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TESTING A STOCHASTIC FORAGING MODEL IN AN OPERANT SIMULATION: AGREEMENT WITH QUALITATIVE BUT NOT QUANTITATIVE PREDICTIONS

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An operant simulation of foraging through baited and empty patches was studied with 4 pigeons. On a three-key panel, side keys were designated as patches, and successive opportunities to complete 16 fixed-ratio 10 schedules on side keys were defined as encounters with feeders. In a random half of the patches in any session, some of the fixed-ratio 10 schedules yielded reinforcement (baited feeders) and the other schedules yielded nonreinforcement (empty feeders). In the other half of the patches, all feeders were empty. Pigeons could travel between patches at any time by completing a fixed-ratio schedule on the center key. An optimal foraging model was tested in Experiments 1 and 2 by varying center-key travel time and number of baited feeders in baited patches. The ordinal predictions that number of feeders visited in empty patches would increase with travel time and decrease as number of baited feeders increased were supported, but pigeons visited far more feeders in empty patches than the optimal number predicted by the model to maximize energy/time. In Experiment 3, evidence was found to suggest that the number of empty feeders encountered before the first baited feeder in baited patches is an important factor controlling leaving empty patches.

Key words: optimal foraging, stochastic model, patch, travel time, operant simulation, fixed-ratio schedule, feeders visited, key peck, pigeon

In some recent experiments, a stochastic model of optimal foraging has been tested with downy woodpeckers (*Picoides pubescens*; Lima, 1984) and with laboratory rats (*Rattus norvegicus*; Roberts, 1991). Animals foraged through patches, each of which contained several food locations or feeders. A random half of the patches contained food in selected feeders (baited patches), and the other half contained no food at any feeders (empty patches). The question of major interest was how many feeders a forager would sample in empty patches before leaving the patch. The stochastic model allowed a calculation of the optimal number of empty feeders that should be visited in empty patches in order to maximize the overall energy obtained for time spent foraging (E/T). The optimal number decreased as the probability of food at feeders in baited patches increased, thus allowing the model to be tested at several levels of patch density.

Assume that patches contain F total feeders and that each baited patch has b randomly baited feeders. If n is the number of empty feeders a forager visits in a patch, a forager cannot logically know whether it is in an empty patch until it has visited $n = F - b + 1$ empty feeders. If it visits this number or more feeders, it risks wasting time in an empty patch. If it leaves before this number, it risks leaving a baited patch with no food. The probability of making this latter error, $P(n)$, is given for any value of n by the following formula:

$$P(n) = \frac{(F - n)!(F - b)!}{(F - n - b)!F!} \qquad n \leq F - b. \quad (1)$$

The average number of baited feeders (BF) encountered on a single foraging bout for different levels of n is calculated as follows:

$$BF = .5[1 - P(n)]b. \quad (2)$$

It is assumed that a forager, once having encountered a baited feeder in a baited patch, will visit all of the feeders in the patch (Stephens & Krebs, 1986). Based on empirical estimates of the search and handling time at baited feeders (t_b) and the search time at empty feeders (t_e), the average time taken in baited patches (T_b) is

$$T_b = bt_b + (F - b)t_e. \quad (3)$$

With a final empirical value calculated for the time to travel between patches, t_t, the total foraging time (FT) per patch can be determined for any value of n:

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$$FT = .5[(1 - P(n))T_b + P(n)nt_e + nt_e] + t_t. \quad (4)$$

For a given level of patch density or b baited feeders, the optimal value of n can be found as that number that maximizes E/T or BF/FT from the above equations.

In Lima's experiments with downy woodpeckers, patches consisted of lengths of tree with 24 holes drilled in each (Lima, 1984). In separate tests, 6, 12, or 24 holes were baited in baited patches. When b equaled 6 and 24 holes, woodpeckers left empty patches at close to the optimal value of n empty feeders visited. When 12 holes contained food, the average number of feeders visited in empty patches exceeded the optimal n value. Roberts (1991, Experiment 1) tested rats on a four-arm radial maze, with 10 feeders located on each arm. When b was varied over values of 3, 5, and 7, the mean number of feeders visited in empty patches overshot the optimal value of n by 0.6 to 1.6 feeders. When the maximum number of 10 feeders was baited, rats almost always left empty patches after visiting the optimum value of one empty feeder. The behavior of both woodpeckers and rats agreed with the ordinal prediction from the optimal foraging model that feeders visited in empty patches would decline as b increased.

