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Using a Touchscreen Paradigm to Evaluate Food Preferences and Response to Novel Photographic Stimuli of Food in Three Primate Species (*Gorilla gorilla gorilla*, *Pan troglodytes*, and *Macaca fuscata*)

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Abstract
Understanding captive animals' preferences is important for their care and management. However, pairwise testing for preference can be time consuming, open to bias, and typically restricted to stimuli that can be presented manually. We tested the efficacy of using touchscreens to test zoo-housed primates' food preferences and evaluated the primates' understanding and interpretation of photographic stimuli. We showed 18 subjects (six gorillas, five chimpanzees, and seven Japanese macaques) four food stimuli (digital photographs of familiar foods presented via touchscreens) to test their preferences in a forced-choice paradigm. We presented preliminary single-food training trials before paired forced-choice test trials, which revealed subjects' relative preferences for the four foods. To distinguish whether the primates' responses represented conditioned associations between the stimuli and rewards, or a true understanding of the food photographs, we ran a follow-up study with novel stimuli (novel photographs of familiar foods). We combined the two novel stimuli with the four stimuli presented in the first experiment in pairwise forced-choice trials (importantly, without training trials). Subjects did not preferentially select or avoid the novel stimuli, suggesting they spontaneously interpreted the stimuli without training. While there was interindividual variation in preferences, subject choices were consistent across studies, even with the

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addition of novel stimuli. These results suggest that preferences for a variety of stimuli could be tested quickly, efficiently, and accurately using touchscreens.

Keywords Photograph · Preference testing · Primate · Touchscreen · Welfare · Worth valuations

Introduction

Understanding the food preferences of captive animals has been an area of interest and emphasis in recent years. Elucidating food preferences can have a variety of applications among managed animals, including use in enhancing husbandry and training (Gaalema *et al.* 2011). Moreover, preferences can inform experimental testing paradigms, such that researchers can provide a more desired and meaningful reward to subjects for cognitive tasks (e.g., Brosnan and de Waal 2003). In general, animals' food preferences reflect choices made based on the interaction of factors such as taste (Drewnowski 1997) or nutritional need (e.g., Brousseau and Baglivo 2005). For instance, captive spider monkeys (*Ateles geoffroyi*) appear to prefer foods high in calories (Laska *et al.* 2000), whereas captive African apes prefer foods high in sugar (Ganas *et al.* 2008; Remis 2002, 2006; Wrangham *et al.* 1998).

The food selections of social animals, such as primates, can be further mediated by extrinsic factors such as the social environment (e.g., Kumpan *et al.*, 2019) or the choices made by their group mates (e.g., Galef and Whiskin 2008; Hopper *et al.* 2011; Wyrwicka 1993). Social factors can inhibit certain individuals' ability to select and eat preferred foods, which are monopolized by higher-ranking individuals (Finestone *et al.* 2014; Hopper *et al.* 2011; Murray *et al.*, 2006). Moreover, primates not only compare the type and quality of food in relation to that obtained by others in their group (Brosnan and de Waal 2003; Hopper and Cronin 2018), but they also compare it to what other food is available in the environment (i.e., "contrast effects," Gibson 2001; Hopper *et al.* 2014; Tinklepaugh 1928, or "decoy effects," Sánchez-Amaro *et al.* 2019). Thus, their choices can also be dictated by their *relative* preference for a food in relation to other options that are available and the "price" they are willing to "pay" to obtain it (Bramlett *et al.* 2012; Schwartz *et al.* 2016). Consequently, food *choice* may not necessarily reflect *preference*, and so developing a bias-free way to test primates' individual preferences has important applications.

In their pilot study evaluating the validity of using touchscreens for preference testing, Hopper *et al.* (2019) presented a single male gorilla with photographs of familiar foods in a pairwise manner to test his choices and to determine his preferences for four foods. While all foods were familiar to the subject, the presentation of photographs of foods on the touchscreen interface was novel to him. Therefore, the investigators first trained the subject on the association between the photographic stimuli and the associated food rewards. Thus, not only were the results restricted to a single species, and a single subject, but they also failed to elucidate the subject's *understanding* of the stimuli. Previous research has suggested that photographic or video stimuli may cause confusion in naïve subjects, as compared to the presentation of the items themselves (Bovet and Vauclair 2000; Fagot *et al.* 2010; Hopper *et al.* 2012; Parron *et al.* 2008). Fagot *et al.* (2010) proposed that animals can either perceive images and their physical counterparts as independent of, or unrelated to, one another, or they can award "equivalence" to both items (i.e., they learn the association between image and item without confusing the two, and thus truly comprehend the photograph). In the present study, therefore, we wished to build upon the pilot study by Hopper *et al.* (2019) to further interrogate the efficacy of touchscreens for preference testing with nonhuman primates and to explore primates' spontaneous interpretation of photographic stimuli of familiar foods presented via touchscreens (see also Tabellario *et al.* 2020, for comparable investigations of food-photograph interpretation by sloth bears, *Melursus ursinus*).

Given the importance of testing captive primates' food preferences for research and husbandry needs, and owing to the myriad of factors that can influence the choices individuals make, we built on the work of Hopper *et al.* (2019) to test more primates' preferences via a touchscreen interface by testing more subjects and more species. We did so to explore the applicability of this method across different species and to gain a better understanding of how primates interpret photographic stimuli presented to them on a touchscreen. We wished to evaluate the broader applicability of using touchscreens to test primate preferences and hence sought to determine if primates can interpret novel photographs on a touchscreen interface without training, such that their preferences can be assessed in such a manner. We adapted a forced-choice, pairwise paradigm for a touchscreen interface by presenting subjects with photographs of two foods in every trial, which they had to choose between, and rewarding subjects with their chosen food item.

Our first aim was to test the efficacy of touchscreens for preference testing with multiple species of primate and with an increased number of subjects as compared to previous work (i.e., Hopper *et al.* 2019; Judge *et al.* 2012). Our second aim was to more robustly evaluate the primates' understanding of photographic stimuli presented on the touchscreen. Our first hypothesis was that we could successfully use touchscreens for testing primates' preferences and that this interface could be easily adapted for presentation to different primate species, including both apes and monkeys. We predicted that all three species we tested (*Gorilla gorilla gorilla*, *Pan trogolodytes*, and *Macaca fuscata*) would be able to make selections using the touchscreen, given these subjects' prior experience with this technology, and that they would select the different stimuli at different rates, reflecting their relative preferences for the foods. Our second hypothesis was that subjects would understand associations between stimuli and rewards, and thus recognize the food items presented via the touchscreens, in spite of not previously being exposed to photographic stimuli. Therefore, we predicted that subjects' selection rates would not change over the course of the study and that they would not preferentially select or avoid selecting novel stimuli presented without training trials.

