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Assessment of Foraging Devices as a Model for Decision-Making in Nonhuman Primate Environmental Enrichment

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Continued progress to move evidence-based best practices into community and regulatory animal welfare standards depends in part on developing common metrics to assess cost, benefit, and relative value. Here we describe a model approach to evidence-based evaluation and an example of comprehensive cost–benefit assessment for a common element of environmental enrichment plans for laboratory-housed nonhuman primates. Foraging devices encourage a species-typical activity that dominates the time budget of primates outside captivity and provide inherent cognitive challenges, physical activity demands, and multi-sensory stimulation. However, their implementation is not standard, and is challenged by perception of high costs and labor; nutritional and health concerns; and identification of best practices in implementation (that is, device types, food type, frequency of delivery and rotation). To address these issues, we directly compared monkeys' engagement with different foraging devices and the comprehensive cost of implementing foraging opportunities. We recorded 14 adult male cynomolgus monkeys' interactions with 7 types of devices filled with a range of enrichment foods. All devices elicited foraging behavior, but there were significant differences among them both initially and over subsequent observations. Devices that afforded opportunity for extraction of small food items and that posed manipulative challenge elicited greater manipulation. The cost of providing a foraging opportunity to a single monkey is roughly US$1, with approximately 80% attributable to labor. This study is the first to perform a rigorous cost–benefit analysis and comparison of common foraging devices included in environmental enrichment. Its broader significance lies in its contribution to the development of methods to facilitate improvement in evidence-based practices and common standards to enhance laboratory animal welfare.

Abbreviations: EEP, Environmental Enrichment Plan;

Opportunities for exploratory behavior, physical manipulation, and cognitive engagement are a central part of many care programs for captive nonhuman primates. Empirical support and rationale for the benefit of providing captive animals with these activities span the past 100 y. Early in the history of research with captive animals, laboratories that focused on scientific questions involving learning, cognition, motivation, curiosity, and problem-solving regularly presented animals with various manipulative tasks, puzzles, and other exploratory opportunities[14,15,43,44] (for review and additional references, see references 11 and 33). Work spanning from 1911 through the 1960s demonstrated intrinsic motivation for exploration,[6,7] a curiosity drive,[9,11] and complex learning abilities in nonhuman animals.[15,19,40] By 1947, psychologist DO Hebb had demonstrated profound effects of experience and enriched environments on the behavior of laboratory animals.[16] By the 1960s, physiologic psychologists identified the effects of environmental enrichment on multiple aspects of neural development and organization[20] (for review, see references 4, 33, 34, and 42). In turn, the efforts and observations of these scientists and other investigations of comparative psychologic research questions provided a strong foundation of empirical evidence from which to recognize the importance of attention to enriched environments for laboratory animals[17,35] (for review, see reference 4).

Engagement in exploratory and manipulatory activities occurs via both research and environmental enrichment aspects of care and husbandry for laboratory animals. Opportunities for such cognitive engagement were provided for many decades via laboratory animals' participation in research that included those activities. Prior to the 1980s, however, there was no regulatory standard that required provision of enrichment for all captive primates. In 1985, changes to federal regulation meant to ensure minimum standards in care practices specifically included consideration of psychologic welfare. The regulation required each facility to have a formal Environmental Enrichment Plan (EEP).[41] The mandate for EEP undoubtedly increased efforts to provide captive primates with enrichment. It also resulted in enhanced record-keeping, better articulation of extant programs, and justification for dedicated resources and professional personnel charged with responsibility for oversight and implementation of EEP. In turn, the number of empirical articles aimed at refining approaches, establishing standards, and evaluating the outcome of these practices increased (for review, see references 22, 24, 25, and 28).

Nonetheless, there remains an absence of clear consensus and uniform implementation of best practices for many aspects of nonhuman primate environmental enrichment. The nature of the regulatory system and guidelines for husbandry and care in the United States, which tend to use 'performance' rather

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than 'engineering' standards, contribute to lack of standardization. The specificity of regulatory standards varies widely across aspects of care. For example, minimum standards for cage size are specific and unambiguous as compared with the broad requirement for an EEP. While performance standards have practical, scientific, and animal welfare advantages, there are also significant downsides. Weak mechanisms to ensure that evidence-based best practices are disseminated and implemented broadly pose challenges to safeguarding both animal welfare and the science that depends on some level of experimental control.

A primary value of uniform standards is to ensure that animals benefit from best practices. In the case of experiential factors that can influence scientific outcomes, some uniformity based in community standards is also important. Environmental enrichment provides a strong example of this need because the same empirical evidence that supports its value for animal welfare also demonstrates its effect on outcome measures that are relevant to a full range of scientific questions. Therefore, the case for attention to greater uniformity in standards rests on protecting both science and animal welfare.

A variety of challenges complicate the process of identifying best practices and broadly disseminating advances in animal care standards. Perhaps primary among them is avoiding the prescription of practices that lack strong empirical evidence or rationale, have high cost and low benefit, lack practicality, or jeopardize scientific objectives. Differing limitations and opportunities as a function of variation in types of research and facility characteristics are also a central consideration in deriving workable standards in some aspects of environmental enrichment. Nonetheless, current regulations provide some examples where community standards for best practices have evolved into specific minimum requirements (for example, cage size, EEPs).

A model process by which environmental enrichment practices move from initial selection to widespread use includes assessments of both cost and benefit to inform relative value. Figure 1 illustrates the process, beginning with an operationalization of benefit (Figure 1 A) and continuing through phases of assessment (Figure 1 B) that can inform analysis of value (Figure 1 C) and ultimately contribute to broad implementation of best practices (Figure 1 D). Of note, the model incorporates incremental progression such that previous data and literature can be recruited to support assessment. In other words, de novo evidence for each aspect of benefit, cost, or feasibility is not required for each effort to evaluate an enrichment or refinement strategy. Thus, effort can be directed to filling gaps rather than duplicating assessment for which considerable evidence has already demonstrated benefit, cost, and feasibility. Finally, the model is one of dynamic process, where standards evolve as a result of continuing evidence-based evaluation and scientific data.

In this model, benefit is considered in terms of the majority of the population of animals. A subset of animals may have specific needs. Some animals may require tailored enrichment or behavioral management strategies, with the goal of treating abnormal behavior. The requirement for environmental enrichment, however, is for all animals, including the majority who do not exhibit abnormal behavior. As a result, assessing benefit simply in terms of reduction of abnormal behavior fails on several grounds. Rather than focusing narrowly on subpopulations and abnormal behavior, the foundational assumption for assessment is therefore measuring effectiveness in promoting species-typical behavior, cognitive engagement, or some other benefit for the larger population. Best practices for the subset of special cases and specific treatment or intervention needs are clearly important and highly relevant. However, adopting a model that allows for distinction between the 2 different goals does nothing to impede refinements intended for a subpopulation. What it does do is ensure that the primary criteria for assessment of benefit for the larger population remains focused on promoting species-typical and other positive behavior.

The study reported here addresses one type of environmental enrichment: foraging devices. Providing foraging opportunities benefits captive primates by promoting curiosity, manipulation, learning, and species-typical behavior. Empirical study of enrichment for captive primates provides demonstration that fairly common strategies for enrichment can successfully induce foraging behavior in laboratory nonhuman primates.[2,8,18,21,38] In this case, the benefit of the enrichment strategy is defined operationally as promoting the manipulation and use of foraging devices among the majority of animals (Figure 1 A).

