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RESEARCH ARTICLE

Multi-Step Routes of Capuchin Monkeys in a Laser Pointer Traveling Salesman Task

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Prior studies have claimed that nonhuman primates plan their routes multiple steps in advance. However, a recent reexamination of multi-step route planning in nonhuman primates indicated that there is no evidence for planning more than one step ahead. We tested multi-step route planning in capuchin monkeys using a pointing device to "travel" to distal targets while stationary. This device enabled us to determine whether capuchins distinguish the spatial relationship between goals and themselves and spatial relationships between goals and the laser dot, allocentrically. In Experiment 1, two subjects were presented with identical food items in *Near-Far* (one item nearer to subject) and *Equidistant* (both items equidistant from subject) conditions with a laser dot visible between the items. Subjects moved the laser dot to the items using a joystick. In the *Near-Far* condition, one subject demonstrated a bias for items closest to self but the other subject chose efficiently. In the second experiment, subjects retrieved three food items in similar *Near-Far* and *Equidistant* arrangements. Both subjects preferred food items nearest the laser dot and showed no evidence of multi-step route planning. We conclude that these capuchins do not make choices on the basis of multi-step look ahead strategies. Am. J. Primatol. 76:828–841, 2014.

Key words: spatial cognition; traveling salesman problem; multi-step route; capuchins

INTRODUCTION

Since organisms have limited time and energy and, since time and energy conserved while traveling can be applied to other important activities, moving to distant resources in an energy-efficient manner should ultimately increase an animal's fitness [Pyke et al., 1977]. Animals may demonstrate energy minimizing strategies when traveling to resource sites and the behavioral mechanism of choosing efficient routes is one means of minimizing the costs of travel. Nonhuman primates in natural environments have demonstrated ranging patterns that appear to reduce foraging distance, such as traplining behavior [Garber, 1988], linear travel segments between foraging sites [Janson, 1998; Normand & Boesch, 2009; Noser & Byrne, 2007; Presotto & Izar, 2010], and a preference for the nearest feeding site [Janson, 1998].

The traveling salesman problem (TSP) is a theoretical mathematical construct which is relevant to the ecological challenge of minimizing travel distance. This problem concerns how one might choose an optimal path through a series of destinations and then return to the origin, much like a traveling salesman might choose a path through a series of cities before returning home at the end of the day. The TSP is a difficult problem to solve and its difficulty increases exponentially as the number of destinations to be visited increases. A similar problem, the one-way TSP, refers to the efficient choice of a path through a series of destinations, without returning to the origin. The one-way version of the TSP is similar to the foraging patterns of many nonhuman primates, and the one-way version TSP and the round-trip TSP (collectively referred to hence as the TSP) are equally difficult to solve. One known strategy that reduces total travel distance for the TSP is the nearest neighbor model [MacGregor et al., 2000] or the one-step look ahead method [Anderson, 1983]. The single heuristic of this method assumes that the traveler always chooses the closest resource to itself and the solutions from this model rank high in terms of efficiency. However, the nearest neighbor

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model does not take into account the global layout of resources and thus tends to produce results that are less efficient than human performance in laboratory TSP tasks [Ormerod & Chronicle, 1999].

In tests of the TSP, nonhuman animals have demonstrated the use of strategies to minimize or reduce travel distances, although their paths have been longer than the optimal least distance path and also longer than human performance. Rats (*Rattus norvegicus*; Long-Evans) performing a modified version of the TSP were shown to use a strategy that resembled the nearest neighbor model [Bureš et al., 1992]. Gibson et al. [2007] studied the performance of humans and pigeons (*Columba livia*) in finding efficient routes between a series of points. Traveling Salesman tasks of three, four, or five points were presented in a single horizontal line on a computer screen. Humans were required to click all points using a mouse while pigeons responded by pecking the screen. This TSP was considered one-way, as subjects were not required to return to the start point in order to complete the trial. Human participants were more efficient than a Monte Carlo model, or a random solution sequence. Humans were also more efficient than the nearest neighbor model, yet less efficient than the optimal route. Pigeons were more efficient than the Monte Carlo model, yet less efficient than the nearest neighbor model. However, when required to choose routes that were in the top 66% of all possible solutions, the pigeons learned to perform more efficiently and their routes became more comparable to the nearest neighbor model. This result indicates that when the costs of inefficiency are high, pigeons can learn to choose more efficient routes. However, in both these previous experiments, the nonhuman animals achieved maximal efficiency by approximating the nearest neighbor model, a model that fails to generate the minimum distance path considering the global distribution of points.

In real-world foraging situations, using a strategy more sophisticated than the one-step look ahead method may be unnecessary for foraging animals. Anderson [1983] demonstrated that the one-step look ahead strategy would perform nearly as well as a few-step look ahead method if not all resources are visited by an animal, and surprisingly, better than a few-step look ahead strategy if all resources are visited. Grove [2013] has also demonstrated that when resources are dense and foragers are highly perceptive of those resources, spatial memory does little to increase the likelihood of resource retrieval. That is, while searching, foragers choose or find the resource nearest to their current location, recreating the one-step look ahead strategy. In effect, the cost of evolving a cognitive strategy that solves the TSP (i.e., finds the minimum distance route between a series of points) would be immense, while the payoff of having such a strategy is likely to be low given moderate to high resource densities.

Despite these findings, several studies have reported that monkeys and apes use multi-step route minimization strategies in TSP tasks, traveling from one simulated foraging patch to another to retrieve remembered food resources [Cramer & Gallistel, 1997; MacDonald & Wilkie, 1990; Menzel, 1973]. In one notable example of route minimization, vervet monkeys (*Cercopithecus aethiops*) minimized their travel distance while retrieving food from baited opaque containers using a strategy that the authors claimed was more sophisticated than the nearest neighbor technique seen in both rats and pigeons [Cramer & Gallistel, 1997]. The authors also indicated that the monkeys demonstrated evidence of planning at least three choices in the future. In this experiment, the monkeys visited baited containers configured as the four vertices of a diamond. In some trials, the monkeys revisited the baited start location using a diamond-shaped route through all four vertices. In other trials, the monkeys did not revisit the start location, using a zigzag route through the three baited locations that they visited. The authors indicated that these route choices maximized the rate of reward and required the subjects to look ahead at least two choices into the future.

In a recent reexamination of Cramer and Gallistel's results [1997] as well as the results of two other experiments indicating multi-step route planning in nonhuman primates [MacDonald & Wilkie, 1990; Menzel, 1973], Janson [2013] finds no evidence for multi-step route planning in nonhuman primates' solutions to the TSP. In the case of the vervet monkeys, Janson states that the monkeys were not preferentially revisiting the start location on the basis of whether a reward existed in that location. Instead, the vervets that did not retrieve a reward in the start location were performing sub-optimally for the four-vertex problem with which they were presented. Given this interpretation of Cramer and Gallistel's results, Janson compared the routes chosen by the vervets, as well as routes chosen by chimpanzees (*Pan troglodytes*) [Menzel, 1973] and routes of yellow-nosed monkeys (*Cercopithecus ascanius whitesidei*) [MacDonald & Wilkie, 1990] to various models of route choice. His results indicate that the subjects in these experiments chose routes that were longer on average than the solutions of the nearest neighbor heuristic. These results call into question the ability of nonhuman primates to execute efficiently multi-step routes that minimize travel distance, instead conforming to the performance of other nonhuman animals on the TSP.

