

Let the pigeon drive the bus: pigeons can plan future routes in a room

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Abstract The task of determining an optimal route to several locations is called the *traveling salesperson problem* (TSP). The TSP has been used recently to examine spatial cognition in humans and non-human animals. It remains unclear whether or not the decision process of animals other than non-human primates utilizes rigid rule-based heuristics, or whether non-human animals are able to flexibly ‘plan’ future routes/behavior based on their knowledge of multiple locations. We presented pigeons in a One-way and Round-Trip group with TSPs that included two or three destinations (feeders) in a laboratory environment. The pigeons departed a start location, traveled to each feeder once before returning to a final destination. Pigeons weighed the proximity of the next location heavily, but appeared to plan ahead multiple steps when the travel costs for inefficient behavior appeared to increase. The results provide clear and strong evidence that animals other than primates are capable of planning sophisticated travel routes.

Keywords Spatial cognition · Navigation · Planning · Traveling salesperson · Pigeon

Introduction

In the beloved children’s book—*Don’t let the pigeon drive the bus!*—a human bus driver pleads with the reader not to let a pigeon drive his bus while he takes a break (Williams

2003). On the one hand, the bus driver might have been concerned that the pigeon would not be able to safely drive the vehicle. On the other hand, maybe the driver was more concerned that the pigeon would not be able to take a route that would efficiently pick up all the passengers at the various stops throughout the city. For example, if the bus had to travel to three sequential stops that were on the same street, it would be more efficient to travel to the stops sequentially rather than to the first stop, followed by the third and then backtrack to return to the second stop before revisiting the third stop as the bus continued down the street.

The task of determining an optimal route to several locations or nodes is called the *traveling salesperson problem* (TSP). The number of possible solutions to a TSP that includes a round trip is defined as $(N - 1)!$, where N is the number of places to be visited. The ability to determine all possible solutions to find the most efficient route becomes more demanding as the number of locations (nodes) in the problem increases. With 5 locations, there are 12 possible routes, but with 10 locations, there are 181,440 possible travel routes! Thus, the task of finding an optimal route can have quite a cognitive demand and many “travelers” may resort to using less cognitively demanding strategies to reduce the task difficulty. The TSP has been used to examine spatial cognition in humans (MacGregor and Ormerod 1996; MacGregor et al. 1999, 2000; Vickers et al. 2006) and non-human animals (Gallistel and Cramer 1996; Gibson et al. 2007; MacDonald 1994; MacDonald and Wilkie 1990; Miyata and Fujita 2010). This laboratory-based work, and related work in the field with non-human primates (Janson 1998, 2007), has shown that people and animal travelers select efficient routes given TSP-like problems.

It remains unclear whether animals, other than non-human primates, are using rigid rule-based solutions when

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solving TSPs, or a more flexible solution in which the animal may plan a future route (Kong and Schunn 2007) based on a consideration of multiple locations (see Cramer and Gallistel 1997; Gallistel and Cramer 1996; Janson 2007; Miyata and Fujita 2008, 2010; Scarf and Colombo 2010 for related work). An example of a rule-based solution would be the nearest-neighbor solution for generating a route. Using a nearest-neighbor solution, a “traveler” selects the location that is closest to its current location and then continues to travel to the next closest location until all potential locations have been visited. The neighbor solution can be characterized as a more local solution in that the traveler identifies the location closest to its current position for selecting the next leg of the route (see Kong and Schunn 2007). The neighbor solution utilizes proximity as a rule for identifying the next leg in the route and does not require that the traveler plan beyond the next step. In contrast, a traveler that plans a route several steps ahead might represent the problem more globally and consider most or all of the legs of the route before setting off on the journey. That is, a traveler could plan beyond just the next step in the route. There is some experimental and field evidence that non-human primates are capable of such planning beyond the next step (Cramer and Gallistel 1997; Gallistel and Cramer 1996; Janson 2007), but it remains unclear whether this is true for other animals (see Miyata and Fujita 2008, 2010).

Note, that a traveler that utilizes a neighbor solution or one that plans a route several steps ahead of its current location may both have efficient routes and also be “planning” future movements. Here, we define planning in its broadest sense, that is, developing a plan for future movements before they actually occur. The scope of the planning, level of analysis, and the cognitive demand may be very different for each type of solution, however. In particular, planning several steps ahead may require an allocentric representation such as a cognitive map—an internal representation of important places that indicates the geometric relationships between them (Gallistel 1990; O’Keefe and Nadel 1978; see Shettleworth 2010 for a review). Such a representation could be used to determine an efficient route to multiple locations. Cognitive maps remain controversial (Bennett 1996) and evidence for such internal representations can often be explained by alternative mechanisms, such as vector addition or learning (see Bennett 1996; Gibson and Kamil 2001; Brown et al. 1993; see Shettleworth 2010).

Here, we examine the ability of pigeons to plan a route to visit multiple locations in a room. Although several studies have shown that animals in the laboratory exhibit efficient traveling behavior, it remains unclear to what extent non-human animals can plan beyond the next step during route development, nor how local and global

strategies may interact (e.g., conditions under which a switch from using a local to global solution would occur). Evidence that an animal could plan a route beyond its next step might suggest that it has a relatively sophisticated representation of the geometric relationships between multiple destinations and can use that information to efficiently guide its behavior.

Methods

Animals

Eight adult White Carneaux pigeons (*Columbia livia*) were examined for their ability to solve traveling salesperson problems. The pigeons were maintained at 85% of their ad lib weight using controlled feedings of mixed grain following daily experimental sessions. The pigeons had ad lib access to grit and water in their home cages.

Procedures

The pigeons were individually transported from their home cage to a start box (*S*) in the experimental room (2.134 m × 2.743 m, see Fig. 1). The start box was always placed in the same corner of the experimental room and had a clear plastic Guillotine door that provided a view of the room from inside. The experimenter remotely opened the Guillotine door from a control room and the birds entered the experimental room and consumed 4 peas that had been placed on the floor to familiarize the birds to the room. This familiarization continued until the birds were freely moving to consume peas that had been placed in locations throughout the room.

