RESEARCH ARTICLE

Playing it safe? Solitary vervet monkeys (*Chlorocebus pygerythrus*) choose high-quality foods more than those in competition

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Abstract

An important goal in foraging ecology is to determine how biotic and abiotic variables impact the foraging decisions of wild animals and how they move throughout their multidimensional landscape. However, the interaction of food quality and feeding competition on foraging decisions is largely unknown. Here we examine the importance of food quality in a patch on the foraging decisions of wild vervet monkeys (*Chlorocebus pygerythrus*) at Lake Nabugabo, Uganda using a multidestination platform array. The overall nutritional composition of the vervet diet was assessed and found to be low in sodium and lipids, thus we conducted a series of experimental manipulations in which the array was varied in salt and oil content. Although vervets prioritized platforms containing key nutrients (i.e., sodium and lipids) overall, we found that solitary vervets prioritized nutrient-dense platforms more strongly than competing vervets. This finding was opposite to those in a similar experiment that manipulated food site quantity, suggesting that large, salient rewards may be worth competing over but slight differences in nutritional density may be only chosen when there are no potentially negative social consequences (i.e., aggression received). We also found that vervets chose platforms baited with oil-only, and oil combined with salt, but not salt-only, suggesting that energy was an important factor in food choice. Our findings demonstrate that when wild vervets detect differences in feeding patches that reflect nutritional composition, they factor these differences into their navigational and foraging decisions. In addition, our findings suggest that these nutritional differences may be considered alongside social variables, ultimately leading to the complex strategies we observed in this study.

KEYWORDS
decision-making, multidestination routes, navigation, nutrient balancing, nutritional ecology, optimal foraging theory

1 | INTRODUCTION

Animals have a multitude of factors to consider while foraging in the wild and attempting to maximize their fitness. The successful acquisition of nutrients is a direct prerequisite for growth and reproduction and thus is a central ecological factor influencing the animal abundance, diversity, and social behavior (Rothman, Chapman, & Van Soest, 2012). However, foraging problems are complex and should be viewed in terms of a combination of the nutritional needs of the animal as well as the biotic and physical environmental variables that determine how an animal is able to meet those nutritional needs (John & Temerin, 1984). Such biotic and physical variables include climate, the physical structure of the environment, predation risk, the presence of sympatric species, and intraspecific competition, among other variables. Foraging sites vary further in patch size, location, distribution, quality, handling time, and renewal rate (Menzel, 1997; Stephens, Brown, & Ydenberg, 2007; Teichroeb & Aguado, 2016). Animals must balance all of these variables and the exact value of resources available in patches may not always be clear to the consumer.

A variety of taxa are known to make foraging trade-offs when dealing with the differential costs and benefits of choosing one food patch over another. For example, female red deer (*Cervus elaphus*) trade-off closed habitats that provide shelter against harsh weather and predators for open pastures with greater foraging opportunities (Godvik et al., 2009). Foraging trade-offs have also been observed in gray partridges (*Perdix perdix*), who have been found to trade-off increased individual access to resources for improved predator detection through increased group size (Watson, Aebischer, & Cresswell, 2007). Similar foraging trade-offs have also been observed in fish (Berumen & Pratchett, 2008) and insects (Berger & Gotthard, 2008). Primates are also well-known to make foraging trade-offs when dealing with the differential costs and benefits of feeding patches, for example trading off predation risk for high reward sites (Cowlishaw, 1997; Janson, 1990), or increased spatial distance for increased foraging reward (Janson, 2007). In a similar vein, Teichroeb and Aguado used a platform foraging experiment to determine whether wild vervet monkeys (*Chlorocebus pygerythrus*) prioritize high-reward food sites over low-reward sites (2016). They found that when one feeding platform was baited to be six times more rewarding than four other platforms, competing vervets prioritized highly rewarding platforms whereas solitary vervets did not. Solitary vervets traveled through the platforms in order of distance, regardless of where the high-reward platform was located, saving on distance and acquiring all the rewards. These findings strongly suggest that social factors add an additional dimension of complexity to the foraging decisions made by wild primates. Simulations of individual-based models have converged on similar results, suggesting that social animals can efficiently track their own nutritional needs in various social contexts, and that competing nutritional requirements (e.g., differing nutritional requirements between males and females) can lead to selection for different foraging strategies and group dynamics (Senior et al., 2016). Thus, different behaviors may be optimal when an individual is foraging alone versus with others and in primates, may depend on the relative dominance rank of competing individuals (Teichroeb, 2015).

Although this previous work has helped to clarify how resource quantity, spatial position, and predation risk may influence foraging decisions (Cowlishaw, 1997; Janson, 1990; Janson, 2007; Teichroeb & Aguado, 2016), the interaction of nutritional density and feeding competition on foraging decisions remain largely unknown. Although no single food item can offer the full complement of requisite nutrients (Lambert & Rothman, 2015), we define nutritionally dense food items as those that provide a relatively high proportion of nutrients or energy per unit. It has been suggested that animals may impose variable selection criteria on different food groups to balance their nutrient intake (Felton, Felton, Lindenmayer, & Foley, 2009; Raubenheimer & Simpson, 2004; Raubenheimer, Machovsky-Capuska, Chapman, & Rothman, 2015; Simpson & Raubenheimer, 2012). This concept of nutrient balancing suggests that animals balance their nutritional needs by mixing food items of varying nutritional composition instead of maximizing intake of any one particular nutrient (Milton, 1982; Westoby, 1974; Whiten, Byrne, Barton, Waterman, & Henzi, 1991). For example, Felton et al. (2009) note that two colobine species studied by Davies, Bennett, and Waterman (1988) selected leaves and seeds based on two different nutritional criteria, preferring high protein in leaves but high lipid concentration in seeds. These and other findings suggest that nutritional goals may serve as the main drivers of animal diet selection (Felton et al., 2009). However, under the assumptions that (a) all animals in a social group are trying to balance their nutritional needs, and (b) each food item may only have small quantities of desired nutrients: How does contest competition for nutritionally valuable resources affect food site selection?