Methods

Study Subjects and Housing

For this study, we tested six western lowland gorillas (*Gorilla gorilla gorilla*), five chimpanzees (*Pan troglodytes*), and seven Japanese macaques (*Macaca fuscata*), all housed at Lincoln Park Zoo, Chicago, IL, USA (Table I). As testing was voluntary, not

Table I The test subjects

Species	Subject	Sex	Age at start of testing (years)	Subject group	Group size	Testing location
Gorilla (*Gorilla gorilla gorilla*)	Amare	M	6	All-male	4	Off exhibit
	Azizi	M	12	All-male	4	On/off exhibit
	Kwan	M	28	Mixed-sex	7	On exhibit
	Mosi	M	10	All-male	4	Off exhibit
	Rollie	F	23	Mixed-sex	7	On/off exhibit
	Umande	M	10	All-male	4	Off exhibit
Chimpanzee (*Pan troglodytes*)	Cashew	F	24	Mixed-sex	6	On exhibit
	Chuckie	F	19	Mixed-sex	6	On exhibit
	Kathy	F	28	Mixed-sex	6	On exhibit
	Optimus	M	27	Mixed-sex	6	Off exhibit
	Magadi	F	19	Mixed-sex	5	On exhibit
Japanese macaque (*Macaca fuscata*)	Akita	M	13	Mixed-sex	11	On exhibit
	Iwaki	F	2	Mixed-sex	11	On exhibit
	Izumi	F	13	Mixed-sex	11	On exhibit
	Mito	F	13	Mixed-sex	11	On exhibit
	Miyagi	M	13	Mixed-sex	11	On exhibit
	Nagoya	F	2	Mixed-sex	11	On exhibit
	Otaru	F	2	Mixed-sex	11	On exhibit

All the gorillas, chimpanzees, and Japanese macaques were housed at Lincoln Park Zoo, Chicago, IL, USA.

all members of every group participated, but our test subjects represent those that showed consistent engagement with the touchscreen. Our subjects represented a range of ages, both males and females, and those of high, mid, and low rank (Table I). Both subjects and non-subjects were managed in the same way outside of testing periods. Primates had access to water *ad libitum* and were given fresh produce and commercial primate chow daily.

The six gorilla subjects belonged to two groups: four males lived together in an all-male group and the other two gorillas (one male, one female) lived in a mixed-sex group comprising three adult females, one adult male, and three juvenile females (including the subjects) (Table I). Four of the five chimpanzees (three females, one male) lived in a mixed-sex social group comprising four females and two males (including the subjects), while the final female chimpanzee subject lived in a different mixed-sex social group comprising three females (including the subject) and two males (Table I). The gorillas and chimpanzees all were housed in the Regenstein Center for African Apes at Lincoln Park Zoo. Their enclosures were around 68,000 m^2 in total area and included both indoor and outdoor areas. Indoor areas all consisted of mulch flooring and climbing structures. These were connected to outdoor areas, which provided extensive climbing structures, via floor-to-ceiling sliding glass doors that allowed natural light inside (Ross *et al.* 2011).

We tested seven individuals (five females, two males) from a group of 11 Japanese macaques (five adult females, three adult males, three juvenile females) (Table I). This group was housed at Lincoln Park Zoo's Regenstein Macaque Forest, an expansive indoor/outdoor exhibit of *ca*. 224,700 m^2. The outdoor area contained natural trees and vegetation, rocks, grass and mulch, and a pool (Cronin *et al*. 2018 provides details).

Testing Environment and Apparatus

We tested all three species using Zenrichment ApeTouch software (Martin 2017) with 55 cm ViewSonic LCD touchscreen monitors (1920 × 1080 resolution). During a testing session, one subject worked per screen. We tested all subjects in their home enclosure, either on exhibit in a group setting or individually in an adjacent off-exhibit holding area, where they could stay within visual, olfactory, and auditory range of the rest of their group mates. As test participation was voluntary, subjects could terminate their session at any time, session lengths were variable, and participants did not always complete the maximum number of trials per day (Egelkamp *et al*. 2019).

We tested the gorillas and chimpanzees on a touchscreen monitor that was mounted on a mobile cart, which could be adjusted for the height of the subject (Cronin *et al*. 2018). We began each subject's testing session by placing the touchscreen flush against its enclosure mesh and verbally inviting the subject to participate. The subjects initiated their session when they touched the screen. We terminated any session if the subject failed to approach the touchscreen within 5 min, stopped participating for 5 min, or completed the maximum-allowed number of trials (30 trials/subject/day). We set the intertrial interval (ITI) at 4 s for all experiments. If the subject was interrupted by another group member, we paused the session and gave the subject another opportunity to participate once the "interrupter" moved away. We tested the remaining five ape subjects (four gorillas, one chimpanzee) in an off-exhibit area, where they were moved temporarily each morning as part of their regular husbandry routine in order to participate in training interactions with their keepers and facilitate exhibit cleaning (*sensu* Egelkamp *et al*. 2019).

We tested the seven Japanese macaques in touchscreen testing booths that they could voluntarily enter directly from their outdoor exhibit and that were in view of zoo guests. Macaques could enter one of two adjacent booths via a swinging door that was unlocked while researchers were present and remained unlocked during *ca*. 60 min of testing. Each booth measured 216 cm × 114 cm x 122 cm and each housed a touchscreen monitor. The booths had a glass panel that divided the two adjacent booths, which allowed the macaques to see inside the booth next to them (Cronin *et al*. 2018). We began a testing session with the macaques by unlocking the doors to the booths and calling out to the macaques to offer an audio cue that the booths were unlocked. We initiated a session when a macaque entered a booth. We paused a session if another macaque entered the same booth or if the subject left the booth. Two macaques could participate simultaneously in adjacent booths, and a session could be resumed when a macaque reentered if it had not yet completed the maximum-allowed number of trials that day (30 trials/subject/day). The session was ended if they completed the maximum number of trials allowed for the day. Given the voluntary nature of the experimental setup, a subject completed a variable number of trials in a single day and all trials completed in 1 day are referred to as a "session" in the text that follows. For all four experiments, macaque subjects were given an ITI of 8 s, owing to the researcher working with two monkeys simultaneously. Further, because macaques can store food in cheek pouches, the longer ITI gave subjects time to consume the food and thus remain cognizant of the foods they were receiving.

Stimuli

We presented each species with images of six different foods (Fig. 1). Although the subjects were naïve to photographic stimuli at the start of testing, they had all previously been provided with these six foods in meals as part of regular husbandry routines. We showed the apes full-color photographs of a piece of carrot, a piece of cucumber, a grape, and a piece of turnip in the first phase of the study, with the addition of photographs of a piece of apple and half a cherry tomato in the second phase of testing. We showed the macaques full-color photographs of a piece of carrot, a piece of celery, a quarter of a peanut, and half of a jungle pellet (Scenic™ Jungle Food, Marion Zoological) in the first phase, with the addition of photographs of a piece of green bean and a piece of toasted oats cereal (Gordon Food Service) in the second phase of the study. We selected the two novel stimuli for the second phase of the study after consultation with animal care staff: we selected foods based on what the subjects would eat but were not necessarily highly preferred or disliked. This was a preemptive effort to avoid strong biases in preference, so that we could disentangle a subject potentially avoiding a food because it was disliked rather than novel, or, conversely, preferentially selecting the food in every pairing because it was highly preferred or due to a novelty effect.

When creating the food photograph stimuli, as well as when preparing the food rewards for testing, we cut all foods to be approximately the same size: for the apes we cut all foods to the size of a grape (weighing 5–7 g each) and for the macaques we cut all the foods to be around the size of a piece of toasted oats cereal (weighing 0.50–0.64 g each).

Following Hopper *et al.* (2019), to create the food stimuli, we photographed all the food rewards using a Canon Powershot S110 digital camera, keeping the camera's

Fig. 1 Photographic food stimuli we presented to primates. We showed the apes (left to right) photographs of grape, cucumber, turnip, and carrot in phase 1 and added two novel stimuli (tomato, apple) in phase 2 that we presented without training trials. We showed the macaques (left to right) photographs of celery, jungle pellet (Scenic™ Jungle Food, Marion Zoological), peanut, and carrot, in phase 1 and in phase 2 we added trials with photographs showing toasted oats cereal (Gordon Food Service) and green bean as the novel stimuli. We used only one photograph of each food type as the stimuli (shown here).

distance and height from the food items constant for every photograph. To ensure consistent lighting, we photographed the food items in a LimoStudio tabletop photography box (41 × 41 cm) using white Bristol paper as the background in order to eliminate shadows and enhance contrast. We resized the stimuli in Adobe Photoshop to be 300 × 300 pixels.