The birds then were randomly assigned to either a one-way ($n = 4$) or round-trip ($n = 4$) group. A second box, an end box (*E*, Fig. 1) identical to *S*, was placed in the corner of the room opposite *S*. During training, a single 60 (height) × 5 (width) cm cylindrical PVC “feeder” was positioned in the room and peas were placed in shallow food wells at the base of the feeder prior to the start of the trial. The floor of the room was represented as a Cartesian grid and the centers of each cell (63 total) were marked as dots on the floor of the room. The centers of adjacent cells were separated by 30.49 cm. This grid was used to determine the position of the feeder(s) during each trial. The birds from both groups were released from *S* as described above. After consuming the peas at the base of the feeder, the experimenter activated a buzzer in the ceiling of the experimental room. For the birds in the round-trip group, the Guillotine door to *S* then was raised. Once the pigeon visited the feeder and returned to *S*, the Guillotine door was closed, and a bucket feeder that was filled with mixed grain

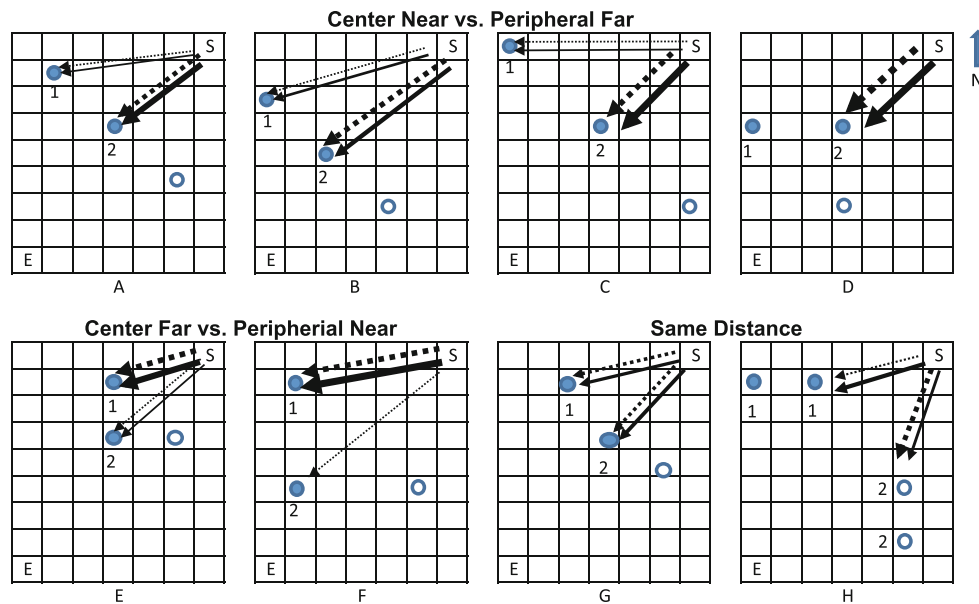


Fig. 1 The performance of pigeons in the round-trip (dashed line) and one-way (solid line) groups during the 16 two-feeder test configurations presented in Experiment 1. Each of the panels a–g shows the first choices averaged across two configurations that were mirrors of each other. For these problems, the position of the feeders for the first of the two test configurations is indicated by the filled circles. The position of the central feeder (number 2 in each panel) remained the same for the second configuration, and the position of the second feeder in the mirror configuration is indicated by the unfilled circle. The data across both problems are shown relative to the first test configuration for each pair of configurations in a panel (filled circles). The location of the start box is indicated by S, and the location of the end box for the birds in the one-way group is indicated by E. The Cartesian grid used to position the feeders is shown for

display purposes, but the lines in this figure were not present (dots indicated the center of each cell in the test room—see text). The number of choices and direction of choices to each feeder is indicated by the arrows. There were a total of 12 first feeder choices for each configuration for each group (12 choices \times 2 mirror configurations = 24 choices/panel/group). The width of the arrow corresponds with the number of choices to a particular feeder; bolder arrows indicate more choices to a feeder (arrow width of 4 font = 24 choices). Panel h also displays two test configurations indicated by the closer and farther pair of open and filled circles relative to S. The arrows show the number of choices to the pair of filled or unfilled circles across both configurations. The arrow with the N to the far right of the panels indicates a northerly direction

and attached to the rear of S was raised for 2 s. The door to the end box (E) remained closed for the duration of the trial for the birds in the round-trip group. In contrast, following the buzzer, the door to E was opened and the bucket feeder in this box was raised for the birds in the one-way group. Thus, the birds in the round-trip group left S, visited the feeder, and then returned to S after consuming the food. The birds in the one-way group departed S, visited the feeder, and then traveled to E to complete the trial. The position of the feeder in the room varied pseudo-randomly across trials, such that the pigeons were familiar with traveling to the different regions of the room. Each daily session consisted of four consecutive training trials for each bird.

The procedures for testing were the same as those for training except that the birds encountered two feeders in the room. During four of the eight trials (randomly determined) in each daily session, the position of the two feeders was determined randomly (random condition) from the total of 48 positions. These trials were used in part to disperse the test trials and maintain traveling performance,

but were otherwise identical to the other four trials of the session. For the other four trials, we presented the birds with one of 16 “problems”—predetermined test configurations of the feeders designed to elucidate the nature of the decision process that pigeons may use to determine their routes (see Fig. 1). These configurations examined whether the birds preferred to go to (1) a central and near feeder versus a more distal and peripheral feeder (Center Near vs. Peripheral Far, Fig. 1) (2) a centrally located and distal feeder versus a far feeder that was closer to S (Center Far vs. Peripheral Near, Fig. 1) and (3) a pair of feeders that were the same distance but in different directions from S (Same Distance, Fig. 1). The order of the random and test trials within a session was randomly determined, and the test configuration that was used on a trial was determined randomly without replacement from the set of 16 predetermined configurations. Testing continued until the birds completed three sets with each test configuration ($3 \times 16 = 48$ total test trials) and a corresponding number of trials with the random configurations. Once a bird had visited each feeder just once and consumed the food, the

buzzer sounded and the end of the trial proceeded as described above. If the pigeon returned to *S* (or *E*) before visiting the second feeder, or to the first feeder again after visiting the second feeder, the lights in the room were turned off, the trial ended, and a correction trial ensued. If a bird failed to visit each of the three landmarks just once, the data from the trial were eliminated from subsequent analysis and the trial redone; this occurred during less than 10% of the trials. We eliminated these trials from the analysis to ensure that all of the data in the analysis were from trials in which the birds did not make a procedural error and were more comparable.

Measures and analyses

We recorded the order of the feeders that the pigeons selected each trial during testing. The distance of these routes closely approximated the actual distance of the birds journey, since the birds rarely deviated (<4.5% of all occasions) from taking a direct line between any two locations. We examined whether the routes the pigeons selected were efficient. For each trial of testing, we calculated the total distance of the route taken by the pigeon. We determined the minimum distance between *S* and the first feeder selected, then the first and second feeder selected, and finally the second feeder and *S* (or *E*). The distance of these three legs then was summed to achieve the total distance of the route. We also calculated a model of chance (Monte Carlo) and ideal (optimal) performance. The random model was generated by having a computer randomly select the sequence of two feeders for a given trial. These choices were then used to determine the distance of the entire journey (see Gibson et al. 2007). For each trial, we also determined the choice of feeders that would lead to the shortest (distance minimization) route. Notably, regardless of which feeder the birds in the round-trip group selected first, the total length of their routes was always the same (only for Experiment 1 with two feeders and only for the analysis that included distance as a measure). Therefore, we only performed the analyses that utilized distance for the birds in the one-way group. We used a mixed ANOVA with Traveler (pigeon, random, and optimal), Problem (1–16), and Set (1–3) as repeated measures and route distance as a dependent measure.

