible, we will examine published enrichment studies to determine whether they support our predictions. Although we will primarily focus on examples from mammalian species, these principles should apply equally well to non-mammalian taxa.

2. First Steps to increasing the effectiveness of environmental enrichment

Early planning is the key to any successful project, and this is no different for environmental enrichment. Before providing enrichment or altering an animal's environment, it is important that caretakers consider several factors. First, they must specify the goal of the enrichment program for each animal. Because an improvement in animal well-being is generally measured as either an increase in desirable and naturalistic behaviors or a decrease in undesirable or stereotypic behaviors, caretakers generally implement enrichment programs to produce one or both of these changes (e.g., Baker, 1997; Carlstead, 1998; White et al., 2003). Increasing desirable behaviors, which are often referred to as species-specific behaviors or species-typical behaviors can best be accomplished by identifying the behaviors that one wants to increase (exploration, activity levels, foraging, social behavior, hunting) and then choosing a form of enrichment that specifically reinforces or strengthens those behaviors. Decreasing or weakening undesirable or stereotypic behaviors can be accomplished through punishment, however, this method may be unethical, difficult to apply, and fail to produce the desired behavioral change. For example, treating fences with an aversive chemical displaced a giraffe's stereotypic licking onto a new surface, but did not reduce the amount of time the giraffe spent licking (Tarou et al., 2003). There are many alternatives to punishment, including eliminating the reinforcement for performing the undesirable behavior and reinforcing another behavior that may be incompatible with the undesirable behavior (e.g., Novak et al., 1998). The former technique involves identifying why the animal is performing the undesirable behavior and either providing it an alternate, more appropriate opportunity to obtain that reinforcement or removing the reinforcement available for that behavior. The latter technique, because it requires a less detailed functional analysis of the undesirable behavior and acts on multiple behaviors simultaneously, may be ideal for animal care providers who are interested in both increasing species-typical behaviors and decreasing undesirable behaviors.

After deciding what behavioral change is desired, the next decision concerns the type of enrichment that will be provided. Bloomsmith et al. (1991) divide enrichment into five general categories: social, physical, feeding, occupational, and sensory. If exploration is the targeted behavior, then changing the environment or introducing a novel object may be the best type of enrichment. On the other hand, if foraging is the targeted behavior, then introducing feeding devices, changing the normal feeding regimen, or supplementing the diet may work best. Enrichment procedures tailored specifically to the targeted behaviors will prove more effective at altering behavior than those in which enrichment is provided without consideration of the relationship between the enrichment and the behavior.

The final consideration is how the enrichment will be presented. This is the factor that may be the most important for maintaining effectiveness. The manner in which enrichment is presented will directly influence the way the animals respond as well as the persistence and strength of their response to the enrichment. Some enrichment items will be reinforcing to the animal every time they are presented, whereas others will produce rapid habituation.

3. Factors that influence enrichment effectiveness

3.1. Intrinsic versus extrinsic reinforcement

Performing behavior related to an enrichment item or procedure can be either intrinsically or extrinsically reinforcing to the animal. Intrinsic reinforcement occurs when simply performing a behavior increases the probability that the behavior will occur again (Hughes and Duncan, 1988). Extrinsic reinforcement occurs when the performance of behavior results in a consequence that is external to the behavior itself and increases the likelihood that the behavior will recur. We will begin our discussion with intrinsic reinforcement, and then move on to extrinsic reinforcement.

Some behaviors that are considered to be intrinsically reinforcing include exploration and novelty-seeking (Mench, 1998), hunting behavior (Hughes and Duncan, 1988), play (Fagen, 1981), nest-building (Hughes et al., 1989), and the performance of stereotypic behaviors (Mason, 1991). Though some of these behaviors (hunting, nest-building, and exploration) may be performed to attain a tangible goal such as food, a place to lay eggs, or access to conspecifics, the ability to obtain this end goal has been argued to be unnecessary to maintain the continued performance of these behaviors. In fact, hens with access to nesting material will construct a nest even if the experimenter has already provided one for them, demonstrating that nest-building behavior is an end unto itself (Hughes et al., 1989). In the absence of a relationship between behavior and an external consequence such as food, interaction with enrichment is intrinsically motivated. As long ago as 1955, Hediger noted that ‘‘many predators are very glad of some pleasant interruption of their rather monotonous existence; that is why they are often given wooden balls and the like to play with’’ (1968 translation, p. 135). Because hunting behavior is intrinsically motivating, some types of objects have been used with success to increase hunting and play in felids, at least immediately following presentation (Markowitz and LaForse, 1987; Wooster, 1997).

