LEAVING PATCHES: AN INVESTIGATION OF A LABORATORY ANALOGUE

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Five pigeons were trained on a procedure that has been used as a laboratory analogue to natural patch residence. Trials commenced with two responses available. One of these might provide a reinforcer if the patch was a prey patch; the other ended the residence time in the patch and, after a fixed travel time in blackout, produced another patch that might or might not provide a reinforcer. Patch residence also ended, and was followed by the same travel time, after a reinforcer was obtained or after a fixed maximum time was spent in the patch. The dependent variable was patch residence time, from the commencement of the patch to the time at which the subject emitted a response to exit from the patch or until the maximum patch residence time had elapsed. In Parts 1 to 3, the duration of the imposed travel time was varied from 0.25 to 16 s at three different probabilities (.05, .1, and .2) of food per second (λ) in prey patches. As reported in previous research, both increasing travel time and decreasing probabilities of reinforcers per second increased patch residence time. In Parts 4 to 7, the probability of prey trials (p) was varied in an irregular order from .1, through .2, .5, and .7, to .9 for different combinations of λ and travel time. Respectively, these were in Part 4, .05 per second and 0.25 s; in Part 5, .05 per second and 16 s; in Part 6, .2 per second and 0.25 s; and in Part 7, .2 per second and 16 s. A previously offered model, based on optimization assumptions, substantially and consistently underpredicted patch residence time. However, a modification of that model, which assumes that the subjects could not accurately discriminate the residence time that provided the minimum interreinforcer interval, described the data well. The same model also described previously reported residence times in a different species with a uniform distribution of prey-arrival times.

Key words: patch residence time, prey probability, patch probability, travel time, peck, pigeons

There has been considerable research into understanding the variables that control the behavior of leaving a patch and moving on to another patch. Some of this research has focused on patches that may contain multiple prey items at fixed locations, and has measured the number of empty locations visited before the animal leaves the patch (e.g., Kamil & Yoerg, 1985; Kamil, Yoerg, & Clements, 1988; Roberts, 1991). Other research has looked at patches that may or may not contain a single prey item at a variable location in the patch, and has measured the time from patch entry until the animal leaves the patch (Kamil, Mishal, & Stephens, in press). This is the patch residence time (and has also been called the "moving-on time" by Brunner, Kacelnik, & Gibbon, 1992). Some of the research has been

carried out within the behavioral ecology literature in natural or seminatural settings, and has often focused on the marginal value theorem (Charnov, 1976). Most of the variations in relevant independent variables have had effects on residence times in the direction predicted by the marginal value theorem (see Shettleworth, 1988), but the predictions are often not quantitatively accurate.

One method for studying a behavioral analogue to natural patch residence under laboratory conditions was developed by Kamil et al. (in press). Their procedure was one in which a single prey item might be found somewhere in a patch. They used this procedure to test a model of patch usage that was suggested by McNamara and Houston (1985). This model attempts to predict the length of time that a subject will spend in a patch that may or may not contain a single prey item as a function of three variables: the probability that the patch contains a prey item (is a prey patch) rather than being an empty patch; the length of time required to move between patches (travel time); and the distribution of the prey item over time in a prey patch. Kamil et al. used blue jays as subjects and tenebrio larvae as reinforcers, and provided no information to the subjects on whether a patch contained prey. The following

We thank the Auckland University Research Committee for equipment grants that helped support this research, Jacqui Barrett and Jamie Gemmell, who looked after the subjects, and the academic staff and graduate students who helped run the experiments. We also thank Al Kamil for extensive, interesting, and informative discussions when he was at Auckland University on sabbatical leave. Address correspondence and reprint requests to Michael Davison, Department of Psychology, University of Auckland, Private Bag 92019, Auckland, New Zealand (E-mail: m.davison@auckland.ac.nz).

procedure was arranged: Each trial started with the birds being presented with a start cue. Responding to this cue produced a patch cue behind one key and an exit cue behind the other key. A reinforcer was available for responding to the patch cue on 50% of the trials (prey trials), and no reinforcer was available on the other trials (no-prey trials). On prey trials, the arrival time of the prey was scheduled according to a probability gate set at .075 and sampled every 1 s ($\lambda = 0.075$ per second), and it was signaled when the prey became available. Trials ended with an imposed travel time following food delivery, or following a leave response, or after 120 s, whichever event occurred first. Kamil et al. varied travel times from 4 to 16 s and obtained mean residence times of 24.5 s (4 s), 30.7 s (8 s), and 39.7 s (16 s). In Experiment 2, Kamil et al. arranged a uniform (rather than exponential) distribution of times to prey in prey patches in the range of 2 to 16 s, and varied travel time from 4 to 16 s. In Experiment 3, they used discriminable patches, one of which gave prey according to an exponential distribution, the other according to the same uniform distribution as was used in Experiment 2, and varied travel time from 3 to 18 s. Kamil et al. reported that increasing travel time increased patch residence times in all experiments, and also found that the subjects consistently stayed in patches longer than necessary to maximize their food rates according to McNamara and Houston's model.