Consensus of common sense holds that animal program practices should be driven by selection of those strategies that result in demonstrable positive outcomes (that is, evidence-based selection[3,5]). Therefore, the provision of foraging opportunities should be highly ranked and prioritized in the design and evaluation of environmental enrichment programs. However, there is no current regulatory requirement or set of community standards that directly address consistency across facilities and improvement of current strategies to promote foraging. For example, the only reference to foraging devices for nonhuman primates in the newly revised *Guide for the Care and Use of Laboratory Animals*[27] is:

"In some species (e.g., nonhuman primates) and on some occasions, varying nutritionally balanced diets and providing 'treats,' including fresh fruit and vegetables, can be appropriate and improve well-being. Scattering food in the bedding or presenting part of the diet in ways that require the animals to work for it (for example, puzzle feeders for nonhuman primates) gives the animals the opportunity to forage, which, in nature, normally accounts for a large proportion of their daily activity." (p 67).

Despite the absence of direct requirement to provide foraging devices, many—perhaps most—environmental enrichment programs for nonhuman primates do so. A nonrandom survey of 22 research facilities showed that all of them use foraging devices in enrichment for caged primates.[1] Providing foraging is not without challenge. Device selection, cost, and rotation as well as frequency, amount, and type of food, potential for weight gain, and increase in labor costs are all common concerns associated with movement toward increased provision of foraging opportunities. Of the institutions surveyed previously,[1] half report time, staff, or cost constraints to implementation of foraging opportunities. Furthermore, only subsets of these challenges are addressed by the current literature, leaving little direct evidence to guide decision-making and behavioral advocacy at the facility level.

Uniform and continued improvement in primate captive care can be assisted by evidence-based cost–benefit analysis to provide a foundation for evolution in best practices that are both feasible and meaningful. To our knowledge, no previous studies have directly compared different types of commonly used primate foraging devices to evaluate both their cost and their benefit. Some studies in the peer-reviewed scientific literature have evaluated primates' use of foraging devices and whether their provision has benefits in terms of measures related to animal welfare. For example, a comparison of 4 types of feeding enhancement, 2 devices and 2 foods, demonstrated

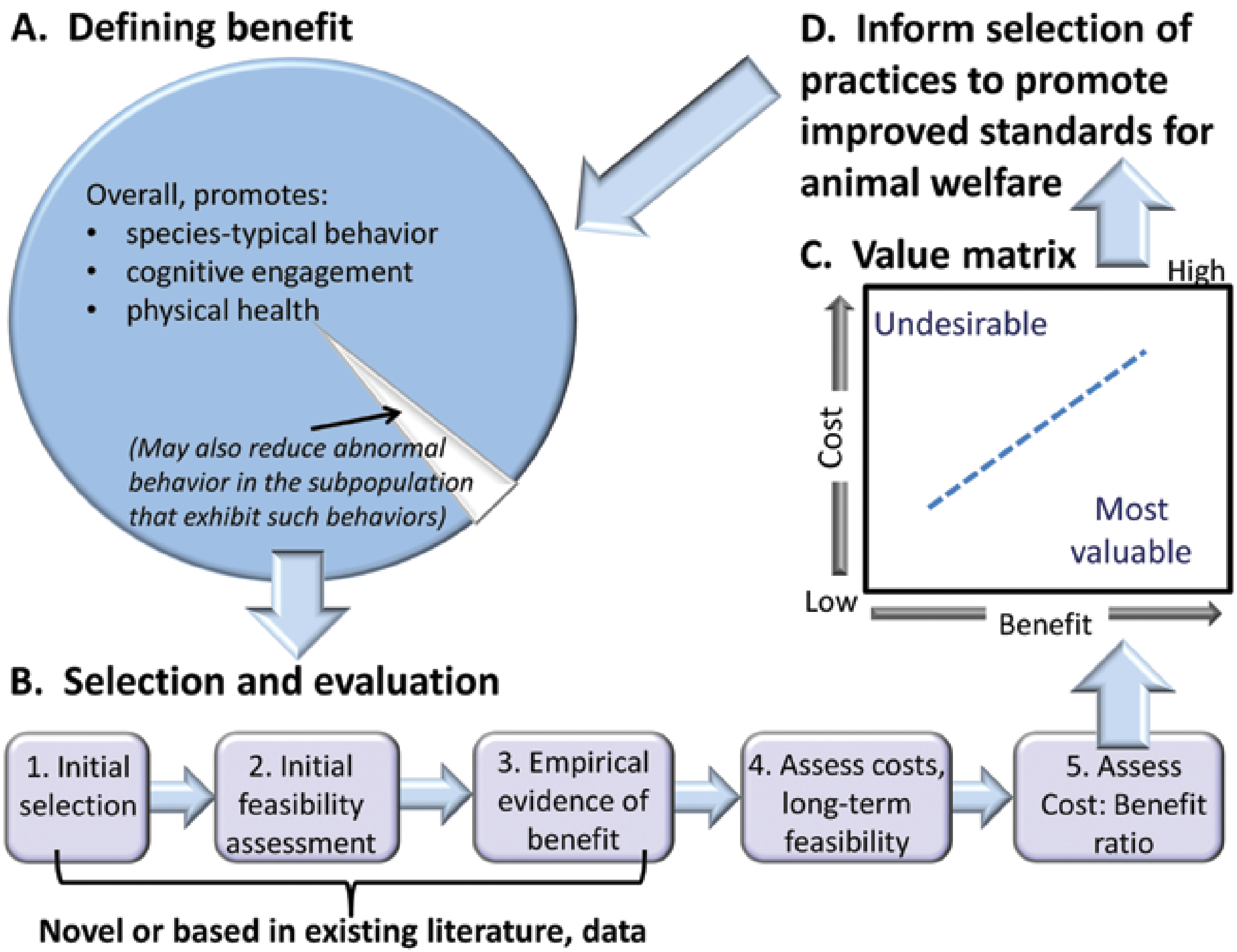

Figure 1. Illustration of model process for assessment of environmental enrichment strategies.

increases in species-typical activity patterns.[37] Furthermore, the findings emphasize the importance of device characteristics, concluding that "since feeding devices were used in species-typical activities in addition to feeding, devices may be more valuable than foods."

The goal of the study reported here is to produce generalizable cost: benefit data on specific methods for refinement in the care of laboratory-housed monkeys, namely, evaluation of foraging devices. For the purpose of this study, benefit is defined as manipulation of foraging devices. The study targets the aspects of cost–benefit assessment represented in Figure 1 B. Two specific aims are addressed. The first is a direct comparison of the length of time monkeys engaged in foraging when the same foods were presented within different devices (Figure 2) and within devices differing in their novelty (Figure 1 B and 3). The second is a comparison of the comprehensive cost of implementing foraging with different devices (Figure 1 B and 4). Consistent with our overall goal of providing information with broad generalizability and utility to the field, we selected foraging devices that are commercially available or easily manufactured, that are commonly used in nonhuman primate laboratory settings, and thus, that have already been screened (Figure 1 B and 2). From a facility management perspective, systems and strategies designed to minimize the cost, labor, and storage associated with providing a diverse and effective set of foraging devices are desirable. Therefore, we evaluated the Primate Enrichment System (PES; Otto Environmental, Milwaukee, WI), which is specifically designed to facilitate rotation of devices (Figure 2). Three additional devices were assessed. Two were made inhouse from common materials, whereas the third is a commercially available ball with holes (challenger ball, Otto Environmental). Two device types were familiar to the animals through use in their enrichment over 8 y, and 4 devices were novel. Our selection of devices provided comparison data on comprehensive cost and effectiveness, both when novel and when familiar.

In addition to selection of specific types of foraging devices as a key to developing a meaningful environmental enrichment program, selection of the type and amount of food provided with each foraging opportunity is important. Nutritional content, palatability, variability, suitability for the device type, and cost are all considerations. We explicitly included caloric analysis and comparison of different food types commonly used in primate enrichment programs. In the first set of assessments (study 1), we used a small, standardized serving size for each foraging opportunity to evaluate the amount of foraging interaction that could be sustained with a relatively low caloric increase from the standard chow-based diet. In the second set of assessments (study 2), we tested the duration of foraging with a greater amount of food. Consequently, we evaluated foraging from a device that was filled to maximum capacity with a mix of popcorn and cereal. In both cases, comprehensive information about serving sizes, caloric content, and cost were calculated in a manner that would easily provide the basis for scaling-up to larger servings or for others to estimate their own local costs.