Animals are also intrinsically motivated to explore new spaces, or examine new sensory information in familiar spaces, even when no resources are used or discovered during exploration (Mench, 1998). Rotating animals among enclosures or even moving them in and out of the same enclosure would, therefore, be predicted to increase behaviors related to exploration, including sensory investigation and locomotion. There is some evidence for this in the enrichment literature. For example, gorillas that were systematically alternated between enclosures showed greater enclosure use, feeding, and activity, especially in the first 4 days after rotation (Lukas et al., 2003). Similarly, adding sensory stimuli to a familiar enclosure can be used to induce an increase in exploration. This has been observed in several species including lions and other cats (Powell, 1995; Wells and Egli, 2004). In addition to increasing exploration, rotating animals among exhibits may also be used to induce scent-marking in territorial animals. Both tapirs and tigers increased marking when placed into exhibits that had recently housed other species (White et al., 2003).

Behavioral changes that occur with intrinsically reinforcing enrichment are often short-lived (e.g., Line et al., 1991; Renner et al., 2000; Vick et al., 2000). Enrichment that provides extrinsic reinforcement generally has longer lasting effects. In this case, the performance of behavior results in an external outcome that increases the likelihood that the behavior will be performed again. For example, the performance of exploratory behavior would be externally reinforced if the behavior results in finding food. Providing hidden food or scattering food items throughout an enclosure provides external reinforcement for exploration, and under these feeding protocols searching behavior increases (e.g., Ings et al., 1997). In addition to food, other external reinforcers for behavior include sensory stimulation and sensory access to a mate or other conspecific. For example, bonnet macaques will press a bar to gain access to a 10-s video of other macaques (Andrews and Rosenblum, 1993).

Knowledge of the motivation for the performance of a behavior may be very important for predicting the effectiveness of the enrichment item that is being provided. When animals are intrinsically reinforced for performing a behavior, merely providing them an opportunity to do so may result in desirable changes in behavior patterns. For example, Hare and Jarand (1998) provided tigers with a dangling burlap bag containing branches and observed an increase in hunting behavior. No external reinforcers were available as a result of interaction with the device, yet behavioral changes were anecdotally reported to be dramatic and to recur with repeated opportunities to interact with the device. Although enrichment techniques that rely on intrinsic motivation may be quick and easy to implement, their effectiveness may be limited. Because of the nature of the reinforcement, animal managers have less control over the effects of enrichment that provides intrinsic reinforcement than they do when extrinsic reinforcers are provided. For example, if the animal is motivated to explore an object because it is new, then that animal will lose interest in the enrichment item following exploration (Vick et al., 2000). It may return to the item periodically but will usually not exhibit the same behavior pattern as observed on its initial encounter (Powell, 1997). This decrease in response is described as habituation.

3.2. *Habituation*

Habituation influences the effectiveness of enrichment and is defined as ‘‘response decrement as a result of repeated stimulation’’ (Harris, 1943, p. 385). It has been known for some time that intrinsically reinforced, unlearned behaviors such as curiosity, play behavior and approach behavior (Thompson and Spencer, 1966) and even sexual arousal (Wilson et al., 1963) will habituate both during one presentation (within a session) and across consecutive presentations (between sessions). The enrichment literature makes it clear that intrinsically reinforced behavior towards simple devices or environmental changes decreases very quickly after repeated presentations (Celli et al., 2003). For example, olfactory enrichment intended to increase activity levels of captive black-footed cats produced large increases in moving and exploration on the first day of presentation but elicited no behavioral changes by the third day of exposure (Wells and Egli, 2004). Moreover, simple toys generally produce high levels of responding in the first few minutes of exposure. Responding quickly diminishes on subsequent days of exposure, suggesting that they are ineffective forms of long-term enrichment (Line et al., 1991). Habituation occurs for enrichment devices that are both unresponsive and responsive to manipulation by the animal (Vick et al., 2000). Even responses to highly manipulable objects such as uprooted trees can habituate quickly. Maki and Bloomsmith (1989) report that chimpanzees performed more than four times as many tree-related behaviors on the second day that the trees were available than on the third day.