We investigated the importance of patch nutritional composition on the foraging decisions of solitary and competing wild vervet monkeys at Lake Nabugabo, Uganda using a multidestination platform array. We used the same pentagon platform array as previously used in Teichroeb and Aguado (2016) but manipulated the quality, rather than the quantity, of food at the sites available to the monkeys to allow direct comparison with this previous study. We assessed the nutritional composition of the natural diet of the vervet monkeys at Nabugabo and we found it to be low in sodium and relatively low in lipids (Table 1;

TABLE 1 Mean ± standard deviation fat and salt concentrations found in foods eaten by vervets at Nabugabo along with recommended intake

	Fat/DM[a]	Salt/DM[a]
Foods eaten by Nabugabo vervets[b]	5.55%	0.03%
Standard deviation[b]	10.12%	0.05%
Recommended Intakes by the National Research Council[c]	2.5% (min)–25% (max)	0.25% (min)–0.65% (max)

[a]Percentage of fat and salt per unit of dry matter (DM).
[b]Collected by C. A. C., J. M. R., and their field assistants. Analyzed by J. M. R.
[c]Recommended for nonhuman primates by National Research Council (2003).

Cancelliere, Chapman, Twinomugisha, & Rothman, 2018). Sodium is critical in supporting overall maintenance and health in nonhuman primates (Robbins, 1993), and is typically limited in wild primate diets due to its lack of abundance in wild herbs, leaves, and fruits (Rode, Chapman, Chapman, & McDowell, 2003; Rothman, Van Soest, & Pell, 2006). Additionally, lipids provide an extremely dense, caloric-rich source of energy to wild animals and also support normal growth and development in nonhuman primates (Reisbick, Neuringer, & Connor, 1996). Thus, this experiment consisted of a series of manipulations in which platforms were baited to vary in their content of these limited nutrients. As in previous foraging experiments with vervets at Nabugabo (Teichroeb, 2015; Teichroeb & Aguado, 2016; Teichroeb & Smeltzer, 2018), solitary individuals were found to leave their group and complete our experiments alone and to also come as part of a group, allowing comparison between social and solitary foraging decisions.

We hypothesized that foraging vervets would more strongly prioritize (i.e., travel further to visit them first) the platforms of higher nutritional composition (i.e., those containing salts and/or fats) when they were foraging in competition with others in their social group but not when they were alone. Since solitarily-foraging vervets could obtain the rewards on all platforms and were guaranteed the high-quality site, we expected them to complete the platform array in order of distance (i.e., beginning at the platform closest to their approaching angle regardless of reward quality), collecting high-quality rewards on the way (e.g., Teichroeb & Aguado, 2016). Optimal foraging theory predicts that animals should choose to maximize their rate of energy gain relative to their energy expenditure. That is, animals should attempt to minimize the distance traveled between feeding patches while simultaneously maximizing their food energy intake (Charnov, 1976; Pyke, 1984). Indeed, previous foraging experiments on vervets involving a platform array have shown that they are adept at minimizing distance in multidestination routes and seem to rely on spatial movement heuristics that allow them to do this (Teichroeb, 2015; Teichroeb & Smeltzer, 2018). Optimal foraging theory further suggests that competing vervets should prioritize the nutrient-dense platforms to a greater degree than solitary foragers due to the increased risk of losing high-quality food rewards to conspecifics (Simpson, Sibly, Lee, Behmer, & Raubenheimer, 2004), as was found in a previous experiment in the same population on the effects of food quantity on foraging decisions (Teichroeb & Aguado, 2016) Thus, competing vervets were expected to alter their behavior by traveling farther to visit high-quality sites first (i.e., bypassing lower-quality platforms in favor of high-quality sites), rather than attempting to complete the route in order of distance, risking loss of the high-quality reward (Teichroeb & Aguado, 2016).

2 | METHODS

2.1 | Animal ethics statement

All applicable international, national, and institutional guidelines for the care and use of animals were followed, and the research adhered to the American Society of Primatologists Principles for the Ethical Treatment of Nonhuman Primates. The methods used in this foraging experiment were approved by the Uganda Wildlife Authority, the Uganda National Council for Science and Technology, and the University of Toronto Animal Care Committee (UACC). Individuals were not captured, handled, or restrained during data collection. Participation was entirely voluntary and opportunistic, and individuals were free to leave the platform set up at any time.