Assessment of relative value depends on information about both benefit and cost. Our approach characterizes the inclusive cost both to implement and to maintain enrichment strategies.

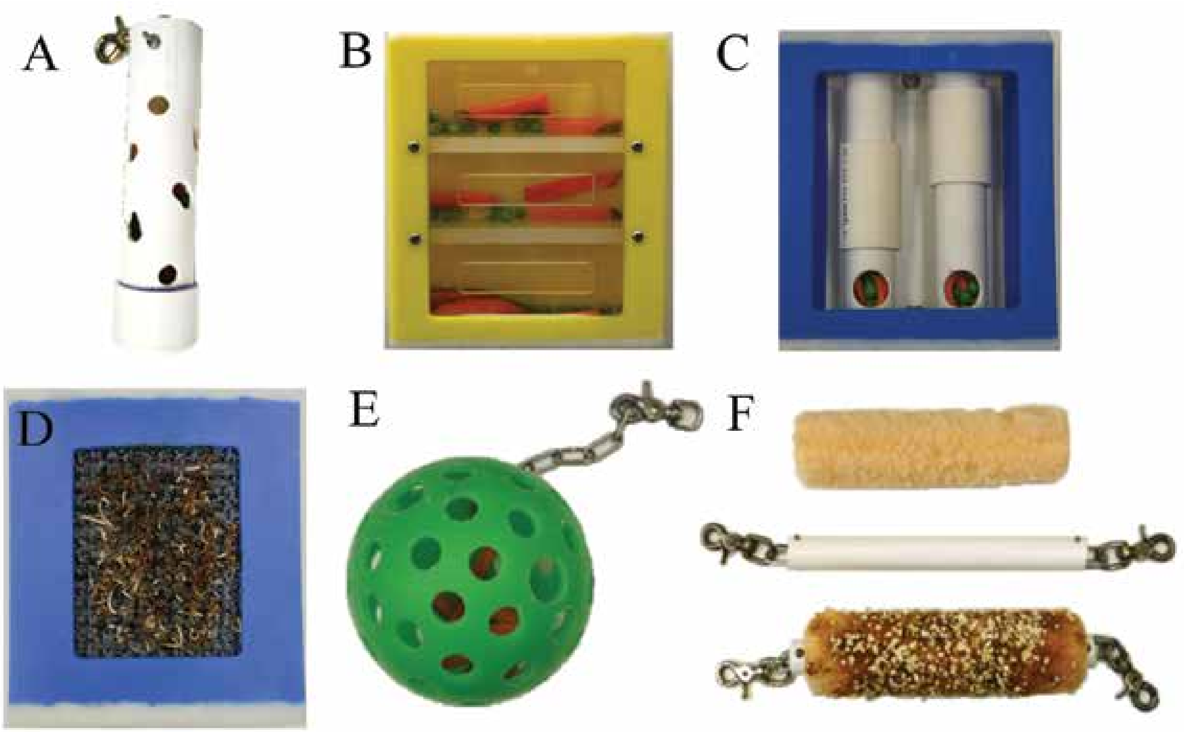

Figure 2. Filled foraging devices used in study 1. Novel devices included a (A) pipe, (B) food feeder, (C) treat dispenser, and (D) combination panel. Familiar devices included a (E) challenger ball and F) paint roller.

We previously developed and implemented methods to perform assessments that provide generalizable results useful to inform the selection of primate environmental enrichment strategies.[5] Primary challenges to cost assessment range from inclusion of all costs (that is, initial purchases, labor, supplies) to estimation of staff time for implementation and maintenance to long-term practicality (that is, safety, ease of cleaning, device durability). Our previous work analyzed the full cost of labor, materials, and consumable supplies associated with providing wood shavings as floor cover for pen-housed monkeys.[5] Our analysis included both cost for initial implementation and for maintenance over several months. We use the same method in the study reported here, including multiple cycles of presentation and cleaning with each device to gauge their long-term practicality.

Materials and Methods

Subjects. Evaluation of the foraging devices was conducted with adult male cynomolgus macaques (*Macaca fascicularis*) housed at the Harlow Primate Laboratory. study 1 involved 14 macaques; study 2 used 9 animals. At the start of data collection, the subjects ranged in age from 129.5 to 138.4 mo (mean, 135.4 mo; 1 SD, 3.1 mo). None of the animals were clinically obese, with weights ranging from 5.44 to 9.39 kg (mean, 7.37 kg, 1 SD, 1.31 kg) at the start of the study and no significant differences in weights afterward. The monkeys were singly housed in quadrant cages (0.71 × 0.75 × 0.79 m or 0.71 × 0.75 × 0.89 m) with visual, auditory, and olfactory access to each other. The evaluation of foraging devices reported here is from animals enrolled in a study for which they are singly housed for clinical and experimental reasons. Enrichment is part of their husbandry and clinical care; they were not singly housed for the purpose of the foraging device assessment. Animal rooms were maintained on a 12:12-h light:dark cycle.

Monkey chow (no. 5038, Purina Mills, St Louis MO) was provided twice daily, once in the morning and once in the afternoon, with water available ad libitum. In accordance with the long-standing facility-wide EEP, fruit, vegetables, and ice treats (approximately 16 oz water containing small fruit, vegetable, rice, split peas, garbanzos, banana chips, peanuts [in shell], oatmeal, or seeds or various combinations thereof) were distributed each afternoon. In-cage manipulatable objects were present at all times, foraging devices were provided at least once each week, fruit or vegetable was given via food hopper 3 times weekly, and ice treats were given once each week. Manipulatable enrichment objects were provided inside the cage (that is, polypropene objects shaped as dumbbells, grenades, or balls; nylon rubber hedgehog; 4-in. nylon rubber kong toy [Kong, Golden, CO]). Objects are rotated every 2-wk such that a specific object type is presented only 2 times over the course of 1 y.

The amount and variety of foods provided to the macaques during the study was similar to what had been routinely given prior to the study. Specifically, animals were provided with fruit via their food hopper on Monday, Wednesday, and Friday; ice treats on Tuesday and Thursday; and foraging devices other than those used in the study on Monday and Wednesday.

The study was conducted in compliance with all regulations, including the University of Wisconsin–Madison IACUC and the NIH *Guide for the Care and Use of Animal Subjects*.[27] Macaques were healthy, with no clinical issues that would affect foraging behavior. Animals were treated humanely, and there were no potentially painful procedures.