Given the challenges of knowing *a priori* all potentially exploitable resource sites in a natural setting, it is unclear from field studies whether nonhuman primates prefer distance minimizing paths between multiple resource sites [Janson & Byrne, 2007]. It is clear that capuchin monkeys in natural settings demonstrate discounting of rewards when delays are incorporated in their retrieval, such that more distant rewards are less valued and proximal rewards are preferred [Janson, 1998, 2000]. This continues to be the case even when the energetic costs of locomotion between reward sites cease to exist. In a previous experiment, capuchin monkeys used a laser pointer to indicate desired food items of different sizes, types and distances from self [Menzel et al., 2008; Stone, 2008; Stone et al., 2008]. The monkeys remained stationary and, after making their choice, a human researcher delivered their chosen food item. When the items were of the same type and size, capuchins significantly preferred proximal food items to foods placed at a greater distance from themselves. Together with results from wild monkeys demonstrating discounting of resource value based on distance of the resource from the group may indicate the use of a strategy resembling the nearest neighbor model, although this has not previously been tested. Also of interest, Fragaszy et al. [2009] demonstrated that capuchins performing a computerized maze task were less likely to take a route that eventually led to the goal, but initially led away from that goal than they were to take a route leading directly to the goal. Taken in conjunction with capuchins' preference for resource proximity, this may indicate a preference for reward immediacy or may demonstrate an inability to plan an efficient path in the two-dimensional space of the computerized maze.

Also relevant to studies of spatial decision making and efficiency is the question of how these animals specify the locations of objects in their environment, or their spatial frame of reference. Specifying the location of an object in space using information about the location of other objects is considered use of an allocentric frame of reference, while specifying that object's location in relation to oneself is egocentric. The use of an allocentric frame of reference by capuchin monkeys has had mixed results in previous studies. Potì [2000] demonstrated that capuchin monkeys (*Cebus apella*) performing a simulated foraging experiment involving rotation of a feeding platform and concealed food items showed a bias for encoding the location of the hidden food item using and egocentric frame of reference; their use of the allocentric frame was relatively weak. This is in contrast with results from field observations which appear to indicate that capuchins (*Cebus nigritus*) use an allocentric frame of reference in the wild [Presotto & Izar, 2010]. Failure to use an allocentric frame of reference when planning a multi-step route may result in inefficient travel sequences, as the spatial relationships between the subject and other objects are prioritized over the spatial relationships between the objects themselves.

Field studies and laboratory experiments have come to different conclusions regarding the multi-step route planning and spatial reference frames of nonhuman primates. The results of Janson's [2013] analysis are in opposition to the interpretations of the authors whose results he reexamined, while also contradicting many primatologists' interpretations of the ranging patterns of nonhuman primates traveling in natural environments. Our study presents the results of two experiments designed to test alternative predictions regarding path choice and spatial reference frame in tufted capuchin monkeys (*Sapajus apella* spp.). We investigated whether capuchin monkeys plan a multi-step route through two and three node, one-way TSPs using a nearest neighbor heuristic or some more complex look-ahead strategy. Since we were interested in efficiency of path choices and spatial frame of reference without the added challenge of spatial memory, subjects in this experiment were allowed visual access to all the goal locations and associated foods throughout each trial. If capuchin monkeys use cognitively complex look-ahead strategies, we expected to see a preference for goal locations in an order that indicates a multi-step look-ahead strategy. If, as Janson [2013] has suggested, capuchins do not execute multi-step route minimization, we expected performance that conforms to the nearest neighbor model. In general, simulated foraging experiments appropriate for this type of test occur in either (A) a three-dimensional testing space with real goal sites or (B) in a virtual space such as a computerized maze task where goal sites and spatial relations between them and the subject are simulated. In real-world foraging situations, initial route planning and subsequent route execution phases occur from distinct visual perspectives on the part of the foraging animal. The change in visual perspective as the array of potential goal sites is progressively exploited and its effect on path choice has not been previously studied. In the current study, the monkeys used a laser pointer apparatus [Menzel et al., 2008; Stone, 2008; Stone et al., 2008] to indicate preferred objects at a distance in real three-dimensional space. The nature of this design means that subjects manipulating the joystick are stationary while the laser dot moves through the environment. Thus, the perspective of the subject is not updated as each subsequent choice is made, the directional effect of any potential nearest neighbor preferences or egocentric frame of reference is constant and unchanging throughout each trial, and nearest neighbor food items are differentiable from foods nearest to the laser dot throughout the course of the experiment. The use of the laser pointer apparatus is useful in keeping the design constant and the subject's perspective stationary throughout the experiment and the trials, making subjects' choices simpler to interpret. Also, the removal of spatial memory from the task's cognitive requirements makes it simpler. We acknowledge, however, that the laser pointer paradigm may have been perceived by the subjects as more foreign, and thus more difficult than the spatial decision making which occurs in real world foraging situations.

Experiment 1 tests the spatial decision making of capuchin monkeys on the basis of the distance between a laser dot and two food items. The laser pointer apparatus keeps the design and subjects' perspective stationary throughout the spatial choice process. The two arrangements of Experiment 1 allow us to test the subjects' ability to dissociate the distance between the laser dot and self from the distance between the laser dot and the foods. This requires an allocentric frame of reference, a prerequisite to spatial planning [Potì, 2000]. Experiment 2 builds upon the results of Experiment 1, testing whether capuchin monkeys look more than one step in the future when making spatial decisions. We continue to test the influence of distance from self on these multi-step spatial decisions in Experiment 2. Multi-step route minimization in both experiments of this study will require the subjects to make their choices using an allocentric frame of reference.

EXPERIMENT 1

Method

Subjects

Two adult male capuchins (Leo and Xenon) (*Sapajus apella* spp.), ages 18 and 25, from the Primate Cognition and Behavior Laboratory at the University of Georgia participated in this experiment. These individuals were pair housed, but their cage mates did not participate in this experiment. The subjects had been previously tested in various behavioral experiments, including computerized maze tasks [e.g., Fragaszy et al., 2009] and laser-pointer tasks [Stone, 2008; Stone et al., 2008]. Subjects had no experience with this design prior to the data presented in this study. However, during Stone's [2008] work, these same subjects gained experience retrieving food items of higher and lower value at distances nearer to and farther from the subject himself. All monkeys were fed a consistent diet of monkey chow and fruit twice a day throughout the experiment, and water was available *ad libitum*. This study complied with protocols approved by the Institutional Animal Care and Use Committee of the University of Georgia and complied with all laws regulating animal care and use in the United States. The study also adhered to the principles of the American Society of Primatologists for the ethical treatment of primates.

