



Foraging vervet monkeys optimize travel distance when alone but prioritize high-reward food sites when in competition



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Optimal foraging theory predicts that animals should attempt to maximize their food intake while exerting minimal energy. Thus, food sites should often be visited in order of proximity. However, resources vary in multiple attributes, so it may be beneficial to bypass some sites to visit others first. We used a foraging experiment on wild vervet monkeys (*Chlorocebus pygerythrus*) at Lake Nabugabo, Uganda to determine whether they prioritize high-reward food sites over low-reward sites. Five baited platforms were set in a pentagon within the range of one group. Trials usually consisted of single foragers but when multiple individuals participated, food competition occurred. In phase 1, platforms were baited equally. Individuals immediately found the shortest path and there was no relationship between experience and distance travelled. From phase 1, expected numbers of first visits to each platform were calculated for phases 2 and 3, where one or two platforms were six times more rewarding than others. In combined results from all trials with high-reward sites, individuals did not travel to highly rewarding platforms first, unless competitors were present. Vervets that foraged alone usually accessed food sites in order of proximity and saved on travel costs (consistent with a nearest-neighbour rule or a convex hull heuristic), regardless of the location of high-reward site(s); while monkeys in competition prioritized high-reward sites (a 'take-the-best' or gravity heuristic) and sometimes bypassed low-reward sites in an attempt to increase food acquisition at the expense of travel costs. When two sites were six times more rewarding, travel patterns changed to a greater focus on high-reward sites by single foragers and a tendency to ignore low-reward platforms. These results confirm that vervets integrate distance/reward information over multiple food sources, show spatial discounting in the right circumstances and optimize their routing decisions in different ways depending on the social context.

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Foraging animals face many challenges that affect individual fitness (Stephens, Brown, & Ydenberg, 2007). They must find food, decide their path between variable resources, and if they live in a group, ensure their own food intake in the midst of competition with others. In theory, animals should strategically exploit food sources in a way that optimizes net energy gain (Charnov, 1976; Stephens & Krebs, 1986; Stephens, Lynch, Sorensen, & Gordon, 1986). However, food sites vary in multiple ways, including location, quantity, distribution (clumped or scattered), quality (nutrition, calorie content, mineral content, etc.), taste, visibility, handling time and renewal rate (Menzel, 1997; Stephens et al., 2007). Resources may also be differentially exposed to predation risk (Stephens, 1981) and depletion by conspecifics and

heterospecifics. Natural selection should have favoured the ability to prioritize certain resources over others, but it is still unknown how all of these factors come into play for foraging animals. The suggestion that some animals may remember resources, rank them along a linear scale, and visit them sequentially based on their expected value has been called the rank-order problem in foraging (Menzel et al., 2008; Sayers & Menzel, 2012); however, this represents ideal decision making, unaffected by the constraints imposed by living with others. Animals also probably vary in their abilities to remember information about each food location and they are usually forced to make foraging decisions with imperfect knowledge (Shettleworth, 2010).

In situations where the food available at each site is known or of equal value, optimizing food intake for a single animal over multiple locations becomes a travelling salesman problem (TSP) (Anderson, 1983; Janson, 2000). In the TSP, an individual must find the shortest distance between multiple destinations by visiting

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each location once before returning to the starting point; a seemingly simple task that quickly becomes intractable as the number of sites to be visited increases (Lawler, Lenstra, Rinnooy Kan, & Shmoys, 1985). If an individual does not need to return to the first location, as is the case for animals that are not central place foragers (e.g. many primates), the problem is referred to as an 'optimal Hamiltonian path problem' (also known as a shortest-path problem or an open-TSP) (Janson, 2013). Without prescribed start and end points, path problems may be even more difficult to solve than classical TSPs (MacGregor & Chu, 2011). Human performance is consistently worse in open versus closed versions of TSPs (Chronicle, MacGregor, & Ormerod, 2006; Vickers, Bovet, Lee, & Hughes, 2003) seemingly because an open problem with N targets is equivalent to a closed problem with $N + 1$ targets (Lawler et al., 1985; Vickers et al., 2003). By visiting food sites in order of distance, animals spend the least amount of energy possible on travel costs and acquire the most resources. When food sites are renewing, this may lead to the development of 'trapline foraging', where food patches are repeatedly visited in a predictable nonrandom order (Thomson, Slatkin, & Thomson, 1997).

However, as discussed above, in the natural world the exact value of the resources in each patch may be difficult for a forager to ascertain, and sites will vary in multiple aspects, including the cost of attaining the food (Menzel, 1997; Stephens & Krebs, 1986). In these situations, it may be beneficial for foragers to bypass less profitable food sites so that more rewarding sites can be visited first (Janson, 2007). Thus, solving a TSP-like problem, where every food site needs to be visited on a foraging route, may not always be the best course of action. Indeed, several studies have shown that foraging animals will sometimes bypass nearby resources on the way to more distant sites (primates: Cunningham & Janson, 2007; Garber, 1988, 1989; Janson, 1998; Menzel, 1973; Noser & Byrne, 2006; Sigg & Stolba, 1981; insects: Janzen, 1971; Lihoreau, Chittka, & Raine, 2011; Ohashi, Thomson, & D'Souza, 2007). However, the situations where it is beneficial to bypass one resource for another may not be common. Sites that are further away may need to contain substantially more food or a different type of resource (Garber, 1989; Janson, 1998, 2007; Kralik & Sampson, 2012; Noser & Byrne, 2007; Sigg & Stolba, 1981). Passing by a food reward also requires a degree of self-control (Tobin & Logue, 1994; Tobin, Logue, Chelonis, Ackerman, & May, 1996), and animals are known to be affected by the psychological process of spatial discounting, where the subjective value of a reward decreases as the distance needed to travel to that reward increases (Green, Myerson, Holt, Slevin, & Estle, 2004; Stevens, Rosati, Ross, & Hauser, 2005). Animals that live in groups face the additional constraint of food competition when making foraging decisions. Different behaviours may be optimal when an individual is foraging alone versus when there is the threat of others usurping a food site (corvids: Dally, Emery, & Clayton, 2006; Kalinowski, Gabriel, & Black, 2015; Legg & Clayton, 2014; primates: Hare, Call, Agnetta, & Tomasello, 2000; Hare, Call, & Tomasello, 2001; Hirata & Matsuzawa, 2001; Menzel, 1974; Teichroeb, 2015).