In a second set of analyses, we examined the first choices the birds made to the feeders after departing *S*. Many of the 16 feeder test configurations were reflections of each other, and the data for the analyses are combined for these (see Fig. 1). We used logistic regression with Group (one-way vs. round-trip), and Test (1, 2, 3) as factors to assess the choice of feeder(s) by the pigeons.

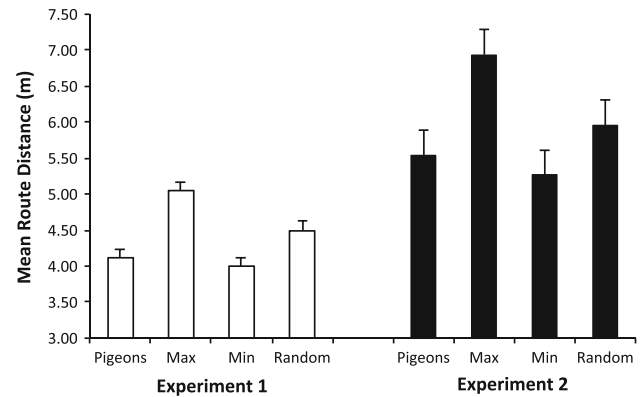


Fig. 2 The distance of the routes taken by the pigeons and the three models during Experiment 1 (2 feeders) and Experiment 2 (3 feeders). The values are taken across all groups and conditions for each traveler

Results

Across all test and random configurations of test trials, the analysis revealed a main effect of traveler $F(3,12) = 12,034.64$, $P < 0.0001$ (Fig. 2). Follow-up comparisons using the Games–Howell procedure indicated that the mean distance of the routes that the birds choose ($\chi = 4.15$ m, $CI = 0.05$) was significantly shorter than the mean distance of the routes indicated by the maximum ($\chi = 4.68$ m, $CI = 0.05$) and the Monte Carlo/random ($\chi = 4.33$ m, $CI = 0.05$) models of performance (P 's < 0.01), but significantly longer than the optimum distance ($\chi = 4.04$ m, $CI = 0.05$, $P = 0.02$) that could be taken (Fig. 2, left).

Center near versus peripheral far configurations

In the center near versus peripheral far test configurations (Fig. 1, panels a–d), the pigeons departed *S* and had to choose between a closer central feeder and a feeder more peripherally located in the room to complete the first leg of their route. The pigeons in both groups chose the central feeder as their first stop in their route on 36 of 48 test trials in panel a ($b = -1.10$, $\chi^2(1) = 10.86$, $P = 0.001$), 33 of 48 test trials in panel b ($b = -0.79$, $\chi^2(1) = 6.41$, $P = 0.01$), 42 of 48 tests in panel c ($b = -1.96$, $\chi^2(1) = 19.88$, $P < 0.001$), and 48 of 48 trials in panel d. Table 1 shows the distance of *S* from the two feeders for each problem as well as the impact of choosing the closest feeder to *S* on the overall length of the route. Notably, for most configurations, choosing the nearest feeder resulted in a large short-term reduction in the distance traveled for the first leg and generally had only a modest positive or negative impact on the total length of the journey (Table 1).

Table 1 Some geometric properties of the 16 test configurations of two feeders used in Experiment 1

Test configuration	Panel in Fig. 1	1st leg diff (m)	Total route diff (m)	Neighbor net impact
1	a	−0.26	0.12	↑
2	a	−0.26	−0.26	↓
3	b	−0.2	0.26	↑
4	b	−0.2	−0.20	↓
5	c	−0.54	0.39	↑
6	c	−0.54	−0.13	↓
7	d	−0.75	−1.00	↓
8	d	−0.75	−1.43	↓
9	e	−0.33	−0.87	↓
10	e	−0.33	−0.71	↓
11	f	−0.6	−1.41	↓
12	f	−0.6	−1.79	↓
13	g	0	NA	
14	g	0	NA	
15	h	0	NA	
16	h	0	NA	

Column 1 identifies the configuration in the analysis, and column 2 indicates the panel in Fig. 1 in which the configuration is displayed. Column 3 shows the difference in the distance between *S* and the two possible feeders ($\Delta \text{dist} = \text{dist}(S \text{ to near feeder}) - \text{dist}(S \text{ to far feeder})$). Column 4 shows the impact of choosing the nearest feeder first after departing *S* (proximity rule) on the total length of the entire route for the one-way group. Column 5 indicates whether choosing the nearest feeder results in a shorter (down arrow) or longer (up arrow) total route for the birds in the one-way group. Negative values indicate the savings in distance traveled. For configurations 13–16, the feeders were all the same distance relative to *S*

Center far versus peripheral near configurations

Panels e and f of Fig. 1 (center far vs. peripheral near) show the results from pairs of test configurations in which the birds had to choose between a central and peripheral feeder as the first leg of their route, but in contrast to the first four pairs of test configurations (Fig. 1, panels a–d), the more proximal of the two feeders was located in the periphery of the room relative to *S*. Now, the birds in both groups preferred to travel to the peripheral feeder—but also the more proximal feeder—as their first choice on 40 of 48 occasions for the configurations in panel e ($b = -1.61$, $\chi^2(1) = 17.27$, $P < 0.001$) and on 48 of 48 trials for the configurations in panel f. For these configurations, choosing the nearest feeder first relative to *S* resulted in a large short-term reduction in the distance traveled for the first leg and the total length of the journey (Table 1).

Same distance configurations

We also presented the birds with pairs of configurations with a peripheral and central feeder (panel g) or two

peripheral feeders (panel h) that were the same distance (on an arc) from *S* (Fig. 1, same distance). The birds chose to travel to the central feeder first on 23 of 48 occasions ($b = 0.08$, $\chi^2(1) = 0.08$, $P = 0.77$) in panel g and on 27 of 48 occasions for the problems in panel h ($b = 0.251$, $\chi^2(1) = 0.749$, $P = 0.39$).