In the experiments reported here, 4 pigeons were tested in an operant simulation of the stochastic problem previously studied with downy woodpeckers and rats. A three-key panel was used, with the two side keys representing two different patches and the center key acting as a travel key. Within each patch, a pigeon could complete as many as 16 successive fixed-ratio (FR) 10 schedules, with each FR 10 defined as an encounter with a potential feeding location or feeder. A pigeon could leave a patch at any time by completing an FR schedule (travel time) on the center key. Completion of the FR darkened the previously lit side key and illuminated the alternative side key. Ten patch visits were allowed on each daily session, with five patches baited and five patches empty. Baited patches contained b baited feeders randomly distributed among the 16 feeders in the patch. Thus, both travel time and patch density could be manipulated, and temporal components of foraging were recorded by computer. The dependent variable of primary interest was the number of feeders visited in empty patches when different numbers of baited feeders were arranged in baited patches. There were two main reasons for doing these experiments. First, they tested the generality of Lima's model with yet another species. Second, the use of successive FR completions as feeders within patches allowed the specific sequence in which empty and baited feeders were encountered to be controlled. Manipulation of this sequence provided an important theoretical test in Experiment 3.

EXPERIMENT 1

Patch-leaving behavior was studied in pigeons over 30 foraging sessions in which patch density in baited patches was held constant at 25% (or $b = 4$). Travel time between patches (t_t) was varied by requiring pigeons to complete an FR 10, FR 30, or FR 60 on the center key in order to enter a new patch. The time components of foraging sessions, t_b, t_e, and t_t, were measured and used to calculate the optimal value of n.

METHOD

Subjects

Four adult White King pigeons (*Columba livia*) served as subjects. These birds had previously served as subjects in delayed matching-to-sample experiments. Each bird was housed in an individual wire cage and had constant access to water and grit. Food access was controlled to keep each pigeon at approximately 80% of its free-feeding weight. Lights in the housing room came on at 8:30 a.m. and went off at 10:30 p.m. Testing was carried out between 9:00 a.m. and 12:00 p.m. 6 days a week.

Apparatus

Two operant conditioning chambers were used that measured 31 cm by 35.5 cm (floor dimensions) by 35.3 cm (height). The front walls contained a row of three pecking keys, level with a pigeon's head, spaced 8 cm apart, center to center. Projectors mounted behind the keys presented black and white patterns or colored fields on each key. An electromechanical food hopper provided mixed grain through an opening (6 cm by 6 cm) centered on the front wall below the pecking keys.

All of the foraging contingencies were controlled by a Commodore® 64 computer and a