We used a foraging experiment on wild vervet monkeys (*Chlorocebus pygerythrus*) at Lake Nabugabo, Uganda to determine (1) whether they could integrate information about the value and location of five different food sites and (2) whether they would prioritize high-reward sites in small-scale space (the area that can be seen from a single vantage point, following Byrne's (2000) definition of 'large-scale space'). Vervet monkeys form cohesive, semiterrestrial groups that are female philopatric with marked dominance hierarchies for both males and females (Struhsaker, 1967; Whitten, 1983). Vervets are known to quickly and efficiently solve multidestination route problems (Cramer & Gallistel, 1997; Gallistel & Cramer, 1996; Teichroeb, 2015), but it is

unknown how varied resource quantities within a path influences their decision making. The vervets were presented with a multi-destination routing problem with five feeding platforms arranged in a pentagon (5 m apart) where resource quantity was varied. This experimental design was inspired by a study on trapline foraging bees (Lihoreau et al., 2011). In the first phase, all five sites were baited equally, while in subsequent phases one or two sites were made six times more rewarding. Previous foraging experiments at Nabugabo (Teichroeb, 2015; Teichroeb & Chapman, 2014) showed that single vervets in our study group would run ahead to participate in trials alone, before rejoining the group to again go through the experiment. These behaviours allowed the strategies used by solitary individuals to be compared with the behaviours used while foraging socially. We predicted that vervets would be able to integrate information on the location and value of all five food sites. Single foragers were expected to adhere to foraging theory and maximize their net energy gain (Stephens et al., 1986) by obtaining all the rewards present using the shortest possible route (i.e. solve the shortest-path problem), regardless of where the high-reward site was located. Conversely, individuals in competition were predicted to go to a high-reward platform first in an attempt to get more food relative to their competitor(s).

METHODS

Study Site and Subjects

This research was done at Lake Nabugabo, Masaka District, Uganda (0°22'–12°S, 31°54'E), a satellite lake (8.2 × 5 km) to Lake Victoria lying at an elevation of 1136 m. Foraging experiments were conducted on one habituated group of vervet monkeys (*C. pygerythrus*) called M group, which has been followed continuously since June 2011 (Chapman, n.d.). All individuals in M group can be identified by their natural markings. At the time of the study, the group contained 21–22 individuals (2–3 adult males, 7 adult females, 2 subadult males, 1 subadult female, 9 juveniles and infants). An incoming male became the alpha male part-way through the study, although former resident males remained.

Data Collection

Route choice experiments were conducted from June through to early September 2013. M group had a relatively predictable daily range due to their use of only two sleeping sites. Five feeding platforms (wooden tables, 0.75 m high, with a square flat top 0.75 × 0.75 m) were arranged in a pentagon (5 m between platforms) in a clearing between the vervets sleep sites (Fig. 1a). With five sites to be visited, there were 120 possible routes that the monkeys could take through the array (calculated as: 5 factorial (5! = 5 × 4 × 3 × 2 × 1 = 120) because after each platform is selected, the forager has the choice of any other remaining platform). M group had been the subject of two previous foraging experiments in the same location with the same platforms (Teichroeb, 2015; Teichroeb & Chapman, 2014), one of which ended just previous to this experiment. Thus, the vervets were used to receiving food rewards at the site and did not need to be habituated to the platforms. The platform arrangement was changed from a prior experiment (Teichroeb, 2015) to the pentagon set-up on the morning of 24 June 2013 and baited with slices of unpeeled banana. Data collection began that day because the speed with which the vervets found the shortest path through the new platform arrangement was of interest. The group passed by the experimental array relatively predictably (usually twice per day) and trials were carried out on most days, whenever the monkeys ranged past the platforms ($N = 500$ trials, mean number



Figure 1. The feeding platform array (a) as it looked in the field and (b) the numbers assigned to each platform. For phase 1, all platforms were baited equally (100 trials). In phase 2, platform 2 (100 trials) and platform 1 (200 trials) were alternately six times more rewarding. In phase 3, platforms 2 and 4 were simultaneously six times more rewarding (100 trials).

of trials per day: 8.33; range 0–30). The monkeys usually appeared interested in acquiring the rewards at every site, so on most trials ($N = 430/500$ trials) they visited every platform, although bypasses and the skipping of platforms did occur and are analysed below. Since the study group was wild and animals were not captured or restrained in any way, their participation in the experiment was voluntary and we were unable to control which individuals participated in each trial. This led to an unequal number of trials per individual (range for single trials: 0–174, range for competition trials: 0–17; [Table 1](#)). Two adult males (JK and NM) dominated the array on many occasions and showed a high number of solitary trials due to their willingness to range away from the group ([Table 1](#)).

In total, 500 trials were completed for the experiment. Initially in phase 1, 100 baseline trials were carried out where all five platforms were baited with identical rewards (a single banana slice). From phase 1, expected numbers of ‘first visits’ to each platform were calculated for the remaining phases of the

experiment (to allow comparison with the observed numbers of first visits; see Data Analyses). In phase 2, one platform was made six times more rewarding (containing three banana slices) relative to the others (containing half a banana slice) for 300 trials. The location of the high-reward platform in this phase was chosen based on a low number of first visits in phase 1. We did this because we wanted to determine when high-reward platforms were chosen first, and also when low-reward platforms were bypassed to get to them, so we did not want high-reward sites to be in a location where the monkeys habitually approached the platform array. During phase 2, the high-reward site was platform 2 for 100 trials and platform 1 for 200 trials ([Fig. 1b](#)). Finally in phase 3 of the experiment, 100 trials were done where two sites were made six times more rewarding than others (platforms 2 and 4). These were chosen because they were not near neighbours in the platform array ([Fig. 1b](#)); thus, the vervets would have to travel a greater distance and bypass less rewarding platforms to prioritize only these high-reward sites.