Unlike enrichment that provides intrinsic reinforcement, habituation towards extrinsically reinforcing enrichment usually occurs during a single exposure (within sessions) but not across multiple exposures (between sessions). The decrease in responding to extrinsically reinforced enrichment within a single exposure could be a result of habituation to the reinforcer itself, rather than the enrichment device. This argument is supported by data showing that the response to an enrichment device wanes even when the enrichment device has not been emptied. For example, Vick et al. (2000) reported that manipulation of a device filled with food by rhesus macaques decreased within a 2 h period of exposure despite the fact that food was still left in the device at the end of the session. The authors hypothesized that this decline in responding may have occurred because the food items became increasingly difficult to obtain. However, recent work in operant conditioning has shown that responding will decrease even when reinforcement is still available and is being provided on the same schedule (McSweeney et al., 1996) because reinforcers lose their effectiveness over time (Murphy et al., 2003b). The response decrement does not seem to be the result of either fatigue or satiation, and instead has been postulated to occur by habituation.

The idea that habituation to extrinsic reinforcement-based enrichment is a result of habituation to the reinforcer suggests that the response rate should decrease more slowly when a variety of reinforcers are available for the behavior than when all reinforcers are identical. Melville et al. (1997) found that the occasional replacement of grape-flavored sugar water with a food pellet eliminated the decrease in responding during a session that occurred when only the sugar water was used as a reinforcer. Similarly, McSweeney and Roll (1998) directly compared animals that received a consistent reinforcer for a task with animals whose reinforcers changed, and found that providing different reinforcers significantly reduced response decrements within sessions. If habituation to the reinforcer is responsible for decreases in behavior towards enrichment in a single presentation, then using a variety of reinforcers could reduce this decrease. For instance, placing a variety of food items in a puzzle feeder, rather than just peanuts, could induce animals to use the device for longer during each presentation.

Despite decreasing within a single presentation, behavior that is extrinsically reinforced remains high at the beginning of each session as long as the item continues to provide reinforcers on subsequent exposures. For example, Platt and Novak (1997) found evidence of habituation in the behavior of male rhesus monkeys toward videotape stimulation but not for video game use. The difference was that correct responses when playing the video game resulted in food pellets (extrinsic reinforcement) whereas the videotape stimulation did not. Other studies have found similar results (Baker, 1997; Markowitz et al., 1995; Markowitz and Line, 1989). As stated by Markowitz and Line (1989), ‘‘an apparatus that the monkey can control, and that responds to the monkey in some way, will be used by a larger proportion of animals, and for a longer period of time, than devices or toys that are not actively responsive.’’

It is important to note that some decrease in responding as a result of habituation is normal and even desirable. In providing enrichment, we would not want an animal to continuously engage in behavior towards an enrichment device any more than we would expect a wild animal to continuously hunt for food all day without breaks. But there may be ways that animal caregivers can maximize sustained interest in a particular type of enrichment. In a recent review of the laboratory work on reinforcer effectiveness, Murphy et al. (2003b) outline several factors that affect habituation to enrichment and extrinsic reinforcers that may be directly applicable to the provision of enrichment designed to reinforce behavior.

Behavior toward enrichment that is thought to have habituated to the stimuli or its reinforcers may reappear if the enrichment is withheld for a period of time (Murphy et al., 2003b). This phenomenon is known as spontaneous recovery, and has been documented in the enrichment literature. Markowitz and LaForse (1987) found that responding to a pigskin sack by servals was high the first morning that it was provided, decreased over the course of the day, and was then ignored for the 2 days during which it remained in the exhibit. However, responding returned at a high rate the first morning of presentation following a 1-week period during which the pigskin was removed. Likewise, Renner et al. (2000) found that investigation of a manipulable object by New World primates habituated within 3 days of exposure but recovered significantly following 2 weeks during which that specific object was not available. Therefore, providing breaks between successive presentations of enrichment should result in spontaneous recovery of the response. This could be accomplished by removing an animal from its environment and then allowing it access to the same environment (McSweeney and Johnson, 1994), by moving animals from indoor to outdoor areas and back more than once a day, or by presenting an enrichment item again after withholding it for a period of time. Unfortunately, the recovered response would be predicted to decrease in intensity with each presentation and subsequent habituation. While spontaneous recovery has been observed, changes in the magnitude of the recovered response have not been directly examined for enrichment programs.