Protocol

All subjects had previous experience using touchscreens (e.g., Cronin *et al.* 2018; Egelkamp *et al.* 2019; Jacobson *et al.* 2019; Ross 2009; Wagner *et al.* 2016); however, the subjects had no exposure to digital photographs of food items before this experiment. Ape subjects had been working with touchscreens for ≥5 yr, although some individuals had been working with touchscreens for ≥10 yr, while the macaques had been working with touchscreens for four years. The responses of one gorilla (Azizi) to the presentation of the initial four foods have been published previously (Hopper *et al.* 2019), but we included his results here as part of our analyses. His responses to the two novel stimuli have not been previously reported. All the other subjects' data have not been published previously.

We first replicated the methods of Hopper *et al.* (2019) with all 18 subjects (Table I). In this task, we presented subjects with four novel photos of familiar food items, first via training trials, in which just one photograph was presented on the screen, and then in a pairwise fashion (test trials). We presented subjects with every possible pairing of four food items in a blocked format, for a total of six food pairings. As all the subjects were inexperienced in responding to photographic stimuli, we used a blocked study design to ensure that they had repeated exposure to each pairing before moving on to a novel pairing in order to maximize their experience with, and understanding of, the stimuli and their associated reward contingencies. We counterbalanced the order in which we presented the pairings to each subject to control for order effects across subjects. For each trial, the screen background was black, and the square stimuli containing photographs of food were presented in random locations on the screen that differed from trial to trial. There were 105 possible configurations in which the two stimuli could appear from a total of 15 locations on the screen (three rows by five columns).

Following the methods of Hopper *et al.* (2019), for each of the six possible food pairings, we first presented all subjects with 50 training trials (presented over one or two sessions). In each training trial, a single food image was shown on the screen, and once the subject touched the image, it was rewarded with that food allowing the subject the opportunity to learn the association between the photographs and receiving those same foods. Across the 50 training trials, we presented an equal number of the two food items in the test pair in a random order (i.e., 25 training trials per food type). In each trial, the location of the food image on the screen was randomized and there were 15 unique locations on the screen where the photograph could be presented. No secondary reinforcers were provided during the training trials.

After a subject had completed the 50 training trials for the two foods in a given food pairing, we then presented the subject with 90 forced-choice preference test trials per food pairing in which the two food photographs were shown on the screen simultaneously. When the subject selected one of the two foods, both images disappeared, and we rewarded the subject with the selected food. As with the training trials, the locations of the two food images were randomized and no secondary reinforcers were provided. After a subject completed the 50 training trials and 90 paired test trials for a given food pairing, we tested the subject with a new pair of foods until it had been tested with all six pairwise combinations of the four foods. Subjects completed a mean of 26 paired test trials per session (SD = 4) and all subjects completed 90 trials per pairing, with the exception of one macaque that completed 89 trials per pairing.

After completing this planned replication of Hopper *et al.* (2019) with more subjects and new species, we presented the same 18 subjects with two photos of novel food stimuli paired with the known stimuli from the previous round of testing. During this second stage of testing, we did not provide subjects with any single-stimuli training trials prior to their paired preference trials (i.e., the first time subjects saw the novel stimuli was in paired test trials). In each test trial we presented subjects with two photographs on the screen and we rewarded the subject with whichever food it selected. We presented the subjects with every possible pairing of two novel stimuli (apple or tomato for the apes, green bean or toasted oats cereal for the macaques) paired with the four familiar food stimuli presented to them initially (Fig. 1). We presented the eight possible food pairings (each of the two novel stimuli paired with the four foods from the previous experiment) in a blocked format, with pairing presentation counterbalanced across subjects, and with 90 trials per pairing as per the first phase. We also presented subjects with novel-novel pairings (see Electronic Supplementary Material [ESM] Table SII). Owing to experimenter error, we only presented 80 trials in one pairing to one macaque (Mito), while two others (Iwaki and Miyagi) received only 89 trials in two novel pairings. We excluded one chimpanzee (Chuckie) from our analyses of response to novel stimuli because we inadvertently did not give her any test trials for one of the novel-familiar food pairings. All remaining subjects received the full 90 trials and subjects completed a mean of 26 trials per session (SD = 3).

Analyses

Following Hopper *et al.* (2019), we used the prefmod package (Hatzinger 2015) in R version 3.5.2 (R Core Team 2018) to calculate each subject's "worth" values for the four foods. Specifically, we used a log-linear Bradley–Taylor model (LLBT) to estimate worth values for each food item (Hatzinger and Dittrich 2012). A higher worth value is indicative of that subject's greater preference for that item relative to another (all worth values combined for a single subject totals 1).

For a standard Bradley–Terry model the probability that a subject will prefer object k to j, and *vice versa*, is

$$p\left(y_{jk}\right) = c_{jk}\left(\frac{\sqrt{\pi_j}}{\sqrt{\pi_k}}\right)^{y_{jk}}$$

where π_j and π_k are worth values for each object on the preference scale, y_{jk} is a response to the comparison of j to k that takes the value 1 if $j > k$ and the value −1 if $k > j$ and c_{jk} is a normalizing constant. For objects j and k, the LLBT model assumes that the observed number of selections for object j instead of k (and *vice versa*) follow a multinomial distribution conditional on a fixed number of trials. Thus, the expected number of selections for a given object over a paired trail is

$$m\left(y_{jk}\right) = n_{jk}p\left(y_{jk}\right)$$

where n_{jk} is the number of trails conducted for a given pair and $m(y_{jk})$ is the expected number of selections (Hatzinger and Dittrich 2012). As a loglinear model, the linear predictor of the LLBT is then

$$\ln m\left(y_{jk}\right) = u_{jk} + y_{jk}\left(\beta_j - \beta_k\right).$$

Here, u_{jk} is a nuisance parameter whereas β_j and β_k correspond to the worth values on the preference scale such that $\ln \pi = 2\beta$ (Hatzinger and Dittrich 2012).

Again following Hopper *et al.* (2019), once we calculated the subjects' worth values for each of the four foods, we used the gnm function (Turner and Firth 2015) to compare each subject's relative preference for the four foods, allowing us to determine which foods they preferred significantly over others. Relative preferences sum to one across the four food types. As the prefmod package uses the multinomial-Poisson transformation (Baker 1994) to fit the LLBT model through maximum likelihood, we specified the family of the gnm function as Poisson (Hatzinger and Dittrich 2012).

To calculate the effect size of each comparison, we calculated the odds of selecting one item over another following the ratio:

$$\frac{p}{q}$$

where p is the relative preference of the first food item (i.e., the food presented in the column in ESM Table SI), and q is the relative preference of a second food item (listed in the row in ESM Table SI).

Once we had calculated the subjects' relative preferences for the four foods, replicating Hopper *et al.* (2019), we then explored their responses to the novel stimuli that we presented without training trials. First we calculated each subject's relative preferences for all six foods by combining data from both phases of the study, again using the prefmod package in R to generate each subject's worth value for each food, as described previously (see also Hopper *et al.* 2019). Next, we compared each subject's worth values for all six foods to see if any were preferred significantly over others using the gnm function, as described previously. We calculated the effect sizes for the six food trials in the same way as for the four food pairwise comparisons described previosuly (see also ESM Table SII).