Table 1

The distribution of participation during 500 trials among individuals in the study group

ID	Age–sex	Dominance rank ^a	N of 500 trials	N – Phase 1 (100 trials)		N – Phase 2 (300 trials)		N – Phase 3 (100 trials)	
				Solitary	Comp.	Solitary	Comp.	Solitary	Comp.
PY	Adult male	1	19	0	0	2	17	0	0
JK	Adult male	1–2 ^b	135	44	9	48	17	6	11
NM	Adult male	2–3	286	33	1	174	9	65	4
OT	Subadult male	3–4	18	0	4	4	8	0	2
CL	Subadult male	4–5	10	1	1	1	7	0	0
GT	Adult female	1	13	0	2	3	6	0	2
MA	Adult female	2	6	0	0	1	4	0	1
TB	Adult female	3	6	0	0	0	5	0	1
LP	Adult female	4	19	0	4	2	2	7	4
RM	Adult female	5	9	0	1	3	2	3	0
DT	Adult female	6	4	0	0	2	2	0	0
TS	Adult female	7	21	11	1	7	2	0	1
PT	Adult female	8	7	0	0	5	1	0	1
GR	Subadult female	9 ^c	5	1	2	1	0	0	1
LT	Subadult female	10	1	0	0	0	2	0	0
DG	Subadult female	11	4	0	0	2	2	0	0
PG	Subadult female	12	1	0	0	0	0	1	0
?	Juveniles		14	0	0	2	7	0	5

^a Within-sex dominance ranking.

^b Drops in rank occurred for the males due to the immigration of a new alpha male (PY) during the study.

^c Although vervet female hierarchies are matrilineal, the subadult females in our sample (with the exception of LT, whose mother died) were still young and physically small and did not win in dyadic interactions with larger adult females.

During trials, we recorded the identity of vervets that approached the platforms and the sequence of events for each trial, including the order that sites were visited and which individual received the rewards. All data were recorded by a single observer on a data sheet using direct visual inspection. The observer habitually stood on one side of the array after baiting, about 5 m away from the platforms and watching from a perspective between platforms 1 and 5, as in Fig. 1b. For all trials, we were able to record the individuals that visited each platform, the order of visits and who received the rewards. Adults and subadults were always identified, and we only missed identifying juveniles at the platforms during eight trials (2 solitary and 6 competitive trials for 14 instances of participation; Table 1). We also recorded the direction of approach for each individual and whether they bypassed platforms that contained rewards to get to a different platform. We did not rebait platforms to start another trial unless all monkeys were at least 20 m away and the entire sequence could be rebaited before an individual could return. Trials usually consisted of single foragers ($N = 436$), but when multiple individuals reached the platforms and participated ($N = 64$), food competition occurred. Trials were also classified as competitive if other vervets were within 20 m of the platform array and were actively approaching the platforms. Thus, an additional seven trials were considered competitive ($N = 71$) even though one individual moved through the array. We did this because decisions made when other vervets were nearby may have differed from those made when an individual was truly alone. We differentiate between these two types of competitive trials in some analyses below.

Just prior to this foraging experiment (April–June 2013), M group was followed for 33 days (average follow: 7 h/day) by J.A.T. to collect scan-sample data for another study. In addition, concurrent with this experiment, M group was followed for another 59 days by W.D.A. to collect focal animal data. The dominance relationships of the adult and subadult members of M group were assessed during these follows based on agonistic interactions (aggression and/or submission) collected both ad libitum and within focal animal samples. Individuals were assigned a sex-specific ordinal ranking based on dyadic interactions (Table 1), which were the type of interactions that occurred during competitive trials. Hierarchies in females were stable and linear during the experiment. The immigration of a prime-aged adult male (PY) to the alpha position partway through the study caused all the males to be bumped down a rank (Table 1).

Ethical Note

The procedures used in these foraging experiments were approved by the Uganda Wildlife Authority (permit no. UWA/TDO/33/02), the Uganda National Council for Science and Technology (permit no. NS537) and the McGill University Animal Care Committee (Protocol Approval no. 5061). Animals were not captured or restrained in any way and indicated their satiation or unwillingness to participate in experiments by leaving the platform array.

Data Analyses

For phase 1, where all sites were baited equally, we investigated the speed with which individuals found the shortest route through the platform array. Thus, for these analyses we only used trials with single foragers where every platform in the route was visited once ($N = 86$ trials with 4 individuals). First, we used a chi-square test for homogeneity to determine whether each route used to solve the path problem was used equally. We used a linear mixed-effects model to determine the influence of experience on the distance travelled through the route. Subject ID and age–sex class were

included as random factors in the model to account for repeated observations on the same individuals over time.