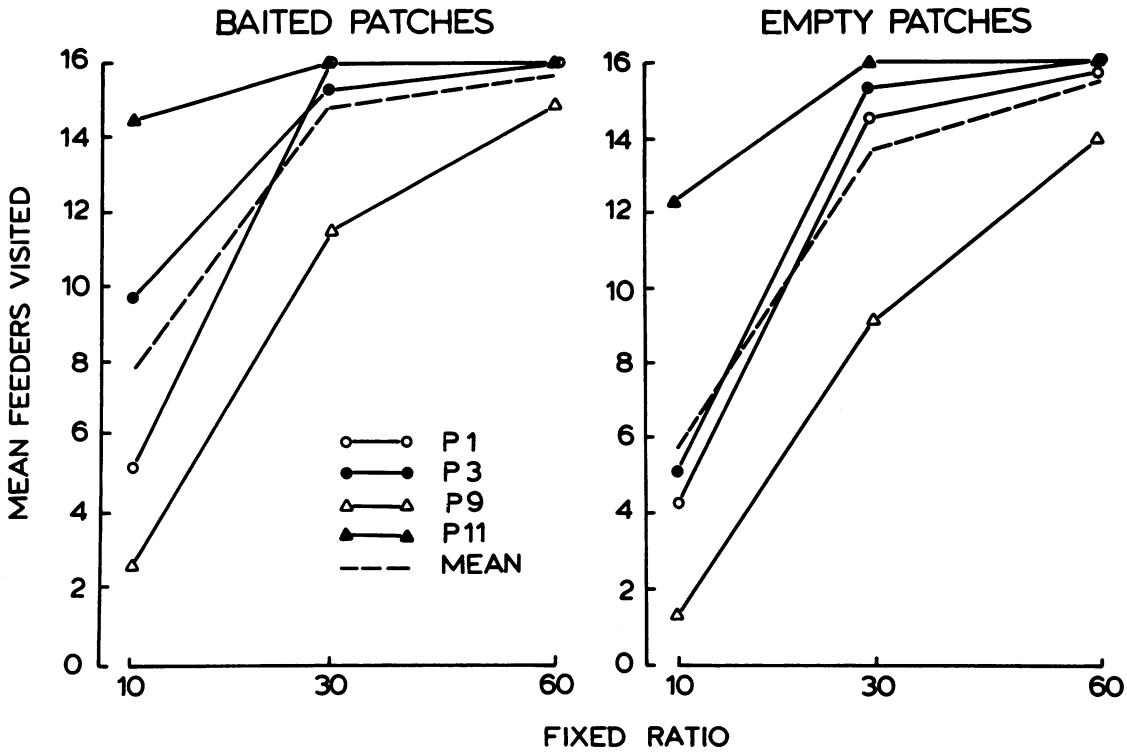

Fig. 1. Mean number of feeders visited before leaving baited and empty patches, plotted as a function of the FR travel requirement for each pigeon.

locally constructed interface. The computer also recorded the time of each foraging component.

Procedure

The side keys in each chamber could be lit with patterns of three black stripes (3 mm wide) on a white background, oriented vertically and horizontally on the left and right keys, respectively. The center key was white and remained lit throughout a session. At the beginning of a session, a pigeon was placed in a chamber with one randomly chosen side key lit and the other darkened. Pecks on the lit side key completed an FR 10 schedule that ended in either a 3-s grain delivery or a 5-s timeout period in which the side key was darkened. Following reinforcement, the side key remained darkened for the 5-s timeout period. If a pigeon completed 16 FR 10 schedules on a side key, the side key remained dark after the timeout. Only the completion of an FR schedule on the white center key would now illuminate the other side key. Once lit, the other side key could be responded to up to a maximum of 16 FR 10 schedules. At any point during a bird's responding to one side key, it could switch to the other side key by pecking on the center key. Completion of the required FR on the center key darkened the first side key and illuminated the second. Once a pigeon initiated pecking on the center key, the previous side key was deactivated, and the subject could only complete the FR and enter a new patch.

During each session, five patches were randomly chosen by the computer as baited patches, and the other five patches were empty. In empty patches, all 16 feeders or FR 10 schedules terminated in nonreinforcement. In baited patches, four feeders randomly chosen by the computer yielded reinforcement. Each pigeon was tested for three successive blocks of 10 sessions at each of three travel time requirements. In order to travel from one side key (patch) to the other, a pigeon had to complete an FR 10, FR 30, or FR 60 on the center key. The center-key FRs were tested in the order 10-30-60 with Pigeon 1, 30-60-10 with

Table 1

Mean travel time between patches (t_t), search and handling time at baited feeders (t_b), search time at empty feeders (t_e), observed number of feeders visited in empty patches (n), and optimal value of n for each pigeon at each travel FR.

Pigeon	t_t(s)	t_b(s)	t_e(s)	Observed n	Optimal n
FR 10					
1	5.29	11.67	8.67	4.20	4
3	5.72	11.24	8.24	5.12	4
9	2.41	11.65	8.65	1.52	3
11	12.60	11.30	8.30	12.24	5
FR 30					
1	105.41	12.79	9.79	14.44	7
3	25.40	11.82	8.82	15.36	5
9	7.88	14.24	11.24	9.24	4
11	43.93	11.21	8.21	16.00	6
FR 60					
1	147.87	11.65	8.65	15.88	7
3	28.26	12.78	9.78	16.00	5
9	28.33	13.52	10.52	13.96	5
11	104.90	11.16	8.16	16.00	7

Pigeon 3, 60-10-30 with Pigeon 9, and 10-60-30 with Pigeon 11.

All statistical tests were considered significant if alpha was less than .05.

Results

All of the data presented were taken from the last five sessions of testing with each pigeon under each FR travel time. Figure 1 presents the mean number of feeders visited up to the point of patch departure for each pigeon at each FR; data from baited patches appear in the left panel, and data from empty patches appear in the right panel. All 4 birds showed an increase in mean number of feeders visited as the travel time FR increased, both within baited and empty patches. The effect of travel time was more marked from FR 10 to FR 30 than from FR 30 to FR 60, and was somewhat stronger in empty patches than in baited patches. Subjects × Travel Time analyses of variance (ANOVAs) yielded statistically significant effects of travel time both in baited patches, $F(2, 6) = 10.44$, and empty patches, $F(2, 6) = 21.56$.

