

Influence of Multiple Factors on Rhesus Macaque (*Macaca mulatta*) Use of a Feeding Enrichment Device

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We studied the effect of different filler items on rhesus macaques' use of a feeding enrichment device called the 'browsing bowl.' We examined use of the device as affected by calories, sugar content, and volume of different fillers as well as the presentation of each filler as 1) whole, loose, or smeared and 2) frozen or not frozen. In addition, we examined the impact of age and sex of the monkeys on use of the device. Fifty-eight macaques were observed across 30-min sessions with the device, with one session for each of 12 different fillers. Scans occurred every 2.5 min, at which point the monkeys were scored as interacting or not interacting with the device. Subjects were recorded as interacting with the device during 47.6% of all observed scans and during 80% of the first 2 scans per session. Frozen items were associated with a significantly higher mean engagement (ME; proportion of observed scans in which animals engaged with the device) than items that were not frozen items ($t(57) = 12.91$, $P < 0.001$). Whole presentations were associated with a significantly higher ME than for smeared ($P < 0.001$) or loose ($P = 0.005$) items. Loose items were associated with a significantly higher ME ($P < 0.001$) than for smeared items. Sugar and calorie content did not impact use of the device. Younger monkeys used the device more than for older monkeys, and female monkeys used the device more than did males. We conclude that some filler items encourage more foraging behavior than others, and that it is possible to generate relatively long (up to 30 min) foraging bouts by altering the presentation of foods rather than increasing calories or sugar content. Indeed, some fillers were still present and engaged with at the end of the observation session.

Abbreviations and Acronyms: B, β coefficient; ENPRC, Emory National Primate Research Center; MD, mean difference; ME, mean engagement; Std., standardized.

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Introduction

Rhesus macaques (*Macaca mulatta*) living in natural environments may spend nearly a third to more than half of their day foraging and consuming food.^{1–3} This natural activity budget is replicated in captive settings by providing food-based foraging opportunities, perhaps by scattering food throughout the animals' enclosure or by implementing enrichment devices that require the animals to work to extract food. Many species have been shown to prefer food that requires effort compared with food that can be acquired through 'freeloading,' a phenomenon first described in laboratory rats.⁴ The described preference for food that requires effort over food that is freely available is referred to as 'contrafreeloading.' Multiple studies have reported that captive macaques engage in contrafreeloading, increasing the amount of effort invested over time to retrieve food from enrichment devices rather than ingesting freely available food.^{5–9} Several different enrichment devices have been demonstrated to induce long bouts of foraging behavior in captive macaques,^{5,10–12} which promotes a more natural activity budget for NHPs living under human care. Some of these

enrichment devices not only encouraged desirable behaviors, such as foraging, but also appeared to reduce undesirable behaviors (that is, overgrooming, stereotypies, and injuries caused by social aggression).^{10,11,13–16}

Not all foraging devices have equivalent impact on behavior, however. Studies that compared the impact of multiple foraging devices have demonstrated that different devices are associated with varied amounts of foraging behavior.^{5,11} Bennett and colleagues reported that devices that required more work to extract food were associated with more manipulation of the devices and their edible contents.⁵ They also reported that when the food inside a device was not clearly visible, the device was manipulated for more time. Familiarity with a particular device did not affect manipulation time.⁵ However, Gottlieb and colleagues reported an increase in stereotyped behavior associated with devices that appeared to be difficult for monkeys to use effectively. They concluded that some devices are too challenging and can lead to frustration-induced behavior.¹¹

The type of food placed in a foraging device also influences use of that device. Although one study reported that novel foods increased use of a foraging device,¹⁷ we were unable to find much research focused on the qualities of food used with foraging devices. These qualities may impact the animals' degree of active engagement with a device and could also potentially impact animal health. It is important that healthy foods be used in foraging devices as much as possible, particularly for

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Table 1. Subject age and housing

Sex	Subject no.	Mean age paired	Subject no.	Mean age single	Mean age across housing
Females	11	11.0	24	11.2	11.1
Males	5	8.0	18	8.8	8.7

frequently used devices. For example, foods that are high in sugar or fat content should be used sparingly. Welfare scientists studying NHPs should identify enrichment devices that are at an appropriate level of difficulty (increasing engagement but not frustration) and which encourage a more natural activity budget for captive-living rhesus macaques. In addition, researchers should assess the value (as far as having the desired impact on behavior) of different food items as incorporated in these devices. Ideally, the foods used in foraging devices should stimulate the animals' engagement while providing benefit to the animals' health or, at minimum, having a neutral impact on their health.

In the current study, we assessed the incorporation of various foods in a specific foraging device, that is, the 'browsing bowl.' Foods selected for assessment varied in type, presentation, sugar and caloric content, and volume. We recorded the macaques' engagement with the browsing bowl to determine the impact of the different food 'fillers' on use of the device. We also examined use of the device as a function of the animals' age and sex. We hoped to identify relatively healthy (but effective) foods to use with enrichment devices and to determine the best method of food presentation, potentially tailoring those choices toward the monkeys based on their age and/or sex.