To determine whether high-reward platforms were visited first by solitary foragers ($N = 340$ trials with 16 individuals) and by those in competition ($N = 60$ trials with 15 individuals) in phases 2 and 3, we used Wilcoxon signed-ranks tests to compare observed frequencies of first visits with expected frequencies. We calculated expected frequencies from the results of phase 1, where the proportion of trials where first-arriving vervets visited each platform first was determined (platform 1: 0.204; platform 2: 0.058; platform 3: 0.107; platform 4: 0.214; platform 5: 0.417). These proportions were then multiplied by the trial sample size for each individual in each phase to arrive at the expected values for that phase. To avoid pseudoreplication within tests, we ran a Wilcoxon test for each phase of the experiment with high-reward sites, and then combined the results with Fisher's log-likelihood method to test the overall hypothesis (Sokal & Rohlf, 1995). These analyses were run twice, once with the whole sample of individuals and once after removing the two males with the majority of trials (JK and NM) to ensure that the results were generalizable. Observations of monkeys bypassing less rewarding platforms to get to high-reward sites were most obvious when only one platform was of high reward. Therefore, in our analyses of bypasses we only used data from phase 2. We compared the proportion of decisions where low-reward sites were bypassed in competitive versus noncompetitive situations using Z ratios. These analyses were also run twice, with and without the two males with high trial number.

In competition trials, we examined the effect of arriving first versus being the dominant animal in an interaction on the number of rewards obtained in phases where high-reward platforms were available. We used t tests for phase 2 but nonparametric Mann–Whitney U and Wilcoxon signed-ranks tests for phase 3 because of smaller sample sizes. We used Z ratios to compare the proportion of trials in phase 3 and in phase 1 that solitary foragers made direct paths between the two high-reward sites. We used Wilcoxon signed-ranks tests in the analysis of phase 3 (1) to examine whether solitary foragers would choose high-reward sites first more often than expected and (2) to examine the differences between the distances travelled for individuals when they moved directly between high-reward sites versus when they did not take this path. Finally, we used a Mann–Whitney U test to determine whether a greater number of platforms were skipped in phase 3 versus phases 1 and 2 and a Spearman correlation to determine whether there was a relationship between skipping sites and the number of trials that an individual participated in that day. Tests were two tailed, with an alpha level of 0.05 set for significance, and run in R v.3.0.2 (R Foundation for Statistical Computing, Vienna, Austria, <http://www.R-project.org/>) and PASW v.22.0 (IBM, Armonk, NY, U.S.A.).

RESULTS

Over all the phases of the experiment, monkeys usually visited every platform at least once on each trial ($N = 430/500$ trials, 86%). Platforms containing rewards were occasionally skipped ($N = 70/500$ trials, 14%), sometimes because of external circumstances such as a disturbance in the area (i.e. a dog or local people nearby), but skipping of low-reward sites became more common in phase 3 ($N = 29/100$ trials, 29%, discussed below). Revisits to platforms by single individuals were rare, only occurring three times in 500 trials (0.006%), and in these instances, the monkey rested on the revisited platform or stood on its hindlegs and looked around. In competitive trials, where more than one monkey got to the platforms, individuals did sometimes visit platforms where the food reward had already been taken by competitors ($N = 23/64$ competitive trials, 35.9%). In competitive trials with high-reward food sites, 11/21

(52.4%) of these visits to already used food sites were to the high-reward site.

In phase 1, where platforms were baited equally, the shortest path was used on 90.8% of trials ($N = 86$) by solitary foragers. Out of 120 possible routes, only 15 were used (Fig. 2), and these were not used with equal frequency (chi-square test: $\chi^2_{14} = 113.25$, $P < 0.0001$). Individuals did not show strong fidelity to a single route (Fig. 2b). All four individuals in this data set found the shortest path: two prime-aged adult males (JK and NM) and one subadult female (GR) found it on their first trial, while one individual (a very old adult female, TS) took four trials to find it. Over all of phase 1, for one male (NM), there was zero variability in route

distance because he found the shortest route on every trial ($N = 34$), despite starting at different points in the pentagon. Overall, there was no relationship between experience and distance travelled (linear mixed-effects model: $F_{1,35} = 1.52$, $N = 86$ trials, $P = 0.097$).

Some Sites Six Times More Rewarding

In combined results from all phases with high-reward sites (phases 2 and 3), solitary foragers travelled to highly rewarding platforms first on 37.4% of trials (127/340), but this was not more often than expected from phase 1 first visits (Fisher's log-