Table 1 shows, for each pigeon at FR 10, FR 30, or FR 60, the median values of travel time between patches (t_t), time for search and handling at baited feeders (t_b), and search time at empty feeders (t_e). Substantial individual differences in t_t were apparent, with Pigeons 1 and 11 taking much longer to complete the FR 30 and FR 60 travel times than Pigeons 3 and 9. By contrast, t_b and t_e were fairly homogeneous across birds and FRs; these times represent the time required to complete the FR 10 on a side key plus the 5-s timeout for t_e and the 3-s grain delivery time for t_b. ANOVAs showed that mean t_t increased significantly as FR increased, $F(2, 6) = 5.28$, but t_b and t_e did not vary as a function of FR, $F(2, 6) = 2.26$.

These time components were used to calculate the optimal n for each pigeon using Equations 1 to 4; the optimal n is an integer value that represents that number of empty feeders a pigeon should visit before leaving a patch in order to maximize BF/FT. The "observed n" column shows the mean number of feeders visited in empty patches for comparison with the optimal n. At FR 10, the observed n agrees fairly closely with the optimal n for Pigeon 1, with Pigeon 3 overshooting the optimal n by 1.12 feeders and Pigeon 9 undershooting it by 1.48 feeders. In sharp contrast to the reasonable approximation by these 3 birds, Pigeon 11's observed n vastly exceeded its optimal n by 7.24 feeders. The optimal n increased for each bird as travel time increased to FR 30 and FR 60. Although observed n also increased with travel time, observed values of n at FR 30 and FR 60 were far in excess of optimal values of n for each subject.

Discussion

Pigeons' patch-leaving behavior, defined as switching from one side key to another, was strongly controlled by the FR travel time on the center key. The increase in feeders visited in empty patches as FR increased clearly agreed with the predicted increase in optimal n as travel time increased. Although the ordinal prediction from Lima's (1984) stochastic model was supported, the precise predictions of optimal n values far underestimated the observed values of n, particularly at the longer FRs.

EXPERIMENT 2

Experiment 1 involved an examination of only one level of patch density, 25% or $b = 4$. In Experiment 2, predictions from the stochastic model were tested over four levels of patch density, $b = 4$, 8, 12, and 16. An ordinal