To evaluate whether subjects responded differentially to the novel vs. the known stimuli, we compared their worth values for novel stimuli with known stimuli to see if they preferentially selected, or avoided selecting, the novel stimuli that had been presented without training trials as compared to the four foods presented with training trials. First, we coded each subject's trials with two possible outcomes: novel stimulus chosen from the pairing (1) or novel stimulus not chosen (0) to create a binary outcome variable. Second, we evaluated and simplified our null models using Z-tests and likelihood ratio tests (LRTs) (Bates *et al.* 2012) to explore the relative contribution of our two potential random effects, "subject" and "trial number," so that we could determine which to include. In our analyses, we did not account for sex or mode of testing (i.e., individually or while other group members were present) owing to our small sample size. Given the binary response variable and the combination of fixed and random predictor variables, we analyzed our data using a binomial generalized linear mixed model in R version 3.5.2 (R Core Team 2018). We fit this model using the Laplace approximation method via the glmer function in the lme4 package (Bates *et al.* 2012) to test the relative effect of our predictor variable “food type.” We used the fixed effects of each species’ GLMM to calculate the odds a novel stimulus was selected over a known stimulus; these odds represent an average effect size across individuals of a species.

Ethical Note

The Lincoln Park Zoo Research Committee approved this study and we conducted it in accordance with the American Society of Primatologists’ Principles for the Ethical Treatment of Nonhuman Primates. Lincoln Park Zoo animal care, veterinary, and nutrition staff approved all foods prior to commencement of research. No modifications were made to animal husbandry schedules. The authors have no conflict of interest to declare.

Data Avalailability The datasets that we analyzed for the current study are available from the corresponding author on reasonable request.

Results

Did the Primates’ Selection of the Stimuli Reveal Differential Food Preferences?

From their responses in the first phase of testing (i.e., paired test trials preceded by training trials), the subjects of all three species exhibited differential selection rates of the four foods, preferring some significantly more than others (in ESM Table SI we provide the results of the every pairwise comparison for each subject). Four of the apes (three gorillas, one chimpanzee) significantly preferred grape over the other three foods [the ranges of apes’ selection odds for selecting grape over the other three foods were: 4.55–17.86 (Amare), 4.06–11.50 (Azizi), 4.92–10.67 (Umande), and 5.23–9.71 (Cashew)], while two gorillas (Kwan and Rollie) did not have significantly different preferences for grape and carrot, which were their most preferred foods [their selection odds for choosing grape over carrot was: 1.07 (Kwan) and 1.27 (Rollie)] (ESM Table SI). In contrast to the strong relative preferences across the four foods that these six apes showed, the selections made by three of the apes (one gorilla, two chimpanzees) revealed only one significant preference among the pairings: Mosi significantly preferred carrot over turnip (selection odds: 1.29), Kathy significantly preferred grape over cucumber (selection odds: 1.29), and Chuckie significantly preferred grape over carrot (selection odds: 1.20) (these three apes selected all other foods at comparable rates). The remaining two apes (chimpanzees Optimus and Magadi) did not show any significant difference across their worth values for the four foods (Optimus’ selection odds range: 0.77–1.29; Magadi’s selection odds range: 0.85–1.17) (ESM Table SI). Generally, the apes’ choices revealed a lack of preference for turnip, selecting this food less than the other three options (selection odds range: 0.09–1.00) (ESM Table SI).

Five of the seven macaques significantly preferred peanut over the other three foods and their selection odds for peanut were all >1.00 [range of macaques' selection odds for peanut over the other three foods were: 1.53–7.67 (Iwaki), 2.15–9.33 (Izumi), 1.56–10.00 (Mito), 3.30–22.00 (Nagoya), and 1.39–11.50 (Otaru)], while the remaining two macaques (Akita and Miyagi) did not show a significant difference in preference for jungle pellet or peanut relative to one another [the macaques' selection odds of selecting peanut over jungle pellet were: 1.03 (Akita) and 1.21 (Miyagi)] (ESM Table SI). Like the apes, the macaques showed a consistency across subjects as to their least-preferred food, and all selected celery the least (selection range: 0.05–1.00). Indeed, all macaques selected celery significantly less than the other three foods, expect for one macaque (Mito) that selected celery and carrot at equal rates (Mito's selection odds for celery over carrot: 1.00) (ESM Table SI).

Did the Primates Treat the Novel Stimuli Differently from Known Stimuli?

Comparing the primates' selection of all six foods (i.e., combining data from both phases of the study including stimuli presented with and without training trials), we found that the subjects did not preferentially select the novel stimuli over the known stimuli, nor did they avoid selecting the novel stimuli (Figs. 2, 3, and 4). Rather, all three species appeared to select the foods according to their relative preference for each food and all subjects showed significant differences in their selection rates of the six foods, apart from chimpanzee Optimus who selected the six food at comparable rates (in ESM Table SII we provide the results of the pairwise comparisons for each subject).

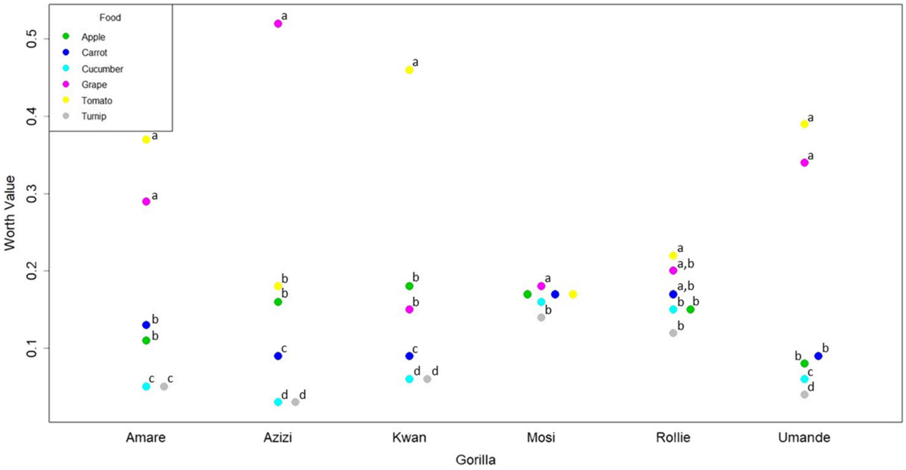

Fig. 2 "Worth" values for each of six foods for six gorillas. We calculated worth values using the prefmod package in R. A subject's worth values for all six foods equal 1, and higher worth values are associated with the subject selecting that food more frequently, suggesting that the subject prefers that food more over others. We calculated relative preferences between the foods using the gnm function in R and letters (a, b, etc.) denote significant differences in worth values between adjacently ranked items. The four foods we presented to the gorillas with training trials were grape, carrot, turnip, and cucumber, while the two novel foods, which we presented without training trials, were tomato and apple. All gorillas were housed at Lincoln Park Zoo, Chicago, IL, USA, and we tested the gorillas' preferences from October 2016 to March 2018.

