



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

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