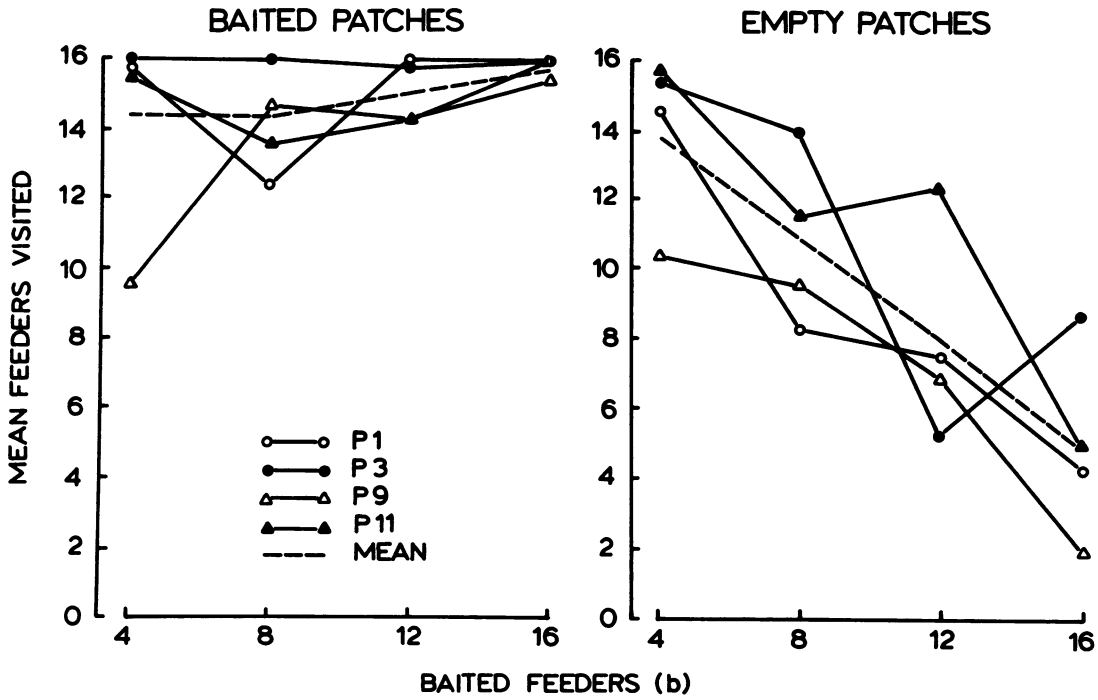

Fig. 2. Mean number of feeders visited before leaving baited and empty patches, plotted as a function of number of baited feeders in baited patches (b) for each pigeon.

prediction from the model is that animals should leave an empty patch sooner the higher the density of baited patches; that is, observed n should decrease as b increases. Further, quantitative predictions about the match between optimal and observed values of n were made at different levels of baited patch density.

Method

Subjects and Apparatus

The same pigeons and apparatus used in Experiment 1 were used in Experiment 2.

Procedure

The experiment was carried out over a period of 40 daily sessions. Each pigeon was tested for 10 sessions with b set at values of 4, 8, 12, or 16 baited feeders in baited patches in each block of sessions. These values of b were tested in the order 4-8-16-12 with Pigeon 1, 8-12-4-16 with Pigeon 3, 12-16-8-4 with Pigeon 9, and 16-4-12-8 with Pigeon 11. As in Experiment 1, pigeons foraged through 10 patches per session, with up to 16 feeders to be visited in each patch. Five patches were randomly selected in each session to have b feeders baited at randomly selected ordinal positions, and the other five patches were empty. The travel-time requirement on the center key was held constant throughout the experiment at FR 30. All of the other parameters of the experiment were the same as those used in Experiment 1.

Results

All data presented were taken from the last five sessions of testing at each level of b. Figure 2 presents the mean number of feeders visited in baited and empty patches as a function of b for each subject. The data for baited patches (shown in the left panel) indicate that pigeons generally visited all or nearly all of the 16 feeders available in baited patches. Only Pigeon 9 showed a sizable reduction in feeders visited at $b = 4$, visiting only 9.60 feeders. An ANOVA indicated that the group average of mean number of feeders visited did not vary significantly as a function of b, $F < 1.0$. By contrast, the mean number of feeders visited in empty patches (shown in the right panel) decreased markedly as a function of b for each pigeon. The mean of all 4 pigeons dropped

Table 2

Mean travel time between patches (t_t), search and handling time at baited feeders (t_b), search time at empty feeders (t_e), observed number of feeders visited in empty patches (n), and optimal value of n for each pigeon at each level of b baited feeders.

Pigeon	t_t(s)	t_b(s)	t_e(s)	Observed n	Optimal n
$b = 4$					
1	28.28	12.49	9.49	14.40	5
3	18.26	11.84	8.84	15.30	5
9	8.77	10.75	7.75	10.28	4
11	25.32	10.69	7.69	15.80	5
$b = 8$					
1	14.20	13.41	10.41	8.30	2
3	23.72	11.07	8.07	14.00	3
9	12.37	11.20	8.20	9.70	2
11	23.43	10.87	7.87	11.52	3
$b = 12$					
1	27.73	12.97	9.97	7.48	2
3	17.98	11.28	9.28	5.24	2
9	8.25	11.30	8.30	6.90	1
11	19.29	11.66	8.66	12.40	2
$b = 16$					
1	19.27	12.01	9.01	4.28	1
3	12.19	11.42	8.42	8.64	1
9	7.11	10.34	7.34	2.00	1
11	13.52	12.18	9.18	5.00	1

from 13.94 at $b = 4$ to 4.98 at $b = 16$, and the effect of b also was statistically significant, $F(3, 9) = 11.45$.

Median values of t_t, t_b, and t_e are presented in Table 2 for each pigeon at each level of b. The travel times to complete an FR 30 (t_t) generally were lower and more homogeneous than those seen in Experiment 1; the means of t_t did not vary systematically across levels of b, $F(3, 9) = 1.81$. As in Experiment 1, t_b and t_e were homogeneous across pigeons and did not vary systematically as a function of b, $F < 1.0$.