Apparatus

The subjects were transported from their home cages to a transparent acrylic testing cage (64 cm × 47 cm × 78 cm cage, sitting 84 cm above the floor) located in a hallway (2.2 m × 12.2 m) of the Primate Cognition Laboratory. Subjects sat on a metal perch (30 cm above the cage floor) while working, and extended their arm through an opening in one side of the testing cage to contact a joystick apparatus (Fig. 1). The metal joystick controlled a projected laser dot by directing a motorized pan-tilt head (Bescor, MP-101b) attached to a laser pointer (Fig. 2). The red laser dot projected onto the gray cement floor of the hallway. The motorized pan-tilt head stood on a tripod 108 cm above the floor on the right side of the testing cage.

Fig. 1. Subject manipulating joystick-controlled laser apparatus.

Procedure

Two food items of equal size and type (e.g., peanut halves, multigrain cereal, fresh fruit) were placed on the floor of the hallway in front of the testing cage.

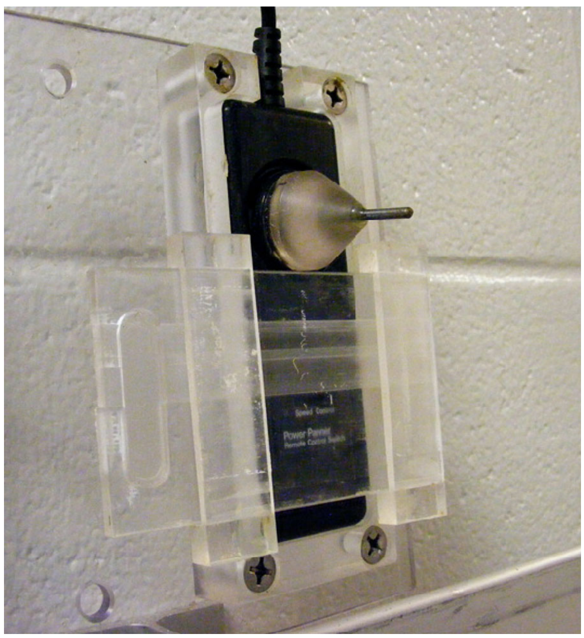

Fig. 2. Motorized pan-tilt head and joystick apparatus.

The food type was varied throughout testing to increase motivation, but in any given trial, the two foods presented simultaneously were identical. The laser dot was placed between the two food items, such that the ratio between the distance from the dot to food A and the distance from the dot to food B was 1:1, 1:2, 1:3, or 1:4. The metric distances of these ratios are provided in Table I, and the relationship between time and distance traveled was equivalent (i.e., the distance ratios were also representative of the ratios of time between the resources). For the experimental layouts described in Experiment 1 and Experiment 2, the velocity of the laser pointer movement as controlled by the pan-tilt apparatus was approximately 50 cm/s. However, the manipulation of the apparatus demanded a great deal of attention on the part of the subjects, and the path taken between two food items usually deviated from a straight line between the two points. Table II shows the cumulative total distance the laser dot needed to travel for each ratio in Experiment 1 and the minimum time required for the laser dot to travel this distance, considering choice of the item nearest the laser dot first or last. Actual trials typically consisted of between 30 sec and 2 min of contact time for the monkeys directly manipulating the joystick. Delivery times (the time required for the experimenter to bend down, pick up the food item and step up to the opening in the front of the testing cage), by contrast, were less than three seconds for any given trial. For this reason, the capuchins' spatial decisions are compared in terms of the total minimum distances the laser dot was required to travel in order to contact the food items in a given order. The food delivery paths were not included in the comparison as the delay to food delivery varied negligibly with the distance between where the laser dot was left and the subject itself.

TABLE I. Distance Ratios Between Food and Laser Dot in Experiment 1

Ratio	Distance
1:1	0.75 m: 0.75 m
1:2	0.5 m: 1 m
1:3	0.375 m: 1.125 m
1:4	0.3 m: 1.2 m

Note: The distances between the laser dot and food items at each distance ratio experimental condition.

TABLE II. Distance and Minimum Possible Time of Total Routes in Experiment 1

Ratio	Total distance (nearest item first) (cm)	Total distance (nearest item last) (cm)	Minimum time (nearest item first) (sec)	Minimum time (nearest item last) (sec)
1:1	225	225	4.5	4.5
1:2	200	250	4	5
1:3	187.5	262.5	3.75	5.25
1:4	180	270	3.6	5.4

Note: The cumulative total distance for each ratio in Experiment 1 and the minimum time required for the laser dot to travel this distance, considering choice of the item nearest the laser dot first or last.

There were two arrangements of resources, resulting in two conditions for Experiment 1, *Near-Far* and *Equidistant* (Fig. 3). The distance ratios between the resources and the laser dot were the same in both *Near-Far* and *Equidistant* conditions. In the *Equidistant* condition, the two resources were placed at equal distances (2.7 m) from the subject. In the *Near-Far* condition, the two resources differed in their distance from the subject, at 0.5 and 2.3 m from the opening in the front of the testing cage. Figure 3 illustrates the starting location of the laser dot for each of the ratios in the *Near-Far* and *Equidistant* conditions.

The design of this experiment simulated real-world foraging situations in which an animal must choose a path by which to retrieve two resources separated by some distance. Unlike real-world foraging, the animal was not required to locomote to retrieve the resources in this experiment, and therefore its perspective was not changed through the course of its spatial decisions. At the beginning of each trial, the animal made a choice between two food items, a choice which it could make by (A) choosing randomly, (B) preferentially traveling in one direction over another, or (C) preferentially choosing to retrieve first the resource that would result in the shortest path between the two points. The *Near-Far* trials placed in opposition an animal's spatial decisions based on proximity of a resource to itself with spatial decisions based on the efficiency of a route between both resources. Unlike some real-world foraging situations, the animal was not required to remember the locations of the resources while making its spatial decisions.