Materials. ***Foraging devices.*** Six foraging devices were evaluated (Figure 2). The devices each fell into 1 of 2 categories: novel or familiar. Novel devices consisted of a pipe feeder (constructed inhouse) and a set of 3 devices as part of the Primate Enrichment System (Otto Environmental). The pipe (Figure 2 A) was constructed of a PVC tube (length, 17 cm; inner diameter, 3.81 cm) fitted with a 4.45-cm PVC cap on one end and a 10.16-cm chain on the other, to attach the device to the cage. Holes that were 1.27 cm in diameter or 1.27 × 2.22 cm were drilled into the PVC tube to provide access to the food placed inside. The

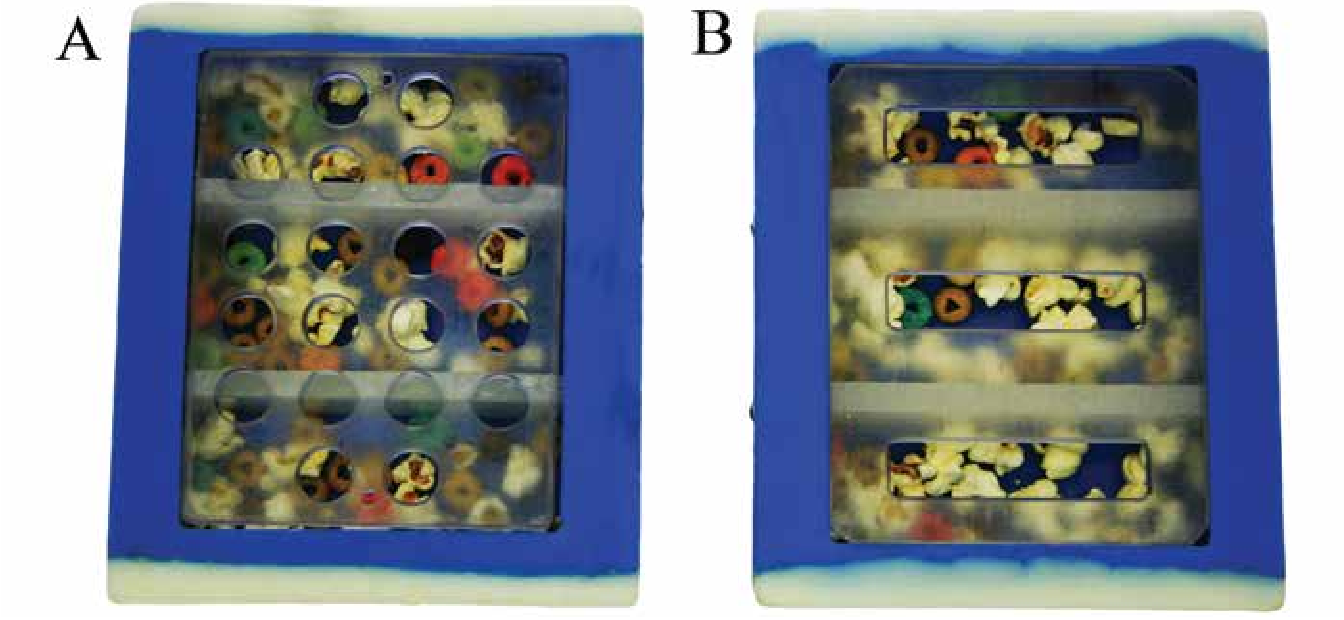

Figure 3. Food feeders with (A) circular hole and (B) rectangular hole covers used in study 2.

devices were hand-constructed with roughly equal numbers and distribution of holes across the surface of the pipe.

The Primate Enrichment System consists of a stainless steel 22.86-cm^2 bracket that attaches to the cage front and a set of 17 interchangeable panels with a wide range of foraging devices (10 panels) and moveable parts to promote exploration and manipulation (7 panels). This enrichment system is a longstanding part of the Harlow Primate Laboratory EEP but was novel to the animals in this study. Three inserts were selected for analysis on the basis of the facility manager's (MLL) previous experience and observation that these devices had the best level of interaction among those inserts in use at our facility: the food feeder, treat dispenser, and combination panel with Astroturf.

The food feeder (Figure 1 B) was a colored acrylic insert of 5 cm deep and divided into 3 sections, each 5 cm tall. The insert has clear acrylic covers with either 3 rectangular openings (Figure 2 B and 3 B) or a series of circular holes (Figure 3 A). The rectangular hole cover that opened was used in study 1. Study 2 compared the rectangular and the circular opening covers. The treat dispenser (Figure 2 C) was a colored acrylic insert with 2 PVC pipes within the acrylic frame; one PVC piece slid to reveal an opening from which food was retrieved. The combination panel (Figure 2 D) was a colored acrylic insert, with an opening to fit a piece of gray artificial turf.

These 4 novel devices were compared with 2 enrichment devices that were familiar to the animals. The first was a commercially available device (challenger ball, Otto Environmental, Milwaukee WI; Figure 2 E). The second was the inhouse-constructed paint roller device, which was composed of a 22.86-cm paint roller fitted over a 1.9-cm diameter PVC tube that was 25.4 cm long (Figure 2 F).

Forage foods. Table 1 provides the serving sizes, cost, and caloric content of all foods used in the study. For phases 1 and 2 of study 1, all devices except the challenger ball and paint roller were filled with frozen peas and apple 'straws,' which were cut by using a 0.95-cm grid potato slicer (FFC-375. Winco, Lodi NJ). The challenger ball could not be filled with peas and so was filled with apple straws to a volume equivalent to that used in the other devices. The paint roller was covered in molasses, grits, and oatmeal (Table 1). For phase 3, each device was filled with a range of food enrichments commonly used with each device. Food feeders were filled with cucumber coins cut in half and pear straws; treat dispensers were filled with orange slices and halved green beans; combination panel turf was coated in molasses, sweetened shredded coconut, and sunflower seeds; challenger balls were filled with orange slices and yam straws; pipes were filled with popcorn and yam straws; and paint rollers were covered in molasses, grits, and sweetened shredded coconut.

In study 2, the food feeder was filled to capacity with a 3:1 mix of popcorn and cereal (Table 1). A mix of cereals purchased in bulk included: Bunch O' Krunch, Cocoa Munchies, Fruit Whirls, Happy Shapes (Hospitality brand, Gilster-Mary Lee, Chester, IL) and Apple Zingers (Malt-O-Meal; Lakeville, MN).

Procedure. For study 1, behavioral observations were collected over a 2-d period during each of three 6-wk phases, such that each device was presented 3 times. Phase 1 provided an assessment of novelty effects, and phase 2 gave a comparison in which all of the devices were familiar. The first and second phases used the same types of food within similar types of devices (that is, fruit or vegetable within 5 devices; molasses mix on paint roller; Table 1). In the final phase, different food types were used (see preceding section). In study 2, behavioral observations were collected over a 2-d period for each cover of the food feeder (rectangular compared with circular opening; Figure 3 A and B, respectively). The devices were not novel to the animals. Study 2 took place 22 wk after study 1.

Food prep and device cleaning. Forage foods consisted of fresh or frozen produce, popcorn, seeds, or dry grains prepared as described previously. Devices were cleaned as follows: when necessary, devices were soaked in a solution of dishwashing soap to loosen and remove remaining food particles. All devices were then rinsed in a bleach solution and sanitized with 2 wash cycles in a high-temperature dishwasher (Avenger HT 208/230/1, Jackson, Barbourville, KY). Devices were left overnight to air-dry and stored until the next use.

Behavioral data collection. To begin an observation session, devices were placed on the front of each animal's cage. Devices in the Primate Enrichment System were affixed to cages via the bracket that remained on cages continuously. Other devices were affixed