The optimal number of empty feeders to visit before leaving a patch was calculated from the times in Table 2 and can be compared with the observed mean values of n in the final two columns of Table 2. Optimal values of n dropped as patch density increased from 25% to 100%, and there was a corresponding drop in observed n, as seen in the table and Figure 2. Nevertheless, all 4 birds consistently stayed in empty patches far beyond the optimal number of empty feeders. When all feeders in the baited patches contained food ($b = 16$), Pigeon 9 visited a mean of 2.00 feeders before leaving empty patches, thus approximating optimal performance. However, the other 3 subjects overshot the optimal value by three or more feeders. This tendency to exceed the optimal n became more marked as b decreased, with observed n exceeding optimal n by 6 to 10 feeders at $b = 4$.

Discussion

The effect of patch density on patch-leaving behavior was clearly in agreement with the ordinal prediction from Lima's (1984) stochastic model; as b increased, pigeons visited markedly fewer feeders in empty patches. However, just as in Experiment 1, pigeons stayed in empty patches far beyond the optimal number of feeders. In this operant analogue of stochastic foraging, pigeons clearly did not leave patches at a point that would maximize BF/FT.

EXPERIMENT 3

Having shown clearly in Experiment 2 that pigeons leave empty patches sooner the higher the density of food in baited patches, Experiment 3 was carried out to examine a possible mechanism responsible for this relation. Roberts (1991) pointed out that an animal visiting feeders in a partially baited patch often encountered a delay before the first baited feeder. This delay can be quantified in several ways: in terms of empty feeders visited, time, or work expended foraging through empty feeders. Using the number of empty feeders visited before the first encounter with a baited feeder, the average delay in empty feeders will increase as b decreases. The stochastic foraging situation used here then could be viewed as analogous to an animal discriminating between periods of varying delay to reinforcement. The delay-reduction hypothesis (Abarca & Fantino, 1982; Fantino & Abarca, 1985) suggests that foragers will choose the baited or shorter delay patch, but discrimination between baited and empty patches must be based on the delay in time or number of empty feeders to first baited feeder in baited patches. Thus, the inverse relation between b and feeders visited in empty patches may represent differences in the ease of discriminating delay to first baited feeder in baited patches from continuously empty feeders in empty patches.

To test the importance of delay discrimination, delay to first baited feeder should be manipulated without the confounding effect of patch density. The importance of delay is difficult to test in open patches in which animals can visit feeders in any order, because the number of empty feeders visited before a baited feeder is encountered in baited patches cannot be precisely manipulated. In the procedure used with pigeons in these experiments, however, feeders are defined as successive opportunities to complete an FR 10 on a side key, and the order of empty and baited feeders can be precisely controlled. In Experiment 3, pigeons foraged through baited patches with patch density held constant at 37.5% (or $b = 6$). Between blocks of sessions, initial delay of the first baited feeder was varied in baited patches by programming short or long strings of encounters with empty feeders before the first encounter with a baited feeder. If delay of encounter with the first baited feeder is an important variable controlling patch-leaving decisions, the number of feeders visited in empty patches should vary directly with delay length in baited patches.

Method

Subjects and Apparatus

The same 4 pigeons and the same apparatus used in Experiments 1 and 2 were used in Experiment 3.

Procedure

Each pigeon was tested over a period of 40 sessions, with 10 patch entries in each session. Five randomly selected patches contained six baited feeders and 10 empty feeders, and the other five patches contained 16 empty feeders. Travel between the side-key patches required the completion of an FR 40 schedule on the center key. All other time and response-ratio parameters were the same as those used in Experiments 1 and 2.

Each session was designated as short delay or long delay, indicating the length of the delay that preceded the first baited feeder in baited patches. On short-delay sessions, the first baited feeder was always encountered after zero or one empty feeder had been encountered. On long-delay sessions, the first baited feeder was not encountered until four to eight empty feeders had been encountered. The remaining five reinforcers were randomly distributed over the remaining feeder visits. An A-B-A design was used with each subject. Pigeons 1 and 9 began the experiment with 10 short-delay sessions, were then given 20 long-delay sessions, and then completed the experiment with 10 short-delay sessions. Pigeons 3 and 11 initially completed 10 long-delay sessions, followed by 20 short-delay sessions and 10 more long-delay sessions.