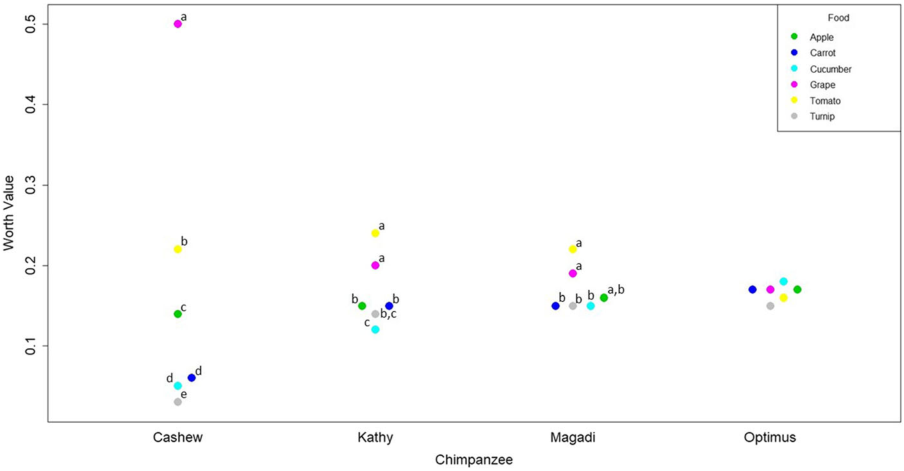

Fig. 3 "Worth" values for each of six foods for four chimpanzees. We calculated worth values using the prefmod package in R. A subject's worth values for all six foods equal 1, and higher worth values are associated with the subject selecting that food more frequently, suggesting that the subject prefers that food more over others. We calculated relative preferences between the foods using the gnm function in R and letters (a, b, etc.) denote significant differences in worth values between adjacently ranked items. The four foods we presented to the chimpanzees with training trials were grape, carrot, turnip, and cucumber, while the two novel foods, which we presented without training trials, were tomato and apple. All chimpanzees were housed at Lincoln Park Zoo, Chicago, IL, USA, and we tested their preferences from October 2016 to March 2018.

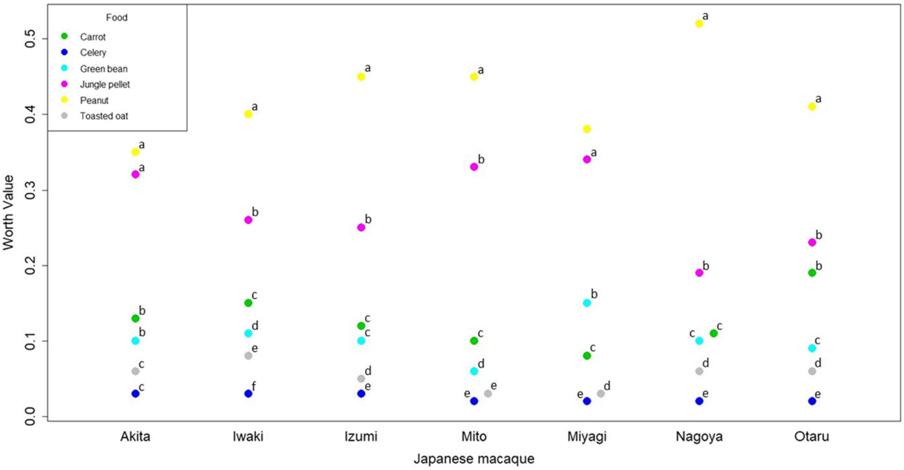

Fig. 4 "Worth" values for each of six foods for seven Japanese macaques. We calculated worth values using the prefmod package in R. A subject's worth values for all six foods equal 1, and higher worth values are associated with the subject selecting that food more frequently, suggesting that the subject prefers that food more over others. We calculated relative preferences between the foods using the gnm function in R and letters (a, b, etc.) denote significant differences in worth values between adjacently ranked items. The four foods we presented to the macaques with training trials were peanut, Jungle Pellet, celery, and carrot, while the two novel foods, which we presented without training trials, were green bean and toasted oats cereal. All macaques were housed at Lincoln Park Zoo, Chicago, IL, USA, and we tested their preferences from October 2016 to March 2018.

While for many of the apes the novel tomato was one of their preferred foods, the apes showed individual variation in their relative selection of the other novel stimuli, apple (Figs. 2 and 3). Specifically, seven of the apes (gorillas Amare, Mosi, Rollie, and Umande and chimpanzees Kathy, Optimus, and Magadi) selected tomato and grape at rates that were not significantly different (their selection odds ranged from 0.94 to 1.28), two (one gorilla, one chimpanzee) selected grape significantly more than tomato [their selection odds for selecting grape over tomato were: 2.89 (Azizi), 2.27 (Cashew)], and one gorilla (Kwan) selected tomato significantly more than grape (selection odds: 3.07) (ESM Table SII). In contrast, there was much greater variation in the apes' relative selection of apple, reflected by their selection odds for apple, which ranged from 0.09 to 4.00 across all subjects (see ESM Table SII for all comparisons). For some subjects, turnip was a significantly less preferred food item (selection odds ranging from 0.06 to 0.94), although five of the ten apes selected it at equal or higher rates than cucumber, although these differences were not significant (selection odds range for these subjects' turnip–cucumber pairings: 1.00–1.17, ESM Table SII).

Similar to the apes, the macaques showed individual variation in their selection of the novel stimuli (green bean and toasted oats cereal), but none preferentially selected or avoided these foods (Fig. 4). The macaques' preferred food remained peanut (selection odds range: 1.09–22.50) and celery remained the macaques' least preferred food (selection odds range: 0.04–0.67).

Did the Primates' Selection Rate of the Novel Stimuli Change over Trials or by Food Pairing?

For the gorillas, the rate of selecting both the novel stimuli varied significantly across subjects (Apple: LRT, $\chi^2(1) = 46.58$, $P < 0.001$; Tomato: LRT, $\chi^2(1) = 148.62$, $P < 0.001$), but not across trials (Apple: LRT, $\chi^2(1) = 0.38$, $P = 0.540$; Tomato: LRT, $\chi^2(1) = 0$, $P = 1.000$). Thus, we included "subject" only as a random effect in our models. After accounting for this individual variation, we found that the gorillas' selection of the novel apple and tomato stimuli varied significantly by which known food stimuli the novel stimuli were paired with (Table II).

Like that of the gorillas, the chimpanzees' rate of selecting the novel tomato stimulus varied by subject (LRT, $\chi^2(1) = 28.37$, $P < 0.001$) but not trial number (LRT, $\chi^2(1) = 2.55$, $P = 0.110$). Thus, we only included "subject" as a random effect in our model. After accounting for this individual variation, we found that the degree to which the chimpanzees selected the novel tomato stimulus varied by food pairing (Table II). In contrast, the chimpanzees' rate of selecting the novel apple stimulus did not vary across subject (LRT, $\chi^2(1) = 3.28$, $P = 0.070$) nor trial number (LRT, $\chi^2(1) = 0$, $P = 1.000$). Our final model, which excluded both subject and trial number as random variables, revealed that the degree to which subjects selected the novel apple stimulus did not vary by pairing except when apple was paired with grape, in which trials the chimpanzees preferentially selected the known, and preferred, grape over the novel apple (Table II).