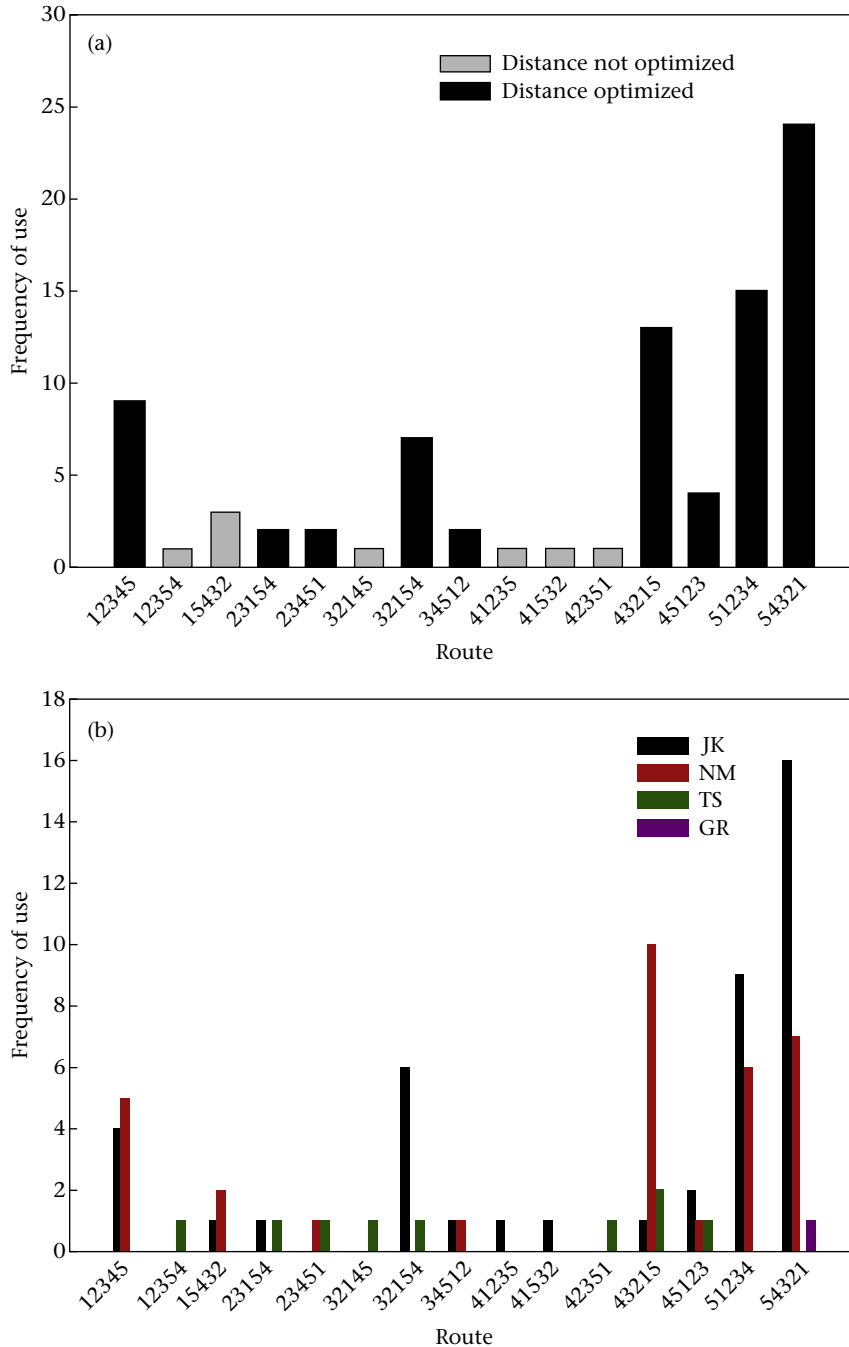


Figure 2. (a) The 15 routes used by solitary vervets out of the 120 possible in phase 1 of the experiment and whether or not they were optimal in terms of distance travelled. (b) Individual fidelity in the use of the 15 routes in phase 1.

likelihood: $\chi^2_6 = 7.81$, $N = 10$ individuals, $P = 0.748$; Fig. 3a). These results persisted when the two males with high trial numbers were removed from the sample ($\chi^2_6 = 8.29$, $N = 8$ individuals, $P = 0.218$). When alone, individuals often began the route at the first platform they came to, regardless of where high-reward sites were located, and the shortest route around the array was taken in 89.2% of trials ($N = 280$ trials with 14 individuals). However, when competitors were present, individuals went to high-reward sites first on 38.2% of trials (21/55), which was more often than expected from phase 1 first visits (Fisher's log-likelihood: $\chi^2_6 = 14.24$, $N = 12$ individuals, $P = 0.027$; Fig. 3b). These results also persisted when the two males with high trial numbers were removed from the data set ($\chi^2_6 = 13.42$, $N = 10$ individuals, $P = 0.037$). Bypassing of low-reward sites to get to highly rewarding platforms was significantly more common when decisions were made during competition ($N = 7/91$ decisions) than when decisions were made while solitary ($N = 6/258$ decisions) (Z ratio: $Z = -2.324$, $P = 0.02$), although sample size did not allow individual analyses to be performed. This difference in bypassing low-reward sites to get to high-reward sites in competitive versus noncompetitive situations did not persist when the two males with large samples were removed (competitive decisions: 5/65; noncompetitive decisions: 5/36; Z ratio: $Z = -0.99$, $P = 0.32$). This indicates that it was individuals other than these males that bypassed low-reward sites. In the noncompetitive situation, the sample of bypassing individuals was made up of all females, while in the competitive situation, males other than JK and NM bypassed the low-reward sites in four of five instances; however, no clear pattern of dominance or arriving first could be determined from such a small sample. While animals usually continued to visit low-reward sites after visiting the more rewarding platform in phase 2 (263/300 trials, 87.6%), they did so less often in phase 3 (71/100 trials, 71%, see below).

Competition and Reward Acquisition

When foraging in competition in phase 2 with one high-reward site ($N = 39$ trials with 17 individuals where all competitors accessed at least one platform), most trials involved two competitors (30/39, 76.9%), several involved three (8/39, 20.5%) and one trial included four competitors (1/39, 2.6%). First-arriving monkeys attained significantly more banana slices (mean = 3.44) than later-arriving competitors (mean = 1.19) (t test: $t_{65} = 8.6$, $N_{\text{first}} = 34$, $N_{\text{later}} = 44$, $P < 0.0001$) because in most instances they got to the high-reward site before the other individual(s) (29/34 trials, 85.3%). Arriving first was more important in acquiring rewards than being the dominant monkey in the interaction; there was no difference in the number of banana slices attained by the dominant monkey

(mean = 2.3) in each dyadic interaction compared to that obtained by the subordinate (mean = 2.63) (paired t test: $t_{29} = -0.55$, $N = 30$, $P = 0.59$). Although dominants could supplant subordinates from platforms, the monkeys generally spread out throughout the array and attempted to retrieve any food rewards that remained.

When foraging in competition in phase 3 with two high-reward sites ($N = 14$ trials with 8 individuals where all competitors accessed at least one platform), most trials (13/14, 92.9%) involved two competitors, and one trial (1/14, 7.1%) involved three competitors. On average, first arrivers attained more banana slices (mean = 4.5) than later-arriving competitors (mean = 2.73) although, now with two high-reward sites, the difference was not significant (Mann–Whitney U test: $U = 68.5$, $N_{\text{first}} = 14$, $N_{\text{later}} = 15$, $P = 0.12$). In dyadic interactions, both competitors managed to obtain one of the high-reward sites in 53.8% (7/13) of trials. Overall, the first-arriving monkey only managed to get both high-reward sites in 42.9% (6/14) of trials. Arriving first still appeared to be more important in acquiring rewards than being the dominant monkey in the interaction; there was no difference in the number of banana slices attained by the dominant monkey (mean = 3.18) in dyadic interactions compared to that obtained by the subordinate (mean = 3.97) (Wilcoxon signed-ranks test: $W = -17$, $N = 13$, $P = 0.56$).