Results and Discussion

Mean numbers of feeders visited in baited and empty patches are plotted across blocks of two sessions in Figure 3, with each subject's data contained in a separate panel. Curves for baited patches show that pigeons visited all or nearly all of the 16 feeders on both short-delay and long-delay sessions. Visits to feeders in empty patches, on the other hand, were strongly controlled by short versus long delays to the first baited feeder. Each pigeon showed a clear tendency to decrease feeders visited over short-delay sessions and to increase feeders visited over long-delay sessions. The mean number of feeders visited over the final five sessions of the short-delay phases was 7.54, and the mean number of feeders visited over the final five sessions of long-delay phases was 13.00; these means differed significantly, $t(3) = 15.91$.

With the food density of baited patches held constant, pigeons' readiness to abandon empty patches was strongly affected by how many empty feeders preceded the first baited feeder encountered in baited patches. This finding supports the hypothesis that length of delay to first baited feeder forms a basis for a patch-leaving rule in pigeons and perhaps other animals. However, if such a rule was applicable, it was used very conservatively. The longest delay on short sessions was one empty feeder, and the longest delay on long sessions was eight empty feeders. The mean number of feeders visited in empty patches exceeded the maximum delay in baited patches by four to six feeders. Thus, the findings of Experiment 3, like those of Experiments 1 and 2, suggest that pigeons did not make optimal use of information from baited patches to depart from empty patches.

GENERAL DISCUSSION

Pigeons were tested in an operant simulation of stochastic foraging between randomly