Discussion

The birds had a strong preference to choose the feeder closest to *S* when selecting the first leg of their route, regardless of whether they were in the one-way or round-trip group. The large weighting of proximity during the choice process was true regardless of whether the feeder closest to *S* was in the center of the room (Fig. 1a–d) or in the periphery (Fig. 1e–f). The pigeons had no preference for moving to the center or periphery relative to *S* when given a choice when the distance to *S* from both feeders was constant (Fig. 1g–h), indicating that side biases were minimal across participants. The birds also chose feeders that were far away and in the periphery relative to *S*, suggesting that they were able to visually detect feeders positioned throughout the room (Fig. 1h).

For problems like the ones displayed in Fig. 1f, the use of a nearest-neighbor solution by the birds in the one-way group is coincident with the most efficient route; that is, going from *S* to feeder 1 (nearest), followed by feeder 2, and then to *E*. Such a route would have a maximal savings of 1.41 m compared to a route that included going to feeder 2 first (slightly different depending upon whether the feeder is in the north or south of the room). Despite the general efficiency the neighbor solution takes, it can be a less efficient approach for some problems. For example, in Fig. 1b, the distance between *S* and feeder 2 is 1.29 m and the distance between *S* and *P* is 1.55 m. Although choosing c minimizes the distance of the first leg, the total length of this route ($S \rightarrow 2 \rightarrow 1 \rightarrow E$) would be 0.26 m longer than if the bird had gone to the *P* as its first choice.

Notably, the peripheral feeder was in the north portion of the room for the problems in Fig. 1, panels a–c, but on half of the occasions *P* was in the south of the room (unfilled circles). During these trials, the nearest neighbor is also consistent with the most efficient route because of the proximity of feeder 2 to *E* (only for the one-way group). If the birds were to maximize their efficiency, then for this subset of problems, they should choose the nearest-neighbor solution when feeder 1 is in the north and select feeder 2 first when feeder 1 is in more southerly. The birds choose c on 36 of 36 occasions when feeder 2 was in the north (when the neighbor solution is less efficient) and on 25 of 36 occasions when feeder 2 was in the south (when neighbor is more efficient) for these problems. Thus, as the

overall results suggest, the birds weighted proximity heavily in the short-term regardless of the later impact on route efficiency. Indeed, a perusal of Table 1 shows that for the problems in Fig. 1, panels a–c, choosing the closest feeder first would bring the pigeons to food more quickly and such a choice has relatively little impact on the total length of the trip (positive or negative). For the configurations in Fig. 1, panels d and f, choosing the most proximal feeder first is also concurrent with a substantial reduction in the total length of the total trip (Table 1). Indeed, only for configurations 1, 3, and 5 (Table 1) would choosing the most proximal feeder first after departing *S* result in a total route that was longer than if the birds had chosen the more distal feeder first. For these configurations, however, the total increase in the total length of the route was small; between 0.12–0.39 m and 2–8% of the total distance of the route for these configurations.

There appears to be much correspondence between pigeons behavior on TSPs provided in past work using operant chambers with computer displays and the current open room task. In both operant and the current open room TSPs, pigeons were less efficient than the optimal model of performance but reliably better than chance. Additionally, in both the operant and ambulatory tasks, the pigeons have a tendency to weight proximity cues when making choices. Thus, the pigeons appear to be utilizing similar spatial cognitive skills in both contexts, consistent with similar findings from people given ambulatory and virtual spatial cognitive tasks (e.g., Richardson et al. 1999).

The results from Experiment 1 indicate that pigeons utilize a local proximity-based solution when solving TSPs. The results from several of the current tests also indicate that the tendency to utilize a local solution is not based on the failure to detect feeders in the periphery (e.g., panel 6), which would be essential to a global solution that considered the location of more than one feeder. Past work with non-human primates in the laboratory and field indicate they are capable of planning one or more steps ahead. One possibility is that the travel costs associated with using a nearest-neighbor solution instead of a more global one were not very large. That is, the assumed costs (e.g., delay to food, energetic costs) for some level of inefficiency were not large enough to cause a shift from a local to a more global solution. We explored this possibility in a second experiment.

Experiment 2

The results from Experiment 1 strongly indicated that pigeons use proximity as a cue to determine the next location when traveling a route, even though such a solution often resulted in a less efficient route. The difference

in cost between a somewhat less efficient route based on proximity and the optimal route were likely quite small, however. In a second experiment, we added a third feeder to increase the complexity and travel costs associated with the TSPs. Additionally, we used test configurations to determine whether pigeons would forgo proximity in favor of a more global solution if travel costs associated with a less efficient route (based on proximity) were more apparent or when proximity differences between feeders at different choice points were held constant.