Materials and Methods

Subjects. We evaluated 58 rhesus macaques (35 females, 23 males) with ages ranging from 1 to 24 y old (mean age = 10.1 y, SD = 5.9). Sixteen subjects (11 females, 5 males) were pair-housed, while the other 42 were singly housed (see Table 1 for further subject descriptions). Housing was decided by other factors unrelated to this study. All subjects lived at the Emory National Primate Research Center (ENPRC) Field Station in Lawrenceville, GA. Subjects were categorized for analysis by age, sex, and social housing status (single compared with paired). Pair-housed subjects were selected only if observed to exhibit minimal competition for food resources. In addition, animals in pairs were always provided with 2 devices containing the same filling type. This selection criterion was implemented to avoid potentially confounding effects of social dominance (such as food hoarding and/or food aggression by the dominant individual) on subjects' interactions with foraging devices.

The ENPRC is accredited by AAALAC International. The housing and care of these subjects is in accord with the *Guide for the Care and Use of Laboratory Animals*¹⁸ and the USDA Animal Welfare Act.¹⁹ Cages consisted of interconnected, stainless-steel mesh cages averaging in size dimensions of 0.8 × 0.8 × 0.7 m. Singly-housed subjects occupied one cage, and pairs occupied 2 adjoining cages. All subjects always had visual, auditory, and olfactory access to other rhesus macaques. Rooms were kept on a 12-h light/12-h dark cycle. No subject was clinically sick or obese at the time of the study, and all subjects had free access to water ad libitum. Monkeys were provided with monkey chow twice daily (PMI LabDiet no. 5037, Richmond, IN) and half of an orange once daily. Enrichment items such as fresh produce, dry cereal, seed mix, uncooked pasta, and/or destructible (paper) items were given every day. Each macaque had a manipulable toy inside the cage, a foraging device hung on the front of the cage (for example, challenger ball), and a forage board attached

to the front of the cage. Toys and hanging devices were rotated biweekly to promote novelty.

Materials. The browsing bowl foraging device was proposed in 2015 by an ENPRC staff member and subsequently pilot-tested for safety. The device consists of a size 2 (2.4-in. inner diameter) polyvinyl chloride cap that attaches to the cage front via a 6- by ¼-in. stainless-steel partially smooth hex screw that is bent into a J-shape at the cage-facing end to hook on to the mesh. A ¼-in. stainless steel wingnut is applied to the back of the bolt so that the device can be attached and tightened until it is flush to the cage. A ¼-in. Nylock nut is permanently secured at the end of the bolt (see Figure 1). The total cost of materials is estimated at \$10 per device.

Twelve browsing bowl fillings were selected for assessment, each defined by the type of food(s), the preparation of the food (frozen or not frozen), and the method of presentation in the device (whole, smear, or loose) (see Table 2). Whole items were presented as a solid item (a frozen cube, a whole unpeeled portion of a banana, or a tightly compressed block of alfalfa) placed inside the bowl. Smear items were semiviscous and smeared on the inner rim of the browsing bowl (not the back because it was beyond the monkeys' reach). The fillings categorized as 'loose' included cubes of alfalfa that, when soaked in juice or water, consisted of loosely-bound pieces of alfalfa that could easily be removed. Also, the vegetable mix and cereal mix were



Figure 1. The browsing bowl device is attached to the cage front with 1-in. mesh.

Table 2. Filling types, nutritional information, and presentation

Filling name	Food type	Volume (Tbsp.)	Sugar (g)	Total calories ^a	Description
Frozen banana	Banana, frozen, whole	4	5	35	~1/3 unpeeled banana, frozen
Regular banana	Banana, not frozen, whole	4	5	35	~1/3 unpeeled banana
Banana mash	Banana, not frozen, smear	3	5	35	~1/3 peeled banana, mashed
Alfalfa cube	Alfalfa, not frozen, whole	4	0	43	Cube of compressed alfalfa
Alfalfa juice cube	Alfalfa, not frozen, loose	8	7	79	Cube of compressed alfalfa, soaked in 4 tbsp. Gerber reduced-sugar apple juice
Alfalfa water cube	Alfalfa, not frozen, loose	8	0	43	Cube of compressed alfalfa, soaked in 4 tbsp. water
Oatmeal	Oatmeal, not frozen, smear	1	12	50	1 tbsp. oats, 1 tsp. honey, 3 raisins, 1/8 tsp. cinnamon, 1 tsp. water
Frozen oatmeal	Oatmeal, frozen, whole	2	12	50	Mix plus 1 tbsp. water, frozen into cube
Peanut butter	Peanut butter, not frozen, smear	1	2	100	Plain peanut butter
Frozen peanut butter	Peanut butter, frozen, whole	2	2	100	Peanut butter plus 1 tbsp. water, frozen into cube
Frozen veggies	Veggies, frozen, loose	4	1	15	Even amounts of carrot, cauliflower, and broccoli pieces, frozen pieces
Cereal with apricots	Cereal, not frozen, loose	8	5	37	2 tbsp. Kix + 2 tbsp. diced, dried apricots in bowl behind 3/4 cup shredded paper compressed into 4 tbsp.

^aCalorie information from Nutritionix.

categorized as loose because they were composed of multiple small food items extracted individually from the bowl. For the purpose of analyses, we recorded the amount of sugar found in each serving (1 serving = the portion included in the device), the volume of the serving as presented in the device, and the total calories in each serving (Table 2). Information about sugar and caloric content was obtained from the nutrition label for a specific item (for example, the Gerber juice bottle) or, if this was not available, from a website (<https://nutritionix.com>). Note that we report the volume of the cereal mix filling including the volume of shredded paper, which was part of that filling. The monkeys often ingested the shredded paper, so for the purpose of analysis we considered it part of the filling volume (the calories for paper are negligible; each cereal mix serving included 2 shredded sheets of 8- × 11-in. white TreeZero copy paper). All foods used in the study were approved by a committee composed of a veterinarian, an operations manager, and the director of behavioral management at the ENPRC. All food items used in the browsing bowl are also routinely fed (for example, in other enrichments or with medications) to the macaques at a frequency determined by ENPRC standard operating procedures. We did not conduct a food preference test prior to the study, so we were unaware of any individual or collective preferences for the foods used.