2.2 | Study site and subjects

This study was conducted at Lake Nabugabo, Masaka District, Uganda (0°22′-12°S, 31°54′E). Lake Nabugabo is a relatively small satellite lake (8.2 × 5 km) on the western side of Lake Victoria, lying at an elevation of 1,136 m. Our research station lies on the western side of Lake Nabugabo, in an area of mixed forest fragments, wetland, farmer's fields, and tourist camps. The study subjects were a habituated group of vervet monkeys (*Chlorocebus pygerythrus*) referred to as the K group, which had been followed continuously for approximately 1 year. All adult and subadult individuals were identifiable by their natural markings; however, some juveniles were not yet individually identifiable. At the time of the study, the group contained 39–40 individuals (5 adult males, 11 adult females, 3 subadult males, 5 subadult females, 15–16 juveniles and infants).

2.3 | Data collection

This experiment was conducted from May through to late July 2017. Five wooden platforms (wooden tables, 0.75 m high, with a square flat top 0.75 × 0.75 m, as in Teichroeb & Aguado, 2016) were arranged in a pentagon with a distance of 5 m between each platform. The K group had a reliable daily range which allowed platforms to be placed in an area among frequently visited feeding patches. The group was experimentally naïve and had not participated in any foraging experiments before data collection. Therefore, individuals required a short adjustment period (~2 weeks) to habituate to the platforms before they readily began to approach the array and take food rewards. Platforms were baited with individual pieces of popcorn that varied in types of nutrients, having been treated according to the experimental phase (6 total, see below). Although popcorn is an anthropogenic food item, previous work conducted with a neighboring group of wild vervets at the research site found that popcorn was palatable to the monkeys and elicited approach behaviors (Teichroeb, White, & Chapman, 2015). In addition, plain popcorn prepared with a hot air-popper, without the use of any additives, served as an easily manipulated carrier for the nutrient treatments used in each experimental condition. Because this group of vervets was wild, popcorn was given only as supplemental food specifically to address the questions we investigate in this study.

FIGURE 1 Orange flagging tape beacon setup beginning in control Phase 2 and later indicating high-quality rewards to the study animals

Before we began collecting data in the experimental phases, we ran two separate controls phases, which we used to assess which platforms in the array the monkeys visited first most often and the effect of a beacon that was to be used in further experimental trials. In the first control, all five platforms were baited equally with one piece of plain air-popped popcorn. In the second control, all five platforms were again baited equally with one piece of plain popcorn, however, a beacon consisting of bright orange flagging tape was wrapped around the top of one platform to serve as an experimental control (Figure 1). The location of the beaconed platform was chosen because it received the lowest number of first visits in the first control phase (platform 1; Figure 2). The second control phase allowed us to determine if the beacon had any effect on first visits to the platform containing the beacon, relative to the first phase where no beacon was used. This was important to assess because in the remaining phases, we manipulated the nutritional composition of the popcorn on the platforms and indicated which

platform(s) had nutritionally different rewards to the monkeys using the flagging tape beacon. Vervets have a trichromatic color vision (Jacobs, 2009) and we knew from a previous experiment that vervets easily learned to associate a beacon with a reward (Teichroeb & Chapman, 2014). The flagging tape beacon was found to work well because it was visible from a long distance and the monkeys did not have to see the top of the platform to see the beacon.

Experimental manipulations began with Phase 1, where four of the platforms were baited with one piece of plain popcorn, but one platform (platform 1 with the beacon; Figure 3a) was manipulated to hold a food reward that was nutritionally different (in either lipids or salt) than other platforms. In this phase, the platform was baited with a piece of popcorn that had been treated with salt. In this phase and all remaining phases, lipid or salt popcorn platforms were selected based on the fewest number of visitations in the preceding phase. Phase 2 included three platforms baited with one piece of plain popcorn and two platforms baited with the salted popcorn (platforms 1 and 4 with beacons; Figure 3b). Phases 3 through 6 proceeded in the same manner, with one or two high-quality platforms, but was changed to popcorn with oil (Phases 3 and 4; Figure 4), and then oil and salt (Phases 5 and 6; Figure 5). Oiled or salted popcorn was on platforms 2 and 5 in Phases 3 and 4, and platforms 4 and 1 in Phases 5 and 6.

In sum, 100 trials were completed for Phases 1, 2, 4, 5, and 6, 104 trials were completed for control Phase 1, 101 trials were completed for control Phase 2, and 101 trials were completed for Phase 3, for a total of 806 trials (n_{trials} = 806, mean$_{trials\ per\ day}$ = 20.15; range, 0–50). We collected an unequal number of trials per individual because our subjects were wild animals and we could not control the participation of individual monkeys. However, overall the platforms were not dominated by a few individuals (range for single individuals participating in repeated trials: 0–69, range for competition trials: 0–42) and 31 individuals participated in trials (see Tables S1 and S2). The majority of trials were solitary, where only one individual was present at the platforms and no other individuals were within 20 m of the experimental setup ($n_{solitary\ trials}$ = 576, $n_{competitive\ trials}$ = 224).