The model that McNamara and Houston (1985) offered for the experimental situation described above ("some patches are empty") predicts that the residence time, t , is the value of the residence time that maximizes the reinforcer rate, γ_t , in the following equation:

$$\gamma_t = \frac{p(1 - e^{-\lambda t})}{\tau + qt + \frac{p}{\lambda}(1 - e^{-\lambda t})}, \quad (1)$$

where p is the probability of a prey trial (and q is the complementary probability of a no-prey trial), τ is the travel time arranged, and λ is the probability of food per second in prey trials. In this equation, the numerator expresses the frequency with which prey are obtained for a given residence time, rate of prey arrival, and probability of a prey trial. The denominator expresses the total time spent for-

aging—the travel time plus the time spent in no-prey trials plus the time spent in prey trials for a given patch residence time. For particular values of λ , p , and τ , Equation 1 is solved for the value of t that gives the maximum value of γ_t . As McNamara and Houston showed, this model predicts that patch residence time will increase with travel time. It also predicts that residence time will decrease with increasing food rate in prey patches and with an increasing probability of a no-prey trial. Although Kamil et al. (in press) showed that the effects of travel time were in the direction predicted by McNamara and Houston's model, they also showed that the model predicted residence times that were consistently too short. They did not examine the predictions of the model for the effects of prey probability or rate of food availability in prey trials.

The present experiment was designed to replicate some of Kamil et al.'s (in press) results using a simplified procedure with pigeons. It is of some interest to make a cross-species comparison with these procedures to see whether such results, which are germane to ecological studies of foraging, generalize across species. We also were interested in more detailed quantitative tests of McNamara and Houston's (1985) model. To this end, we arranged a greater number of travel times over a larger range than did Kamil et al., and also arranged three levels of prey rates in prey patches. In addition, we varied the probability of prey trials for both 0.25-s and 16-s travel times and λ values of .05 and .2. Assuming, on the basis of Kamil et al.'s results, that the McNamara-Houston model is incorrect, we hoped that a parametric study of travel time and prey rate would provide sufficient data to be able to develop a more accurate model to predict residence time. In particular, the arrangement of very short travel times is important. As can readily be seen from Equation 1, if travel time tends towards 0 s, then residence time also tends to 0 s. This seems to be an illogical prediction. It has been argued that when there is no travel requirement, the forager effectively remains in the same patch, but if this is the correct interpretation, then the procedure described by McNamara and Houston and employed by Kamil et al., in which an exit response defines movement to a new patch with new contingencies is incompatible with the mathematical model. Thus, in the

present experiment, travel times were varied from 0.25 to 16 s in six steps with three different probabilities of food: $\lambda = .05, .1$, and $.2$ per second.

METHOD

Subjects

Five homing pigeons, numbered 21, 23, 24, 25, and 26, were maintained at $85\% \pm 15$ g of their ad-lib body weights. They had previously been trained on a signal-detection procedure in which they discriminated the amount of grain displayed on slides. They had continuous access to water and grit in their home cages, and were fed an amount of mixed grain, sufficient to maintain their set weights, immediately after their daily training sessions.

Apparatus

The subjects worked in a standard sound-attenuating experimental chamber (330 mm high, 300 mm wide, and 330 mm deep). Two pecking keys, 20 mm in diameter, were located on one wall of the chamber, 130 mm apart and 260 mm above the grid floor. Each key, when illuminated, required a peck of about 0.1 N for operation. Centered beneath the keys, and 100 mm from the floor, was a food magazine. During reinforcement, the keys were darkened and the food magazine containing wheat was lit for 3 s. There was no chamber illumination other than the key and the magazine lights.

Procedure

Sessions commenced in blackout. A few minutes later, the left key was illuminated white and the right key was illuminated red. The keys-on period simulated being in a patch. The patch might contain either a single prey item (food delivery), or contain no prey, with a probability p (Table 1). Pecks to the white left key (prey key) occasionally produced a food delivery according to the probability per second (λ , Table 1) with which such a delivery was arranged, and prey arrival was not signaled. A single peck to the right red key (patch exit response) turned off both keys and started a fixed-duration travel time in blackout. The same travel time also followed a food delivery, and also commenced when 120 s had been spent in the patch without a food delivery or

Table 1

Sequence of experimental conditions, probability of reinforcement per second in a prey trial (λ), travel time in seconds, probability of prey trial, number of sessions to stability, and the parts of the experiment to which the conditions contributed. The data from Condition 32 were lost, so the condition was later arranged as Condition 38.