A trial began with both food items placed on the floor. A human experimenter stood to the right of the subject, removing and replacing the joystick apparatus from the front of the acrylic testing cage. A second human experimenter stood by the initial location of the laser dot. The subject manipulated the joystick controlling the laser dot to contact the food. When the laser dot came within approximately 2.5 cm of the food, the subject was verbally praised and the joystick was withdrawn. Following each choice, the chosen food was delivered to the subject. Once the subject had consumed the food, the joystick was returned to him. The subject completed the trial by retrieving the second food item in the same manner as the first. Trials in which the subject did not retrieve the second food item were discarded. While the experimental setup involved interruptions between each choice of

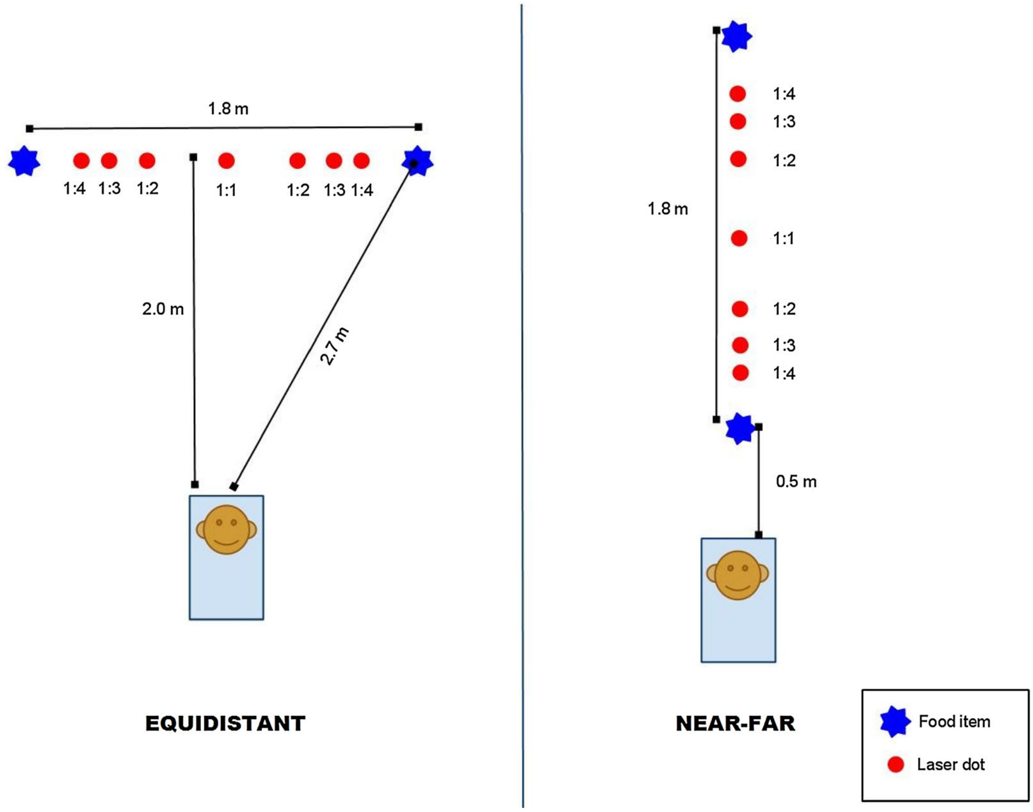

Fig. 3. Experiment 1: Equidistant and Near-Far conditions. Red dots depict starting points for the laser dot at each distance ratio.

food item, we believe that these choices were not considered as distinct problems by the subjects. The subjects were motivated to continue testing until all food items had been retrieved from the testing space during each trial and were frustrated by any delays in access to the joystick as long as there was food to be retrieved. We believe that this behavior is an indicator of continued attention to the remaining food items in the experimental space even while retrieving one food item at a time.

The distance traveled by the laser dot was the dependent variable of this experiment. It was important that the manner in which the food was delivered to the subject did not confound the distance traveled by the cursor. Therefore, the distance traveled by the experimenter in delivering the food was designed to replicate the distances between the food choices made by the subjects. An experimenter stood directly behind (in the *Equidistant* condition) or beside (in the *Near-Far* condition) the laser dot as the subjects made their food choice. After the subject's choice, the experimenter walked in a straight line path from her start location to the location of the first food item, retrieved the food item, and then took a straight-line path to deliver the food to the subject (Fig. 4). These delivery routes were not marked on the floor of the array to prevent the subjects from directing the cursor to these marks. The experimenter then stood directly behind or beside the laser dot again, in the location where the subjects paused the cursor after their first choice. Occasionally, the subjects continued to manipulate the joystick after their first choice, and before the joystick was removed from their reach. These manipulations of the joystick did not appear to be visually guided, as the subjects were visually tracking the experimenter walking toward the food item, and not the laser dot. In the *Equidistant* condition, this often resulted in the laser dot being left on the wall of the hallway. In these trials, the experimenter placed the laser dot back upon the floor of the experimental space before the joystick was returned to the subject.

A single least distance path existed for each distance ratio and condition. For the subject, the only disadvantage to an inefficient route was the time delay in receiving the food reward. Subjects were apparently sensitive to the time required to complete the task, refusing to participate if the laser dot moved more slowly than usual (due to battery condition). Thus, while there was no upper limit on the duration of the trials, we believe subjects were sensitive to minimizing time to resource retrieval. In this experiment, the most efficient path was always to choose the food item closest to the laser dot first. In an *Equidistant 1(left):3(right)* trial (i.e., 1: 3 distance ratio in the distance between food item A and the

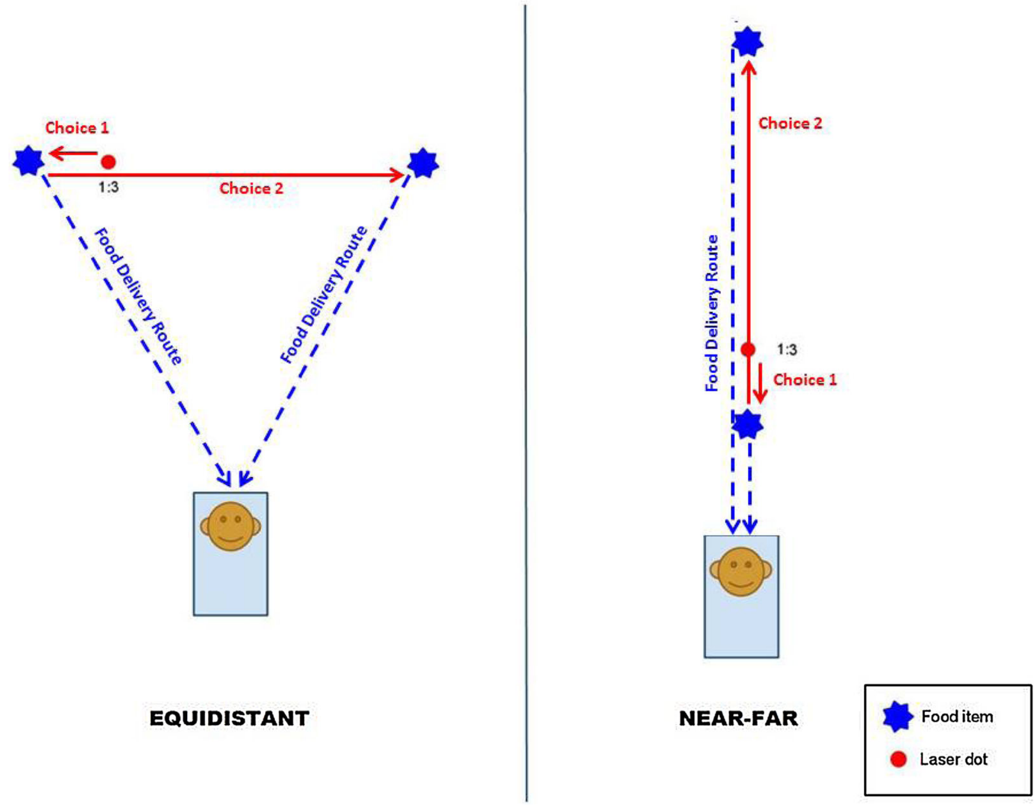

Fig. 4. Least distance paths and food delivery routes for Equidistant and Near-Far 1:3 distance ratio in Experiment 1.