We calculated the expected number of "first visits" for each platform from control Phase 2 (the beacon control trials), for comparison with the number of first visits to nutritionally dense platforms in experimental trials. During trials, the researcher recorded
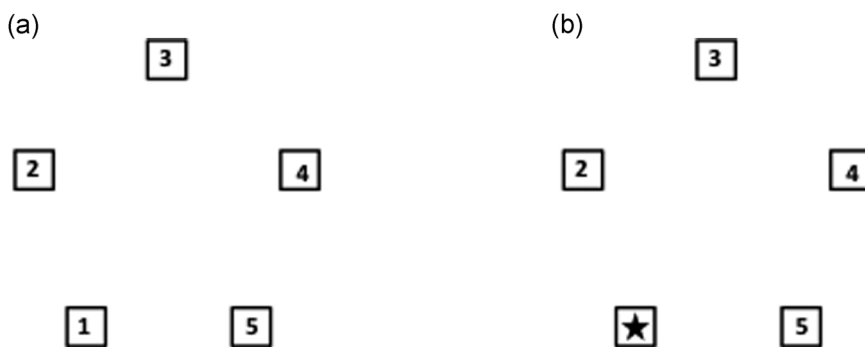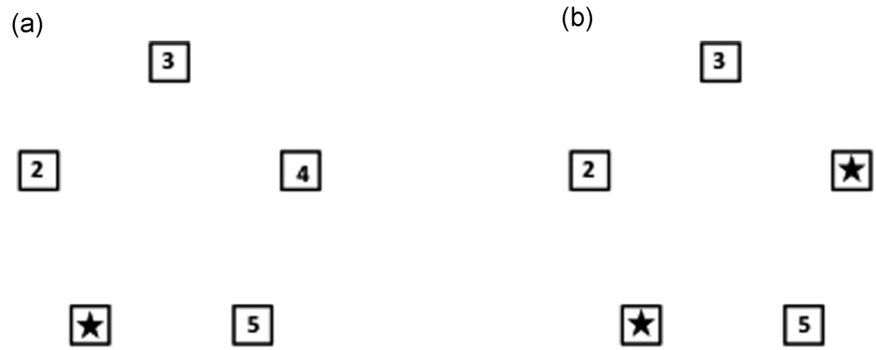
(a)

(b)

FIGURE 2 Control Phases 1 (a) and 2 (b): (a) All platforms baited with plain popcorn (n_{trials} = 104) and (b) all platforms baited with plain popcorn and an added beacon on platform 1 (n_{trials} = 101)

FIGURE 3 Experimental Phases 1 (a) and 2 (b). (a) Platform 1 baited with salt-treated popcorn (n_{trials} = 100) and (b) platforms 1 and 4 baited with salt-treated popcorn (n_{trials} = 100)

the number of individuals present, the identity of the individual(s) participating, the sequence of platform visitation, the direction of approach for each individual, and the reward(s) taken by each individual. Instances, where a platform that contained a reward was bypassed for a different platform, were also recorded. The researcher stood in the vicinity of platform 3 (~5 m away) during all phases of data collection, and recorded all data onto a data sheet using direct visual observation. Platforms were not rebaited to begin a new trial until all monkeys were a minimum of 20 m away and the researcher could easily rebait the entire setup before any monkeys returned. Adults and subadults were always reliably and consistently identified based on individual markings. However, due to the high number of juveniles ($n_{juveniles}$ = 16), not all juveniles were consistently individually identified. As a result, juveniles were not identified for a total of 91 trials (21 solitary and 70 competitive), out of a total of 265 juvenile visits.

2.4 | Nutritional analyses

Before this foraging experiment, a neighboring vervet group (M group) that overlaps the home range of K group was followed for 10 days a month, from June 2011 to May 2014 (36 months; approximately 9 hr/day) by C. A. C. and his field assistants to determine their diet (Cancelliere et al., 2018). J. M. R. collected and analyzed the nutritional content of plant parts that were consumed by the M group using analyses described in Cancelliere et al. (2018). We then analyzed the same samples for sodium using methods described in Rothman et al. (2006), because primate diets in tropical areas are typically deficient in sodium (Rode et al., 2003; Silver, Ostro, Yeager, & Dierenfeld, 2000; Wambeke, 1992) and we suspected the same for these monkeys. Average levels of salt and

fat in the foods eaten by vervets at Nabugabo are included in Table 1, with recommended levels of salt and fat intake for primates also included for reference ("Nutrient Requirements for Nonhuman Primates", 2003). The treatment of the popcorn for the nutritionally dense platforms (salt and/or oil) was selected on the basis of these data, which suggests that vervets in this area obtain a low level of fat and an inadequate level of salt relative to recommended levels of intake for primates. During the experiment, the popcorn was treated with 2.0 ml of salt per 50 popped kernels in the salt-only trials (Phases 1 and 2), and 4.0 ml of canola oil per 50 popped kernels in the oil-only trials (Phases 3 and 4). In the salt and oil combined trials (Phases 5 and 6), the popcorn was treated with 2.0 ml of salt and 4.0 ml of canola oil per 50 kernels.

2.5 | Data analyses

To assess whether the beacon alone (without any change to the nutritional value of food) had an effect on the vervets behavior, we first compared the proportion of first visits to platform 1 (the platform that would be the first baited with a high-quality reward) in the two control phases (control Phases 1 and 2). The results of a z-ratio test for the significant difference between two independent proportions suggested that the beacon alone did not alter the behavior of the vervets (z = −1.449, p = .147). Thus, the beacon was used as an additional visual aid for high-quality platforms in the remaining phases.