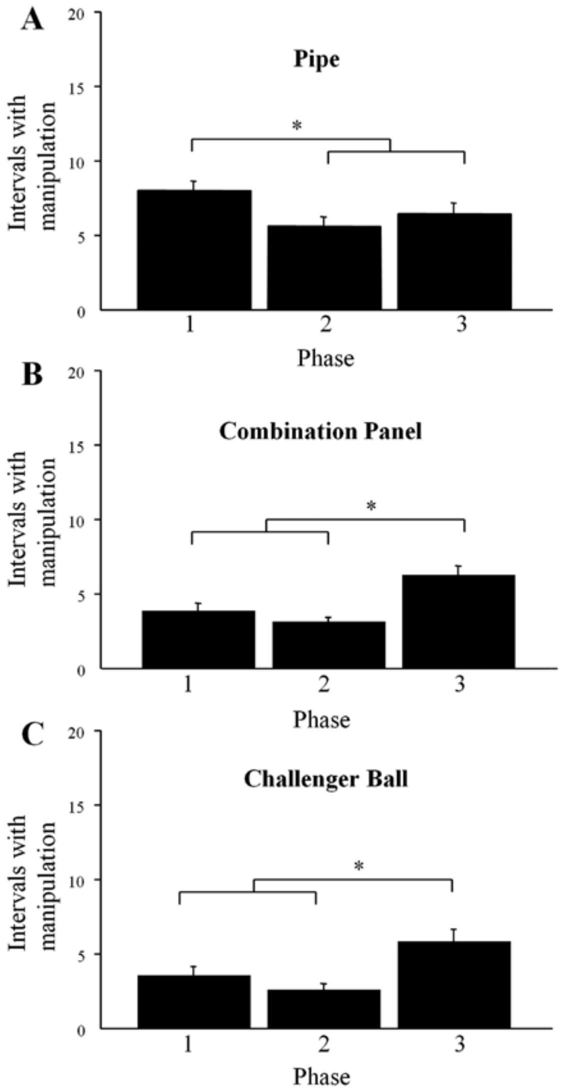

Figure 4. Number of intervals (mean ± SEM) with manipulation for (A) pipe, (B) combination panel, and (C) challenger ball averaged across all observation periods for each of the 3 phases. Symbols refer to significant differences between devices. Post hoc tests showed that for the pipe, manipulation during Phase 1 was significantly higher than that during phase 2 ($P < 0.0001$) and phase 3 ($P = 0.001$). For the combination panel, manipulation in Phase 3 was significantly higher than during phase 2 ($P < 0.0001$) or phase 1 ($P = 0.0004$). For the challenger ball, manipulation in Phase 3 was significantly higher than Phase 2 ($P = 0.0003$), and Phase 1 ($P = 0.006$).

to the cage mesh with swivel clips. Behavioral observations were conducted at 4 time points: within the first 20-min of device placement (Initial), 1 and 2 h later (Sustained), and the following day (24 h; Next Day). Early during the study, observations also were made at 25 and 26 h, but these time points were subsequently dropped because data from the first 8 sessions indicated that the macaques did not interact at those points. Study 2 followed the same behavioral observation procedure.

Each observation session included 20 time bins of 1 min each in which manual, pedal, or oral contact and manipulation of the device were coded as present or absent for each animal. After entering the room at the start of each observation period, the observer sat in a central location and recorded any contact or manipulation for each animal over each 1-min observation time bin. The observer left the room after each observation period. After the final observation period (24 h), the observer removed each device. Data were recorded by observers to whom the animals were well habituated and who met high interrater reliability standards (Cohen κ = 0.995). For data analysis, the number of 1-min time bins in which device contact or manipulation occurred was summed for each 20-min observation session.

Cost calculations. Cost analysis was divided into 3 major categories: 1) initial costs for purchase or manufacture of devices; 2) cost of foods used in the foraging devices; and, 3) costs related to husbandry (food preparation, device placement, and cleaning). All costs were evaluated. Initial cost for devices of the Primate Enrichment System is the cost to purchase the bracket and one of each of the 3 inserts. Challenger balls were purchased commercially (Otto Environmental, Milwaukee, WI) also. For the 2 devices made inhouse (paint roller, pipe), the initial cost was determined by adding the construction labor cost and cost of materials.

To provide the most generalizable information, the cost of foods used for foraging opportunities were calculated as a range, with small-quantity purchases from local grocery stores and large-quantity purchase from a bulk food vendor (Table 1). To determine cost per serving, the cost per pound, ounce, or whole item was divided by the number of servings each quantity would provide. Bulk prices were used for the final summary cost analysis.

The amount of time required for husbandry was assessed by using our previous method for cost–benefit assessment of primate environmental enrichment.[5] In brief, actual labor time (in minutes) was recorded by 2 staff members performing each of the husbandry tasks related to the study: preparing food, cleaning the preparation tools and area; and filling, attaching, removing, and cleaning each device. The time for each task was recorded on 3 occasions by each person, with the average used for subsequent calculations. Labor cost was calculated by using the average salary plus fringe benefits of existing staff that would normally perform this job function. Both the time and cost of labor are reported here to provide more generalizable information for use in comparisons and cost projection.

Calorie calculations. The caloric content of each food was determined on a per-serving basis by using data from the National Nutrient Database (http://ndb.nal.usda.gov/). The caloric content of the cereal mix used in study 2 was obtained from the manufacturers' information.

Data analysis. Data analysis for study 1 began with a 3 (phase) × 6 (device) repeated-measures ANOVA, with manipulation averaged across all observation periods and serving as the dependent variable. Differences between phases for each device were assessed via follow-up analysis with one-way ANOVA and Fisher post hoc comparisons between the 3 phases for each of the devices. To provide the most meaningful comparison of devices, data from the phase in which manipulation was highest was used in subsequent analyses for each device with significant differences between the phases. Data were averaged across phases for those devices that did not differ significantly by phase. These data underwent ANOVA, with device serving as the within-subjects factor. For study 2, manipulation data were analyzed with a 2 (device cover) × 3 (observation period) analysis of variance followed by post hoc comparisons by using the Fisher least significant difference analysis. The α level was set at 0.05 for all analysis of variance tests.

Results

Study 1: behavioral data. Significant main effects were observed for device ($F_{5,65} = 10.33$, $P < 0.001$) and phase ($F_{2,26} = 20.63$, $P < 0.001$). There was also a significant interaction

Table 1. Serving size, cost, and caloric content of foods used in foraging devices

	Serving size	Cost	Calories (kcal)
Food feeder, treat dispenser, pipe, challenger ball (various phases)			
Apple	1/4 whole	$ 0.08–0.18	24
Navel Orange	1/4 whole	$ 0.04–0.17	35
Pear	1/4 whole	$ 0.07–0.22	25
Green Bean	4 whole	$ 0.23–0.70	4
Popcorn	1/2 cup	$ 0.007–0.014	20
Cucumber	1/3 cup	$ 0.05–0.08	8
Yam	1/3 cup	$ 0.09–0.18	54
Green peas	1/8 cup	$ 0.04–0.09	13
Combination panel (phase 3)			
Molasses	1 Tbsp	$ 0.03–0.14	58
Unshelled sunflower seeds	1/8 cup	$ 0.03–0.05	93
Sweetened shredded coconut	1/8 cup	$ 0.09[a]	73
Oatmeal	1/8 cup	$ 0.03[a]	38
Food feeder (study 2)			
Popcorn	3 cups	$ 0.04–0.08	120
Cereal	1 cup	$ 0.17[a]	143
Paint roller			
Molasses	1 Tbsp	$ 0.03–0.14	58
Oatmeal	1 Tbsp	$ 0.03[a]	19
Grits	1/2 Tbsp	$ 0.01–0.02	18
Sweetened shredded coconut (phase 3)	1 Tbsp	$ 0.09[a]	73

Cost range reflects purchasing individual compared with bulk quantities.
[a]No cost difference between bulk and nonbulk purchases.

between device and phase ($F_{10,130}$ = 4.92, P < 0.001). Follow-up analysis demonstrated that 3 devices were significantly affected by phase, whereas 3 were not. Only one device, the novel pipe feeder, elicited greater manipulation at its initial presentation (phase 1; ($F_{2,26}$ = 16.04, P < 0.0001; Figure 4 A).

Two devices, one novel (combination panel) and one familiar (challenger ball), elicited greater manipulation at the third presentation in this study. The aim in study 1, phases 1 and 2 was to hold food type and amount relatively similar across novel and repeated presentation and across similar devices. Phase 3 provided data on manipulation when devices were loaded with a range of common enrichment foods. In the case of the combination panel, these were foods optimally suited to the device (that is, synthetic turf of combination panel was filled with molasses, coconut shavings, and sunflower seeds rather than peas and grated apple). For both the combination panel and challenger ball, manipulation was significantly higher in phase 3 ($F_{2,26}$ = 15.80, P < 0.0001 and $F_{2,26}$ = 9.37, P < 0.0009, respectively; Figure 4 B and C). For the remaining 3 devices (paint roller, food feeder, and treat dispenser), there was no significant difference in manipulation across the 3 phases.