Generalization and dishabituation also affect habituation to stimuli and reinforcers (Murphy et al., 2003b), and both have been reported in the enrichment literature. Generalization refers to the fact that the response habituates not only to the exact stimulus provided, but also to other similar stimuli. For example, Carlstead et al. (1991) examined feeding enrichment for zoo-housed bears and found that, after honey-filled logs were depleted and exploratory behavior towards the logs had habituated, lower levels of exploratory behavior were directed towards novel but similar-looking logs that were not filled with food. However, providing new stimuli can sometimes reduce habituation to old items. The introduction of a new honey-filled log increased exploratory behavior toward not only the new log, but also toward old, empty logs to which a brown bear had habituated (Carlstead et al., 1991). This is referred to as dishabituation and suggests that the provision of new enrichment devices or environmental changes could cause a return of responding toward the original enrichment devices or environmental changes. As with spontaneous recovery of responses, the strength of the dishabituation response would be predicted to habituate with repeated presentations of the dishabituating stimulus. However, this also remains to be systematically investigated in the enrichment literature.

There are many other factors that have yet to be specifically investigated for enrichment. The first is the frequency with which the stimulus is presented. According to laboratory research, the more frequently a stimulus is presented, the faster and more pronounced the habituation (Murphy et al., 2003b). In terms of providing enrichment, this leads to the prediction that behavior towards enrichment would habituate more quickly when the enrichment is left in enclosures for extended periods of time or if provided often within a short period of time. For extrinsic reinforcement, the rate of habituation is determined by how quickly reinforcers are obtained by the animal, such that a higher frequency of reinforcement produces faster and more pronounced habituation. For example, feeders from which food is easy to obtain should maintain an animal's behavior and attention for shorter periods of time than feeders from which obtaining food is more difficult, assuming that the feeder is not so difficult as to fail to provide sufficient reinforcement.

Second, the weaker the stimulus, the faster and more pronounced the habituation (Murphy et al., 2003b). Small changes (e.g., adding a scent to the environment) should produce less exploratory behavior than large changes (e.g., moving an animal to a new environment). Interestingly, effects of stimulus strength also leads to the prediction that the more a stimulus resembles an animal's environment, the smaller the response to that stimulus will be and the faster the response will disappear. For intrinsically reinforcing enrichment, the less similar to the enclosure the stimulus is, the larger the response should be and the slower habituation should occur. If this prediction holds for enrichment, then in a naturalistic enclosure, enrichment items that are not naturalistic should be more effective than those that blend into the environment. Consistent with the effects of strong stimuli, Powell (1995, p. 368) suggested ''animals are likely to be stimulated only by objects and practices that are not part of the daily caretaking routine.'' For extrinsically reinforced behavior, less preferred food items, smaller quantities of food items, or food items more similar to the regular diet should produce faster habituation than highly preferred foods, large quantities of food, or rarely available foods as reinforcers.

Third, habituation is specific to the characteristics of the stimulus (stimulus specificity: Murphy et al., 2003b). Habituation can be disrupted by changes to the original stimulus, so old enrichment items could be modified to produce a return in responding. For example, Hare and Jarand (1998) described an artificial prey device for tigers that resulted in increased hunting behavior, but the hunting response habituated over the course of five trials. A simple modification of the device in which the bag could easily be pulled away from its attachment and successfully ''captured'' by the tigers caused a resurgence in responding to a regularly constructed device on the next trial. Though systematic data were not collected in this study, it does illustrate that periodic changes to a device may help sustain interest in the device. Finally, habituation to stimuli presented at fixed or predictable intervals would be expected to proceed more quickly than habituation to stimuli presented at variable or unpredictable intervals (Murphy et al., 2003b). This suggests that enrichment would be more effective if provided to animals at unpredictable times of the day as opposed to at scheduled or regular times. While a complete discussion of the effects of predictability is beyond the scope of this paper, it is examined in more detail elsewhere in this volume (Basset and Buchanan-Smith, 2007). Systematic data on the effects of presentation frequency, stimulus strength, and stimulus specificity could help animal care providers minimize habituation in enrichment programs.