Con- dition	λ	Travel time (s)	p (prey trial)	Ses- sions	Parts
1	.2	4.00	.5	20	1
2	.2	8.00	.5	25	1
3	.2	16.00	.5	34	1, 7
4	.2	2.00	.5	26	1
5	.2	12.00	.5	23	1
6	.2	0.25	.5	23	1, 6
7	.1	2.00	.5	24	2
8	.1	12.00	.5	21	2
9	.1	4.00	.5	23	2
10	.1	16.00	.5	22	2
11	.1	8.00	.5	25	2
12	.1	0.25	.5	23	2
13	.05	0.25	.5	27	3, 4
14	.05	2.00	.5	22	3
15	.05	12.00	.5	23	3
16	.05	4.00	.5	25	3
17	.05	16.00	.5	21	3, 5
18	.05	8.00	.5	21	3
19	.05	0.25	.5	27	3, 4
20	.05	0.25	.8	23	4
21	.05	0.25	.1	23	4
22	.05	0.25	.9	23	4
23	.05	0.25	.2	19	4
24	.05	16.00	.5	23	5
25	.05	16.00	.2	22	5
26	.05	16.00	.9	43	5
27	.05	16.00	.1	21	5
28	.05	16.00	.8	26	5
29	.2	0.25	.8	31	6
30	.2	0.25	.1	26	6
31	.2	0.25	.9	24	6
33	.2	16.00	.5	23	7
34	.2	16.00	.2	22	7
35	.2	16.00	.9	25	7
36	.2	16.00	.1	24	7
37	.2	16.00	.8	22	7
38	.2	0.25	.2	41	6

a patch exit response. Sessions lasted until either 40 food deliveries had been obtained or until the termination of the first patch after 44 min had elapsed, whichever event occurred sooner.

The sequence of experimental conditions is shown in Table 1. In Part 1 (Conditions 1 to 6), λ , the probability of reinforcement per second in a prey trial, was set at $.2$, and across conditions the travel time was varied from 0.25 to 16 s in six steps. In Part 2 (Conditions 7 to

Fig. 1. Parts 1 to 3. The percentage of all trials that ended after 120 s without food or an exit response as a function of travel time and the probability of a reinforcer per second in prey trials. The data have been averaged over the last five sessions of each experimental condition and across all five subjects.

12), λ was reduced to .1, and in Part 3 (Conditions 13 to 19) to .05, with the same manipulation of travel times in each series. In all these conditions, p , the probability of a prey trial, was .5. In Parts 4 to 7, λ was either .05 or .2, travel time was either 0.25 or 16 s, and the probability of a prey trial was varied from .1 to .9 in five steps for each value of λ and travel time. The number of direct replications is also shown in Table 1.

Training in a condition continued until each of the subjects had reached a defined stability criterion. After 10 sessions on an experimental condition, the ratio of the time spent in prey patches to the time spent in no-prey patches

was calculated for each session and for each subject. Successive, overlapping triplets of these values were compared pairwise. If this measure increased and then decreased, or vice versa, a minor stability criterion was achieved. When this had occurred five (not necessarily consecutive) times for a subject, the performance of that subject was taken as stable. When the behavior of all 5 subjects was stable according to this criterion, the experimental conditions were changed for all subjects. The number of training sessions given in each experimental condition is shown in Table 1.

During each session, the times at which various events (trial starts, trial type, responses, food deliveries, exit responses, and trial endings without exiting) occurred were recorded, and the data from the last five sessions of each experimental condition were analyzed. The main dependent variable was the patch residence time. This is the mean time between the commencement of a trial (of either type) and a subsequent exit response or the end of a trial without an exit response. Note that trials that ended in food deliveries did not contribute to this measure, but that exit responses made on prey trials did contribute to this measure. Trials on which the subject did not obtain a reinforcer and did not emit an exit response also contributed.

RESULTS

All data reported here are taken from the last five sessions of each experimental condition, and these data are provided in the Appendix.

Parts 1 to 3

The subjects clearly used the exit response consistently, and exited the patches on most no-prey trials and on some prey trials. The subjects rather seldom failed either to exit or to gain a reinforcer, resulting in the trial ending after 120 s. Figure 1 shows the percentage of trials that ended after 120 s without food or an exit response, averaged across subjects. It is evident that there was a general increase in this percentage as travel time was increased. Nonparametric trend tests (Ferguson, 1971) showed that the percentage of such trials was not significantly related to travel time when λ was .05, but did increase significantly ($p < .05$) when λ was .1 and .2. Similarly, Figure

$$p(\text{FOOD}) = 0.2/s$$

Fig. 2. Part 1. Mean residence times over the last five sessions of each experimental condition as a function of the travel time imposed for each subject. The value of λ was .2.

1 suggests that there was a general increase in the percentage of uncompleted trials as λ was decreased. But statistical analyses showed that changes in λ did not significantly affect the number of uncompleted trials, except for Bird 26 at a travel time of 12 s, when increasing λ significantly decreased the number of trial endings. Because of the procedure, then, that arranged a maximum time of residence in a patch, we may expect that long mean residence times will be somewhat underestimated.