Study 1: device comparisons. A significant ($F_{5,65}$ = 6.93, P < 0.0001) difference between devices was evident in the amount of manipulation at initial placement of the device (Figure 5 A). Overall, the paint roller and combination panel elicited significantly greater interaction than did the other devices, with the exception of the pipe. The pipe elicited greater manipulation than did either the food feeder or treat dispenser, whereas manipulation of the challenger ball was higher than that of the treat dispenser.

None of the devices effectively elicited manipulation beyond the 2-h period, although we observed that some food often remained in the objects for many animals. Therefore, to compare the effect of device type on sustained manipulation, the average number of intervals with manipulation and contact at 1 and 2 h after device placement was analyzed. Follow-up tests to a significant main effect of device type ($F_{5,65}$ = 3.46, P = 0.008) indicated that only one device (pipe) differed in terms of eliciting higher sustained manipulation (Figure 5 B).

Study 2: behavioral data. When presented with food feeders filled to maximum capacity, macaques engaged in levels of manipulation that were influenced by both the device cover and by the observation period (Figure 6). The device with circular holes promoted greater manipulation ($F_{1,8}$ = 26.2, P = 0.001) than did the one with rectangular holes. Device manipulation was significantly ($F_{1,8}$ = 101.3, P = 0.0001) higher initially than in the sustained and next day observations. Follow-up tests revealed differences between observation periods. Manipulation was sustained significantly longer when the circular hole cover was used, as indicated by a significant interaction between cover type and observation period ($F_{1,8}$ = 20.25, P = 0.0002). For the cover with circular holes, manipulation remained at an average of 75% of intervals at 1 and 2 h after placement of the device. Consistent with the results of study 1, manipulation dropped to relatively low levels (less than 25% of intervals) for both covers the next day (24-h observation).

Cost data. Comprehensive cost data are provided in Table 2. The initial cost for purchasing or manufacturing devices varied, from the relatively low-cost devices built inhouse to the higher cost of commercially available devices. These initial costs ranged from a low of US$5.75 (pipe) to a high of US$70 for the treat dispenser of the Primate Enrichment System, with an additional US$69 for the holding frame. Labor for inhouse device construction was included in cost calculation for those devices. Supply costs were variable, ranging from US$0.07 to US$0.21. There was little variance in labor time, and thus in labor cost, across the devices. On average, the labor time as-

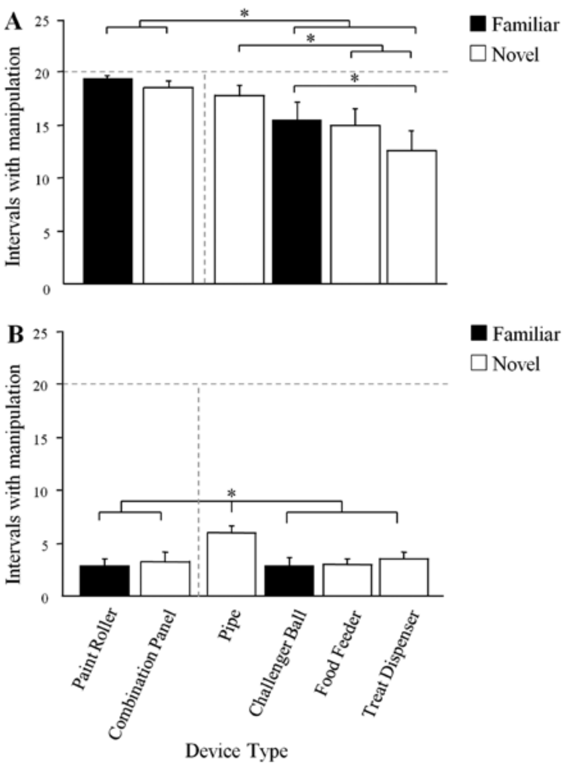

Figure 5. Number of intervals (mean ± SEM) with contact for all devices during (A) the initial observation period and (B) averaged for the 1- and 2-h observation periods. The dashed horizontal lines indicate the maximum possible number of observation intervals. The dashed vertical lines separate the 2 devices that held small forage foods from those that held larger fruit or vegetable pieces. Symbols refer to significant differences between devices. Post hoc tests showed that for the initial observation, manipulation of the paint roller was significantly higher than that for the challenger ball ($P = 0.006$), food feeder ($P = 0.002$), and treat dispenser ($P < 0.0001$). Manipulation of the combination panel was significantly higher than that of the challenger ball ($P = 0.04$), food feeder ($P = 0.01$), and treat dispenser ($P < 0.0001$). Manipulation of the pipe was significantly higher than that for the food feeder ($P = 0.04$) and treat dispenser ($P = 0.0003$). Manipulation of the challenger ball was significantly higher than the treat dispenser ($P = 0.04$). For sustained contact across the 1- and 2-h observation periods, manipulation of the pipe was significantly greater than that of the paint roller ($P = 0.0014$), combination panel ($P = 0.004$), challenger ball ($P = 0.001$), food feeder ($P = 0.002$), and treat dispenser ($P = 0.009$).

sociated with providing a monkey with a foraging opportunity was 2.5 min (range, 2.1 to 2.9 min). Together, the ongoing costs associated with the providing foraging opportunities through use of these devices averaged US$0.94 each, with a range from US$0.74 (paint roller) to US$1.13 (food feeder filled to maximal capacity).

Discussion

Overall, the results of this comprehensive evaluation of devices and strategies to promote foraging demonstrate that attention to choice of devices and foods are the significant and primary factors that influence both initial and sustained manipulation. From a broader perspective, the findings provide an example and model for a process of empirical cost–benefit analysis. The behavioral data verify that provision of foraging devices promote manipulation and engagement in captive macaques, which is a central part of the rationale for environmental enrichment (Figure 1 A).

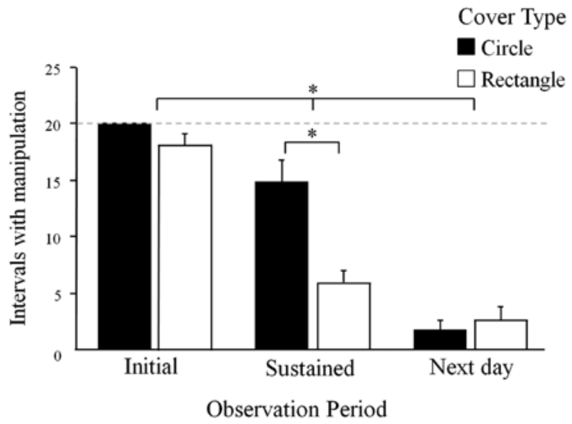

Figure 6. Number of intervals (mean ± SEM) with contact for food feeders having 2 types of covers during the initial observation period, the average of the 1- and 2-h observation periods, and the 24-h observation period. The dashed horizontal lines indicate the greatest number of observation intervals possible. Asterisks indicate significant ($P < 0.05$) differences between covers. Significant main effects for device cover and observation period were observed, as well as a significant interaction between them. Post hoc tests showed that manipulation of the food feeder was significantly ($P = 0.0001$) higher for the circular cover than for the rectangular cover for the sustained manipulation at the 1- and 2-h observations.

Some devices were more effective in promoting greater manipulation both after initial presentation and over a sustained period of 1 to 2 h. Familiarity with the devices did not appear to affect the animals' engagement. In fact, both devices with which the animals had years of experience, the paint roller and the challenger ball, elicited significantly more foraging than did some of the novel devices. Furthermore, with a single exception (the pipe), manipulation failed to decrease with repeated presentation. Efforts to promote diversity and novelty via rotation of foraging devices may not, in general, be an effective route to increase foraging behavior. In addition, previous studies have reported little habituation to enrichment.[3,31] Rotating devices is a common practice in nonhuman primate laboratory facilities, with 58% reporting rotation on a scheduled basis and 32% on a random basis.[1] The data reported here suggest that additional efforts are needed to evaluate whether rotation and novelty have other beneficial effects, given that these features do not appear to directly affect manipulation.