Methods

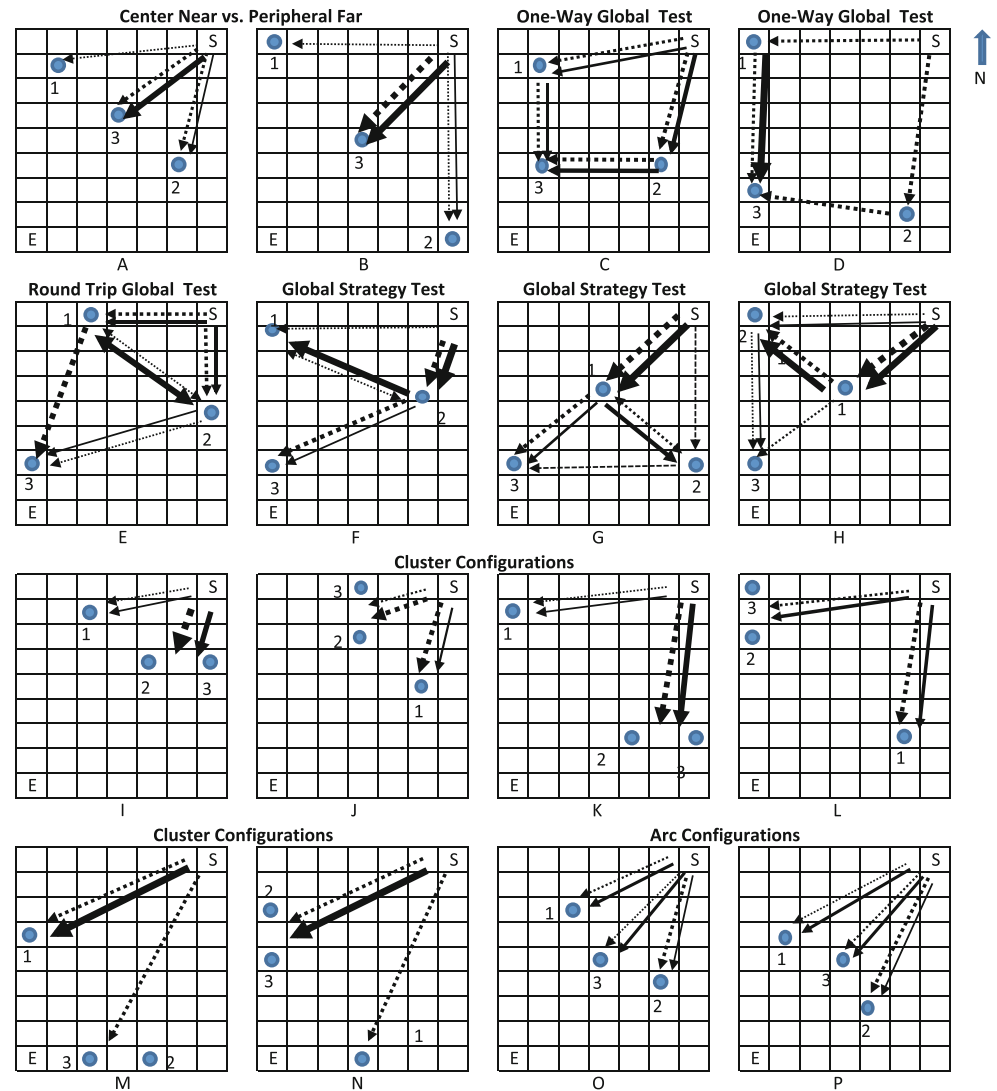
Animals

The same pigeons used in Experiment 1 were again used in Experiment 2. The pigeons were maintained as in Experiment 1.

Procedures

Training with three feeders began immediately following the conclusions of Experiment 1. The procedures for training were identical to those described above for Experiment 1. Testing began once the birds were reliably and directly traveling to all three feeders without an error (feeder revisit or omission, see Experiment 1) on three of four trials for two consecutive days. The procedures for testing in Experiment 2 were similar to those in Experiment 1. Four random and four test configurations of feeders were presented during each daily session using the procedures described in Experiment 1. The birds were presented with a series of test configurations that examined whether they preferred to go to a nearby central feeder or one of two more distal feeders in the periphery after departing *S* (Center Near vs. Peripheral Far Configurations, Fig. 3a, b). We also gave the pigeons test configurations to examine whether they would choose an efficient global solution instead using a more proximal strategy (one-way/round-trip global configurations, Fig. 3c–e). For test configurations a–e (Fig. 3, global solution tests), the pigeons had to make a second choice between two feeders, one of which was at a different angle and distance from their current location. For test configurations f–h (Fig. 3, global strategy configurations), the feeders for the second choices were always the same distance and angle from the feeder that we predicted the birds were likely to choose first. Thus, proximity (neighbor) or other geometric factors were less likely to play a role in the second choices for either group. We also tested the pigeons with clusters of feeders to see whether these would be preferred initially after departing *S* compared to a lone feeder (Fig. 3, cluster configurations).

Fig. 3 The performance of pigeons in the round-trip (dashed line) and one-way (solid line) groups during the 16 three-feeder test configurations presented in Experiment 2. Each of the panels **a–p** shows the first or second choices (see text) for that configuration. The position of the feeders is indicated by the filled circles. The location of the start box is indicated by *S*, and the location of the end box for the birds in the one-way group is indicated by *E*. The Cartesian grid used to position the feeders is shown, but was not visible to the birds. The number of choices and direction of choices to each feeder are indicated by the arrows. There were a total of 16 first feeder choices for each configuration for each group. The width of the arrow corresponds with the number of choices to a particular feeder; bolder arrows indicate more choices to a feeder (arrow width of 4 font = 16 choices). The arrow with the *N* to the far right of the panels indicates a northerly direction



Finally, we tested the birds with two configurations (arc configurations, Fig. 3) in which all three feeders were on an arc whose geometric center was either toward (configuration o) or away (configuration p) from *S*. All three feeders on the arc were spaced equally apart in both configurations.

In contrast to Experiment 1, testing continued until the birds completed four sets with each test configuration ($4 \times 16 = 64$ total test configuration trials) and a corresponding number of trials with the random configurations. As before, if a bird failed to visit each of the three feeders just once (either revisit or omission) the data from the trial were eliminated from subsequent analysis and the trial redone; errors occurred during less than 10% of the trials. The analyses using choice and distance measures were performed, similar to that described for Experiment 1. For the choice analyses, we now considered the first and/or second feeder choices by the pigeons (depending upon the

configuration). Also, we conducted the analyses using route distance for both the round-trip and one-way groups.

Results

The analysis using distance as a measure revealed a main effect of traveler $F(3,28) = 18,906.05$, $P < 0.0001$ across all configurations of feeders used during testing. As can be seen in Fig. 2 (right), follow-up comparisons using the Games–Howell Procedure revealed that the mean distance of the routes that the pigeons selected ($\chi = 5.54$ m, CI = 0.35) was significantly shorter than the mean distance of the routes indicated by the maximum ($\chi = 6.93$ m, CI = 0.35) and the Monte Carlo ($\chi = 5.95$ m, CI = 0.35) models of performance (P 's < 0.01) and not significantly longer than the optimum ($\chi = 5.27$ m, CI = 0.35, $P < 0.35$) route that could be taken.

Table 2 Some geometric properties of 8 of the first 16 test configurations used in Experiment 2

Test configuration	Panel in Fig. 3	Choice (1st/2nd)	Proximal versus distal feeder (diff m)	Round-trip		One-way	
				Total route diff (m)	Neighbor net change	Total route diff (m) ²	Neighbor net change ²
1	a	1	0.26	0.6	↑	0.66–0.97	↑
2	b	1	1.22	1.83	↑	0–1.21	↑
3	c	1	–0.61	0–1.11	↔ ↓	0.31–1.79	↓
4	d	1	0.33–0.76	0–1.82	↔ ↓	1.98–2.59	↓
5	e	1	1.37	1.17	↑	0.85–1.48	↓
6	f	1	0.89–1.65	–0.89 to 1.64	↑ ↓	1.06–3.47	↑ ↓
7	g	1	0.76–1.3	0–0.76	↔ ↓	0.39–2.47	↓
8	h	1	0.76–1.3	0–0.76	↔ ↓	0.12–2.47	↓
3	c	2	–0.5	–1.11	↓	0.31–0.69	↑
4	d	2	–0.79	–1.22	↓	1.98–2.59	↑
5	e	2	0.19	1.17	↑	1.79–2.11	↓
6	f	2	ND	ND	ND	ND	ND
7	g	2	ND	ND	ND	ND	ND
8	h	2	ND	ND	ND	ND	ND

Column 1 (test configuration) shows the test configuration for which the analysis is being performed (letter in column 2 references the same configuration in Fig. 3)