Data collection. All subjects were exposed to the browsing bowl device at least once weekly for 4 wk prior to beginning observational data collection. For 2 wk prior to data collection, 5 observers were trained to reliability on the ethogram during in-room observation sessions so that training sessions also allowed the animals to acclimate to the observers. We gave the monkeys a filled device for 2 h on 6 different days over 2 wk. This was done to reduce the potential impact of subjects' responses to novel objects. Fillers during this period included yogurt, applesauce, frozen juice cubes, or other similar items that were not going to be part of the study. Afterward, behavioral data were collected using a scan-sample method in which each subject was observed for 2 s at intervals of 2.5 min (shorter intervals were difficult for obtaining reliability across observers). Multiple subjects might be observed simultaneously if they were in proximity, in which case scans started with one

subject and rotated through all observed in the same order at each scan point. Filler types were provided in random order to the subjects, and washout periods (minimum of 24 h) between sessions with the browsing bowl were similarly incorporated into the study design to reduce potential carryover effects.^{20,21} At each scan point, subjects were recorded as interacting or not interacting with the device and/or its filling material. Interactions included manual, oral, or pedal manipulation of the device/filling and are referred to as 'engagement.' Each observation session was 30 min long and included 13 scans per subject. At the end of each session, the device was removed, and any remaining contents were noted. If all food was removed from the device (less than about a 1/4 tsp. of edible content remaining), the filler was considered 'fully consumed.' If not, this was recorded as 'leftovers.' We chose to conduct 30-min observations because we had previously noted (during the 2-wk exposure phase) a decline in use of the device within that period and minor change beyond the 30-min marker. At the end of each 30-min session, observers noted whether there was leftover filler in the device. All 58 subjects completed observation sessions with peanut butter, frozen veggies, oatmeal, and a cereal/apricot mix, while 57 completed frozen banana and alfalfa cube sessions, 52 completed banana mash and regular banana sessions, 51 completed alfalfa juice cube, frozen peanut butter, and frozen oatmeal sessions, and 50 completed alfalfa water cube sessions. Across all subjects, we collected data from 653 subject/filler sessions, with many of these recorded simultaneously, for a total of 64 h of observation time. Observation sessions started at least 2 h after routine feeding times or stocking of devices such as forage boards or challenger balls, which were always available to the monkeys, and were not part of the current study. Observations occurred between 1200 and 1400 or between 1500 and 1700.

Data analysis. Data were analyzed based on filler type ($n = 12$ filler types) and on subjects' engagement with the device ($n = 58$ subjects). Each subject's mean proportion of intervals interacting with the enrichment device (hereafter referred to as mean engagement [ME]) across all filler types was calculated. A linear regression was used to determine the relative impact of age (in years), sex (coded 0 = female, 1 = male), and housing status (singly housed = 1 or paired = 2) on ME across all fillers.

This was done to ensure that housing was not impacting overall use of the device. Following this test, filler types were categorized as frozen or unfrozen, and as whole, loose, or smeared (see Table 2). A ME score for fillers within each category was calculated for all subjects. A repeated-measures multivariate ANOVA was used to analyze the impact of age and sex on fillers that were frozen or not and on fillers that were whole, loose, or smeared. Post hoc tests were conducted to compare whole, loose, and smeared ME scores. We also ran correlation tests between all subjects' average ME with the browsing bowl for each filler type at scan 13 and the percent of sessions with that filler type that had documented leftovers ($>1/4$ tsp. of edible content remaining). This was to determine whether a lower ME at scan 13 was a result of the filler being fully removed prior to that point. Statistical analysis was performed using the SPSS software package.

Results

General findings. The browsing bowl device proved to be effective, as all subjects were recorded to use the device with an ME across all scans of 47.6% ($n = 58$, range from 20.5% to 70.5%, $SD = 12.2\%$). The ME was highest at scan 1 ($ME = 93.8\%$) and decreased at each subsequent scan point, with an ME at scan 13 of 15.7%. Frozen banana maintained the $ME > 80\%$ until the 11th scan, at which point it dropped to 70%; at scan 13, frozen banana still had an $ME > 65\%$ (Figure 2). In addition, frozen banana sessions had documented leftovers ($>1/4$ tsp. remaining) after the 13th scan 59.6% of the time.

Paired compared with singly-housed subjects. A linear regression ($F(3,54) = 3.20$, $P = 0.031$, $n = 58$) assessing the impact of age (in years), sex (0 = female, 1 = male), and housing status (1 = single, 2 = paired) on ME of all subjects with the device (across all fillers) found a significant impact of age (β coefficient [B] = -0.60 , $SE = 0.27$, standardized [$Std.$] $B = -0.29$, $t = -2.25$, $P = 0.028$) and of sex ($B = -8.11$, $SE = 3.20$, $Std. B = -0.33$, $t = -2.53$, $P = 0.014$) but not of housing ($B = -1.93$, $SE = 3.43$, $Std. B = -0.07$, $t = -0.56$, $P = 0.576$). The negative value of the slope of each predictor indicates that as animals aged, ME decreased, that ME was lower for males than females, and that the ME for paired animals was lower than for singletons. However, comparison of the relative impact of each predictor ($Std. B$) indicates that the

impact of housing was minimal (and not significant) compared with that of age and sex. Age and sex were thus included in further analyses to account for those effects, but housing was not.