Profitability of the Entire Route

In phase 3, when two platforms were six times more rewarding, results indicated that vervets often took into consideration the location and profitability of all five food sites within the pentagon when choosing their routes. When foraging alone ($N = 82$ trials with 5 individuals), monkeys moved to high-reward platforms first more often than expected (Wilcoxon signed-ranks test: $W = -15$, $N = 5$, $P = 0.05$), which they did not do in phase 2. We investigated whether this could be partially explained by a high-reward site now being located at platform 4. The monkeys' tendency to approach the array from the side of platform 5 may have meant that they had to veer slightly to arrive at platform 4 first. However, just over half (55.6%, 25/45) of the first approaches to high-reward platforms by solitary foragers in this phase were to platform 4, while the rest were to platform 2. Clear swerving from platform 5 to platform 4 was only observed twice in 86 trials, while swerving from platform 1 to platform 2 was also observed once. In addition, 34.1% of solitary trials in phase 3 showed individuals moving directly between the two high-reward food sites (platforms 2 and 4), which were located on opposite sides of the pentagon. In comparison, movements between these two platforms only occurred in 1% of trials in phase 1,

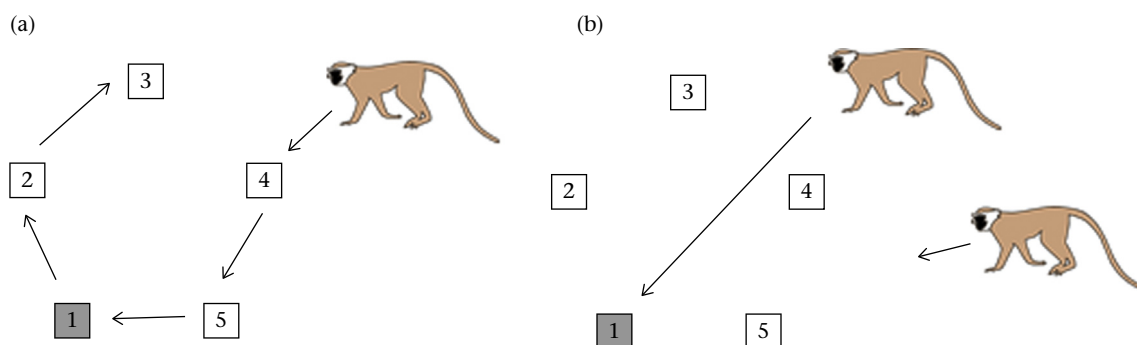


Figure 3. When high-reward platforms were present (shaded platform 1 in this example), (a) lone foragers often started the route at the closest platform and took the shortest path around, regardless of where the high-reward site was located, while (b) foragers in competition were significantly more likely to start the route at a high-reward site, sometimes bypassing low-reward sites to get to a high-reward platform first.

where all sites were equal (Z ratio: $Z = 6.09$, $P < 0.0002$). When monkeys took this direct path between the two high-reward sites and actually finished the entire route, they ended up moving a longer distance overall than when they did not take this direct path (Wilcoxon signed-ranks test: $W = -15$, $N = 5$, $P = 0.05$). However, there was a tendency for individuals to ignore some of the low-reward sites (29% of trials) (Fig. 4a). When multiple trials per day were run by the same forager, more of the platforms were ignored in phase 3 than in phases 1 and 2 combined (Mann–Whitney U test: $U = 24.5$, $N_{\text{phase3}} = 12$, $N_{\text{phases1\&2}} = 15$, $P = 0.0015$; Fig. 4b). To investigate whether this new tendency to ignore some of the low-reward sites was due to foragers being satiated, we examined when

low-reward sites were skipped relative to the number of trials run by each individual that day. There was no correlation between the number of platforms skipped and the number of trials per day in phase 3 (Spearman rank correlation: $r_s = 0.351$, $N = 12$, $P = 0.26$; Fig. 4b).

DISCUSSION

In the first phase of this study, where resources were of equal value, vervet monkeys at Lake Nabugabo very quickly and easily found the shortest path among the five food sites. In fact, three of four individuals did this on their first trial. The speed with which