Figures 2, 3, and 4 show the mean residence times for the three arranged λ values of .2, .1, and .05, respectively, for all 5 subjects as a function of the imposed travel time. Residence times generally increased with travel time for all subjects, and across subjects these increases were statistically significant on a nonparametric trend test for each of the λ values ($N = 5$ subjects, $k = 6$ conditions, replications averaged, $p < .05$). This result replicated that of Kamil et al. (in press). Residence times fell significantly with increasing λ values (nonparametric trend test, $N = 5$ subjects, $k = 3$ conditions, replications averaged, $p < .05$), and this result is in the direction predicted by McNamara and Houston's (1985) theory.

Parts 4 to 7

Figures 5 and 6 show mean residence times for all subjects in Parts 4 and 5, respectively, in which λ was .05, travel time was 0.25 s (Part 4) and 16 s (Part 5), and the probability of a prey trial was varied from .1 to .9. When the probability of a prey trial was .1 or .2 in Part 4, Bird 21 showed extremely long residence times, and essentially stopped working on the procedure. Apart from this subject, the general result from Part 4 was that residence times increased with increasing probabilities of prey trials (e.g., Birds 23, 24, and 25), although this increase was not statistically significant. A similar, but clearer, result can be seen in Part 5 with the 16-s travel time. It is of some interest that Bird 21 did not cease responding at low probabilities of prey trials with the longer travel time. In general, residence times at higher prey probabilities were greater with the longer travel time (Figure 6)

than with the shorter travel time (Figure 5), but this difference was not evident at lower probabilities.

Figures 7 and 8 show data equivalent to those shown in Figures 5 and 6, but for these data the value of λ was .2 rather than .05. The fourfold increase in the probability of prey per second significantly (binomial test, $p < .05$) decreased residence times with both the 0.25-s travel time (Figure 5 vs. Figure 7) and the 16-s travel time (Figure 6 vs. Figure 8). The tendency for residence times to increase with increasing prey-trial probability was much less evident with the higher value of λ than with the lower value, and in neither case was the trend significant at $p = .05$.

DISCUSSION

The results of Parts 1 to 3 of the present experiment, in terms of the effects of travel time on residence time, are entirely consistent with those of Kamil et al. (in press), and, directionally, they are consistent with the predictions of McNamara and Houston's (1985) theory. Parts 4 to 7 investigated the effects on residence time of the probability of a prey trial, a variation not carried out by Kamil et al. (in press).

Are the data, rather than the trends, well predicted by McNamara and Houston's (1985) theory? Figure 9 shows the obtained data (mean residence times averaged across the 5 subjects) as a function of the predictions of McNamara and Houston's theory (Equation 1) for each condition of the present experiment. It is clearly evident that the theory substantially and consistently underpredicts residence times, and *none* of the data from the 37 conditions were shorter than the predictions, a result that is statistically significant beyond $p = .05$ on a binomial test. McNamara and Houston's approach is not an accurate theory of residence time in the present procedure.

Alternative Models

Mazur and Vaughan (1987) investigated the situation in which pigeons chose between a fixed-ratio schedule and a progressive-ratio

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Fig. 3. Part 2. Mean residence times over the last five sessions of each experimental condition as a function of the travel time imposed for each subject. The value of λ was .1.

Fig. 4. Part 3. Mean residence times over the last five sessions of each experimental condition as a function of the travel time imposed for each subject. The value of λ was .05.

Fig. 5. Part 4. Mean residence times as a function of the probability of a prey trial. λ was .05, and the travel time was 0.25 s.

Fig. 6. Part 5. Mean residence times as a function of the probability of a prey trial. λ was .05, and the travel time was 16 s.

Part 6: $R/s = .2$, $t = 0.25$ s

Fig. 7. Part 6. Mean residence times as a function of the probability of a prey trial. λ was .2, and the travel time was 0.25 s.

Fig. 8. Part 7. Mean residence times as a function of the probability of a prey trial. λ was .2, and the travel time was 16 s.

Fig. 9. Obtained residence times as a function of predictions of the McNamara and Houston (1985) theory (Equation 1) for all experimental conditions. The data are mean data averaged across subjects.

schedule, with the option to reset the progressive schedule by emitting a single fixed-ratio response. They found that the subjects spent considerably more time working on the progressive schedule before resetting it than would be predicted if they were using an optimization rule. They also found that intertrial intervals further increased the time before resetting. The results, therefore, were similar to those reported here. Although Mazur and Vaughan's procedure was very different from that used here, their model could be applicable to the present results. On the basis of intertrial interval length affecting progressive-ratio stay time, Mazur and Vaughan suggested that the behavior of resetting might be controlled by the summed value of delays to reinforcers, either calculated hyperbolically (e.g., Mazur, 1984) or reciprocally (Shull & Spear, 1987). Mazur and Vaughan did not attempt a quantitative fit, and only ordinal support for the model was given. Mazur and Vaughan's approach strongly influenced our initial analysis of the present data. We assumed that subjects might leave patches when the hyperbolic value of the reinforcers likely to be available in a patch after a specified time in the patch became equal to the hyperbolic value of the delays that would ensue on switching at that point. Whether obtained or theoretical delays were used, the model produced good ordinal predictions but poor quantitative predictions. The