Nutritional content. The volume, sugar, and total calories associated with a serving of each filler was assessed for correlation with the ME for the device with each filler type. There was not a significant correlation between any of these nutritional measures and average use of the device.

Filler and subject characteristics. Two repeated-measures multivariate ANOVAs were conducted to assess the relationship between age, sex, and 1) subjects' ME with fillers that were frozen or not frozen as well as 2) subjects' ME with fillers that were presented whole, loose, or smeared. We could not include both categorizations in one test because not all resulting cells had data (for example, there were no frozen and smeared items). If a particular subject did not have data for all filler types within a category, the ME was calculated for all filler types within the category for which we did have data. All 58 subjects were thus included in analyses (35 females, 23 males).

For frozen compared with not frozen items, multivariate tests indicated no significant interaction between filler category and age or between filler category and sex. There was a significant main effect of category, however (Wilk test = 0.478 , $F(1,55) = 59.97$, $P < 0.001$, partial eta squared = 0.52), as well as a smaller but significant main effect of age ($F(1,55) = 6.07$, $P = 0.017$, partial eta squared = 0.10) and of sex ($F(1,55) = 5.24$, $P = 0.026$, partial eta squared = 0.09). When the browsing bowl device was filled with frozen items, the ME was higher than when it was filled with nonfrozen items (mean difference [MD] = 18.7 , $SE = 1.45$, $t = 12.91$, $df = 57$, $P < 0.001$; Figure 3). Regardless of category, females had higher ME scores than did males, and older animals used the device less than did younger animals (Figure 4).

When the same subjects were compared for ME with fillers categorized as whole, loose, or smeared, no significant interactions between presentation type and either age or sex were found, but there was a significant effect of presentation type on ME (Wilk test = 0.495 , $F(2,54) = 27.52$, $P < 0.001$, partial eta squared = 0.51). Age and sex both retained significant main effects along with a main effect of presentation category, although these effects were still small (age: $P = 0.021$, partial eta squared = 0.09 ; sex: $P = 0.014$, partial eta squared = 0.10).

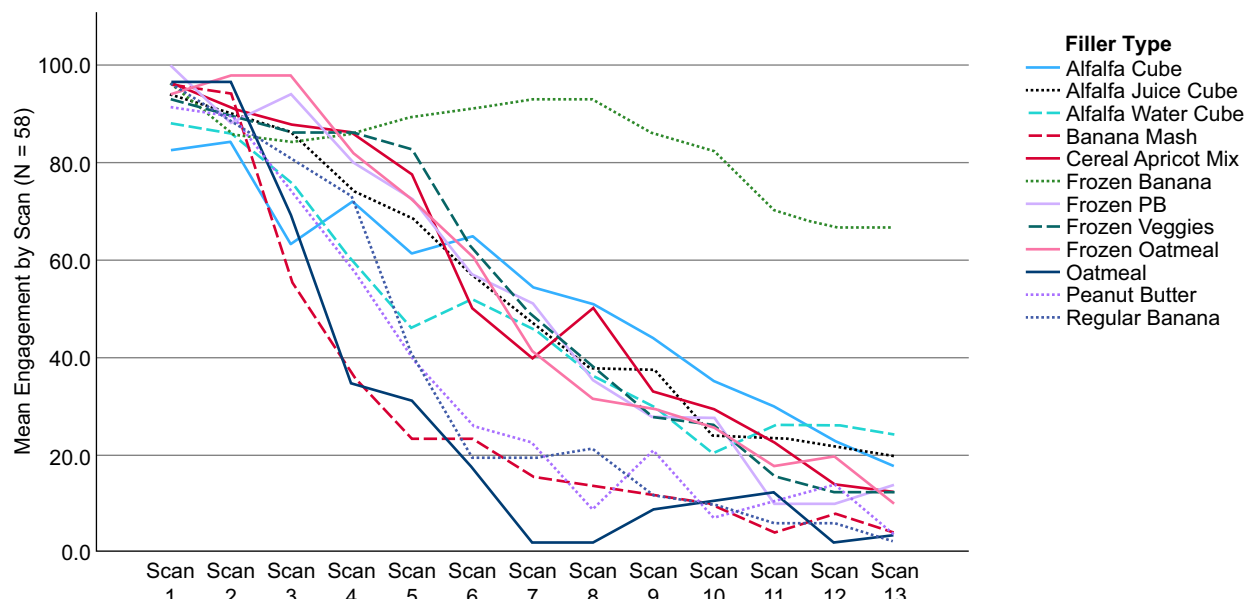


Figure 2. Proportion of subjects engaging with the browsing bowl at each scan based on filler type.