laser dot, and food item B and the laser dot, with the closest food on the left), the least distance path was to direct the laser dot 37.5 cm to the left in the first choice, followed by 1.5 m to the right in the second choice (Fig. 4). An inefficient first choice (e.g., directing the laser dot to the right in the previous example) caused an increase in total trip length proportionate to the distance ratio of the trial. For example, a first choice of the food item on the right in the *1(left):3(right)* trials would mean an increase in total trip length of 0.75 m. In *Near-Far* trials, the least distance path required the subject to direct the laser dot both toward and away from himself in successive choices, and sometimes away from himself first. For example, the least distance path for a *Near-Far 1(far):3(near)* trial (i.e., 1:3 distance ratio, closest food to laser dot is the food farther from the subject) required the subject to direct the laser dot 37.5 cm away from himself, followed by 1.5 m toward himself. This response was expected to be more challenging for the capuchins than first choosing the food item closer to self.

Analysis

A binomial test was conducted to analyze the frequencies of the subjects' preferences for food items proximal to the laser dot and proximal to the subject himself. For distance ratios 1:2, 1:3, and 1:4, a one-tailed binomial test was performed to determine if the frequency of distance minimizing choice was significantly greater than the null hypothesis of 0.5. For the 1:1 distance ratio, a two-tailed binomial test was performed to test whether subjects significantly preferred either of the two equidistant food items.

Results

In the *Equidistant* condition, Leo consistently chose the food item closer to the laser dot for distance ratios greater than and equal to 1:3 (*1(left):3(right)*, $P = 2 \times 10^{-5}$; *1(right):3(left)*, $P = 0.02$; *1(left):4(right)*, $P = 0.006$; *1(right):4(left)*, $P = 2 \times 10^{-4}$), and had an insignificant preference for the food item closer to the laser dot in the 1:2 distance ratio (*1(left):2(right)* and *1(right):2(left)*, $P = 0.06$) (Table III). In the 1:1 distance ratio, although neither food item was closer to the laser dot, Leo showed a significant preference for the left-most food item ($P = 0.003$) (Table IV). Xenon significantly preferred the food items closest to the laser dot in all ratios of the *Equidistant* condition greater than and equal to 1:2 (*1(left):2(right)*, $P = 0.02$; *1(right):2(left)*, $P = 0.006$; *1(left):3(right)*, $P = 0.006$; *1(right):3(left)*, $P = 9.5 \times 10^{-7}$; *1(left):4(right)*, $P = 2 \times 10^{-4}$; *1(right):4(left)*, $P = 2 \times 10^{-5}$) (Table III). In the 1:1 ratio, Xenon did not show any preference for the left or right food item ($P = 0.3$) (Table IV).

TABLE III. Frequency of Choosing the Closer Food Item across Trial Types for 1:2, 1:3, and 1:4 Distance Ratios in Experiment 1

		1:2		1:3		1:4	
Condition	Subject	Left	Right	Left	Right	Left	Right
Equidistant	Leo	14	14	19^{**}	15^{*}	16^{*}	18^{**}
	Xenon	15^{*}	16^{*}	16^{*}	20^{**}	18^{**}	19^{**}
		Near	Far	Near	Far	Near	Far
Near-Far	Leo	20^{**}	13	20^{**}	10	20^{**}	9
	Xenon	18^{**}	13	20^{**}	18^{**}	20^{**}	20^{**}

Note: Leo preferred the food item closer to the laser dot for distance ratios greater than and equal to 1:3 in the Equidistant condition. Xenon significantly preferred the food items closest to the laser dot in all distance ratios of the equidistant condition greater than and equal to 1:2. In the Near-Far condition, both subjects significantly preferred the least distance route in every distance ratio when the food closest to the laser was also closest to himself. All trial types $n = 20$.
$^{*}P < 0.05$.
$^{**}P < 0.001$.

In the *Near-Far* condition, Leo significantly preferred the least distance route in every distance ratio when the food closest to the laser was also closest to himself. Leo chose the least distance route in all 20 trials of the 1:2, 1:3, and 1:4 distance ratios ($P = 9.5 \times 10^{-7}$) (Table III). In the 1:1 ratio, neither first food choice yielded a more efficient route, but Leo showed a significant preference for the food item closer to himself ($P = 0.01182$) (Table IV). Xenon chose the food item closest to the laser dot in every distance ratio of the *Near-Far* condition when that food item was also closest to himself (*1(near):2(far)*, $P = 2 \times 10^{-4}$; *1(near):3(far)*, $P = 9.5 \times 10^{-7}$; *1(near):4 (far)*, $P = 9.5 \times 10^{-7}$) (Table III). Xenon also chose the item closes to the laser dot first in the *1(far):3(near)* and *1(far):4(near)* distance ratios when this item was further from himself ($P = 9.5 \times 10^{-7}$). Xenon did not, however, first choose the food item nearest the laser dot in the *1(far):2(near)* condition when the laser dot was closer to the far food item (*1(far):2(near)*, $P = 0.1$) (Table III). In the 1:1 *Near-Far* condition, Xenon did not have a significant preference for either food item, although the front food item was closer to the subject himself ($P = 0.1$) (Table IV).

TABLE IV. Frequency of Food Item Choice for the 1:1 Distance Ratio in Experiment 1

		1:1
Condition	Subject	Left
Equidistant	Leo	17^{*}
	Xenon	7
		1:1
Condition	Subject	Near
Near-Far	Leo	16^{*}
	Xenon	14

Note: In the 1:1 distance ratio, Xenon did not have a significant preference for food item in the Near-Far or Equidistant conditions. Leo showed a significant preference for the left and near food items. All trial types $n = 20$.
$^{*}P < 0.05$

Discussion

In real-world foraging situations, route planning and execution occur from distinct visual perspectives on the part of the foraging animal. Experiment 1 tested whether monkeys make efficient route choices independent of the location of the desired resources in relation to their current position. The two subjects tested varied in their ability to disambiguate the distance between their goal and themselves and the distance between their goal and the laser dot. These results indicate that some individual capuchins disassociate their current position from a location outside of themselves when making spatial decisions, a skill that may be necessary for multi-step route planning.

In the *Equidistant* condition, when there was a large difference between choosing the nearest food item first versus last (i.e., 1:3 and 1:4 distance ratios), both subjects chose the food item closest to the laser dot significantly more often. When these choices were more similar (i.e., 1:2 distance ratio) in the *Equidistant* condition, Leo showed an insignificant preference (70% of trials) for the item closer to the laser dot, while Xenon still significantly preferred the most efficient route. These results indicate that at least one capuchin monkey used the allocentric frame of reference in his choices of food item, contrasting with the findings of Potì [2000] which showed weak use of the allocentric frame of reference in capuchin monkeys.