Fig. 10. A diagram showing the relation between residence time and the interreinforcer intervals thus produced in one experimental condition. The shape of this function is similar for all conditions. The minimum of the function (designated A) is the prediction of McNamara and Houston's (1985) model (Equation 1), and it falls at a residence time of 13 s. The horizontal line shows an assumed threshold of discrimination, which is an interval 0.5 times greater than the minimum. The mean of this range (designated B) is the prediction of the present approach. For this condition, the prediction is 22 s.

quantitative predictions were not helped by changing the values of the free parameter K (Mazur & Vaughan, Equation 2) or by raising the delay to powers other than 1.0 (see Mazur, 1984). We must conclude that the hyperbolic delay model is not applicable to the present results.

An alternative possibility is that the present analysis might be applicable to the Mazur and Vaughan (1987) results. In the absence of their detailed data, this is difficult to assess qualitatively, although it seems very likely that the ordinal predictions would be correct.

Can a theory that predicts the present data, and those of Kamil et al. (in press), be developed?

A Threshold-Maximization Model

The model of patch residence time suggested by McNamara and Houston (1985) proposes that the mean residence time in a patch, when some are empty, should be that time that maximizes the overall rate of obtaining prey. As shown by Kamil et al. (in press) and the present experiment, subjects do not stay in patches for the predicted time; rather, they stay longer. One theoretical problem inherent in most

maximizing models is that they generally assume that subjects, through their interaction with the environment, can accurately determine the maximum of the function relating such variables as reinforcer rate as a function of some behavior. The finding of such a maximum (or minimum) requires that differential performance can be controlled by vanishingly small marginal changes in reinforcer rates—hardly a parsimonious assumption. Davison (1990) noted the same logical problem in melioration models, in which an exact point of equality needs to be discovered by the subject. His solution was to propose a “threshold-melioration” model, in which differential performance could be controlled by differences in reinforcer rates only down to a certain level. Beyond that level, responding was random. Such an approach predicts that a subject’s performance will continually be driven into an envelope in which outcomes are not discriminable from the best possible (melioration or maximizing) outcome. If the distribution of outcomes as a function of performance (e.g., obtained interreinforcer times as a function of patch residence time) is not symmetrical around the theoretical point of maximum return, and if the subject behaves randomly within the subthreshold area, then the threshold-modified prediction will be different from the theoretical maximal prediction. Davison (1990) showed that such a threshold approach, in combination with melioration theory, predicted undermatching in concurrent variable-interval schedules.

The prediction from McNamara and Houston’s (1985) approach (Equation 1) is the residence time that maximizes the overall rate of reinforcement, and thus minimizes the average interreinforcer interval. Focusing on the interreinforcer intervals, if differences could not be discriminated perfectly, how would the predictions be changed? Figure 10 shows a typical function relating mean interreinforcer interval to residence time for one condition of the present experiment. The shape of this function is typical for all conditions: It is steeper to the left of the minimal (McNamara–Houston) point than to the right of this point. An approach that assumes a threshold in discriminability could be represented by the horizontal line cutting the interreinforcer interval in Figure 10. Assuming stochastic performance within such a subthreshold area, the prediction

of residence time would be given by the mean of the intersections of the threshold line and the interreinforcer time function (shown as B in the figure). Thus, a threshold approach will predict patch residence times that are longer than those that give the maximal return, as we have consistently found (Figure 9). Ordinarily, then, a threshold assumption moves the predictions in the correct way.

The following discussion is intended to be a didactic approach to the formation of an effective model of residence times. It is not meant to be any more than an approximate model, because it assumes a fixed threshold of temporal discrimination, and, as Davison (1990) pointed out, fixed thresholds are unacceptable. A complete model would need to consider discriminability levels between temporal stimuli, and presumably a differential effect on residence times as a function of discriminability. Such a model is too complicated to develop here, and the fixed-threshold model is, for the present purpose, a satisfactory approximation to show that such a model is viable.

We shall also assume a scalar property on the temporal threshold (see, e.g., Gibbon & Church, 1990). In a full model, this would simply assume that the standard distribution of errors around a mean time (be it on perceived interreinforcer time and/or on emitted residence times) is a function of the mean. In the present approximate approach, it simply implies that the size of the fixed threshold is a function of the mean interreinforcer interval.