Habituation poses serious challenges for animal care providers who are limited financially and have a difficult time creating novelty in environments. It may be that the only way to entirely prevent habituation toward enrichment that involves intrinsic reinforcement is to either consistently introduce novelty into the environment or to continually rotate a large number of items at irregular intervals (Mellen and Shepherdson, 1997; Renner et al., 2000). Furthermore, it is possible that as environments become more naturalistic, exploratory behavior toward novel objects could decrease unless they are very artificial (Zimmermann et al., 2001), making it increasingly difficult to maintain responding to intrinsically reinforcing enrichment. As described above, there are many factors that influence habituation and the recovery of a habituated response. However, extinction of behavior maintained by external reinforcers may be less difficult to overcome.

3.3. Extinction

For extrinsically reinforced types of enrichment such as puzzle feeders, scatter-feeding, food-hiding, etc., decreases in responding are more likely to result from extinction than habituation. Extinction occurs when reinforcement is no longer provided for a behavior, resulting in a decrease in the performance of the behavior (Powell et al., 2005). For many devices designed to provide extrinsic reinforcement of behavior, the reinforcement does not last forever (i.e., the food runs out, the trials end). Behavior towards enrichment items that produce extrinsic reinforcement, as well as other behaviors they are intended to increase or decrease, are maintained only as long as the external reinforcers are being provided (Novak et al., 1998). Although extinction and habituation share some commonalities, extinction is different from habituation in that reinforcement is no longer being provided. For example, a foraging animal may continue searching for some period of time even after all of the food has been obtained but will eventually cease if its efforts continue to go unreinforced. Ideal enrichment programs would produce desired behaviors that resist extinction, or those in which responding persists after a loss of reinforcement (Powell et al., 2005). This concept may be most applicable to enrichment that targets feeding-related behaviors such as foraging, food searching, or hunting, in which the reinforcers may be depleted at some point following exposure. Research in operant conditioning suggests that several factors affect the rate of extinction: schedules of reinforcement, history of reinforcement, magnitude of the reinforcer, degree of deprivation, previous experience with extinction, and the presence of distinctive signals for extinction.

Schedules of reinforcement describe the conditions by which an animal can obtain a reinforcer for performing a desired behavior. These schedules vary on two dimensions: the frequency with which a behavioral response must be performed and the duration of time that must elapse before the next reinforcer can be obtained. On a continuous schedule of reinforcement, each response made by an animal is reinforced. Devices that provide continuous reinforcement are often used for enrichment. For example, in a study conducted by Celli et al. (2003), chimpanzees were provided with bottles containing honey that could be accessed with a tool. Each time the individual used the tool correctly it was reinforced. Markowitz and his colleagues have been quite successful over the years at maintaining behavior with enrichment devices that continuously deliver reinforcers, particularly when animals are reinforced for performing complex patterns of behavior (Markowitz and Aday, 1998). Although these schedules are initially effective at producing and maintaining the desired behavior, they present three problems. First, continuous reinforcement may result in more rapid satiation and, therefore, more rapid decreases in the rate of behavior within sessions. Celli et al. (2003) report that variation in chimpanzees' honey-fishing across test sessions could be explained by satiation. Second, even when satiation does not occur, continuous reinforcement usually results in more rapid presentation of reinforcers and therefore produces faster rates of habituation, as discussed in the previous section (McSweeney and Roll, 1998). Finally, behaviors that have been continuously reinforced extinguish (i.e., stop occurring) quickly when reinforcers are no longer provided. For example, when a puzzle feeder provided continuous reinforcement, rhesus macaques ceased interacting with it after all the peanuts were removed (Novak et al., 1998).

One way to maximize time spent using an enrichment device is to use a partial reinforcement schedule in which not every response made by the organism is reinforced. Under partial reinforcement, the delivery of the reinforcer can occur after a certain number of responses have been completed (a ratio schedule) or for the first response after a particular time (an interval schedule). We will not discuss in depth the difference between these schedules, however, ratio schedules tend to produce greater response rates than interval schedules. Increasing the complexity or number of behaviors required to obtain reinforcement, therefore, should result in greater responding and slower extinction. For example, when a puzzle feeder for rhesus macaques was modified so that the desired behavior (sliding a peanut across the feeder) had to be performed several times before the peanut could be removed, macaques spent more time interacting with the feeder, showed slower habituation of responding to the feeder over time, and took longer to obtain all of the available peanuts than when the desired behavior was continuously reinforced (Novak et al., 1998).