In the *Near-Far* condition, Leo did not prefer the food item closest to the laser dot first in any ratios when this food was farther from himself. However, in these trials, Leo also did not significantly prefer the food item closest to himself. These results may indicate a bias for items closest to self, which interfered with the choice of an efficient route.

Xenon chose the shorter cumulative path significantly more often than the longer path in almost every ratio across both the *Equidistant* and *Near-Far* conditions, demonstrating a preference for the food item nearest to the laser dot. The only condition in which Xenon did not significantly prefer the food item closest to the laser dot first was the 1:2 *Near-Far* condition in which the laser dot was closer to the food item that was farther from the subject himself. This indicates a bias for items closest to self, given that Xenon chose the most efficient route in the 1:2 distance ratio in the *Equidistant* condition. At larger distance ratios, placement of the food items nearer or farther from himself did not affect Xenon's choice of route.

When the laser dot was placed at a 1:1 distance ratio between the two food items, there was no least-distance path, since choosing either of the two food items would have resulted in the same total path length. Therefore, we expected that if a bias for objects closer to self influenced their choices, subjects would demonstrate a preference for the item closest to self in the *Near-Far* condition, but show no preference for either direction in the *Equidistant* condition. Xenon demonstrated no bias for any food location, left/right or near/far, when the two food items were equidistant from the laser pointer. In the 1:1 distance ratio, Leo preferred the food item to his left in the *Equidistant* condition, and the food item closest to himself in the *Near-Far* condition. The preference for the near food item was predicted by a bias for items closest to self, and indeed, Leo did not choose the most efficient route in any of the trials in the *Near-Far* condition, a result we attribute to his bias for items closest to self. The left side bias demonstrated by Leo in the *Equidistant* condition was not expected, however, and was only seen in this 1:1 distance ratio. When both choices were equal, Leo demonstrated a prepotent motor response, first directing the laser pointer to the left food item, then to the right.

The results of Experiment 1 partially conform to the observation by Fragaszy et al. [2009] that capuchins performing a computerized maze task were less likely to take a route that eventually led to the goal, but initially led away from that goal than a route leading directly to the goal. In this experiment, the necessity of initially moving the laser pointer away from himself interfered with Leo's choice of a route that would eventually efficiently retrieve all the food items of the array. Xenon did not share this bias, nor a side bias, as he chose efficient routes in both experimental conditions.

EXPERIMENT 2

This experiment tested the influence of items nearer to the subject in selecting an efficient route with three, rather than two goal locations, and concurrently, whether capuchin monkeys using a laser pointer to indicate desired food items would plan an efficient route at least two goal sites in the future. The choice of either of the two food items nearest to the laser dot would yield an equal distance to the first and second choices. However, choosing the most efficient path through all three food items required the subjects to look ahead to the third food choice.

In addition to retrieving more food items, the subjects had to complete the entire route before receiving a food reward. In this way, the experiment differed from experiment 1 in which rewards followed each choice. However, this design allowed the movement of the experimenter delivering the food items to duplicate the movement of the laser pointer, and avoided the problem of the experimenter's path differing from the path chosen by the subjects.

Method

Subjects and apparatus

The subjects and apparatus of Experiment 2 were the same as Experiment 1. The trials took place in the same test space described in Experiment 1. Adherence to institutional, local, and societal legal requirements was the same as described in Experiment 1.

Procedure

Following completion of Experiment 1, both subjects completed 24 training trials in which they were required to contact first two, then three food items with the laser dot before these items were given to the subject. These training trials increased in distance from 60 cm between food items until reaching to the final testing distance. From the very first training trial, subjects contacted all available food items, despite the delay in reward.

In the testing phase of Experiment 2, three food items of equal size and type were placed in a straight line on the floor in the hallway in front of the testing cage (Fig. 5). The laser dot was placed between two of the three food items, 76 cm from two and further (1.5 m) from the third food item. There were two arrangements of the food items, resulting in two conditions for Experiment 2 similar to the *Equidistant/Near-Far* conditions in Experiment 1. For each condition, the laser dot was positioned equidistant between two of the three food items (Fig. 5). In the *Near-Far* condition, the laser dot was either between the two food items nearer to the subject or between the two food items farther from the subject. In the *Equidistant* condition, the laser dot was between the two left-most food items, or the two right-most food items. Thus, there were four possible arrangements of the food items and the laser dot: *Near-Far(near)*, *Near-Far(far)*, *Equidistant(left)*, *Equidistant(right)*, with the parenthetical word indicating the location of

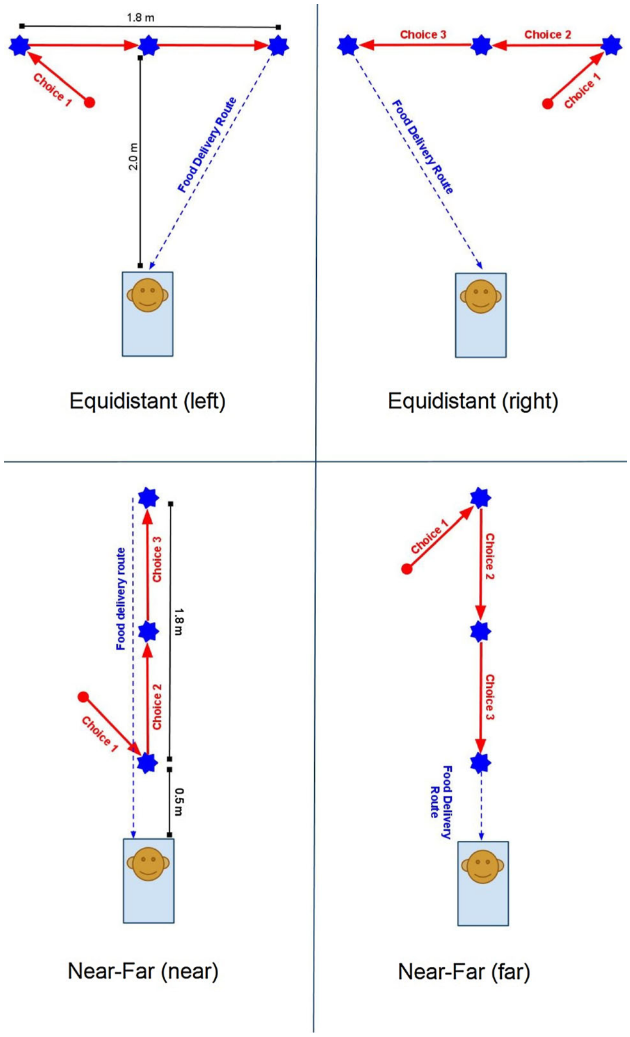

Fig. 5. Least distance paths and food delivery routes for Equidistant and Near-Far conditions in Experiment 2.

the laser dot between either the nearest, farthest, left-most, or right-most pairs of food items. The arrangements of the food items and locations of the laser dot are depicted in Figure 5.