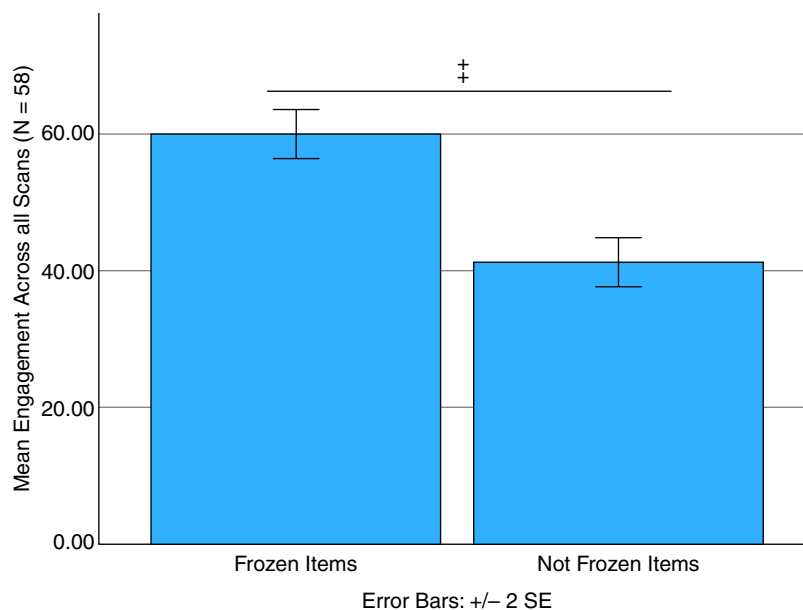


Figure 3. Mean engagement of subjects with the browsing bowl based on frozen or not frozen. ‡, $P \leq 0.001$.

Post hoc t tests found that animals had a higher ME with the browsing bowl when it was filled with whole items than with loose (MD=5.30, SE=1.8, $t=2.91$, $df=57$, $P=0.005$) or smeared items (MD=24.00, SE=1.8, $t=13.14$, $df=57$, $P<0.001$) and had a higher ME if the device was filled with loose items rather than smeared items (MD=18.70, SE=2.1, $t=8.93$, $P<0.001$) (Figure 5).

A Pearson correlation test between ME with the device at scan 13 (per filler, and across all subjects) and the percent of observed sessions with that filler that had documented leftovers was significant ($r=0.62$, $n=12$, $P=0.03$; Figure 6).

Discussion

Our findings suggest that the browsing bowl is effective as a foraging device for cage-housed rhesus macaques, with an ME

of >93% when the device was first presented, averaging 47.6% over 30-min observation periods, and maintaining 15% ME at the conclusion of observations. Published macaque studies on feeding enrichment devices report use over varying time periods using different observational methods, so that making direct comparisons to previous findings is not possible. However, there are several feeding devices reported to elicit species-typical feeding and foraging behaviors at rates that, at least for discrete periods of time, are similar to those of wild macaques.¹⁻³ We observed mean engagement with our device that is similar to that reported elsewhere, ranging from 25% to 52%.^{5,10-12}

Previous studies^{5,22} have emphasized the importance of food types incorporated into enrichment devices, suggesting that

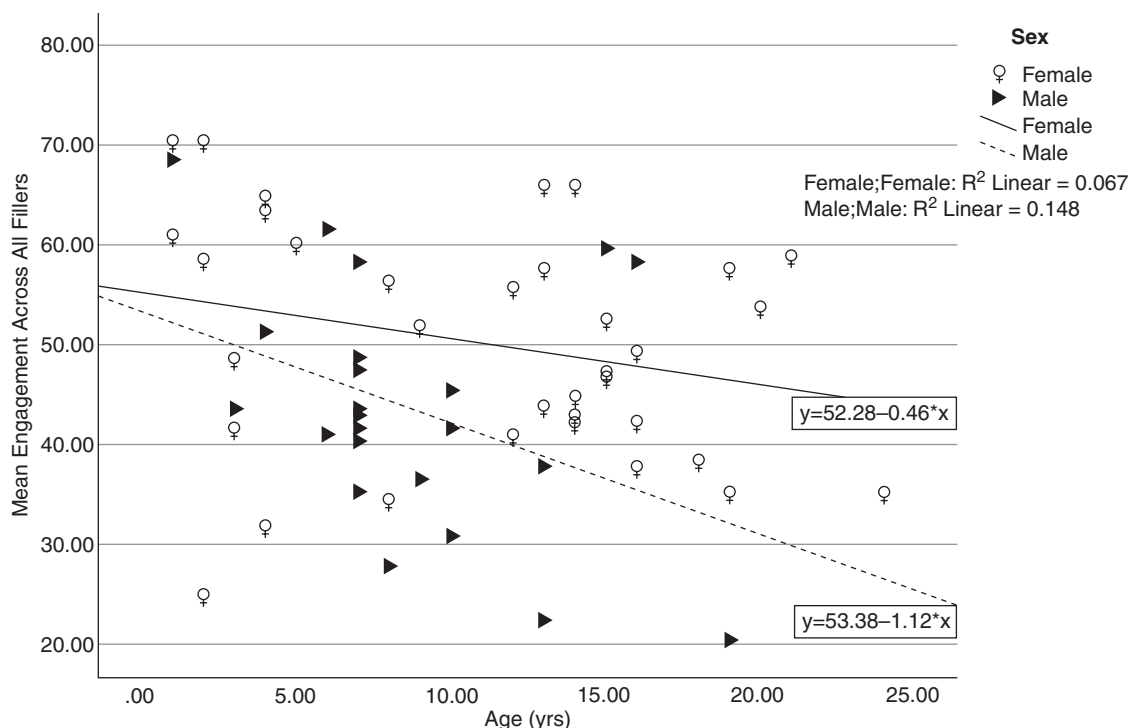


Figure 4. Mean engagement across all fillers as a function of age (in years) and sex of subject.