Scattering or hiding food results in variable reinforcement of food-searching behavior, because food is not encountered on each search or after a set number of search behaviors. This type of enrichment has been shown to be quite effective. For example, adding buried food and sunflower seeds to woodchip litter for rhesus macaques (Byrne and Suomi, 1991), hiding peanuts for African elephants (Wiedenmayer, 1998), scattering forage for chimpanzees (Baker, 1997), and hiding meatballs for bush dogs (Ings et al., 1997) all increased exploration and foraging behavior in the location where food items were hidden. The chimpanzees showed no evidence of habituation of the searching response across time. Though the bush dogs spent less time searching as they became more efficient over 10 days with hidden food, they still showed higher rates of searching in the hidden food condition than in baseline conditions.

To avoid providing continuous reinforcement, animal care providers may also turn to providing food at different intervals throughout the day (e.g., Bloomsmith and Lambeth, 1995). Evaluations of variable feeding schedules have produced mixed results. They have been effectively used to reduce agonism and abnormal behavior (e.g., Bloomsmith et al., 1988), yet they also have failed to increase species-typical behavior (e.g, Carlstead et al., 1991), and may result in greater levels of undesirable behavior in anticipation of reinforcer delivery (Waitt and Buchanan-Smith, 2001). While a full discussion of the effects of predictability is beyond the scope of this paper (see Basset and Buchanan-Smith, 2007), one factor that influence the outcome of predictability studies is whether the delivery of the reinforcer is contingent on the behavior of the animal (for discussion see Carlstead, 1998). For example, when Carlstead et al. (1991) delivered food to American black bears at variable times of the day using a mechanical feeder, changes in exploration and foraging were much less dramatic than when food was hidden in the exhibit. This may have been because of the fact that the availability of food from the feeder required no response on the part of the bears, whereas obtaining hidden food required active search behavior. There have not yet been any direct comparisons between similar enrichment procedures that provide reinforcement on fixed schedules and those that provide enrichment on variable schedules, so the prediction that variable schedules should produce greater responding remains untested.

Despite the effectiveness of using partial reinforcement schedules, continuous reinforcement may be useful in some circumstances. Continuous schedules of reinforcement are commonly used in training when an animal is first learning a behavior, and this method may serve to attract the animal's attention to an enrichment device when it is first introduced. Reinforcing behavior on a continuous schedule before tapering back to partial reinforcement increases the total number of reinforcers an individual animal has received for a desired behavior. Because behavior is more susceptible to extinction when fewer reinforcers have been provided for that behavior in the past (Powell et al., 2005), continuously reinforcing a behavior at the outset of an enrichment program may increase resistance to extinction, resulting in effective enrichment that requires less reinforcement to maintain.

In addition to the schedule of reinforcer delivery, the quality of the reinforcer itself can affect the rate of extinction. In a training session, an animal may receive a ‘‘jackpot’’ reinforcement when it accomplishes a particularly difficult task (Pryor, 1984). The large size of this reinforcer means that animals will respond more and continue to perform the response for longer periods without any reinforcement, producing slower rates of extinction. Furthermore, preferred foods should also produce slower extinction rates. In training, performance is maintained longer when highly preferred food items are used as reinforcers. In enrichment, this effect (in addition to the intrinsic reinforcement for hunting) could help explain the absence of extinction over 2 months of technical difficulties for a leopard that had previously been reinforced for hunting behavior using a highly preferred reinforcer, such as quartered chickens (Markowitz et al., 1995).

Extinction and rate of responding are also affected by the recent history of food consumption (Powell et al., 2005). The larger the amount of food an animal eats prior to its opportunity to respond for food reinforcement, the lower that animal's overall rate of responding and the faster the animal's behavior is extinguished (Demarse et al., 1999). For example, servals performed less hunting behavior in response to enrichment presented after their daily meal than to the same enrichment presented before their meal (Markowitz and LaForse, 1987). Furthermore, Murphy et al. (2003a) showed that less habituation occurs when the food items given in the pre-feeding meal are different from food items used as reinforcers. This suggests that animals may work longer for food when it differs from their regular diet. Animals undergoing training often have their favorite food removed from their diet and available only as a reinforcer, which increases their willingness to respond for that reinforcer. Similarly, providing preferred foods only in the context of enrichment may increase the rate of behavior performed towards the enrichment and decrease the speed of extinction.