The subject manipulated the joystick controlling the laser dot to contact the food item. When the laser dot came within 2.5 cm of the food item, the subject was verbally praised and Experimenter 1 withdrew the joystick. Experimenter 2 immediately walked along a predetermined route (Fig. 5) to collect the food item, but no food was delivered until the end of the trial. Once Experimenter 2 was standing stationary at the location where the first food item had been retrieved, Experimenter 1 returned the joystick, and the subject made the second choice. This procedure was repeated for the third food item. Following the third choice, Experimenter 2 walked along the predetermined route to deliver all three food items to the subject. Subjects completed all three choices in every trial of Experiment 2.

For the *Equidistant(left)* and *Equidistant(right)* conditions, the laser dot was positioned directly between two of the three food items, while the third food item was farther away. If a subject considered only his first choice, the left or right nearest neighbor food item would have equally minimized travel distance of the first leg of the trip. However, the first choice impacted the second and third choices, such that there existed a single least distance path to collect all food items (Fig. 5). A single, straight-line path across the plane of food items minimized the distance of the route. For example, the most efficient first choice considering the entire array in the perpendicular-left condition would be the left-most food item. A first choice of the center food item would cause an increase in the length of the total route of the laser dot by 0.9 m. A first choice of the far food item would increase the length of the total route of the laser dot by 0.74 m. This was true for all the other tested conditions as well. Table V shows the cumulative total distance for each possible choice pattern in Experiment 2 and the minimum time required for the laser dot to travel this distance. In the *Near-Far(Near)* and *Near-Far(Far)* trials, the distance ratios of choices were the same as in the *Equidistant* conditions. However, the proximity of food items to the subjects themselves was expected to impact choice.

Experiment 2 was similar to a real-world foraging situation in which an animal must choose a path by which to retrieve three resources separated by some distance, where two of those resources are equidistant from the start location, while a third resource is located farther away. At the beginning of each trial, the animal made a choice among three food items, a choice which it could make by (A) choosing randomly among the three food items, (B) preferentially traveling in one direction over another (i.e., left/right; near/far), (C) preferentially choosing the food items nearest to the start point, with no specific

TABLE V. Distance and Minimum Possible Time of Total Routes in Experiment 2

A---------------------B---------------------C

x

Choice order	Total distance (cm)	Minimum time (nearest item first) (sec)
A, B, C	256	5.12
B, A, C	346	6.92
C, A, B	346	6.92
A, C, B	346	6.92
C, B, A	330	6.6
B, C, A	420	8.4

Note: The cumulative total distance for each possible choice pattern in Experiment 2 and the minimum time required for the laser dot to travel this distance, considering that items A and B are the two items closest to the laser dot, while item C is farthest from the laser dot.

preference for one of the two nearest food items, or (D) preferentially choosing to retrieve first the one nearest food item that would result in the shortest path among all three points. The *Near-Far* trials placed in opposition an animal's spatial decisions based on proximity of a resource to itself with spatial decisions based on the efficiency of a route between both resources.

Analysis

A one-tailed binomial test was used to evaluate the hypothesis that the monkeys would prefer the two food items nearest the laser dot, with the probability (P) that the monkeys would choose a nearest neighbor option in any trial equal to two thirds. A one-tailed binomial test also was used to evaluate the hypothesis that subjects would prefer a first food choice that would minimize the total route distance. Although there were three possible first food choices, the two of interest were the two food items closest to the laser dot, one of which resulted in the most efficient route to all three food items. Thus, the null hypothesis predicted that the probability of first choosing the food item that would produce the most efficient route (hereafter the most efficient first choice) would not be significantly greater than 0.5.

Results

Both subjects significantly preferred the nearest neighbor choices in the *Near-Far(near)* and *Equidistant(left)* conditions, choosing one of the two food items nearest the laser dot in 12 out of 12 trials (Table VI). Leo also selected the nearest neighbor choices in 12 of 12 trials in the *Equidistant(right)* condition. In the *Near-Far(far)* condition, both subjects chose the nearest neighbor choices in 11 out of 12 trials. In the *Equidistant(right)* condition, Xenon selected the nearest neighbor food item in 9 of 12 trials.

Of the two nearest neighbor food items, one represented the most efficient first choice for every trial type considering the entire array of available food items. That is, first choice of the item at the far end of the array and not the middle item would minimize total travel distance. Leo did not prefer the item at the far end of the array significantly for any of the trial types in the *Near-Far* or *Equidistant* conditions. In the *Near-Far(far)* condition, Leo significantly chose the middle food item that was closer to himself first ($P = 0.04$). However, in the *Near-Far(near)* condition, Leo did not significantly prefer the food item closer to himself ($P = 0.15$) (Table VII). Xenon preferred the item at the far end of the array in the *Near-Far(near)* condition when this item was closest to himself ($P < 0.01$), but he showed a significant preference for the middle item as a first choice (the item closer to himself) in the *Near-Far(far)* condition ($P < 0.001$). In the *Equidistant(left)* condition when the item at the far end of the array was to his left, Xenon preferred this distance minimizing option ($P < 0.01$). However, in the *Equidistant(right)* condition, Xenon did not significantly prefer either of the two nearest neighbor choices. Following a choice of the most efficient first food item, both subjects most often chose the nearest neighbor second food item (Table VIII).

TABLE VI. Frequency of Nearest Neighbor First Choices in the Near-Far and Equidistant Conditions in Experiment 2

	Leo	Xenon
Near-Far		
Near	12*	12*
Far	11	11
Equidistant		
Left	12*	12*
Right	12*	9

Note: Both subjects significantly preferred the food items nearest the laser dot in the *Near-Far(near)* and *Equidistant(left)* conditions. All trial types $n = 12$.
*$P < 0.05$.

Discussion

In Experiment 1, we demonstrated that some capuchin monkeys disambiguate the distance between resources and themselves from the distance between a laser dot and the resource. Experiment 2 investigated route choice more closely, testing whether capuchin monkeys choose multi-step routes between three resource sites by looking ahead multiple steps in the future or by using a simpler strategy that does not prioritize route minimization. The results of Experiment 2 demonstrate that

TABLE VII. Frequency of Efficient First Choices in the Near-Far and Equidistant Conditions in Experiment 2

	Leo	Xenon
Near-Far		
Near	9	12**
Far	2*	0**
Equidistant		
Left	8	11*
Right	5	3

Note: Leo did not prefer the most efficient first choice significantly for any of the trial types in the Near-Far or Equidistant conditions. In the *Near-Far(far)* condition, Leo significantly preferred the inefficient first choice. Xenon preferred the most efficient first choice in the *Near-Far(near)* condition when the most efficient first choice was closest to himself and significantly preferred the inefficient first choice in the *Near-Far(far)* condition. In the *Equidistant(left)* condition when Xenon preferred the most efficient first choice and in the Equidistant(right) condition, Xenon did not significantly prefer either of the two nearest neighbor choices. All trial types $n = 12$.
*$P < 0.05$.
**$P < 0.001$.