The macaques' rate of selecting novel stimuli varied by subject (Toasted oats cereal: LRT, $\chi^2(1) = 12.39$, $P < 0.001$; Green bean: LRT, $\chi^2(1) = 34.43$, $P < 0.001$) but not trial number (Toasted oats cereal: LRT, $\chi^2(1) = 0$, $P = 1.000$; Green bean: LRT, $\chi^2(1) = 0$, $P = 1.000$). Thus, we included "subject" only as a random effect in our models. After

Table II Comparison of the relative rate of selection of novel food stimuli over the known food stimuli in three species of primate

Species	Food pairing (novel–familiar)	Z value	*P* value	Effect size
Gorilla	Apple–cucumber	8.33	< 0.001*	2.63
	Apple–grape	−6.29	< 0.001*	0.39
	Apple–turnip	9.58	< 0.001*	3.20
	Apple–carrot	−8.33	< 0.001*	0.88
	Tomato–cucumber	1.94	0.051	6.16
	Tomato–grape	−10.75	< 0.001*	0.80
	Tomato–turnip	3.09	0.002*	5.07
	Tomato–carrot	−1.94	0.052	3.74
Chimpanzee	Apple–cucumber	1.29	0.200	1.52
	Apple–grape	−6.38	< 0.001*	0.49
	Apple–turnip	0.76	0.450	1.59
	Apple–carrot	−1.30	0.200	1.31
	Tomato–cucumber	0.72	0.470	2.15
	Tomato–grape	−6.52	< 0.001*	0.69
	Tomato–turnip	0.72	0.470	2.15
	Tomato–carrot	−0.72	0.470	1.92
Macaque	Toasted oats–celery	19.69	< 0.001*	12.44
	Toasted oats–jungle pellet	−4.79	< 0.001*	0.12
	Toasted oats–peanut	−8.30	< 0.001*	0.03
	Toasted oats–carrot	−19.70	< 0.001*	0.26
	Green bean–celery	16.07	< 0.001*	24.52
	Green bean–jungle pellet	−8.095	< 0.001*	0.18
	Green bean–peanut	−12.09	< 0.001*	0.04
	Green bean–carrot	−16.07	< 0.001*	0.59

In pairings where $P \leq 0.05$, subjects were significantly more (designated by positive *Z*-value) or less (designated by negative *Z*-value) likely to select the novel stimulus over the known food. We calculated effect sizes (ES) using the exponential function on estimated model values for each pairing, representing the “odds” or ratio of choosing novel item over the familiar item. ES > 1 indicates that the novel food (listed first in the pair) is more preferred, whereas ES < 1 indicates that the familiar food is more preferred. ES = 1 shows that neither food is preferred over the other (Lincoln Park Zoo, Chicago, USA, October 2016–March 2018). *statistically significant relative preferences.

accounting for this individual variation, we found that the macaques’ selection of both novel stimuli was significantly predicted by food pairing (Table II).

Discussion

We provide further evidence of the efficacy of touchscreens to evaluate primate food preferences, testing this paradigm with three primate species and demonstrating that multiple trials can be administered quickly and without experimenter bias. Our forced-choice touchscreen experiments revealed the primates’ individual preferences for six different foods and suggested that the subjects understood the photographic representation of the foods. The individual variation across the subjects' relative preferences of the six foods further highlights the importance of preference testing for individually tailored reward validations for experimental or husbandry needs.

From the primates' differential choices of the six foods, it was evident that the subjects did not require training to associate a photo with the food item that it depicted. We interpret our results to mean that our subjects attributed "equivalence" (Fagot *et al.* 2010) to the images and associated rewards, rather than confusion or a lack of understanding, potentially because the foods were familiar to them at the start of the study, even though photographic stimuli were not. Given the primates' interpretation of equivalence between known foods and their photographs suggests that future applications of this paradigm, whether testing preferences for known foods or other familiar items, should not require a time-intensive training phase to obtain meaningful results. It also suggests that such a protocol could be used with other primates, even those less experienced with touchscreens, given the spontaneous success shown by the subjects we tested, all of which were all naïve to photographs of foods at the beginning of this study. However, subjects' experience with touchscreens likely influenced their response to the stimuli as well as their familiarity with the objects portrayed with photographs.

The responses of the subjects in the second phase of the study demonstrate the variation in subject preferences across the foods but also suggested that the subjects did not show overt evidence of neophobia towards the novel food stimuli (*cf.* Addessi *et al.* 2004; Maratos and Staples 2015), attraction simply to novelty, nor a change in their preference for the stimuli over time (*cf.* Hardus *et al.* 2014; Visalberghi *et al.* 1998). Primates have been shown to increase their consumption of novel foods as they become more familiar (Hardus *et al.* 2015; Visalberghi *et al.* 1998), but we saw no change across trials in the subjects' selection rates of the two novel foods. This suggests that there was no learning involved in the apes' and macaques' understanding of the food stimuli, likely because although the *stimuli* were novel to the subjects, the *foods* that they depicted were not. An alternative explanation of our findings that the subjects' selection rates of the novel foods did not change across trials is because, rather than a spontaneous recognition of the photographs, they simply stuck with their first-trial choice, irrespective of their understanding of the stimulus. Looking at the data, however, the subjects sampled all stimuli at least once over the course of their trials and no subject avoided either novel stimuli altogether. With regard to individual food preferences, we saw a difference in subjects' propensity to select the novel item when paired with certain foods: items that were more preferred were generally selected preferentially over the novel stimulus and items that were less preferred were selected less often than the novel stimulus. In some cases, the novel food stimulus was not significantly different in preference to the familiar food item across subjects. Based on these findings, we think that the primates' responses reflect their relative preferences for the six foods and indicate some understanding of the photographs' content. In future adaptations of this touchscreen preference testing method, truly novel foods (i.e., those not already a part of daily diets) should be included to assess response to novel stimuli and to further determine if subjects have a preference for, actively avoid, or are indifferent to truly novel foods.

As many of the underlying factors behind individual preference are of a social nature, it may be the case that subjects may have been influenced by the choices of their group mates, potentially accounting for the intraspecific consistency. This is particularly so for the macaques, whose order of preferences were virtually identical. Given the macaques' testing setup, in which they were able to make selections while a second monkey made theirs in the adjacent booth, the presence of the second monkey, or the specific choices they were making, may have influenced the subjects' selections. While the mere presence of group mates can influence an individual's decision making (Belletier *et al.* 2019; Huguet *et al.* 2014), we do not think it likely that the presence of group mates influenced the subjects' choices in our study. For our apes, which were tested in a social setting, individuals typically did not approach others as they participated in touchscreen testing, and for the monkeys, which could be tested simultaneously in adjacent booths, because we counterbalanced the order of pairing presentation, any monkeys that tested simultaneously would have been selecting from different food pairings. Although we chose not to separate many of our subjects from their groups for testing to increase welfare and ecological validity (Cronin *et al.* 2017), testing subjects individually could help determine the full extent of the impact of social influence on subject choices. In addition to potential social influences on subjects' choices, a second limitation is that we were not able to test the validity of our findings: we do not know if the primates' selections on the touchscreens relate to their selections of real food items. Future work is needed to explore this. However, we know that at least for some of our subjects their relative selection of some of the foods reflects their real-world choices, as revealed by preference testing for previous research protocols (i.e., that they prefer grape to carrot; see Bonnie *et al.* 2019; Hopper *et al.* 2015). In addition, when subjects were presented with pairs of two low-value foods, we often observed that they often did not eat the food they selected, further reinforcing that it was not preferred. Conversely, our subjects always ate high-value foods they selected.