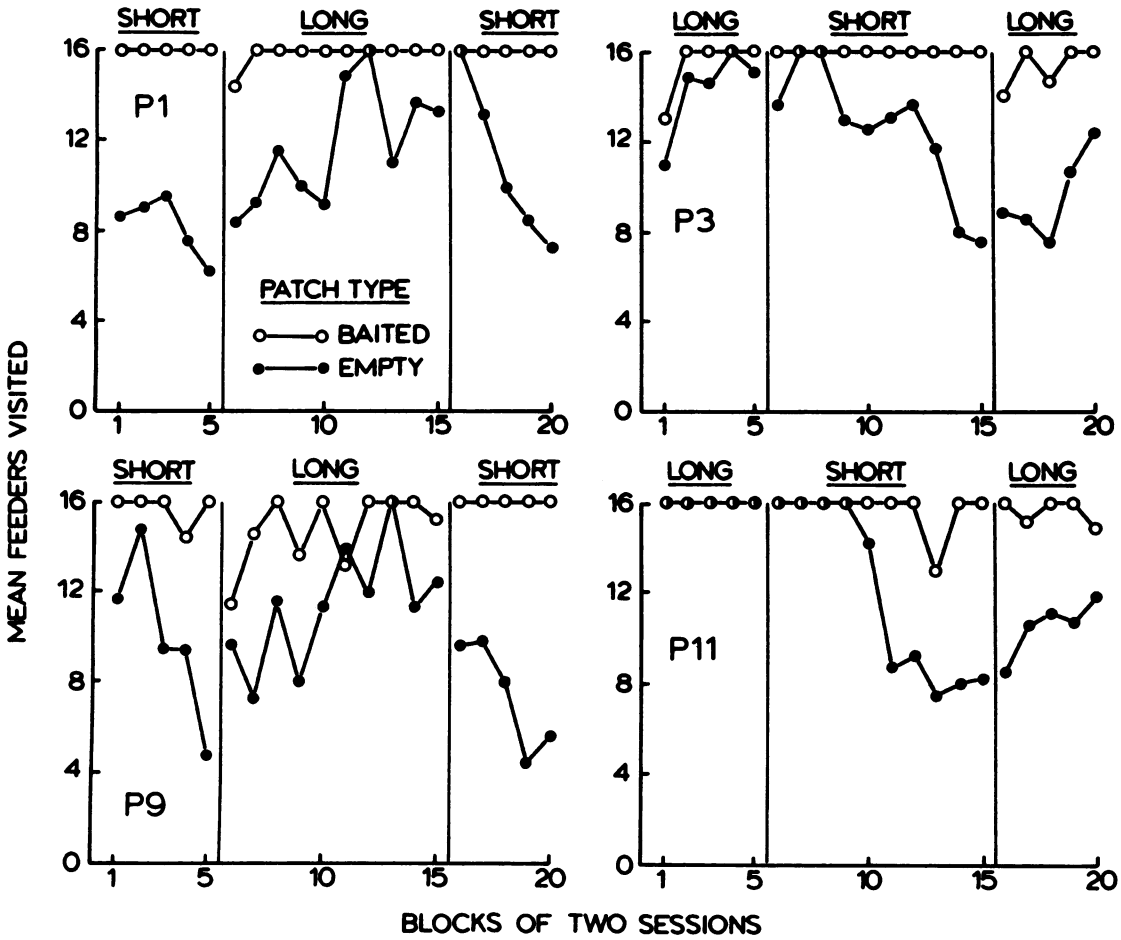

Fig. 3. Mean number of feeders visited before leaving baited and empty patches, plotted over blocks of two sessions, with separate panels for each pigeon. "Short" and "long" refer to the length of delays encountered in baited patches before the first baited feeder.

occurring baited and empty patches. Ordinal predictions derived from Lima's (1984) model about how certain variables should affect pigeons' readiness to leave empty patches were supported. Specifically, pigeons left empty patches later the greater the travel FR on the center key, and pigeons left empty patches sooner the higher the patch density in baited patches. Both of these findings agree with changes in optimal n as travel time or patch density is varied.

In contrast to the ordinal agreement between theory and data, the quantitative match between optimal n and pigeons' observed n was poor. Pigeons consistently stayed in empty patches far longer than was optimal for maximizing BF/FT. This finding is particularly striking when it is aligned with findings of other tests of the model. Downy woodpeckers (Lima, 1984) diverged from the model's predictions when baited patch density was 50% and clearly visited more than the optimal number of holes. Rats (Roberts, 1991) somewhat exceeded the optimal number of empty feeders at each patch density on the radial maze. These findings, combined with the present observations that pigeons tested in an operant conditioning chamber vastly exceeded optimal predictions under all conditions tested, suggest that animals do not forage optimally in the stochastic situation modeled.

Recent work with concurrent schedules has shown that choice between schedules is strongly affected by changeover requirements. Pliskoff, Cicerone, and Nelson (1978) and Pliskoff and Fetterman (1981) found undermatching for

time spent in variable-interval schedules when an FR 1 was required for changeover, but found overmatching when higher FRs were required. Similar results have been found by Davison (1991) when fixed-interval schedules of different length were required for changeover, and by Baum (1982) when pigeons were required to walk around a partition and climb over a hurdle to reach the alternative key. Baum (1982) suggested that overmatching found with increased changeover requirements might represent optimal foraging under increased travel time. However, no precise criterion for optimal foraging was used in those experiments. The experiments reported here tested a foraging model that provided exact quantitative predictions of optimal behavior. The results clearly fail to support Baum's speculation. With an FR requirement of several pecks on the center key to travel between patches, pigeons stayed in empty patches far longer than the model predicted. Further, the tendency to exceed optimal predictions increased as the FR was raised in Experiment 1.

Why did pigeons stay in empty patches far longer than was optimal? The results of Experiment 3 clearly suggested that leaving empty patches was partially controlled by the delay to first baited feeder, or reinforced FR 10, in baited patches. In Experiment 2, the maximum delays to a baited feeder in baited patches were 12, 8, 4, and 0 empty feeders when b = 4, 8, 12, and 16, respectively. The subjects' mean visits to feeders in empty patches tended to somewhat exceed these maximum delays. It could be argued that pigeons learned the maximum delays and exhibited a conservative strategy of slightly exceeding them before leaving a patch. Unfortunately, the results of Experiment 3 discourage this interpretation. When the delay to first reinforcement in baited patches was held constant at zero or one, pigeons still visited a mean of 7.54 feeders before leaving empty patches. In this case, the number of empty feeders visited far exceeded even a conservative estimate of the number needed to conclude that the patch was empty.

Switching from a mechanistic to a functional approach, it could be argued that the model did not work because it does not contain all of the constraints that acted on the evolution of pigeon foraging (Shettleworth, 1988). Other factors, in addition to maximizing energy accumulation over time, might have shaped patch-leaving behavior. For example, travel between patches in the real world entails the risk of predation (Lima, 1985; Phelps & Roberts, 1989) and the possibility that food in other patches has been consumed by predators or conspecifics. If such factors were used as further constraints in a stochastic model, predictions about optimal patch-leaving decisions might be more conservative than those predicted by the model tested here. A new model would have to quantify these factors and show how they influence patch-departure decisions. Although such a model may be developed in the future, the contribution of these experiments is to show that the current stochastic model, based only on maximizing E/T, appears to be inadequate.

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