We separated solitary and social trials in the remaining analyses, where we determined whether the high-quality, beaconed platforms were visited first significantly more often than expected by comparing with the beacon control trials (control Phase 2), using
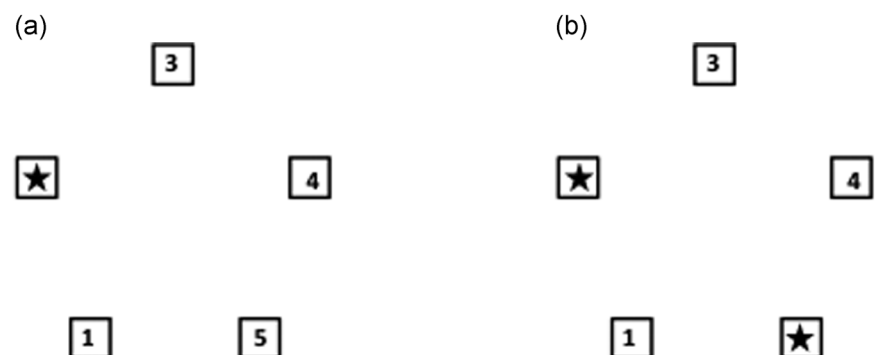
FIGURE 4 Experimental Phases 3 (a) and 4 (b). (a) Platform 2 baited with oil-treated popcorn (n_{trials} = 101) and (b) platforms 2 and 5 baited with oil-treated popcorn (n_{trials} = 100)
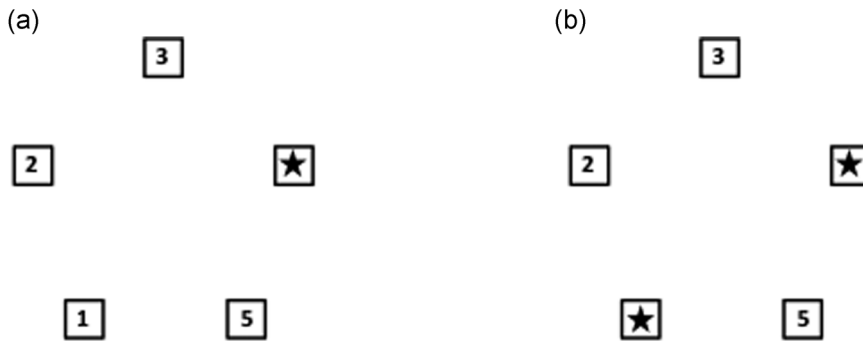
(a)

(b)

Wilcoxon signed-rank tests. The observed frequencies of first visits were compared with expected frequencies from control Phase 2 where the proportion of first visits to each platform were as follows: platform 1, 0.228; platform 2, 0.059; platform 3, 0.277; platform 4, 0.317; and platform 5, 0.109. To calculate the expected values for each phase, these proportions were then multiplied by the total number of trials in each phase per individual. In phases with one rewarding platform in the pentagon, we compared the proportion of first visits to high-quality sites between solitary and competitive trials with McNemar's tests, which allow comparison between proportions that are not independent (i.e., samples from the same individuals).

In addition to the Wilcoxon signed-rank tests, the results from related phases were combined using Fisher's log-likelihood method to test for the overall prioritization of each separate type of nutritional manipulation (i.e. salt, oil, or oil and salt combined). So, the results from Phase 1 (one piece salted popcorn) were combined with those from Phase 2 (two pieces salted popcorn), Phase 3 (one piece oiled popcorn) results were combined with Phase 4 (two pieces oiled popcorn) results, and Phase 5 (one piece oiled and salted popcorn) results were combined with Phase 6 (two pieces oiled and salted popcorn) results. After this, the results from all phases involving higher-quality popcorn (Phases 1 through 6) were combined using Fisher's log-likelihood method to analyze the overall prioritization of platforms baited with any of the included nutritional types.

Bypassing of platforms, where one platform was skipped over in favor of a nutritionally supplemented platform with popcorn, was analyzed for both solitary and competitive trials using Wilcoxon signed-rank tests. However, bypassing was only assessed for phases where only one platform contained a salt or oil reward (Phases 1, 3, and 5) because it was difficult to be sure of bypassing when two platforms of the five in the array had higher-reward food. Competitive trial analyses were run by calculating each individual's frequency of bypassing for dense platforms in solitary trials versus their frequency of bypassing for dense platforms in competitive trials. Further, additional analyses were run using data from Teichroeb and Aguado (2016), who conducted a similar foraging experiment with a neighboring group of vervets using a pentagon platform setup with rewarding sites containing six times more food than low-reward sites (i.e. 3 banana slices vs. one half of a banana slice). To determine if solitary foragers in this experiment

prioritized nutritionally dense platforms more than solitary foragers prioritized high-quantity platforms in the Teichroeb and Aguado (2016) experiment, we used z-ratio tests for the significance of the difference between two independent proportions. This was done only for solitary foragers where nutritionally dense platforms were baited with salt (Phase 1), oil (Phase 3), or salt and oil combined (Phase 5). Tests were two-tailed and run using SPSS, version 24 (IBM Corporation) and the Vassar Stats website (www.vassarstats. net), with an α = .05 set for significance.

3 | RESULTS

When alone, the monkeys minimized the distance they traveled around the platform array on 97.9% of trials (all phases). Incomplete trials, where an individual left due to unknown circumstances, were very rare and occurred only three times in 806 trials (0.003%). Revisits to empty platforms were not seen during this experiment. Results from each phase are reported according to food reward treatment, and solitary and competitive foraging results.