Overall, our testing methodology was successful among our subjects and may be adapted to carry out an array of preference tests, both with food stimuli and, potentially, with nonfood items. For example, it may be possible to use these touchscreen paradigms in a more applied context and present captive animals with images of objects that cannot be presented in a typical manual preference task (e.g., presenting photographs of incoming group members in order to increase familiarity upon their arrival). From a management standpoint, gaining insight into individual food preferences can be used to shape husbandry and training routines, as highly preferred items may to more effectively elicit desired behaviors and encourage novel behaviors (Gaalema *et al.* 2011). In addition, preferred foods may be used to "bait" enrichment devices such as puzzle feeders in order to encourage animal activity. While observation and anecdotal reports may provide a good starting point for determining preference, systematically testing preferences can be a more accurate and effective means of gathering this information and here we have demonstrated that touchscreens offer a reliable way of gathering such information, particularly for other institutions with established touchscreen programs. Nevertheless, while touchscreen technology may initially be an investment in terms of money and animal training, it may be ideal as it offers a means to test multiple animals safely and efficiently while they remain in their home enclosure (e.g., Gazes *et al.* 2019), increasing the validity of the data and the welfare of the animals (Cronin *et al.* 2017).

We hope that the variety of testing paradigms presented here could be adapted for other species, including nonprimate species, provided that the species has acute vision and the ability to make choices on a touchscreen; i.e., such methods may be less suited for animals with poor eyesight, such as Asian elephants (*Elephas maximus*) or black rhinoceros (*Diceros bicornis*). To date, touchscreen studies have been conducted with a variety of species, such as sun bears (*Helarctos malayanus*: Perdue, 2016), black bears (*Ursus americanus*: Johnson-Ulrich *et al.* 2016), dogs (*Canis lupus familiaris*: Zeagler *et al.* 2016), tortoises (*Chelonoidis carbonaria*: Mueller-Paul *et al.* 2014), rats (*Rattus norvegicus*: Cook *et al.* 2004), and pigeons (*Columba livia*: Fortes *et al.* 2017) (Egelkamp and Ross 2019 provide a review), suggesting that these preference-testing methods have applicability beyond primates, and for use in a variety of settings. Furthermore, as we found that our subjects spontaneously interpreted photographic stimuli of novel foods, despite lacking prior exposure to photographs, it is likely that minimal training may be required to implement such protocols with naïve animals (Parron *et al.* 2008; Tabellario *et al.* 2020). The methods detailed here are a strong starting point for developing further comparative protocols, as they use readily accessible technology and allow for timely data collection.

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Author Contributions LMH conceived and designed the experiments. SMH, SLJ, and CLE performed the experiments. SMH and LMH analyzed the data. SMH wrote the manuscript; other authors provided editorial advice.

References

Addessi, E., Galloway, A. T., Birch, L., & Visalberghi, E. (2004). Taste perception and food choices in capuchin monkeys and human children. *Primatologie, 6*, 101–128.

Baker, S. G. (1994). The multinomial-Poisson transformation. *Journal of the Royal Statistical Society: Series D, 43*, 495–504.

Bates, D., Maechler, M., & Bolker, B. (2012). lme4: Linear mixed-effects models using "Eigen" and S4. *R package version, 1*, 1–21 https://cran.r-project.org/web/packages/lme4/lme4.pdf.

Belletier, C., Normand, A., & Huguet, P. (2019). Social-facilitation-and-impairment effects: From motivation to cognition and the social brain. *Current Directions in Psychological Science, 28*(3), 260–265.

Bonnie, K. E., Bernstein-Kurtycz, L. M., Shender, M. A., Ross, S. R., & Hopper, L. M. (2019). Foraging in a social setting: A comparative analysis of captive gorillas and chimpanzees. *Primates, 60*(2), 125–131.

Bovet, D., & Vauclair, J. (2000). Picture recognition in animals and humans. *Behavioural Brain Research, 109*, 143–165.

Bramlett, J. L., Perdue, B. M., Evans, T. A., & Beran, M. J. (2012). Capuchin monkeys (*Cebus apella*) let lesser rewards pass them by to get better rewards. *Animal Cognition, 15*(5), 963–969.

Brosnan, S. F., & de Waal, F. B. M. (2003). Monkeys reject unequal pay. *Nature, 425*, 297–299.

Brousseau, D. J., & Baglivo, J. A. (2005). Laboratory investigations of food selection by the Asian shore crab, *Hemigrapsus sanguineus*: Algal versus animal preference. *Journal of Crustacean Biology, 25*, 130–134.

Cook, R. G., Geller, A. I., Zhang, G.-R., & Gowda, R. (2004). Touchscreen-enhanced visual learning in rats. *Behavior Research Methods, Instruments, & Computers, 36*(1), 101–106.

Cronin, K. A., Jacobson, S. L., Bonnie, K. E., & Hopper, L. M. (2017). Studying primate cognition in a social setting to improve validity and welfare: A literature review highlighting successful approaches. *PeerJ, 5*, e3649.

Cronin, K. A., Bethell, E. J., Jacobson, S. L., Egelkamp, C., Hopper, L. M., & Ross, S. R. (2018). Evaluating mood changes in response to anthropogenic noise with a response-slowing task in three species of zoo-housed primates. *Animal Behavior and Cognition, 5*(2), 209–221.

Drewnowski, A. (1997). Taste preferences and food intake. *Annual Review of Nutrition, 17*, 237–253.

Egelkamp, C. L., & Ross, S. R. (2019). A review of zoo-based cognitive research using touchscreens. *Zoo Biology, 82*(2), 220–235.

Egelkamp, C. L., Jacobson, S. L., Cronin, K. A., Wagner, K. E., Ross, S. R., & Hopper, L. M. (2019). A comparison of sequential learning errors made by apes and monkeys reveals individual but not species differences in learning. *International Journal of Comparative Psychology*, *32*. https://escholarship.org/uc/item/024578f5

Fagot, J., Thompson, R. K. R., & Parron, C. (2010). How to read a picture: Lessons from nonhuman primates. *Proceedings of the National Academy of Sciences of the USA, 107*(2), 519–520.

Finestone, E., Bonnie, K. E., Hopper, L. M., Vreeman, V. M., Lonsdorf, E. V., & Ross, S. R. (2014). The interplay between individual, social, and environmental influences on chimpanzee food choices. *Behavioural Processes, 105*, 71–78.

Fortes, I., Case, J. P., & Zentall, T. R. (2017). Pigeons, unlike humans, do not prefer near hits in a slot-machine-like task. *Behavioural Processes, 138*, 67–72.

Gaalema, D. E., Perdue, B. M., & Kelling, A. S. (2011). Food preference, keeper ratings, and reinforce effectiveness in exotic animals: The value of systematic testing. *Journal of Applied Animal Welfare Science, 14*, 33–41.

Galef, B., & Whiskin, E. (2008). "Conformity" in Norway rats? *Animal Behaviour, 75*, 2035–2039.

Ganas, J., Ortmann, S., & Robbins, M. M. (2008). Food preferences of wild mountain gorillas. *American Journal of Primatology, 70*, 927–938.

Gazes, R. P., Lutz, M. C., Meyer, M. C., Hassett, H. C., & Hampton, R. R. (2019). Influences of demographic, seasonal, and social factors on automated touchscreen computer use by rhesus monkeys (*Macaca mulatta*) in a large naturalistic group. *PLoS ONE.* https://doi.org/10.1371/journal.pone.0215060.

Gibson, L. A. (2001). Seasonal changes in the diet, food availability and food preference of the greater bilby (*Macrotis lagotis*) in south-western Queensland. *Wildlife Research, 28*, 121–134.

Hardus, M. E., Lameira, A. R., Wich, S. A., de Vries, H., Wahyudi, R., et al (2015). Effect of repeated exposures and sociality on novel food acceptance and consumption by orangutans. *Primates, 56*, 21–27.