Two devices—the treat dispenser and the circular cover food feeder—were effective in eliciting continued manipulation. The treat dispenser device is designed such that food is not visible unless the device is manipulated by raising a PVC ring to reveal the hole from which food can be retrieved. The device is regularly used in the Harlow Primate Laboratory's enrichment program, and staff have observed continued interaction with it across multiple days. The observations suggest the possibility that tying food visibility to manipulation may be an important design consideration for developing new foraging devices that promote continued engagement.

Although all devices elicited some manipulation that was sustained 1 and 2 h after their initial presentation, the amount of manipulation was not high for many devices. On average, manipulation occurred during less than 25% of the observation intervals during the 1- and 2-h time points as compared with more than 50% and as much as 100% of the intervals during the initial placement. The animals made few contacts with the devices at 24 h after their placement, despite the fact that some food remained in the majority of them.

Table 2. Initial and supply costs per foraging device

	Total labor (min)	Ongoing costs			Initial cost
		Labor	Supplies	Total	
PES frame					$69.00
Food feeder	2.4	$0.76	$0.18	$0.94	$59.50
Food feeder (study 2)	2.9	$0.92	$0.21	$1.13	$59.50
Treat dispenser	2.6	$0.81	$0.12	$0.93	$70.00
Combination panel	2.6	$0.81	$0.18	$0.99	$45.00
Pipe	2.4	$0.76	$0.18	$0.94	$ 5.75
Challenger ball	2.5	$0.78	$0.16	$0.94	$39.50
Paint roller	2.1	$0.67	$0.07	$0.74	$ 9.27
Range	2.1–2.9	$0.67–0.92	$0.07–0.21	$0.74–1.13	$5.75–70.00
Average	2.5	$0.79	$0.16	$0.94	$38.17

Relatively small amounts of food were used in all devices here in study 1. The results of the study are important for uncovering differences between devices and amount of manipulation when typical amounts of enrichment food are used. They do not, however, fully address the amount of manipulation that could occur with a larger volume of food. Study 2 addressed this issue by comparing 2 devices filled to maximal capacity. The results provide evidence that foraging can be sustained at higher levels with a greater amount of food, but that the relationship depends on features of the device. At 1 to 2 h, the manipulation of the cover with circular holes device remained high and significantly greater than manipulation of the rectangular hole device. Further study would be useful to determine the interaction between increasing amounts of food, device type, and increases in sustained manipulation. The current results provide a basis for selecting devices that are likely to be most successful in promoting sustained engagement with a range of food types and amounts.

One device characteristic associated with highest foraging during the initial presentation was its affordance to capture small bits of food that required continued effort to extract. The combination panel with artificial turf and the paint roller both offered this possibility and elicited the greatest amount of interaction during the first interval after placement on the cage. In addition, the results of study 2, with greater sustained manipulation for the circular-hole device, provide confirmatory evidence that relative difficulty of food extraction is a significant factor in increasing manipulation. Our findings are convergent with previous work that has successfully demonstrated significant increases in foraging behavior when small food items, including crumbled chow, are presented via various forms of artificial turf or other devices that require increased effort for food removal (for examples, see references 2, 10, 12, and 31). A comparison of the use of a fleece grooming board and a tube device with peanut butter by singly housed baboons[31] found individual differences in animals' engagement with the 2 devices, reduction of abnormal behavior, and evidence of interaction sustained over a 24-h period. A study that compared foraging time elicited by 3 devices found both significant differences between devices as well as increased foraging at 25 and 43 h after presentation of the devices.[12] The authors did not, however, include any cost analysis. Furthermore, the device associated with the highest sustained foraging later was discontinued from use due to practical challenges in staff labor and time for cleaning.

Several studies compared foraging time for standard chow when administered as biscuits and via different types of devices. One group demonstrated that foraging and consummatory behaviors increased by 52% when crumbled food was provided via an artificial turf board compared with biscuits delivered in a standard food hopper.[2] Similarly, another researcher[32] found that foraging increased 69-fold– from 23 seconds to 25 min– when chow biscuits were presented in a food puzzle hopper rather than a standard device. Reinhardt observed increased foraging time after 30 d of exposure to the puzzle hopper. By contrast, other authors observed 240% to 1200% increases in foraging time when familiar and novel foods were presented via a pipe feeder as compared with a standard hopper, although the increase associated with familiar food extinguished in 5 d.[18] Together the findings underscore the importance of explicitly evaluating whether strategies to increase foraging depend on food type and whether the effects are sustained over time. Although it seems obvious and intuitive that foraging behavior will increase when animals are presented with devices and foods that require extended effort for extraction, this principle may not uniformly guide decision-making in implementing EEP.

In addition, direct comparisons can be valuable in focusing development and continued improvement of foraging devices. A broad informal consideration of commonly used devices for nonhuman primate foraging shows that many are constructed in a manner that does not allow them to effectively present or hold small food items. Devices with large holes are fairly limited to presentation of foods that will not quickly fall out and thus that are commensurately large. For example, observations in our laboratory and in the larger colony at our facility show that popcorn, seeds, many cereals, cut beans, and so forth readily fall out of many foraging balls and similar devices. This experience is common across nonhuman primate facilities and a practical constraint to promoting diversity in devices and foods. Less obvious is that even those foods that are cut to fit the devices and that pose some extractive challenge often fail to engage nonhuman primates in foraging for a greater amount of time than the time required of staff to prepare those foods.

The issue is addressed in part by some commercially available devices with food treats manufactured to fit them. Unfortunately, there are few data on the effectiveness of these food–device combinations in eliciting prolonged foraging. Furthermore, because custom treats often exceed the cost of other foods, they may not be the optimal choice in the absence of evidence for higher value. Overall, practical considerations, along with the results of this study and others, point to the ongoing need for targeted development of devices based on comprehensive cost–benefit data from direct comparisons made with standard metrics for evaluation.

Careful specification and control of food type is important from a methodologic and replicability perspective. At the same time, it is difficult to conduct controlled comparisons with devices and foods that are commonly used in laboratory settings. Similarly, and as demonstrated by the results of our study, generalizing beyond specific food–device combinations poses some challenges. In the context of informing development and implementation of foraging components of EEP, food type and choice are also centrally important because nutritional and caloric factors are among the concerns frequently raised in association with efforts to increase the frequency of foraging opportunities for captive animals.

Best practices for the selection of the type and amount of food used in nonhuman primate foraging opportunities have not yet been addressed well in the empirical literature. As a result, environmental enrichment is widely viewed as a source of uncontrolled variance in research animals' dietary intake, a possible confound in research projects, and a potential contributor to weight gain and adverse health outcomes.[30] These are reasonable concerns in light of the fact that personnel often view calorically dense (for example, peanut butter, peanuts) or high-sugar foods as preferred 'treats' for these animals. Many treat foods also have characteristics that make them desirable from a practical perspective for those charged with maintaining enrichment programs. For example, apples, peanut butter, peanuts, cereal, and marshmallows have relatively low perishability, low cost, high suitability for common foraging devices, and—likely—high potential to elicit sustained interest and foraging.

Effectively providing foraging opportunities for nonhuman primates can be achieved in a way that does not compromise the animals' nutrition, lead to unwanted weight gain, or result in excessive increased costs. For example, one study provides strong demonstration via a direct comparison of monkeys' foraging from turf for particulate monkey chow compared with particulate fruit-flavored treats that showed neither differences between the foods nor weight gain associated with twice-daily provision of foraging.[2] Explicit attention to both nutritional composition and serving size to guide selection of specific foods is also an obvious way to address concerns about environmental enrichment providing excess calories, fat, or sugar.