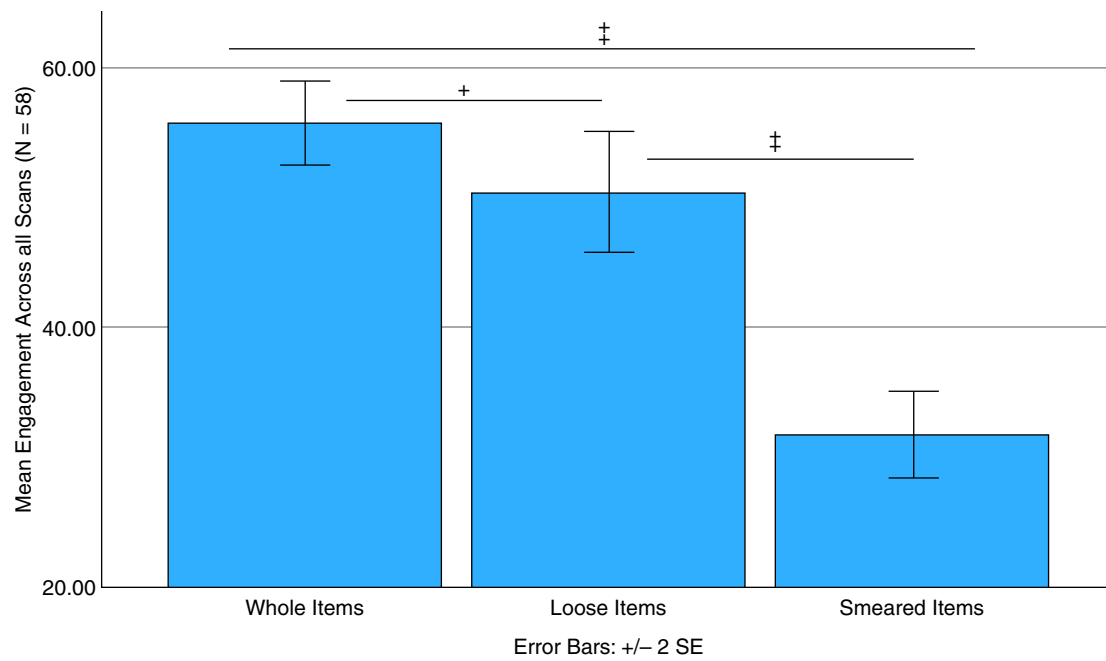


Figure 5. Mean engagement of subjects with the browsing bowl based on whole, loose, or smeared. †, $P \leq 0.01$; ‡, $P \leq 0.001$.

food items such as peanut butter or banana mash are more likely to encourage interaction with the device than standard monkey chow, but hypothesizing that this was due to higher sugar content in the preferred foods.^{5,22} In contrast, our findings indicate that sugar content is not necessarily related to a monkey's interest in a particular food; that is, higher engagement with an enrichment device for a longer amount of time may result from simply freezing a low-calorie, low-sugar item. The quality of the filler we used did have a significant impact on use of the browsing bowl, but this effect was not a function of caloric or sugar content of the foods.

We did not find previous studies regarding characteristics of the monkeys using a device as a factor impacting use of the

device. We found that the browsing bowl was an effective device for caged rhesus macaques, regardless of age or sex. Although females had higher rates of ME with the browsing bowl, males were also engaged in use of the device (>20% of the time). Similarly, although older animals engaged less with the device than did younger animals, they still used it a substantial percentage of time (>20%). There are few studies that have examined the relationship between individual traits (such as age and sex) and use of enrichment devices, and we encourage more assessment of these factors in future studies.

It is possible that there were carryover effects due to the order in which fillings were presented to the monkeys, as we did not include order of treatment in our statistical analyses, but as we