TABLE VIII. Frequency of Choosing a Nearest Neighbor Second Food Item After the Choice of an Efficient First Food Item in Experiment 2

	Leo	Xenon
Near-Far		
Near	9 (9)*	12 (12)*
Far	2 (2)	0 (0)
Equidistant		
Left	7 (8)	11 (11)*
Right	4 (5)	2 (3)

Note: After choosing the most efficient first food item, both subjects most often chose the nearest neighbor second food item. Numbers in parentheses represent the total number of trials in which the subject made the efficient first choice for that condition. Numbers before the parentheses represent the number of second choices.
*$P < 0.05$.

capuchin monkeys do not appear to use a complex multi-step look ahead route choice strategy. Capuchins showed a preference for items nearest the laser dot, but did not consistently choose the one nearest food option that would result in the most efficient multi-step route through all three food items. Subjects' preference for items closest to themselves, as well as side biases, also influenced the choice of routes for both subjects.

Neither subject chose minimizing routes through all three food items consistently, even in the *Equidistant* condition, indicating that they did not make their first food choices on the basis of the entire multi-step route. The subjects did, however, significantly prefer the two food items nearest the laser dot over the further resource in their first and second choices. The capuchins chose randomly between the two nearest neighbor resources, without considering the global problem set, and proceeded through the remaining resources choosing the subsequent closest resource significantly more frequently than the third, farther resource. These results are in agreement with the analysis of Janson [2013], indicating that capuchin monkeys do not plan multi-step routes using a complex look ahead strategy, even when their task did not require spatial memory of hidden objects. Anderson's [1983] study established that spatial choice patterns like those observed in this experiment were to be expected, since always moving to the closest resource site is an effective foraging strategy under most reward conditions and resource distributions. These results may more broadly lend support to the work of Higgins and Strauss [2004] stating that evolution is not likely to have selected for multi-step look ahead strategies in spatial decision making.

GENERAL DISCUSSION

In this work, capuchin monkeys were presented with a TSP to test the influence of the proximity of resources to self and to examine whether capuchin monkeys plan multi-step routes through visible goal locations. The monkeys remained stationary with respect to the resources and used a laser pointer to "travel" to choices. The array was fully in view throughout each trial, and this experimental design allowed us to examine the capuchins' spatial choices without the limitations imposed by spatial memory. When the distance ratio between the two resources and the laser dot was large (i.e., $\geq$1:3), one subject systematically chose the closest resource to the laser dot, even when this meant first choosing an item further away from himself. These results suggest that, in at least one of our subjects, disassociating the location of self from the choice of a route was possible. The other monkey adopted choices reflecting a bias for resources closer to himself, even at the cost of a longer overall path and increased time to reward. These results are the first indication from a captive study that the use of an allocentric frame of reference, specifying the location of an object in relation to other objects in one's environment, is possible for some capuchin monkeys. This result contrasts with Potì's [2000] captive study, but agrees with Presotto and Izar's [2010] analysis of the natural ranging behavior of capuchin monkeys in an Atlantic forest habitat. As stated by Potì, the use of an allocentric frame of reference in this way may be a necessary prerequisite to planning a multi-step route minimizing distance between multiple resources. However, this trend did not extend to minimizing distance between three choices in sequence, as examined in Experiment 2.

In Experiment 2, both subjects demonstrated a preference for food items nearest the laser dot with no apparent consideration for the global problem set. Subjects did not consistently execute distance-minimizing multi-step routes through all three resources, as they had no preference for the nearest neighbor food item that would result in the most efficient multi-step route. Instead, subjects sometimes demonstrated a preference for one or the other nearest neighbor food item on the basis of its proximity to self in the *Near-Far* condition and on the basis of side bias in the *Equidistant* condition.

The lack of multi-step route planning in nonhuman species, as evidenced by Janson [2013] and supported by our work, contrasts with the ready use of route planning typical for adult humans. Gibson et al. [2007] demonstrated that human performance on a laboratory TSP task exceeded the efficiency of the nearest neighbor model. So, while capuchin monkeys in this study appear to be less efficient than humans, their efficiency is similar to that of rats [Bureš et al., 1992] and pigeons [Gibson et al., 2007]. For nonhuman animals, a preference for nearby resources may represent a less cognitively demanding strategy that reliably resolves the Traveling Salesman Problem with a high relative degree of efficiency. In the wild, nonhuman primates are known to use strategies that minimize distance traveled between goal sites including a preference for the nearest feeding site [Janson 1998] and integration of reward size and distance when visiting baited feeding platforms in the wild [Janson 2007]. In natural environments, where resources are often ephemeral and many ecological and social constraints exist on choosing appropriate resource sites, this strategy may produce sufficient resource exploitation and travel costs. Grove [2013] and Higgins and Strauss [2004] have demonstrated that knowledge of resource site location does not necessarily dramatically enhance route efficiency and Anderson [1983] indicates that complex multi-step look ahead strategies were not likely to have been favored by natural selection. Based on our results and the results of Janson [2013], it seems likely that the execution of efficient routes by primates in the wild reflects a strategy that does not involve consideration of the global layout of resources, and also that this lack of optimal route choice may not be due to limitations imposed by spatial memory, but rather by a spatial decision making strategy that does not prioritize route optimality. Results from previous studies indicating that nonhuman primates planned their routes with multi-step look ahead strategies [Cramer & Gallistel, 1997; MacDonald and Wilkie, 1990; Menzel, 1973] are likely more accurately explained by the use of a spatial decision making process that does not mandate route minimization.

The laser pointer apparatus used in this study allowed us to test whether capuchins could reason about the distance ratios between two resources, and could make decisions regarding those ratios, rather than the distance between the goal and the subject himself. However, the degree of explanatory power gained by our procedure may have come at the loss of relevant ecological context. For example, remaining stationary may have interfered with subjects' reasoning about the distances between multiple goal sites, or with planning an efficient route to three goal sites. Previous experiments with human infants indicate that experience with self-produced locomotion enhances infants' spatial memory when tested in novel spaces [Uchiyama et al., 2008]. In natural situations, moving in their environment might enhance reasoning about the spatial relationships between monkeys and familiar goal sites, as well as the spatial relationships among multiple familiar goal sites. Further testing is necessary to determine the influence of moving among resources on capuchins' choice of efficient multi-step routes.

Given that most animals must move from sites of rest and safety to resource sites, it is important to understand how they manage the costs and benefits of these travel decisions when traveling between multiple goals. This study indicates that some capuchins can look at an array of resources and make spatial choices allocentrically, on the basis of the spatial relationship between a point outside themselves and those goal sites. This may be a prerequisite to advanced multi-step route planning for nonhuman primates, and is an interesting avenue for future research.

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