Distinctive signals that extinction is going to occur (i.e. stimuli that tell an animal that reinforcers are no longer available) can also reduce resistance to extinction (Powell et al., 2005). Markowitz and LaForse (1987) suggest that enrichment items should not be visible to the animals unless they are being used, thus providing a clear signal when reinforcement is available. Removing enrichment items when reinforcement is not available prevents extinction of responding, but likely also eliminates the behavioral change produced by the presence of the item. If the potential reinforcers are detectable to the animal, as when chimpanzees could see the level of honey in a honey-fishing task (Celli et al., 2003) and when rhesus macaques could see the absence of peanuts in puzzle feeders (Novak et al., 1998), then animals stop responding once reinforcers are no longer present. Other distinctive signals that indicate no reinforcement is possible and therefore promote extinction might include an absence of the sound of food when a feeder is shaken, a lack of smell of food in the device, changes in the weight of a device, and the disappearance of a human that provides reinforcement. Enrichment techniques that limit the ability of the animal to detect the presence or absence of a reinforcer should therefore result in slower extinction. The extinction of responding when reinforcement is unavailable may not sound like a problem, but the greater an animal's past exposure to extinction, the faster that animal's behavior is extinguished the next time reinforcement is removed (Powell et al., 2005). As animals better learn to discriminate between periods of differential reinforcement availability, it may become more difficult to use enrichment techniques to promote long-term changes in behavior. For this reason, the removal of devices that will no longer provide reinforcement may not only prevent habituation to that individual device, but may also increase the effectiveness of future enrichment procedures.

4. Age and enrichment effectiveness

Very little research has been conducted to examine possible differences in the effectiveness of enrichment for different age groups of animals (Mench, 1998). However, those studies that have examined age as a variable indicate that subadult or young animals may differ from adults with respect to use of intrinsically and extrinsically reinforced enrichment items. For example, Swaisgood et al. (2001) found a significant difference between subadult and adult giant pandas in preference for enrichment items that differed in intrinsic and extrinsic reinforcement. Specifically, adult pandas preferred fruitcicles and puzzle feeders that offered extrinsic food reinforcers over Boomer balls, Boomer bobbins, burlap sacks and fresh-cut branches that offered intrinsic reinforcement, whereas subadults showed no preferences among these items. Similarly, Lambeth and Bloomsmith (1992) found mirror use habituated across 11–13 trials for the adult chimpanzees but increased in use by the immature chimpanzees. It has been hypothesized that the greater intrinsic reinforcement for play in young animals (Fagen, 1981) may underlie this age difference. However, Powell (1995) failed to find age-related differences in responses to enrichment in lions, leaving some question as to whether the greater response of young animals to enrichment that provides only intrinsic reinforcement is generalizable across species.

5. Conclusion

This paper highlights some of the principles of behavior analysis that can contribute to understanding the efficacy of enrichment. However, it is by no means a complete review of the literature, nor does it encompass all the possible applications of the experimental analysis of behavior to enrichment. Instead, we have provided a theoretical framework for thinking about

Table 1
Summary of predictions relevant to enrichment from the experimental analysis of behavior literature