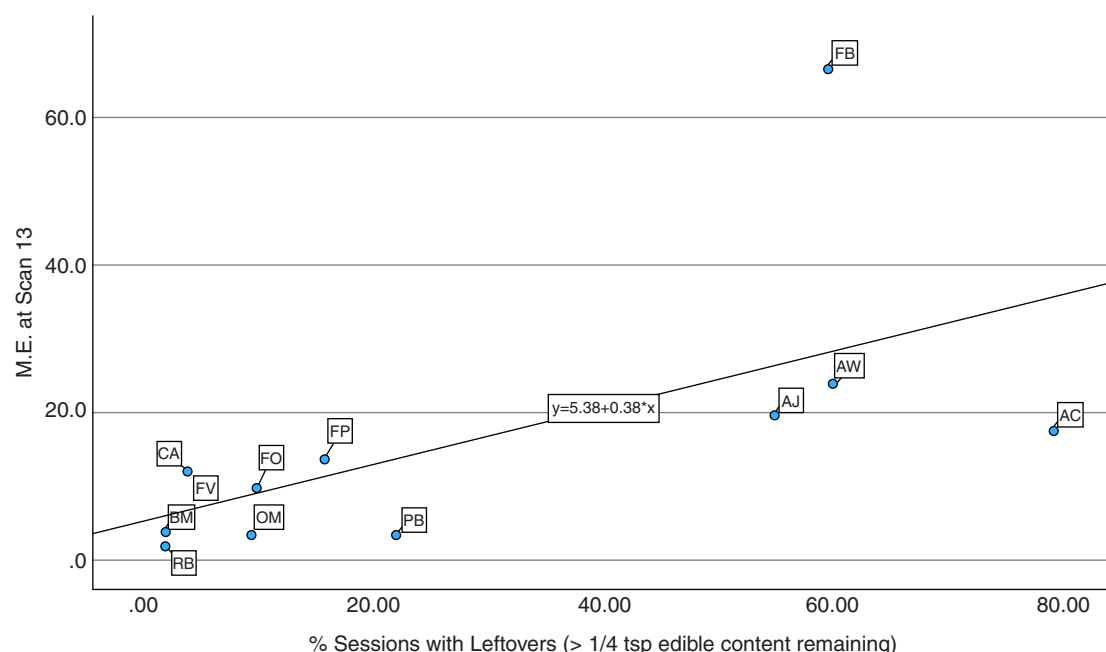


Figure 6. Mean engagement at scan 13 for each filler item as a function of percent of sessions with documented leftovers (> 1/4 tsp. of edible content remaining). AC, alfalfa cube; AJ, alfalfa juice cube; AW, alfalfa water cube; BM, mashed banana; CA, cereal/apricot mix; FB, frozen banana; FO, frozen oatmeal; FP, frozen peanut butter; FV, frozen veggie; OM, oatmeal; PB, peanut butter; RB, regular banana.

Table 3. Percent of sessions (per filler type) with leftovers at the end of session and ME at scan 13

Filler	% Sessions with leftovers	ME at scan 13 (%)
Regular banana	1.9	1.9
Banana mash	1.9	3.8
Frozen veggie	3.8	12.1
Cereal/apricot mix	3.8	12.1
Oatmeal	9.4	3.4
Frozen oatmeal	9.8	9.8
Frozen peanut butter	15.7	13.7
Peanut butter	22.0	3.4
Alfalfa juice cube	54.9	19.6
Frozen banana	59.6	66.7
Alfalfa water cube	60.0	24.0
Alfalfa cube	79.2	17.5

incorporated washout periods between treatments (minimum of 24 h) and randomized the order of presentation, we can be relatively certain that potential order effects were balanced by our study design.^{20,21} We found that 2 qualities of filler items had significant impact on ME with the device: frozen foods generated a significantly higher ME than foods that were not frozen, and items that were presented whole generated significantly higher use than loose foods. Both whole food items and loose items generated a significantly higher ME than smeared foods. Visual inspection of ME with different fillers at each subsequent scan point indicates that all 3 smeared foods (along with regular banana) were lower than all the other filler items at most scan points (Figure 2), also appearing to show the steepest and earliest decline in engagement around 12.5 min after the device was stocked with food. Interestingly, however, this does not seem to be due to the monkeys' retrieval and consumption of all smeared filler in a shorter amount of time. Peanut butter was left in the bowl at the end of a session 22% of the time, for example, whereas frozen oatmeal, frozen vegetables, and cereal/apricot mix, which generated higher levels of ME than any of the smeared items, were fully consumed by the end of the session >91% of the time (Table 3). Our findings, which indicate that food items requiring more work to extract (for example due to freezing banana with peel on) were associated with more manipulation, align with findings by Bennett and colleagues,⁵ as reported previously in this paper.

Based on our findings, we conclude that rhesus macaques will engage in foraging behavior across a variety of healthy food options, and that it is not necessary to provide high-calorie items to stimulate foraging. Fillers incorporated with the browsing bowl in this study were in the same caloric range as foraging foods studied by Bennett and colleagues,⁵ which they described as 4% to 15% of daily caloric intake for a 10-kg adult monkey (assuming the monkey is maintained on a 100 kcal/kg diet of monkey chow). We did find that the ME was higher at the end of a 30-min period for items with a higher volume, but this difference is quite small for all fillers other than the frozen banana, and for our fillers, volume did not vary with caloric content. A 35-calorie portion of banana generated the highest ME of any filler we provided. Peanut butter, at 100 calories per serving, was the highest calorie item we studied but generated one of the lower MEs. Peanut butter mixed with water and then frozen increased the volume without increasing calories and stimulated a significantly higher ME than did peanut butter alone. It appears that caloric content is not important, but rather the method of presentation is crucial toward encouraging

more foraging behavior over time. A higher ME can be achieved simply by freezing or compressing ingredients to require more effort, which aligns with the principle of contrafreeloading.

The results of our study support the use of the browsing bowl to encourage foraging bouts in cage-housed macaques. The browsing bowl device is practical to use, as its construction, installation, stocking of foods, and cleaning are all relatively simple and efficient. The device is low-cost, durable, and requires little or no maintenance. Furthermore, our findings show that macaques will use this foraging device for up to 30 min to extract foods with low caloric and low sugar content. Simple preparation methods can increase the amount of time macaques use the device: a portion of unpeeled banana, if frozen, can stimulate greater use across 30 min than the same chunk of unpeeled banana left at room temperature. Indeed, the same amount of banana, if mashed, generates significantly less engagement with the device while requiring more preparation time. Compressed alfalfa cubes also require no preparation and yet were among the highest ME items assessed in this study. Future studies should include assessment of the browsing bowl midway through an observation to determine how much food is left in the device at that point and should focus on making whole items more difficult to remove from the bowl. We found that some items could be removed in large chunks (particularly the unfrozen, unpeeled banana) and this reduced foraging time. It would also be beneficial to assess other behaviors while the browsing bowl is provided to determine if it reduces some abnormal behaviors or whether it may lead to frustration.¹¹ However, this study is a key step toward maximizing foraging behavior in cage-housed macaques without contributing to obesity or other health problems. In addition, by identifying some foods that require minimal preparation time from humans while also generating high engagement with a foraging device (for example, frozen banana was at an ME of >65% at the end of 30 min), we are contributing to the design of efficient feeding enrichment programs that focus on limited resources toward maximal improvement in animal behavior and welfare.