3.1 | Salt phases

In Phase 1, platform 1 was baited with one piece of salted popcorn and all other platforms were baited with one piece of plain popcorn (n_{trials} = 100). Solitary foragers in Phase 1 visited high-quality sites first 28.36% of the time (19/67) and minimized the distance around the platform array on 100% of trials. When compared to individual expected frequencies calculated from control Phase 2, the frequency of first solitary visits to high-quality sites was not higher than expected (Wilcoxon signed-ranks test: W = 40, n = 16, p = .308). Competitive foragers in Phase 1 visited high-quality sites first 21.21% of the time (7/33), and these visitation rates were also not significantly higher than expected (Wilcoxon signed-ranks test: W = −12, n = 11, p = .610). These two proportions were found to differ significantly, however (McNemar's test: p < .0001), with solitary foragers more likely to visit salt sites first (odd's ratio = 6.875) relative to vervets in competition.

In Phase 2, platforms 1 and 4 were each baited with one piece of salted popcorn and all other platforms were baited with one

piece of plain popcorn (n = 100 trials). Solitary foragers in Phase 2 visited high-quality sites first 64% of the time (48/75) and minimized the distance around the platform array on 98.7% of trials. When compared to expected frequencies calculated from control Phase 2, the frequency of first visits to high-quality sites was not higher than expected (Wilcoxon signed-ranks test: W = 46, n = 15, p = .197). Competitive foragers in Phase 2 visited high-quality sites first 44% of the time (11/25), but this frequency was not higher than expected (Wilcoxon signed-ranks test: W = −30, n = 12, p = .246).

Initial visits to high-quality platforms were combined for solitary and competitive foraging trials in both salt-treated popcorn phases (Phases 1 and 2), and we found that overall high-quality sites were not visited first significantly more often than expected (Fisher's log-likelihood: χ^2 = 4.623, df = 4, n = 23 individuals, p = .328). Although we were interested in analyzing the frequency of bypassing in solitary Phase 1 trials, and comparing bypassing rates to the frequency of bypassing for high-quantity sites in Teichroeb and Aguado (2016), the frequency of bypassing by foragers in this phase of the experiment was too low to analyze using a z-ratio test (3/67 bypassing trials).

3.2 | Oil phases

In Phase 3, platform 2 was baited with one piece of oiled popcorn and all other platforms were baited with one piece of plain popcorn (n_{trials} = 101). Solitary foragers in Phase 3 visited high-quality sites first 20.55% of the time (15/73) and minimized the distance around the platform array on 94.52% of trials. When compared to individual expected frequencies calculated from control Phase 2, the frequency of first solitary visits to high-quality sites was not higher than expected (Wilcoxon signed-ranks test: W = 46, n = 15, p = .197). Competitive foragers in Phase 3 visited high-quality sites first in 14.29% of the time (4/28), and this was also not higher than expected (Wilcoxon signed-ranks test: W = −24, n = 11, p = .298). The proportion of solitary foragers that visited high-quality sites first was again significantly higher in this phase (McNemar's test: p < .0001), compared to competitive foragers (odd's ratio = 14.5).

In Phase 4, platforms 2 and 5 were each baited with one piece of oiled popcorn, and all other platforms were baited with one piece of plain popcorn (n_{trials} = 100). Solitary foragers in Phase 4 visited high-quality sites first 43.68% of the time (38/87) and minimized the distance around the platform array on 98.85% of trials. When compared to expected frequencies calculated from control Phase 2, the frequency of first visits to high-quality sites was significantly higher than expected (Wilcoxon signed-ranks test: W = 81, n = 15, p = .011). Competitive foragers in Phase 4 visited high-quality sites first 61.54% of the time (8/13), but this frequency was not higher than expected (Wilcoxon signed-ranks test: W = 16, n = 7, p = .172).

Initial visits to high-quality platforms were combined for solitary and competitive foragers in both oiled-treated phases (Phases 3 and 4), and we found that overall high-quality sites were

visited first significantly more often than expected (Fisher's log-likelihood: χ^2 = 12.197, df = 4, n = 18 individuals, p = .016). In addition, we analyzed the frequency of bypassing in solitary Phase 3 trials (3/73) and compared it to the frequency of bypassing for high-quantity sites in (6/258) using a z-ratio test (Teichroeb and Aguado, 2016). We found that vervets in Phase 3 of our foraging experiment did not bypass low-quality sites in favor of high-quality sites more often than vervets in bypassed low-quantity sites in favor of high-quantity sites (z = 0.8274, 0.8274, p = .407; Teichroeb and Aguado, 2016).

3.3 | Salt and oil combined phases

In Phase 5, platform 4 was baited with one piece of oiled and salted popcorn, and all other platforms were baited with one piece of plain popcorn (n_{trials} = 100). Solitary foragers in Phase 5 visited high-quality sites first 48.72% of the time (38/78) and minimized the distance around the platform array on 98.72% of trials. When compared to individual expected frequencies calculated from control Phase 2, the frequency of first solitary visits to high-quality sites was significantly higher than expected (Wilcoxon signed-ranks test: W = 61, n = 13, p = .035). Competitive foragers in Phase 5 visited high-quality sites first 45.45% of the time (10/22), but this frequency was not higher than expected (Wilcoxon signed-ranks test: W = 8, n = 8, p = .57). Once again, solitary foragers visited high-quality sites first significantly more often (McNemar's test: p < .0001) than vervets in competition (odd's ratio = 4).