Column 3 shows the choice on which the analysis is being constructed. Column 4 indicates the difference in the distance between moving to the nearest feeder or a more distal feeder (as calculated in Table 1) relative to the current location given the choice. Columns 5 and 6 display the impact of choosing the nearest feeder (proximity rule) for a given choice on the total length of the entire route for the round-trip group; identical calculations are presented for the one-way group in Columns 7 and 8. Negative values indicate the savings in distance traveled, positive values represent additional distance. For problems f–h, the second choice to either feeder was the same distance and some calculations based on differences between proximal and distal choices could not be calculated. “ND” indicates that there is no difference between the local and global legs for that choice

Center near versus peripheral far configurations

The birds in both groups preferentially selected the nearest feeder for the center near versus peripheral far test configurations [a (feeder 1 = 1 choice; feeder 2 = 10 choices; feeder 3 = 21 choices; $\chi^2(2) = 18.43$, $P < 0.0001$), and b (feeder 1 = 1, feeder 2 = 2, feeder 3 = 29; $\chi^2(2) = 46.58$, $P < 0.0001$), as was the case given similar configurations in Experiment 1. The tendency to choose the most proximal feeder from *S* is consistent with the nearest-neighbor rule, which consequentially resulted in a relatively inefficient total route for both groups for both of these configurations (see Table 2).

One-way/round-trip global configurations

The pigeons in both groups again choose the closest feeder as their first choice for test configuration c (Fig. 3). The birds distributed their first choices between feeders 1 and 2, which were equidistant from *S*. The second choice is informative for this test configuration. The birds in the round-trip group should select feeder 3 based on a neighbor solution, but such a choice also would be consistent with a more global solution of route efficiency for returning home

(see Table 2). The birds in the one-way group should take the longer diagonal leg after their first choice (e.g., if at feeder 1 cross to feeder 2) if they are planning beyond the next step, as choosing feeder 3 (based on proximity) would result in a somewhat longer total route (Table 2). Notably, 16 of 16 second choices for the birds in the round-trip group were to feeder 3; consistent with either the global or neighbor solution. All 16 of the second choices for the birds in the one-way group were also distributed to feeder 3, documenting the use of the neighbor solution over a more efficient crossing route based on the global layout of the feeder configuration. Test configuration d (Fig. 3) is similar to configuration c except that the distance between the feeders is somewhat greater. Again, the pattern of first and second choices for both groups was nearly identical to that observed for configuration c. The first of these was a test to examine whether the birds in the round-trip group at a critical decision point would select a feeder consistent with a more global solution than a more proximal feeder. The first choices for the birds in both groups were again distributed between feeders 1 and 2 for test configurations e (Fig. 3). The birds in the round-trip group should subsequently choose feeder 3 if using a global solution (a savings of 1.17 m in the total distance of the route; see

Table 2) and choose feeder 1 if at feeder 2 (or vice versa) if using a neighbor solution. Thirteen of the 16 second choices subsequently were to feeder 3 ($\chi^2(1) = 5.24$, $P = 0.022$), consistent with a global, rather than a neighbor solution. In contrast, 14 of the 16 second choices for the birds in the one-way group crossed between feeders 1 and 2 ($\chi^2(1) = 6.63$, $P = 0.01$), consistent with either a neighbor or global solution. The difference in the pattern of choices between the groups was reliable, $\chi^2(1) = 5.75$, $P = 0.016$.

Global strategy configurations

All 16 of the first choices for the birds in the one-way group were to feeder 2 for testing with configuration f (Fig. 3). Of those birds, 15 of 16 of the second choices were subsequently to feeder 1, $\chi^2(1) = 6.88$, $P = 0.009$; if the birds had instead traveled to feeder 3, the *total* length of their route would be 7.04 m instead of 5.21 m, a choice consistent with planning based on a more global consideration of the problem. The birds in the round-trip group made 13 choices to feeder 2 as their first choice for the same configuration. The pigeons in the round-trip group should select feeder 3 next instead of feeder 2 if choosing the more efficient global solution (savings of 0.75 m, Table 3). Ten of the second choices by the round-trip group were to feeder 3 and three to feeder 1; the difference in second choices to these two feeders approached significance ($\chi^2(1) = 3.35$, $P = 0.07$). The difference in the

pattern of choices between the groups again was significant, $\chi^2(1) = 10.12$, $P = 0.001$. Thus, when proximity and other geometric features were held constant, the pattern of choices for both groups was consistent with planning ahead beyond the movement to the next feeder.

Test configurations g and h of Fig. 3 are mirror images of each other and similar to that shown in panel f in that proximity was held constant for the second choice. Across tests with configurations g and h, 29 of 32 and 31 of 32 first choices for birds in the one-way and round-trip groups were to feeder 1, respectively. The second choices for the birds in the one-way group were highly consistent with planning ahead, as 25 of 31 of their choices were to feeder 2, $\chi^2(1) = 9.86$, $P = 0.002$ (a savings of 1.32 and 1.83 m for problems, g and h respectively, Table 3). The second choices for the birds in the round-trip group were divided, as 14 of the choices were to feeder 2 and 15 to feeder 3, $\chi^2(1) = 0.034$, $P = 0.853$. The difference in the distribution of choices between the two groups was significant, $\chi^2(1) = 6.04$, $P = 0.014$.

Cluster configurations

As was the case for Experiment 1, for the birds in the round-trip group traveling to the cluster or the lone feeder first did not impact the total length of their route (the birds selected both feeders in the cluster before moving on to their next location). Thus, the pigeons in this group would be expected to first choose the cluster after departing *S* to maximize the rate of reward at the beginning of the route. In contrast, the birds in the one-way group potentially had to factor both the rate of reward and the total length of the route into their decision. Across test configurations i–l (Fig. 3), the birds in the one-way group made 44 of 64 ($b = 7.88$, $\chi^2(1) = 8.55$, $P = 0.003$) of their choices to the cluster first, whereas the round-trip group made only 36 of 64 ($b = 2.51$, $\chi^2(1) = 1.00$, $P = 0.319$) first choices to the cluster. Configurations m and n were cluster configurations that were similar to configurations i–l. Because of the geometric relationship between the *S*, the feeders, and *E*, for the birds in the one-way group it was 1.21 m more efficient if these birds traveled to the feeder(s) that was positioned vertically (in Fig. 3) relative to *e* in panels m and n regardless of whether or not a cluster was in that location. The same consideration applied for the one-way group for configurations i–l, but the maximum increase in distance for not going to this location first was only between 0.05 and 0.61 m for these problems. The birds in the round-trip group showed no preference for going to either the cluster or lone feeder first. Sixteen of the 32 choices were to the cluster across both test configurations for this group. In contrast, the birds in the one-way group had a strong preference to go to the location in the room

Table 3 Difference in the distance (m) of local versus global routes for test configurations in Experiment 2