Topic	Prediction for enrichment	Supporting enrichment work
Type of enrichment	Reinforcement will be more effective than punishment	Not yet examined
	Extrinsic reinforcement will be more effective than intrinsic reinforcement	Platt and Novak (1997)
Habituation (occurs for both intrinsic and extrinsic reinforcement)	Habituation will be slower for extrinsic than intrinsic reinforcement	Platt and Novak (1997)
	For intrinsic reinforcement, habituation will occur both within an exposure and across exposures	Celli et al. (2003) and Wells and Egli (2004)
	For extrinsic reinforcement, habituation will primarily occur within an exposure	Not yet examined
	For extrinsic reinforcement, habituation can be reduced by offering a variety of reinforcers	Not yet examined
	Habituated responses will spontaneously recover after removal and replacement of enrichment	Markowitz and LaForse (1987) and Renner et al., 2000
	Spontaneously recovered responses will decrease in magnitude over exposures	Not yet examined
	Habituation will generalize to similar stimuli	Carlstead et al. (1991)
	Dishabituation of behavior towards enrichment will occur when new stimuli are provided	Carlstead et al. (1991)
	Dishabituated responses will decrease in magnitude over exposures	Not yet examined
	Presenting the same enrichment at a lower frequency will result in slower habituation	Not yet examined
	Presenting the same enrichment for a shorter duration will result in slower habituation	Not yet examined
	For extrinsic reinforcement, obtaining reinforcers at a lower frequency will result in slower habituation	Not yet examined
	Stronger stimuli or reinforcers will result in greater responses and slower habituation, where strength is positively related to size, preference, and difference from the environment	Not yet examined
	Changing the characteristics of the stimulus may result in recovery of a habituated response	Hare and Jarand (1998) (anecdotal)
	Enrichment provided unpredictably will be more effective than enrichment provided predictably	Basset and Buchanan-Smith (2007)
	Rotation of enrichment items will reduce habituation	Mellen and Shepherdson (1997) and Renner et al. (2000)
Extinction (occurs for extrinsic reinforcement only)	Behavior toward enrichment should stop occurring when reinforcers are no longer available	Novak et al. (1998)
	Partially reinforced behaviors should extinguish slower than continuously reinforced behaviors	Novak et al. (1998)
	Behaviors reinforced on a variable schedule should extinguish slower than behaviors reinforced on a fixed schedule	Not yet examined
	Increasing the history of reinforcement for a behavior should increase its resistance to extinction	Not yet examined
	Higher quality reinforcers should produce slower rates of extinction, where quality is positively related to size, preference, and difference from the regular diet	Not yet examined

	Responses to reinforcers provided before meals should be greater and extinguish slower than responses to those provided after meals	Markowitz and LaForse (1987)
	Responses to reinforcers different from the regular diet should be greater and extinguish slower than responses to those similar to the diet	Not yet examined
	Responses for preferred food reinforcers should be greater and extinguish slower than those for non-preferred food reinforcers	Not yet examined
	Enrichment for which it is difficult to detect the availability of reinforcement should result in slower extinction than enrichment for which a clear signal of availability is provided	Not yet examined
Age	Younger animals should show greater responses and slower habituation to enrichment relying on intrinsic reinforcement than older animals	Swaisgood et al. (2001) and Lambeth and Bloomsmith (1992) but see Powell (1995)

enrichment, illustrated how the current enrichment literature supports the use of this framework, and made concrete suggestions to improve the efficacy of enrichment programs. If the goal for an enrichment program is to improve well-being by increasing species-typical behaviors or decreasing undesirable behaviors through reinforcement, then enrichment that provides intrinsic or extrinsic reinforcement contingent upon those specific behaviors should be used. The results of basic laboratory studies conducted in the experimental analysis of behavior allow us to make testable predictions, as outlined in Table 1, concerning the circumstances under which habituation and extinction may be reduced in environmental enrichment programs. For example, enrichment providing intrinsic reinforcement will be most effective in promoting behaviors that are strongly motivated (like hunting and play), and will work best for young animals. Rotating enrichment items, altering the appearance or properties of the items, and increasing the difference between the item and the rest of the animals' environment should all result in greater responding and slower rates of habituation.

Enrichment that provides extrinsic reinforcement offers animal caregivers more control over an animal's activity than enrichment that is intrinsically reinforcing. Extrinsic reinforcement may initially be provided on a continuous basis, but after responding is consistent it should be switched to a partial schedule to promote the highest rate of responding and the lowest chance of habituation and extinction across all individuals. In addition, enrichment using extrinsic reinforcement will be more effective if it exploits high quality reinforcers and does not occur concurrent with or following mealtime. Removing enrichment prior to extinction may be especially important to maintain the effectiveness of both the item in question and the enrichment program in general.

Although some of these predictions are consistent with published reports of enrichment, and none of them are contradicted by published enrichment studies, many cannot be adequately validated because of a lack of relevant empirical data. Future research directly testing each of these predictions as they relate to environmental enrichment is crucial for understanding and increasing the efficacy of enrichment programs, especially studies of the long-term effects of enrichment and patterns of habituation and extinction on behavior.

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