In Phase 6, platforms 4 and 1 were each baited with one piece of oiled and salted popcorn, and all other platforms were baited with one piece of plain popcorn (n_{trials} = 100). Solitary foragers in Phase 6 visited high-quality sites first 65.63% of the time (42/64) and minimized the distance around the platform array on 96.88% of trials. When compared to expected frequencies calculated from control Phase 2, the frequency of first visits to high-quality sites was significantly higher than expected (Wilcoxon signed-ranks test: W = 67, n = 14, p = .037). Competitive foragers in Phase 6 visited high-quality sites first 75% of the time (27/36), but this frequency was not significantly higher than expected (Wilcoxon signed-ranks test: W = 31, n = 14, p = .337).

Initial visits to high-quality platforms were combined for solitary and competitive foragers in oil- and salt-treated phases (Phases 5 and 6), and we found that overall high-quality sites were visited first significantly more often than expected (Fisher's log-likelihood: χ^2 = 13.326, df = 4, n = 20 individuals, p = .010). Additionally, we analyzed the frequency of bypassing in solitary Phase 5 trials (8/78) and compared it to the frequency of bypassing for high-quantity sites in (6/258) using a z-ratio test (Teichroeb and Aguado, 2016). We found that vervets in Phase 5 of our foraging experiment in bypassed low-quality sites were in favor of high-quality sites significantly more often than vervets in bypassed low-quantity sites that were in favor of high-quantity sites (z = 3.072, p = .002; Teichroeb and Aguado, 2016).

3.4 | All phases with high-quality foods combined

In combined results from all phases with high-quality sites (Phases 1 through 6), solitary foragers traveled to highly rewarding platforms first on 49.32% of trials (219/444), and competitive foragers traveled to highly rewarding platforms first on 42.68% of trials (67/157); proportions that differed significantly (McNemar's test: $p < .0001$, odd's ratio = 3.358). In combined results from all phases with high-quality sites for both solitary and competitive foragers, highly rewarding platforms were visited first on 47.59% of trials (286/601). This was significantly more than expected from control Phase 2 (i.e., the beacon control trials) first visits (Fisher's log-likelihood: χ^2 = 30.146, df = 12, n = 30 individuals, p = .004).

4 | DISCUSSION

In the experimental phases of our foraging study overall (Phases 1 through 6), we found that solitary foragers chose the nutritionally supplemented platforms by visiting these high-quality sites first significantly more often than low-quality sites. This was not the case with competing foragers, who did not visit high-quality sites first significantly more often than low-quality sites. This is in stark contrast to previous results observed by Teichroeb and Aguado (2016), who found that vervets *only* prioritized high-quantity sites when in competition. These observations were unexpected and did not support our hypotheses, as we expected competing foragers to prioritize high-quality sites more strongly than solitary foragers.

This effect may have occurred for several reasons. First, in our experiment, we baited all platforms with a single piece of popcorn, and the only difference between high-quality and low-quality sites was the treatment of that single piece of popcorn (i.e., salted, oiled, or salted and oiled). However, in Teichroeb and Aguado (2016) the high-quantity sites were perceptually very different from low-quantity sites, being baited with six times the reward quantity. Food quantity is an extremely basic and salient factor relevant to survival, and a variety of species, from salamanders to elephants, have been found to be adept in quantity discrimination tasks (Parrish, Evans, & Beran, 2015). Visual cues in foraging may be even more important in catarrhine primates who possess enhanced visual abilities (e.g., trichromacy) relative to other sensory capabilities such as olfaction (Teichroeb & Kumpan, 2017). Indeed, previous foraging experiments have shown that vervets predominantly rely on visual signals to locate food rewards (Teichroeb & Chapman, 2014). It is thus possible that the differences in quantity in Teichroeb and Aguado (2016) were easier for the monkeys to differentiate based on visual cues than the differences in quality in this study, which did not impart any unique visual signals (each piece of popcorn looked the same regardless of nutritive quality). As such, the high reward ratio in Teichroeb and Aguado (2016) may have been significantly more salient to the vervets than the single-pieces of popcorn in our experiment and may have triggered a different suite of behaviors in solitary and competitive foraging

contexts. It may be the case that a higher number of rewards is perceived as being worth the risk of receiving aggression in competitive foraging contexts regardless of their quality, but a single reward of higher quality is not worth the risk of a fight.

Second, the lack of selection of high-quality sites in competitive trials may have been due to the relatively small increase in the reward (from low-quality to high-quality reward) in our experiment. A single piece of popcorn that had been treated with oil, or salt and oil, represents an increase in nutritional quality relative to other pieces of untreated popcorn in the array, but it may have been that this increase in quality was too small to motivate prioritization of high-quality sites in high-stakes competitive foraging. Vervets may have determined that prioritization of slightly higher-quality sites was beneficial in solitary contexts, but not worth the risk of a potential fight, with the associated risk of injury, in competitive contexts.

Third, although achieving a balance of a variety of nutrients throughout the day is thought to be an important foraging goal of many taxa, competing foragers must meet this goal while also considering complex social factors, such as dominance rank and the potential risk of a physical confrontation. A solitary animal may prioritize a nutritionally dense feeding patch to obtain a variety of nutrients and to maximize their health, but this benefit may no longer be worth the risks when in competition with another individual. Instead, it may be more beneficial to collect the food rewards at the nearest available platform regardless of quality, than to risk bodily harm that has the potential to greatly reduce future fitness. In the immediate context, it may be optimal for competing foragers to lose out on the nutrients that help them to maximize their health, because in the long-run they may come across other opportunities to obtain key nutrients without risking bodily harm.