To demonstrate the effectiveness of the approximate model, we calculated the minimum interreinforcer interval and residence times (the McNamara–Houston prediction), then the lower and upper bounds of residence times for a particular threshold value, and finally the midpoint between these times, giving the threshold-minimization prediction of residence time. The process is shown in Figure 10. After a relatively brief search of scalar threshold values, a reasonably satisfactory fit (although not necessarily the optimal fit) was found when the threshold value in seconds was the minimal interval plus 0.5 times the minimum interval. The mean obtained residence times (averaged across subjects) are shown as a function of these predictions in Figure 11. The obtained data followed the predictions from the threshold approach. Residence times

were generally overpredicted at longer residence times, which may result from the arrangement of a maximum 120 s in a patch, and hence the underestimation of longer residence times, as discussed in relation to Figure 1. It may also suggest that a smaller threshold multiplier would have been more satisfactory. Similarly, the current model, as fitted, does predict rather longer residence times than were obtained for the higher prey-trial probabilities when λ was .2 (Parts 6 and 7), but not when λ was .05. This cannot result from the maximum time allowed in a patch. Although this result might indicate a problem with the model, it may simply represent the fact that we did not try to find an optimal value for the threshold.

In their Experiment 2, Kamil et al. (in press) arranged the availability of food items in prey patches according to a uniform distribution that provided no reinforcers before 2 s, or after 16 s, had elapsed. Between these times, reinforcers were equally likely to be obtained. As Kamil et al. pointed out, in such a procedure, McNamara and Houston's (1985) maximizing approach predicts that subjects should spend a mean residence time of 16 s, independent of travel time. Kamil et al. found that mean patch residence times were always longer than optimal times, and that they increased with travel times. For travel times of 4, 8, and 16 s, they reported mean residence times of approximately 24, 26, and 30 s. If the threshold-interreinforcer-interval approach taken here is applied to Kamil et al.'s uniform-distribution procedure, using the same (0.5) threshold multiplier as above, we predict residence times of 21, 23.5, and 28 s, respectively. Not only does the present approach predict that the subjects will stay longer than the optimal time, it also correctly predicts that increases in travel time will increase residence time. A search of the parameter space for the multiplier would doubtless provide better predictions; it seems unlikely that blue jays and pigeons would have similar threshold values.

It could well be argued that the scalar multiplier of 0.5 that was used to provide the threshold value is too large, and that pigeons and blue jays can discriminate temporal stimuli much better than this. Two points can be said in mitigation: First, discrimination was between continuously and widely varying temporal stimuli, confounding discrimination con-

Fig. 11. Obtained residence times for all conditions of the present experiment (with replications averaged) as a function of residence times predicted from a threshold modification of McNamara and Houston's (1985) theory. The threshold multiplier was 0.5. The data are averaged across subjects.

siderably. Second, we have already noted that in a full model, for the same interreinforcer interval (y axis), the moment propelling the residence time from the left of the function rightwards will be greater than that propelling it in the opposing direction. Such an effect is captured, in the present analysis, by the multiplier. In a full model, these differential moments may be able to predict the frequency distributions of residence times.

Gibbon and Church (1990) discussed a model, based on scalar timing and memory variance, to predict how long animals would remain in a patch beyond the time at which the patch ceased to provide food. This measure, often called "giving-up time," is also affected by travel time in much the same way as is residence time. Gibbon and Church also discussed a model, described in more detail by Brunner et al. (1992), in which animals leave patches "when the elapsed time since the last feeding exceeds some fraction beyond the expected time to the next feeding" (p. 31). This fraction is a threshold, and, as they argue, this threshold must be relative to the delay, rather than absolute, and such was the approach taken here. We, however, focused on the overall times between reinforcers, rather than on times between reinforcers in patches. Gibbon and

Church go on to consider comparator variance and current-time variance, as well as memory variance, which together rather overdetermine the prediction of giving-up times. After considering nine possible models, they concluded that only two models that assume variable memory and variable threshold(s) survive. Although Gibbon and Church's approach is conceptually similar to our own, we have had to assume no memory variance; instead, we have used the distribution of reinforcers in time that arises from the subject's interaction with its environment. It may be that when prey arrive at variable times (as in the present experiment) rather than at fixed times (as in Brunner et al.), most of the variance that affects patch residence is determined by the environment rather than by the perception of, and memory for, times to reinforcement.

Kamil et al. (in press) concluded that their data were incompatible with reinforcer-rate-maximizing models of foraging under patch uncertainty. However, they did discuss the possibility that their subjects misperceived prey-arrival times—that is, they consistently overestimated these times. They argued against such an explanation on two grounds: (a) The size of the overstaying was very large, and (b) when choosing between patches with one uniform and one exponential arrival-time distribution, the jays were sensitive to the relatively subtle differences in the distributions (their Experiment 3). The present approach is also, in some sense, a "misperception" approach, although it would be better characterized by a term such as "limited discrimination" or "less-than-perfect discrimination." Unlike Kamil et al.'s conclusion, we find that rate maximization (interreinforcer interval minimization) is compatible with our results and those of Kamil et al., although it is not quantitatively accurate. We propose, rather, that McNamara and Houston (1985) were correct in focusing on the overall reinforcer rate (reciprocal of interreinforcer interval) as the controlling variable of residence time, but that their model needs to be extended by incorporating a threshold (or dynamic-discrimination process) for it to predict correctly.