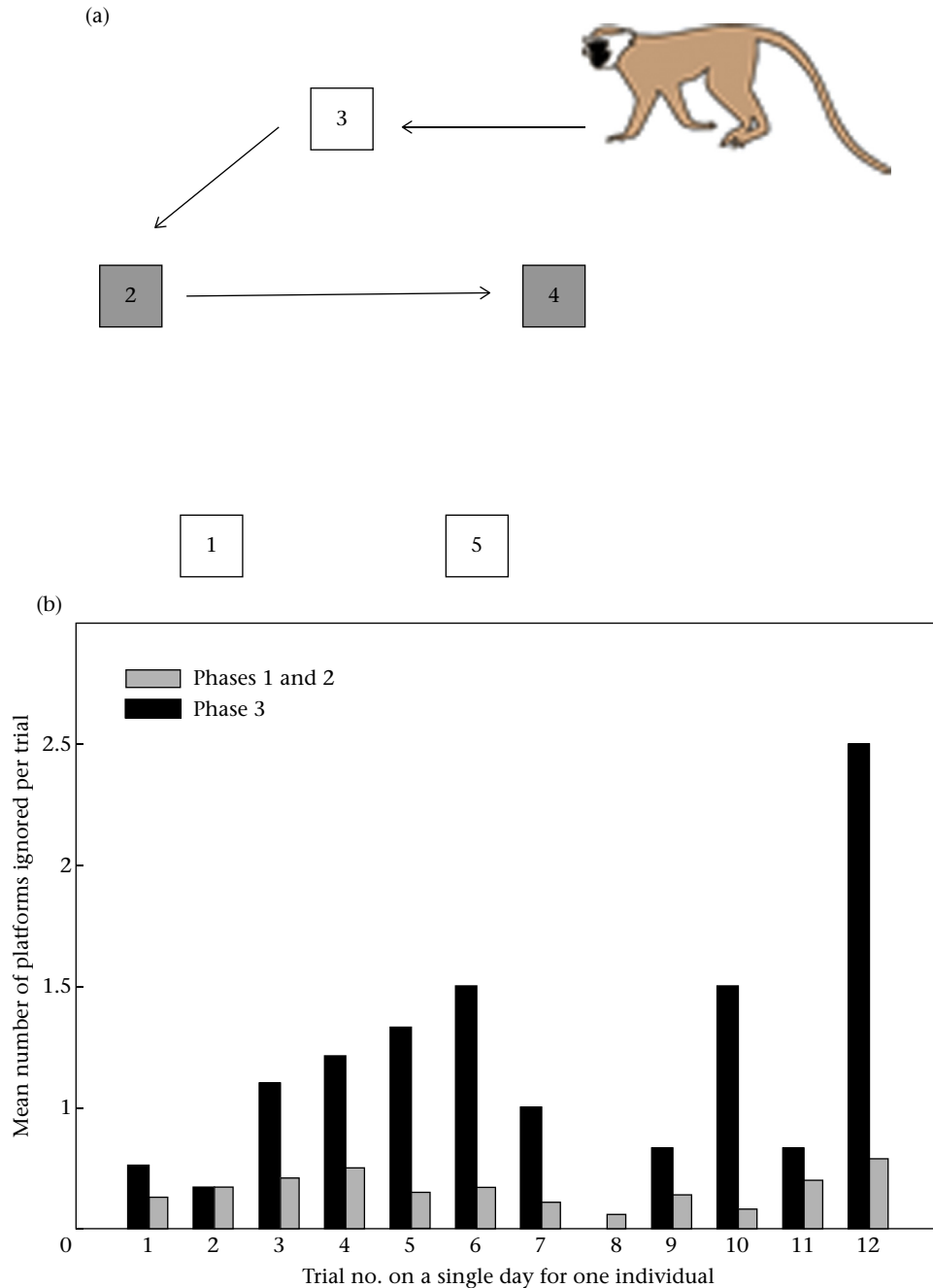


Figure 4. (a) When two sites were six times more rewarding, there was an increasing tendency for lone foragers to move directly between the two high-reward sites and ignore some low-reward platforms. (b) Mean number of platforms containing rewards that were ignored when multiple trials were run in 1 day on the same individuals for phases 1 and 2 versus phase 3.

they solved this path problem, with 120 possible routes, suggests either that this was an easy problem to solve, or that vervets used very simple rules-of-thumb (heuristics) to navigate. Cognitive heuristics are adaptive decision rules that can be quickly applied to arrive at near-optimal solutions to many problems (Gigerenzer & Todd, 1999). These evolved presumably because animals often have to make decisions when they are time constrained and are lacking full information. In a previous path problem examined by Teichroeb (2015) on the same vervet group, the results were consistent with individuals quickly switching among several different heuristics, dependent on the situation and their dominance rank. Vervet paths were often consistent with (1) the nearest-neighbour rule (NNR): go to the closest unused resource that has not been visited before; and (2) the convex hull heuristic: put a mental loop around the outside of the sites to be visited and then sequentially include inside points, beginning with those closest, to determine the order of visits (Golden & Stewart, 1985; Janson, 2000; Teichroeb, 2015). The use of either of these heuristics within the pentagon array used in this study would have led to individuals finding the shortest route, so it is probable that the vervets were applying one (or both) of these rules to solve this path problem quickly and easily. It is also possible that other heuristics that were not examined in Teichroeb (2015) were used by the vervets.

Vervets were only found to prioritize highly rewarding food sites in this experiment when they were in competition with group-mates. These results support our hypotheses. We expected that the vervets would save on travel costs when alone but try to obtain high-reward food when in competition because these choices are most profitable using the economic reasoning of foraging theory (Stephens et al., 2007; Stephens & Krebs, 1986). Indeed, when foragers were alone and knew they were going to be able to acquire all available food resources, they visited food sites in order of proximity, regardless of where the high-reward platform lay. This contrasts with laboratory studies where individual primates showed a strong selection bias to choose larger rewards over smaller ones, even when the experimental protocol dictated that they would receive the smaller reward after pointing to the larger one (reviewed in Vlaming, Uher, & Call, 2006). When presented with the direct perceptual and/or incentive features of larger food arrays, primates often lack the inhibitory control needed not to reach for them (Boysen & Berntson, 1995). However, in most instances in this study, due to the placement of the highly rewarding platform(s), extra travel was required for vervets to go to the high-reward platform first and solitary foragers did not show a selection bias for the larger food reward when this cost had to be paid. Indeed, the knowledge that all of the food rewards would be available to lone foragers seemed to allow them to begin the route at the closest, low-reward platform. Although the monkeys may have leapt onto the first platform they encountered in order to assess the status of the other platforms, they appeared to know when all the platforms were baited based on the presence of an observer and their awareness of where the rest of their group was located. It is also evident that individuals had the inhibitory control needed to bypass low-reward sites (Tobin & Logue, 1994; Tobin et al., 1996), because this is exactly what often occurred when monkeys were in competition at the platforms. When other group-mates were present during the experiment, individuals usually attempted to run straight towards the highly rewarding platform(s), sometimes bypassing low-reward sites, in an effort to acquire the larger resource before their competitors. This led to competition trials starting out as a race towards high-reward sites by competitors and a quick scramble afterwards to see what resources could be acquired. It is notable here that the vervets' behaviour during competitive trials conforms to the use of two