Test configuration	Panel in Fig. 3	Local versus global (diff m) across all choices			
		RT	Net change	One-way	Net change
1	a	0.6	↑	0.6–0.97	↓
2	b	0.6–1.21	↑	1.21–1.82	↓
3	c	NA	↔	0.31–.69	↑
4	d	NA	↔	0.16–1.37	↑
5	e	1.17	↑	NA	↔
6	f	0.75	↑	1.83	↑
7	g	0.76	↑	1.32	↑
8	h	0.76	↑	1.83	↑

Column 1 (test configuration) shows the test configuration for which the analysis is being performed (letter reference configurations in Fig. 3). Columns 3 and 5 show the differences in distance between routes based on local–global principles for the round-trip (RT) and one-way groups, respectively. Negative values indicate the savings in distance traveled, and positive values represent additional distance (meters). The arrows in columns 4 and 6 show the net change in choosing a route based on proximity versus a more global consideration of the problem

that would minimize the distance of their route, regardless of whether a cluster or lone feeder was present (Fig. 3). All 32 of the choices were to the location (16 choices to feeders 1, configuration m; 16 choices to the cluster for configuration n) that minimized the total distance of their route.

Arc configurations

There was a non-significant difference in the distribution of first choices across both groups to the three feeders for configuration o (7 choices to feeder 1, 15 choices to feeder 2, 10 choices to feeder 3) (all P 's ≥ 0.05). For configuration p, the pigeons across both groups had a preference for traveling first to feeder 3 after departing S ($b = -18.75$, $\chi^2(1) = 158.80$, $P < 0.0001$).

Discussion

The results from test configurations a and b demonstrate that pigeons will prefer a proximal over a distal feeder even if it results in a longer overall route. Choosing the most proximal feeder after departing S had a savings of between 0.26 and 1.22 m for the first leg for both groups, but resulted in between a 0.6 and 1.83 m increase in the length of the route for the round-trip group and between a 0 and 1.21 m increase in the total length of the trip for the one-way group (Table 2). These findings are similar to those reported in Experiment 1 and corroborate the role of proximity in past work with pigeons in operant tasks using TSPs (e.g., Gibson et al. 2007; Miyata and Fujita 2010). However, we also found evidence that the pigeons were capable of planning beyond their next choice.

The birds in the one-way group showed evidence of planning beyond their next step during configurations e–h for their second choices. For these configurations, the pigeons either rejected a proximal feeder for a feeder that was farther away to ensure a more efficient route (configuration e) or chose feeders that were consistent with a more efficient global route when proximity between second choices was held constant (configurations f–h). So why did the birds in the one-way group fail to show evidence of planning with configurations a–d of the current experiment, and for the test configurations used in Experiment 1? Hints of an answer may be found in Table 2. The net increase in the distance for the total route after using a local solution compared to a global solution for configurations a–d in Experiment 2 was relatively small (last column: minimally, 0.66, 1.21, 0.31, and 0.16 m). For example, the length of the routes using a neighbor solution for configurations c and d was 5.46 m and 6.77–7.98 m (depending upon direction) and the route predicted based on planning ahead was 5.77 and 6.61–7.22 m, respectively. The differences in

the routes produced by these two strategies were relatively small and may have been hard to discriminate or not terribly costly (e.g., delay in getting food or return to the box). However, for configurations f, g, and h, in which the pigeons in the one-way group showed evidence for planning ahead, the difference between the local and global solution was larger: 1.83 m for f, 1.32 m for g, and 1.83 m for h (Table 2). Likewise, for this group of birds, the large benefit for making a first choice based on proximity was in some cases large (e.g., configuration b) and might have weighted more heavily into the birds' choice.

The pigeons in the round-trip group also showed evidence for planning beyond the next step with configurations f–h. Again, the net increase in the distance of the total route associated with a proximity rule (where inconsistent with the global solution) was higher from these problems than for configurations a–d (Table 2), perhaps accounting for more reliance on planning. For example, the difference in distance between the predicted neighbor and global routes (6.29 m vs. 7.46 m) for the birds in the round-trip group was 1.17 m for configuration e, a sizable increase from minimal values for the first four problems and likely accounted for why the pigeons in this group did not base their second choice on proximity. The behavior of the birds in the round-trip group was more variable than that of the one-way group for the configurations that pitted local versus global strategies against each other (e.g., configurations e–h). The net difference between the local and global strategies was larger for the one-way group than the round-trip group (0.76–1.17 m round-trip vs. 1.32–1.83 m for the one-way group; Table 2) and may have accounted for these group differences, however.

The results from the tests with the cluster configurations indicated that the pigeons in both groups did not have a strong preference for the cluster of feeders. This appears to be in contrast to other work using TSP-like paradigms with pigeons in operant chambers that have shown a preference for clusters of nodes (e.g., Gibson et al. 2007; Miyata and Fujita 2010). It would appear that obtaining food from a nearby compared to a far feeder was not particularly attractive in the current study. Perhaps, the birds were somewhat satiated by consuming four peas initially from the first feeder, so that obtaining an additional four peas from the adjacent feeder in the cluster was devalued. Observations indicated that the birds were not subsequently slower or less efficient on later trials in the daily session, however. In addition, the birds in both groups appeared motivated to display evidence of efficient behavior in Experiment 2. Another possibility is that the birds failed to recognize the group of two feeders as a “cluster” as the two feeders were always separated by approximately half a meter. In the operant studies in particular, the groups of objects were proportionally closer together in the cluster.

This hypothesis could be investigated by moving the pair of feeders closer together during testing in future work in the room environment. Finally, it may have been the case that returning to the enclosed box (start or end) was more motivating than the food (though the birds typically consumed all of the peas at a feeder). The distance of the route (or time to complete the trial) was the same regardless of whether the birds selected the cluster or the lone feeder first during the cluster tests. The pigeons in the one-way group appeared to be influenced more by minimizing the total distance of the route for the problems in which the difference between efficient and inefficient routes was larger. Again, this might be accounted for by the motivation to move as efficiently as possible to the end box to complete the trial. Thus, whereas the pigeons in the operant projects mentioned above were likely influenced more by going to the clusters to minimize their delay to food, the pigeons in the current study were likely influenced more by minimizing their delay for returning to shelter.