Hatzinger, R. (2015). Package "prefmod": Utilities to fit paired comparison models for preferences. https:/CRAN.Rproject.org/package=prefmod

Hatzinger, R., & Dittrich, R. (2012). Prefmod: An R package for modeling preferences based on paired comparisons, rankings, or ratings. *Journal of Statistical Software, 48*. https://doi.org/10.18637/jss.v048.i10.

Hopper, L. M., & Cronin, K. A. (2018). What did you get? What social learning, collaboration, prosocial behavior and inequity aversion tell us about primate social cognition. In L. D. Di Paolo, F. Di Vincenzo, & A. F. d'Almeida (Eds.), *Evolution of primate social cognition. Interdisciplinary Evolution Research*. Cham, Switzerland: Springer International.

Hopper, L. M., Schapiro, S. J., Lambeth, S. P., & Brosnan, S. F. (2011). Chimpanzees' socially maintained food preferences indicate both conservatism and conformity. *Animal Behaviour, 81*, 1195–1202.

Hopper, L. M., Lambeth, S. P., & Schapiro, S. J. (2012). An evaluation of the efficacy of video displays for use with chimpanzees (*Pan troglodytes*). *American Journal of Primatology, 74*(5), 442–449.

Hopper, L. M., Lambeth, S. P., Schapiro, S. J., & Brosnan, S. F. (2014). Social comparison mediates chimpanzees' responses to loss, not frustration. *Animal Cognition, 17*(6), 1303–1311.

Hopper, L. M., Kurtycz, L. M., Ross, S. R., & Bonnie, K. E. (2015). Captive chimpanzee foraging in a social setting: A test of problem solving, flexibility, and spatial discounting. *PeerJ, 3*, e833.

Hopper, L. M., Egelkamp, C. E., Fidino, M., & Ross, S. R. (2019). An assessment of touchscreens for testing primate food preferences and valuations. *Behavior Research Methods, 51*, 639–650. https://doi.org/10.3758/s13428-018-1065-0.

Huguet, P., Barbet, I., Belletier, C., Monteil, J.-M., & Fagot, J. (2014). Cognitive control under social influence in baboons. *Journal of Experimental Psychology: General, 143*, 2067–2073.

Jacobson, S. L., Kwiatt, A., Ross, S. R., & Cronin, K. A. (2019). The effects of cognitive testing on the welfare of zoo-housed Japanese macaques (*Macaca fuscata*). *Applied Animal Behaviour Science, 212*, 90–97.

Johnson-Ulrich, Z., Vonk, J., Humbyrd, M., Crowley, M., Wojtkowski, E., et al (2016). Picture object recognition in an American black bear (*Ursus americanus*). *Animal Cognition, 19*(6), 1237–1242.

Judge, P. G., Kurdziel, L. B., Wright, R. M., & Bohrman, J. A. (2012). Picture recognition of food by macaques (*Macaca silenus*). *Animal Cognition, 15*, 313–325.

Kumpan, L. T., Rothman, J. M., Chapman, C. A., & Teichroeb, J. A. (2019). Playing it safe? Solitary vervet monkeys (*Chlorocebus pygerythrus*) choose high-quality foods more than those in competition. *American Journal of Primatology.* https://doi.org/10.1002/ajp.23002.

Laska, M., Salazar, L.T., & Luna, E.R. (2000). Food Preferences and Nutrient Composition in Captive Spider Monkeys, Ateles geoffroyi. *International Journal of Primatology, 21*, 671–683.

Maratos, F. A., & Staples, P. (2015). Attentional biases towards familiar and unfamiliar foods in children: The role of food neophobia. *Appetite, 91*, 220.

Martin, C. F. (2017). ApeTouch software suite [Computer software].

Mueller-Paul, J., Wilkinson, A., Aust, U., Steurer, M., Hall, G., & Huber, I. (2014). Touchscreen performance and knowledge transfer in the red-footed tortoise (*Chelonoidis carbonaria*). *Behavioural Processes, 106*, 187–192.

Murray, C. M., Eberly, E. E., & Pusey, A. E. (2006). Foraging strategies as a function of season and rank among wild female chimpanzees (*Pan troglodytes*). *Behavioural Ecology, 17*, 1020–1028.

Parron, C., Call, J., & Fagot, J. (2008). Behavioral responses to photographs by pictorially naïve baboons (*Papio anubis*), gorillas (*Gorilla gorilla*) and chimpanzees (*Pan troglodytes*). *Behavioural Processes, 78*, 351–357.

Perdue, B. (2016). The effect of computerized testing on sun bear behaviors and enrichment preferences. *Behavioral Sciences, 6*(4), 19.

R Core Team (2018). R: A language and environment for statistical computing. In *R Foundation for Statistical Computing*. Vienna: Austria. URL w. R-project.org/.

Remis, M. J. (2002). Food preferences among captive western lowland gorillas (*Gorilla gorilla gorilla*) and chimpanzees (*Pan troglodytes*). *International Journal of Primatology, 23*, 231–249.

Remis, M. J. (2006). The role of taste in food selection by African apes: Implications for niche separation and overlap in tropical forests. *Primates, 47*, 56–64.

Ross, S. R. (2009). Sequential list-learning by an adolescent lowland gorilla (*Gorilla gorilla gorilla*) using an infrared touchframe apparatus. *Interaction Studies, 10*, 115–129.

Ross, S. R., Calcutt, S., Schapiro, S. J., & Hau, J. (2011). Space use selectivity by chimpanzees and gorillas in an indoor–outdoor enclosure. *American Journal of Primatology, 73*(2), 197–208.

Sánchez-Amaro, A., Altinok, N., Heintz, C., & Call, J. (2019). Disentangling great apes' decoy-effect bias in a food choice task. *Animal Behavior and Cognition, 6*(3), 213–222.

Schwartz, L. P., Silberberg, A., Casey, A. H., Paukner, A., & Suomi, S. (2016). Scaling reward value with demand curves versus preference tests. *Animal Cognition, 19*, 631–641.

Tabellario, S., Babitz, M. A., Bauer, E. B., & Brown-Palsgrove, M. (2020). Picture recognition of food by sloth bears (*Melursus ursinus*). *Animal Cognition, 23*(1), 227–231.

Tinklepaugh, O. L. (1928). An experimental study of representative factors in monkeys. *Journal of Comparative Psychology, 8*, 197–236.

Turner, H., & Firth, D. (2015). Generalized nonlinear models. http://go.warwick.ac.uk/gnm

Visalberghi, E., Valente, M., & Fragaszy, D. (1998). Social context and consumption of unfamiliar foods by capuchin monkeys (*Cebus apella*) over repeated encounters. *American Journal of Primatology, 45*, 367–380.

Wagner, K. E., Hopper, L. M., & Ross, S. R. (2016). Asymmetries in the production of self-directed behavior by chimpanzees and gorillas during a computerized cognitive test. *Animal Cognition, 19*(2), 343-350

Wrangham, R. W., Conklin-Brittain, N., & Hunt, K. D. (1998). Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. *I. Antifeedants. International Journal of Primatology, 19*, 949–970.

Wyrwicka, W. (1993). Social effects on the development of food preferences. *Acta Neurobiologiae Experimentalis, 53*, 485–493.

Zeagler, C., Zuerndorfer, J., Lau, A., Freil, L., Gilliland, S., Starner, T., & Jackson, M. M. (2016). Canine computer interaction: Towards designing a touchscreen interface for working dogs. In *ACI '16: Proceedings of the Third International Conference on Animal–Computer Interaction (Article 2)*. New York: ACM Press. https://doi.org/10.1145/2995257.2995384.