The present theory can be subjected to further empirical testing. For instance, it should be possible, by manipulating the probability of a reinforcer per second in prey patches, to

design situations in which the mean residence time is *less* than that at which interreinforcer intervals are minimized. This would require a within-patch feedback function (interreinforcer interval vs. residence time, see Figure 10) that is less steep to the left of the minimization point and more steep to the right of that point. Indeed, for a particular predicted minimization point, it should be possible to produce a wide range of residence times by changing the relative steepness of the two limbs of the feedback function.

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Received August 3, 1993
Final acceptance January 28, 1994

APPENDIX

Experimental data for each subject and experimental condition summed over the last five sessions of each condition. The data from Condition 32 were lost, so the condition was later run as Condition 38.

Subject	Condition	Prey trial	No-prey trials	Exit responses	Reinforcers obtained	Exits after 120 s	Residence time (s)
Bird 21	1	220	257	282	200	0	15.26
	2	218	202	220	200	0	16.23
	3	214	220	238	196	0	15.52
	4	258	275	333	200	0	10.56
	5	210	190	199	200	1	17.85
	6	289	316	405	200	0	6.85
	7	253	220	273	200	0	19.87
	8	157	181	193	145	0	35.88
	9	227	214	241	200	0	22.36
	10	125	156	159	116	6	39.98
	11	206	195	209	192	0	27.00
	12	253	247	300	200	0	17.03
	13	258	261	353	158	8	26.95
	14	262	218	292	183	5	29.82
	15	155	147	178	117	7	38.78
	16	195	214	264	145	0	32.65
	17	113	122	125	106	4	53.68
	18	152	178	214	115	1	36.31
	19	290	248	338	197	3	25.25
	20	237	59	85	200	11	44.10
	21	12	101	4	11	98	118.18
	22	213	40	38	200	15	68.51
	23	17	107	11	16	97	112.27
	24	114	136	149	89	12	41.88
	25	51	195	207	30	9	37.55
	26	200	19	10	198	11	100.93
	27	19	179	144	14	40	49.89
	28	180	49	35	177	17	89.50
	29	262	63	125	200	0	8.87
	30	82	738	753	65	2	15.56
	31	260	42	102	200	0	10.38
	33	182	173	176	179	0	29.76
	34	60	262	261	53	8	25.95
	35	200	20	19	200	1	48.74
	36	33	326	330	28	1	19.93
	37	201	54	54	200	1	30.20
	38	236	966	1,015	187	0	9.43
Bird 23	1	225	209	239	200	0	12.11
	2	208	217	225	200	0	20.77
	3	180	153	146	179	8	38.20
	4	253	257	310	200	0	10.08
	5	186	187	185	183	5	30.61
	6	302	296	398	200	0	6.45
	7	331	359	490	200	0	9.57
	8	143	157	152	134	14	44.73
	9	254	277	332	199	0	18.41

APPENDIX (Continued)

Subject	Condition	Prey trial	No-prey trials	Exit responses	Reinforcers obtained	Exits after 120 s	Residence time (s)
	10	133	153	155	124	7	41.36
	11	196	190	202	184	0	35.34
	12	352	347	499	200	0	9.21
	13	428	425	672	173	8	14.14
	14	225	254	320	154	5	27.60
	15	103	116	105	91	23	65.27
	16	182	154	160	161	15	46.05
	17	94	114	126	69	13	55.62
	18	126	140	150	105	11	52.76
	19	457	395	663	187	2	13.06
	20	696	178	674	200	0	7.78
	21	73	643	657	26	33	17.54
	22	209	15	17	200	7	69.43
	23	142	502	581	51	12	19.94
	24	102	87	59	94	36	80.68
	25	47	190	188	33	16	40.43
	26	201	15	1	200	15	117.14
	27	14	155	121	10	38	60.64
	28	202	39	28	196	17	91.08
	29	227	57	84	200	0	11.98
	30	136	1,113	1,140	104	5	10.09
	31	223	28	51	200	0	15.14
	33	181	175	178	178	0	29.51
	34	61	239	240	58	2	30.41
	35	201	17	18	200	0	34.64
	36	17	195	149	17	46	46.00
	37	200	64	64	200	0	28.37
	38	340	1,478	1,625	193	0	5.50
Bird 24	1	235	267	307	200	0	11.34
	2	210	237	247	200	0	16.33
	3	199	181	187	193	0	17.30
	4	284	272	356	200	0	6.82
	5	211	201	212	200	0	16.42
	6	401	375	576	200	0	4.12
	7	314	316	430	200	0	10.27
	8	189	170	181	178	0	29.93
	9	253	246	299	200	0	17.66
	10	164	175	189	149	1	29.06
	11	225	251	289	187	0	21.99
	12	313	326	439	200	0	14.68
	13	520	529	854	195	0	10.63
	14	289	232	325	196	0	22.99
	15	164	154	191	124	3	35.83
	16	250	253	330	173	0	24.29
	17	127	128	135	118	2	47.39
	18	199	203	257	145	0	28.04
	19	565	599	970	194	0	9.97
	20	248	48	90	200	6	39.09
	21	58	588	568	8	70	18.87
	22	200	25	7	200	18	105.87
	23	74	323	316	29	52	32.18
	24	122	120	140	99	3	47.20
	25	40	187	181	34	12	43.89
	26	201	21	16	197	9	99.36
	27	23	194	166	12	39	43.48
	28	199	56	65	188	2	62.28
	29	235	53	88	200	0	11.48
	30	219	2,091	2,175	135	0	5.08
	31	229	21	50	200	0	10.70