General discussion

Past work has indicated that animals can take efficient routes when solving TSPs, but the spatial cognitive strategies that are used to solve these problems have remained elusive, particularly for animals other than non-human primates. In addition, the conditions in which animals other than primates might change strategies also remain unclear. In the current study, we presented pigeons in one-way and round-trip groups with TSPs involving two and three feeders. We documented that pigeons show a strong preference for selecting locations that are close to their current position when developing a route. The results from nearly every test configuration used in Experiment 1 indicated that pigeons weighted the proximity of the next potential feeder relative to their current location heavily when determining where to go next. Likewise, the results from configurations a and b (and to a lesser extent configurations c and d) in Experiment 2 demonstrate that pigeons preferred a shorter leg to a nearby feeder even if it resulted in a longer total route (and any associated costs, e.g., total trip length, delays to subsequent feeders). The results are consistent with past working showing that pigeons and non-human primates prefer nearby locations when solving TSP-like tasks. Miyata and Fujita (2010) found that in an operant version of the one-way TSP, pigeons tended to travel to goals that were closer in proximity to a start location than goals that were farther away. Likewise, Janson (1998) found that capuchin monkeys moved more often to nearby destinations than would be expected by chance. Perhaps, the weight given to proximity should not be surprising since many animals prefer choosing a smaller immediate

reward rather than waiting for a larger one later (see Stevens and Stephens 2008 for a review). Choosing to travel to a closer feeder rather than a farther one would appear to minimize the amount of time a pigeon would have to wait to get food in the short term. However, as mentioned in the Discussion for Experiment 2, the birds in the current experiment may have been influenced also by minimizing the time to complete the trial and enter the end box.

The use of proximity would appear to be a relatively local solution—one in which pigeons do not need to consider their choice of feeders beyond their next move. It is also possible that by utilizing such a solution, the pigeons could determine their route “on the go” as they traveled from feeder to feeder. A local proximity-based solution would appear to be less cognitively demanding, as the pigeon would not be required to represent multiple locations in memory, nor spend cognitive resources calculating routes. Instead, using proximity, the pigeon could stick with a simple rule to guide their behavior, which in many cases would lead to an efficient route.

Proximity does not, however, provide a good account for performance during other tests in Experiment 2, however. The results from the one-way group for test configurations e–h show strong evidence for planning. For these problems (and for this group in particular), the additional costs associated with choosing a less efficient route (i.e., one selected using proximity only) may have driven more efficient behavior that required planning beyond just the next step. Likewise, the pigeons in the round-trip group also showed evidence for planning with configurations e–g. These birds also made choices that were consistent with planning beyond the next step. Indeed, our data suggest that pigeons were likely looking two steps ahead in order to make the choices we observed. During each test with three feeders, the birds had four legs (between two locations) for each trip. Our analysis focused primarily on the decision point around the second choice or leg of the journey. In order to make an efficient decision at this point, the bird had to consider the geometry of the remaining two legs of the journey. The finding is consistent with other work, suggesting that pigeons may be capable of planning one or two steps ahead (Miyata and Fujita 2006, 2008).

It does appear that proximity did play a role, particularly for the first choice after departing *S*, even when there was evidence that the birds planned beyond the next step. For instance, the birds in the round-trip group almost always chose the closest feeder from *S* during configurations f–h as their first choice in Experiment 2, even though choosing feeder 1, 2, or 3, respectively, would have resulted in a route with an identical length. The arrangement of the feeders in these configurations, however, still allowed the pigeons to plan ahead after their first choice and subsequently choose an efficient route, in contrast to

configurations a and b in which a proximal first choice resulted in a less efficient route. Perhaps, the pigeons were able to represent the problem more globally, but only showed evidence of planning beyond the next step when costs associated with a proximity-based rule increased.

Another concern is that the pigeons in each group may have used a general response solution during Experiment 2 which would mimic planning ahead. Specifically, the pigeons in the one-way group may have learned to perform a Z-pattern and the birds in the round-trip group may have had a tendency to perform in circular path to the feeders before returning home. It is difficult to completely eliminate this possibility without further work, but there are several bits of evidence which suggests that these response strategies may not have been used extensively. First, the pigeons in both groups show evidence of planning during the early phases of testing in Experiment 2, prior to having extensive experience with the three feeder displays and the development of the aforementioned response tendencies. Second, we intentionally dispersed test configurations with random configurations to disrupt the formation of such tendencies. Future work will be required to explore the role of learned response patterns and planning ahead as it relates to the TSP.

It is difficult to know the nature of the pigeons' spatial representation when we found evidence for planning beyond the next step in Experiment 2. There are several points to consider here. The first is whether the birds were using a cognitive map when planning future movements. Certainly, the evidence suggests that the birds were aware of multiple feeders and the geometric relationships between them to make the observed decisions. An awareness of the geometric relationships between multiple feeders is consistent with a more "global" perspective than simply using proximity as a cue—which is consistent with the notion of a cognitive map (e.g., Gallistel 1990). Past work has demonstrated, however, that improved spatial performance during spatial tasks may be due to other processes. For example, Brown and Drew (1998) found that perceptual learning could improve the ability of rats to discriminate between familiar and unfamiliar spatial locations, which might require a somewhat different type of representation than a cognitive map.

A related issue is at what point in the route did the pigeons' detect most or all of the feeders in the problem? Certainly, the pattern of the pigeons' behavior in Experiment 1 suggests that they were able to detect feeders that were well distributed in the room (some pigeons travel to more remote feeders first). The behavior of the pigeons in Experiment 2 showed evidence that they were able to plan several steps ahead in the problem, suggesting that they likely detected most or all of the feeders at *S* or shortly thereafter. Of course this is an observation only, and future

empirical work will need to be conducted to examine this issue more closely.

A third consideration regarding representations is whether the pigeons were using prospective or retrospective information about visited feeders during their decision-making process. Cook et al. (1985) examined the performance of rats on a 12-arm radial maze and found evidence for a dual-code process. Specifically, rats appeared to be using retrospective information early during the trial, but prospective information after about half of the choices had been made. It would be interesting if pigeons, particularly given more feeder choices, use a dual-code process when solving TSPs. Future empirical work will be required to determine the nature of the spatial representations that the pigeons may be using to solve traveling problems like the ones used in the current study.

Finally, our results have demonstrated that the spatial cognitive mechanisms used to solve TSPs in an operant environment would appear to be similar to those utilized in the tasks in which pigeons have to move through a room. While the principles guiding the pigeons' searching behavior would appear to be best applied to how they may move or forage in relatively small environments in nature, they may also apply to navigation on a larger scale. Further work will need to be done to explore this possibility.

The results from the current experiment show that pigeons weight proximity heavily when determining a route to multiple locations. The use of proximity-based solutions like the nearest neighbor can result in efficient travel behavior. In addition, our work provides further documentation that pigeons can plan several steps ahead along the route (Miyata and Fujita 2008, 2010) when the differences in travel costs between efficient and less efficient routes based on proximity become larger. Thus, an animal other than a primate would appear capable of planning a complex route, suggesting the use of a relatively sophisticated spatial cognitive ability.

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