The range of calories provided here per foraging opportunity was roughly 40 to 150 kcal, or approximately 4% to 15% of the intake of a 10-kg adult monkey maintained on a 100 kcal/kg chow diet. The animals in this study did not show weight gain associated with enrichment. There is no accepted or widely used standard for the proportion of calories or specific nutrients captive primates receive via nonchow dietary sources that include enrichment. In absence of specific published guidelines, observation of animals' health and weight, reference to the composition of the species' natural diet, and recommendations for human primate nutrition may provide the appropriate guidance for best practices in selection of foods for enrichment.[26]

In the study reported here, one explicit goal was to evaluate foraging across device types with food type and amount held relatively low and constant. This goal was not possible with all devices. However, we were able to compare multiple devices that held the same types of food, as well as the same devices with a range of foods typical of primate enrichment programs. As a result, the differences between devices with similar affordances (that is, greater foraging with challenger ball compared with treat dispenser and pipe compared with food feeder and treat dispenser) can be attributed to the device type rather than food type. The results are likely to generalize over a broader range of produce. Finally, because we specified the amount of food used, its caloric value, and cost range, the data presented here should allow for scaling up to increase duration of foraging. The data also allow for calculation, or for projection, of the potential contribution of foraging enrichment to animals' daily caloric intake.

To our knowledge, this study is the first to perform a comprehensive cost–benefit analysis and comparison of commonly used strategies included in the food-foraging component of nonhuman primate EEP. The results demonstrate that the devices did not differ a great deal in terms of costs beyond the initial purchase or construction. Furthermore, the analysis provides evidence that the full cost of providing a foraging opportunity is roughly US$1.00. Nearly 80% of that cost is attributable to the labor time associated with preparing forage foods and with attaching, removing and cleaning devices. Direct time–labor analysis of each of these activities showed that personnel time associated with a foraging opportunity was roughly 2 to 3 min per animal, or approximately 5 h for 100 animals. This point is important from the perspective of facility management, budget projection, and decision-making. It is also true, however, that the actual cost of implementing foraging may be less, because the staff are already engaging in feeding or other activities that can partially be combined with enrichment. For example, in a survey of 22 facilities, enrichment technicians and animal care technicians account for 63% and 37%, respectively, of the personnel charged with distributing and implementing foraging devices.[1] In general, these activities also provide good opportunities for developing and enhancing a 'culture of care' among personnel, because animals respond with more complex engagement than is elicited by simply providing food via hoppers or in the cage.

The other ongoing cost for provision of foraging is the foods themselves. In this work—with the exception of study 2—we used relatively small amounts of food, but we provide the information in a way that it can easily be used to estimate the cost of scaling up to larger servings. Again, however, this cost is likely already in place at most facilities, given that most provide produce, nuts, seeds, popcorn, and other foods to supplement the standard chow diet.[1] Some facilities provide supplemental foods via food hoppers or by hand. Our results demonstrate that the additional cost to provide the food via foraging devices may be a relatively small increase and one with high value for animal welfare.

The final consideration in decision-making about enrichment devices and in cost comparison is their durability, maintenance, and replacement over the longer-term. The devices evaluated here have been in use in our laboratory for over a decade. All are outstanding in terms of long-term durability. The commercial frames that attach to cages have been in place for 13 y and have required little maintenance. The device shells are of molded plastic that is unbreakable and that withstands frequent use and high-temperature disinfection. The internal components are also durable and have required little maintenance or replacement. Similarly, the challenger ball and the devices made in-house are all robust and long-lasting.

In the context of the model presented in Figure 1, the results of this study provide data and an example of an approach to assess the relative value of different environmental enrichment strategies. Table 3 illustrates how this type of cost analysis might be used in budget projections to inform selection and decision-making about foraging components of EEP. Cost is estimated on the basis of providing different levels of foraging for 100 macaques for a 1-y period. Initial device cost and supplies are shown separately from labor, which is estimated as hours/week. However, that these estimates may be high because they do not account for efficiency of scale. In other words, some labor costs would not increase proportionately to the number

Table 3. Example of cost projections over 1 y for 100 animals

Amount of foraging	Device and frequency	Initial device cost	Cost of food supplies	Labor (hours per week)
Low	Pipe with forage food once weekly	$575	$936	4
Medium	Food feeder with forage food 3 times each week	$5950	$2808	12
High	Combination panel with forage food daily	$11,400	$6552	30

of animals served. Costs for 3 levels of foraging provision are estimated, by using the results of the study reported here to select those device and food combinations that result in the highest manipulation. The costs are projected based on frequency of provision—comparing once weekly, 3 times per week, and daily. What the projection shows is that daily foraging can be provided for a relatively low cost when considered within the context of all other costs associated with laboratory animal care (that is, clinical care, husbandry, record-keeping, facility maintenance, and so forth).

There are many obvious sources of variance between facilities in terms of costs and in practical considerations. Nonetheless, the kind of analysis performed here fills a gap in the literature by providing a model for a relatively straightforward empirical approach to evaluate resources needed to implement one part of most nonhuman primate facilities' EEP (Figures 1 B and 4). In turn, the approach allows for comparison of different practices and, ultimately, sufficient data from which to identify best practices that are beneficial for animal welfare, feasible, and of high value (Figure 1 C).

Our study aimed to provide a cost–benefit analysis. It did not focus on outcome measurements in terms of effects of foraging on animals' health and wellbeing. As discussed earlier, ample strong evidence demonstrates the benefit of, and need for, exploratory, manipulatory, and cognitively engaging activities for nonhuman primates. In fact, the beneficial effects of providing captive animals foraging opportunities is well-established and has become a community standard—if not a regulatory requirement—for laboratory-housed primates in the United States. Therefore, we operationalized benefit as manipulation and engagement with foraging devices (Figure 1 A), with the majority of animals as our target population. Species-typical foraging behaviors were sustained by all devices in this study, which suggests their inherent value to the psychologic wellbeing of the animals. Evaluating the effects of foraging enhancements as behavioral treatments for untoward behaviors (excessive self-grooming or abnormal behaviors) was not our aim. Furthermore, a number of studies suggest that foraging, device interaction, or other enhancements do not always produce an expected direct benefit for animals that exhibit abnormal behavior[10,12,13,23,29,36,39] (for additional discussion, see references 24 and 37). Finally, the evaluation of foraging as a remediation for abnormal behavior requires a sufficient sample of animals that exhibit the behavioral problem. The participants used in this study did not provide such a sample.

The body of empirical literature aimed at evaluating multiple aspects of foraging opportunities for nonhuman primates provides ample evidence that it has potential to be a high-priority activity for EEP. At the same time, practical and other concerns continue to be obstacles to uniform practices. Among the challenges are perceived high costs and labor; nutritional and health concerns; and identification of best practices in implementation (that is, device types, food type, and frequency of delivery and rotation). The focus of this study was to produce comprehensive data that would address practical challenges to implementation and improvement of foraging components within EEP, including data about inclusive cost. The primary results of this study and others provide an empirical basis to guide specific recommendations about strategies for selection and implementation of food-foraging strategies. Among those recommendations are 1) devices that permit small food items or pose manipulative challenges should be prioritized; 2) devices should be filled at least daily, or more frequently, if the objective is provision of daily foraging; and 3) device novelty and rotation are less important than are device characteristics. Furthermore, these data demonstrate that foraging opportunities can be provided for a relatively low cost and in a manner that does not compromise nutrition. Finally, our study provides a conceptual approach and illustration of workable methods to support direct comparisons of different implementation strategies both within and across facilities, as well as a method for cost projection to inform decision making.

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