Bypassing of low-quality sites in favor of high-quality sites was not frequently observed, and when it was observed it did not happen significantly more often in competitive trials, as Teichroeb and Aguado (2016) observed for high-quantity sites in their foraging experiment. The reasons for this are likely similar to those we presented in the previous section for competing foragers who did not visit high-quality sites first significantly more often than low-quality sites, namely, high-quality sites were less salient and differed relatively little from low-quality sites, in comparison to the six times greater, salient reward in Teichroeb and Aguado (2016). However, we found that solitary foragers in Phase 5 (i.e., oil- and salt-treated popcorn) bypassed low-quality sites in favor of high-quality sites significantly more often than foragers in Teichroeb and Aguado (2016) bypassed low-quantity sites in favor of high-quantity sites, even when they were six times more rewarding. This suggests that food of higher nutritional quality may be more important to solitary foragers than a larger amount of food of the same type. Solitary foragers likely benefit in the long-run by prioritizing nutritionally dense patches, as this maximizes health and thus the potential for successful reproduction. The increased frequency of bypassing in our high-quality trials relative to high-quantity trials in Teichroeb and Aguado (2016) may, therefore, indicate an increased

value placed on nutritionally dense food by solitary foragers, but not competing foragers due to the additional social risks when others are present. This is perhaps unsurprising given that micro and macronutrients are known to play important roles in the survival and fitness of primates. Body fat is well-known to provide an essential energy reserve, for example, Vogel et al. (2012) found that Bornean orangutans (*Pongo pygmaeus wurmbii*) were able to rely on body fat stores for energy during low-fruit periods avoid tissue wasting. Further, variability in the intake of critical nutrients is a known factor influencing primate infant and juvenile growth, as well as maternal effects and female reproductive success (Altmann & Alberts, 2005; Righini, 2014; Thompson, Kahlenberg, Gilby, & Wrangham, 2007).

Differences in prioritization were additionally found when we analyzed our data according to the different treatment types of the experiment (i.e., salt, oil, or salt and oil). We found that solitary vervets visited nutritionally dense platforms first significantly more often when they were treated with oil (Phases 3 and 4), or oil and salt (Phases 5 and 6), but not when they were treated with salt alone (Phases 1 and 2). In our case, it is possible that the vervets in this experiment were obtaining salt from a source that we had not tested, as we had only tested their natural foods. There were two compost heaps located near the foraging array (50–100 m) that we had not analyzed for nutritional composition, as food types present in the heaps were mixed and not natural. Obtaining salt from such point sources can occur very rapidly and thus not appear to be an important component of the diet based on intake (grams/second). Further, human-sourced foods are likely to contain a relatively high amount of sodium compared to natural foods (Milton, 1999). Therefore, it is possible that compost heaps or other feeding locations (e.g., soils) contained foods that were high in salt, and vervets were not motivated to select salted popcorn in our experiment.

Another contributing factor may have been that the salted popcorn phases were the first set of experimental trials where we baited beaconed platforms with high-quality nutritionally dense popcorn. The participating vervets may not have had enough time to learn that higher-quality rewards were present at the site at fixed platforms, or to associate the beaconed platforms with higher-quality rewards. This effect may also have been enhanced because the preceding phase was the beacon control phase, where the beacon was baited with the same low-quality reward as all other platforms so that we could assess whether the beacon alone had an effect on the vervets behavior. This essentially created a period in which the vervets had learned that the beacon contained a low-quality reward, which we then switched to a high-quality reward in the proceeding salt treatment phases. This is akin to a reversal learning task used to analyze flexibility in learning, where object-reward associations are established and then immediately switched (Bitterman, 1965; Rumbaugh & Pate, 1984). The vervets in this experiment may have needed more time to effectively extinguish this learned association and to create a new association whereby the beacon became a rewarding stimulus. In the future, it would be beneficial to look at the effects of salt-only on vervet foraging, especially as it appeared to be important in the final two phases where oil and salt were combined (Phases 5 and 6).

5 | CONCLUSION

The combined impacts of patch nutritional composition and feeding competition on the foraging decisions of animals are poorly studied. Obtaining key nutrients is a pervasive problem faced by wild animals, as the acquisition of nutrients is a direct prerequisite for normal growth patterns, successful reproduction, and fitness. The strategies that animals use to maximize intake of key nutrients during feeding bouts are as such subject to the same selective pressures as other foraging strategies. Our findings demonstrate that when wild vervets are aware of differences in feeding patches that reflect nutritional composition, they factor these differences into their navigational and foraging decisions. To our knowledge, our study is the first to manipulate nutritional variables in an experimental foraging setup with primates and has found that nutritional variables appear to influence site selection and navigation in wild vervets in a complex way. Although we found that vervets prioritized platforms containing key nutrients overall, solitary vervets appeared to prioritize nutritious patches more heavily than competing vervets. Our results also demonstrate that the strategies that animals use to maximize nutrient intake seem to vary in social and asocial conditions.

CONFLICT OF INTERESTS

The authors declare that there are no conflict of interests.

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