additional heuristics relative to their behaviour during noncompetitive trials. By running first to the high-reward sites, the monkeys may have been using either a take-the-best heuristic (Gigerenzer & Goldstein, 1996, 1999), or a gravity heuristic (Haynes & Fotheringham, 1984). To use the take-the-best heuristic, an individual must infer the value of two or more alternatives by examining cues, stopping their search when the higher-value alternative is discriminated and selecting it (Gigerenzer & Goldstein, 1996). In the gravity heuristic, food sites differ in the quantity of the resources they offer: larger, more productive sites are more attractive to foragers, and thus are visited before nearer, less productive sites (Janson, 2000). Since the value of the rewards on each platform was the same for many trials within each phase of this experiment, the monkeys knew which platform(s) were high value and could easily apply one or both of these decision rules when competitors were present.

Competition is a fundamental aspect of primate social life (Hare, 2001), and this paper echoes the findings of Teichroeb (2015), which showed that vervets make different foraging decisions when they are in a social situation compared to when they are alone. Social environments are complex and unpredictable (Byrne & Whiten, 1988; Humphrey, 1976), and the vervets appeared to make faster movement and site selection decisions when faced with competitors, striving to get the best reward before others. Movements and site selection have also been observed to differ in solitary and social foraging food-caching birds. Western scrub-jays, *Aphelocoma californica*, vary their cache sites depending on whether they have been observed by a conspecific and the identity of that individual (Clayton, Dally, & Emery, 2007; Dally, Emery, & Clayton, 2004; Dally et al., 2006). Additionally, Stellar's jays, *Cyanocitta stelleri*, hide food nearby when alone, travel further to hide it when with their mate, and move the greatest distance before caching food when a neighbouring competitor is present (Kalinowski et al., 2015). For gregarious primates, both solitary and social foraging may not occur, so a comparison between decisions in these situations may not be possible for all species. However, contrived competitive situations are where primates have been shown to display their most impressive cognitive feats in psychological experiments (e.g. rhesus macaques, *Macaca mulatta*: Flombaum & Santos, 2005; Santos, Nissen, & Ferrugia, 2006; chimpanzees, *Pan troglodytes*: Hare et al., 2000; Hare et al., 2001; Hirata & Matsuzawa, 2001; Melis, Call, & Tomasello, 2006; Menzel, 1974), and competition appears to be an important selective pressure for primate cognitive abilities (Hare, 2001; Hare & Tomasello, 2004; Herrmann, Call, Hernández-Lloreda, Hare, & Tomasello, 2007; Herrmann & Tomasello, 2006).

The results of the competitive trials in this study also show the importance of food patch size and distribution in the ability of primates to exclude others from food sites (Elgar, 1986; van Schaik, 1989; Whitten, 1983; Wrangham, 1980). First-arriving vervets were able to get more food than later-arriving competitors when there was only a single high-reward site. However, they were not able to acquire significantly more food when two high-reward sites were available.

The trade-off between travel distance and reward size for foraging primates has also been examined at the group level by Janson (2007) in wild capuchin monkeys (*Cebus apella*). Unlike this experiment, which examined individual decision making in small-scale space, Janson's experiment was explicitly set up to understand spatial movements by a group in large-scale space. However, similar to our results, he found that capuchins appeared to evaluate the profitability of the entire foraging route (three sites) rather than evaluating each goal separately. The capuchins behaved in a way that was consistent with an energy-maximizing rule. After foraging at the first experimental site, the monkeys were given a choice

between two goals, a lower-reward food site located as a detour to a high-reward site, and they only took the detour when the distance/reward trade-off was profitable (Janson, 2007).

This experiment also supports the supposition that vervets can remember and integrate distance and reward information over five feeding platforms. This is not surprising since monkeys, including vervets, have previously been shown to remember the location of at least six feeding sites (*M. mulatta*: Tinkelpaugh, 1932; *C. pygerythrus*: Cramer & Gallistel, 1997; Gallistel & Cramer, 1996). The profitability of the entire route appeared to be considered by the monkeys in this experiment. This was most strongly demonstrated by the third phase of the experiment, where two of the five food sites were six times more rewarding. In this phase, vervet travel patterns changed relative to what they were in the first two phases. Individual foragers began to visit the two high-reward sites first, located on opposite sides of the pentagon, and often travelled directly between the two sites, which lengthened their overall path once they had finished the route. However, even though low-reward platforms contained the exact same amount of food as they had in phase 2, vervets now began to ignore some low-reward platforms, which they had not done in previous trials with high-reward sites. The distance that needed to be travelled through the route never changed, but providing the monkeys with two rich food sites, that were renewing (because we kept baiting them if the monkeys moved off a certain distance), seemed to make it less worthwhile to travel a few extra metres to the get small food rewards. Thus, it appears that in this situation the monkeys were discounting the value of the small rewards because of the extra travel required to get them (i.e. spatial discounting; Stevens et al., 2005). This result brings up new questions about where the threshold of reward profitability to travel distance lies for vervets and whether it varies for different individuals in different situations (e.g. differing levels of hunger). Although there was no clear relationship between the number of trials run by a single vervet in a day and the number of food sites that they ignored, animals could be satiated by foods that they foraged for naturally before participating in the experiment. It is also interesting that the distance required to travel to low-reward sites (5–10 m) was a small proportion of the relatively large travel distances that this group moves every day (mean daily path length = 987.6 m, $N = 36$ days; Teichroeb, n.d.), yet appeared to be significant enough to avoid. This study is one small step towards clarifying how animals make foraging decisions given the large variability in food site characteristics (Menzel, 1997; Stephens, 1981; Stephens et al., 2007). Much more work is needed to parse out the influence of all of the variables that foraging animals encounter every day.

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