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Conflict of Interest

The authors have no conflicts of interest to declare.

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Author Contributions

Jason M Cowan-Brown conceived of the project, designed the project and associated ethogram, trained observers to reliability, collected data, and assisted in data analysis and writing of the manuscript; Andrea W Clay managed and analyzed data and wrote the final manuscript for

publication; Jaine Perlman assisted in experimental design; Celeste Lam and Adele Kramer collected data and assisted in manuscript preparation; and Mollie A Bloomsmith assisted in research design, data analysis, and manuscript preparation.

Data Sharing

The authors are willing to share data from this study upon request.

References

- Goldstein SJ, Richard AF. Ecology of rhesus macaques (*Macaca mulatta*) in northwest Pakistan. *Int J Primatol*. 1989;10(6):531–567.
- Jaman MF, Huffman MA. The effect of urban and rural habitats and resource type on activity budgets of commensal rhesus macaques (*Macaca mulatta*) in Bangladesh. *Primates*. 2013;54(1):49–59.
- Seth PK, Seth S. Ecology and feeding behaviour of the free ranging rhesus monkeys in India. *Indian Anthropologist*. 1985;15(1):51–62.
- Jensen GD. Preference for bar pressing over ‘freeloading’ as a function of number of rewarded presses. *J Exp Psychol*. 1963;65(5):451–454.
- Bennett AJ, Perkins CM, Harty NM, et al. Assessment of foraging devices as a model for decision-making in nonhuman primate environmental enrichment. *J Am Assoc Lab Anim Sci*. 2014;53(5):452–463.
- Evans HL, Taylor JD, Ernst J, Graefe JF. Methods to evaluate the wellbeing of laboratory primates: comparisons of macaques and tamarins. *Lab Anim Sci*. 1989;39(4):318–323.
- Line SW, Markowitz H, Morgan KN, Strong S. Evaluation of attempts to enrich the environment of single-caged nonhuman primates. In Driscoll JW, ed. *Animal Care and Use in Behavioral Research: Regulations, Issues, and Applications*. Animal Welfare Information Center; 1989:103–117.
- Reinhardt V. Using the mesh ceiling as a food puzzle to encourage foraging behaviour in caged rhesus macaques (*Macaca mulatta*). *Anim Welf*. 1993;2(2):165–172.
- Reinhardt V. Caged rhesus macaques voluntarily work for ordinary food. *Primates*. 1994;35(1):95–98.
- Bayne K, Mainzer H, Dexter S, Campbell G, Yamada F, Suomi SJ. The reduction of abnormal behaviors in individually housed rhesus monkeys (*Macaca mulatta*) with a foraging grooming board. *Am J Primatol*. 1991;23(1):23–35.
- Gottlieb DH, Ghirardo S, Minier DE, Sharpe N, Tatum L, McCowan B. Efficacy of 3 types of foraging enrichment for rhesus macaques (*Macaca mulatta*). *J Am Assoc Lab Anim Sci*. 2011;50(6):888–894.
- Schapiro SJ, Suarez SA, Porter LM, Bloomsmith MA. The effects of different types of feeding enhancements on the behavior of singly-caged, yearling rhesus macaques. *Anim Welf*. 1996;5(2):129–138.
- Beisner BA, Isbell LA. Ground substrate affects activity budgets and hair loss in outdoor captive groups of rhesus macaques (*Macaca mulatta*). *Am J Primatol*. 2008;70(12):1160–1168.
- Lam K, Rupniak NMJ, Iversen SD. Use of a grooming and foraging substrate to reduce cage stereotypies in macaques. *J Med Primatol*. 1991;20(3):104–109.
- Novak MA, Kinsey JH, Jorgensen MJ, Hazen TJ. Effects of puzzle feeders on pathological behavior in individually housed rhesus monkeys. *Am J Primatol*. 1998;46(3):213–227.
- Wooddell LJ, Beisner BA, Hannibal DL, Nathman AM, McCowan B. Increased produce enrichment reduces trauma in socially-housed captive rhesus macaques (*Macaca mulatta*). *Am J Primatol*. 2019;18(12):1–11.
- Holmes SN, Riley JM, Juneau P, Pyne D, Hofing GL. Short-term evaluation of a foraging device for non-human primates. *Lab Anim*. 1995;29(4):364–369.
- Institute for Laboratory Animal Research. *Guide for the Care and Use of Laboratory Animals*. 8th ed. National Academies Press; 2011:246.
- Animal Welfare Act Amendments. Pub. L. No. 99 - 198, 1985.
- Díaz-Uriarte R. Incorrect analysis of crossover trials in animal behaviour research. *Anim Behav*. 2002;63(4):815–822.
- Ratkowsky DA, Evans MA, Alldredge JR. *Cross-Over Experiments: Design, Analysis, and Application*. Marcel Dekker; 1993.
- Nash R, Johnston H, Robbins AM, Descovich K. The effect of enrichment filling and engagement time on regurgitation and reingestion behaviour in three zoo-housed orangutans. *JZBG*. 2021;2(1):10–20.