APPENDIX (Continued)

Subject	Condition	Prey trial	No-prey trials	Exit responses	Reinforcers obtained	Exits after 120 s	Residence time (s)
Bird 25	33	197	213	219	191	0	19.63
	34	90	270	270	88	2	22.92
	35	202	26	28	200	0	28.77
	36	29	254	243	29	11	30.87
	37	201	51	52	200	0	31.63
	38	381	1,279	1,460	200	0	4.73
	1	219	256	280	200	0	12.04
	2	205	194	199	200	0	17.06
	3	198	214	224	186	2	21.07
	4	210	239	249	200	0	14.74
	5	201	188	189	200	0	23.15
	6	238	227	265	200	0	11.00
	7	217	216	230	200	3	30.93
	8	170	172	182	157	3	35.68
	9	221	226	247	200	0	27.12
	10	154	133	130	151	6	44.78
	11	204	183	194	193	0	34.04
	12	265	249	313	200	1	18.19
	13	276	294	412	152	6	23.22
	14	219	249	291	176	1	29.45
	15	131	129	132	120	8	52.90
	16	197	220	260	153	4	32.79
	17	90	117	111	79	17	60.43
	18	150	135	152	132	1	50.60
	19	319	332	467	181	3	19.82
	20	285	68	152	200	1	28.52
	21	87	748	785	30	20	14.93
	22	227	25	45	200	7	45.21
	23	228	979	1,133	69	5	9.96
	24	102	98	72	85	43	66.54
	25	44	209	205	28	20	35.78
	26	200	19	0	200	19	120.00
	27	29	256	243	14	28	28.78
	28	198	48	49	188	9	77.10
	29	230	62	92	200	0	10.04
	30	211	2,075	2,181	105	0	5.17
	31	226	25	51	200	0	10.73
	33	178	168	174	172	0	33.07
	34	53	219	209	53	10	35.54
	35	202	19	21	200	0	33.45
	36	38	314	313	35	4	21.05
	37	201	36	37	200	0	36.00
	38	330	1,369	1,499	200	0	5.24
Bird 26	1	207	173	185	200	0	17.87
	2	203	202	203	201	1	22.72
	3	190	199	203	183	3	22.44
	4	267	248	315	200	0	7.58
	5	211	206	216	199	2	21.79
	6	282	260	342	200	0	8.96
	7	287	311	398	200	0	15.35
	8	202	181	202	179	2	28.65
	9	232	228	258	200	2	24.55
	10	164	167	180	149	2	29.98
	11	214	209	237	185	1	25.91
	12	327	349	478	198	0	14.79
	13	269	280	375	154	20	25.56
	14	144	140	114	118	52	58.90
	15	137	144	166	100	15	40.94

APPENDIX (Continued)

Subject	Condition	Prey trial	No-prey trials	Exit responses	Reinforcers obtained	Exits after 120 s	Residence time (s)
	16	149	177	188	124	14	44.70
	17	124	133	146	95	16	42.71
	18	170	162	205	122	5	37.57
	19	427	410	649	171	17	15.06
	20	350	100	248	200	2	16.70
	21	20	248	188	11	69	47.46
	22	236	18	50	200	4	32.34
	23	156	634	725	48	17	15.45
	24	130	138	165	91	12	37.04
	25	63	222	237	34	14	30.23
	26	204	24	13	199	16	92.50
	27	40	301	310	6	25	20.85
	28	254	67	155	156	10	27.49
	29	268	73	140	200	1	10.98
	30	155	1,483	1,552	77	9	7.45
	31	237	30	67	200	0	11.04
	33	186	172	172	186	0	30.46
	34	72	273	277	63	5	23.16
	35	201	30	30	200	1	42.07
	36	22	234	212	19	25	34.94
	37	201	51	52	200	0	40.34
	38	368	1,505	1,673	200	0	5.62