RESIDENCE TIME AND CHOICE IN CONCURRENT FORAGING SCHEDULES

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Five pigeons were trained on a concurrent-schedule analogue of the "some patches are empty" procedure. Two concurrently available alternatives were arranged on a single response key and were signaled by red and green keylights. A subject could travel between these alternatives by responding on a second yellow "switching" key. Following a changeover to a patch, there was a probability (p) that a single reinforcer would be available on that alternative for a response after a time determined by the value of λ , a probability of reinforcement per second. The overall scheduling of reinforcers on the two alternatives was arranged nonindependently, and the available alternative was switched after each reinforcer. In Part 1 of the experiment, the probabilities of reinforcement, p_{red} and p_{green} , were equal on the two alternatives, and the arranged arrival rates of reinforcers, λ_{red} and λ_{green} , were varied across conditions. In Part 2, the reinforcer arrival times were arranged to be equal, and the reinforcer probabilities were varied across conditions. In Part 3, both parameters were varied. The results replicated those seen in studies that have investigated time allocation in a single patch: Both response and time allocation to an alternative increased with decreasing values of λ and with increasing values of p , and residence times were consistently greater than those that would maximize obtained reinforcer rates. Furthermore, both response- and time-allocation ratios undermatched mean reinforcer-arrival time and reinforcer-frequency ratios.

Key words: foraging, concurrent schedules, matching, residence time, key peck, pigeons

Recently, there has been increased interest in experimental analyses of contingencies that simulate natural foraging situations. In the "some patches are empty" paradigm, discussed by McNamara and Houston (1985), two discriminated response alternatives are concurrently available: responding (or foraging) in a patch, and initiating travel to another patch. Upon entry to a patch, a set probability determines whether that patch does or does not contain a single food item. If the patch does contain food, this food can be obtained after a period of responding usually specified by a probability per second. At any time after entering a patch, the animal can terminate that patch and initiate a fixed travel time to another patch by emitting an exit response. The dependent variable of interest in this procedure is the residence time in a patch, which is the time at which a subject exits from a patch without having ob-

tained a reinforcer. McNamara and Houston offered a theory of patch-residence times that assumed that subjects would adjust their residence times in order to maximize the overall frequency of obtaining food. However, Kamil, Mishal, and Stephens (1993) using blue jays, and Davison and McCarthy (1994) and McCarthy, Voss, and Davison (1994) using pigeons, all found that this theory systematically underestimated mean residence times. Davison and McCarthy provided an alternative theory to predict residence times that assumed subjects were unable to discriminate different rates of reinforcement below some threshold and so maximized their obtained food rates within a range, rather than completely maximizing them.

The purpose of the present experiment was to investigate behavior in a modified "some patches are empty" procedure that was closer to a standard concurrent schedule of reinforcement than the original paradigm. The procedure that we used here allowed the measurement of response and time allocation in a foraging procedure when two discriminable, and potentially different, patches were available. By arranging a modified switching-key concurrent schedule (Findley, 1958), we used changeover responses as patch-exit responses and so could measure residence

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times in the two patches. Each concurrent alternative consisted of a patch that, once selected, either contained a food item (with a probability p) or did not contain a food item (with a probability $1 - p$). If the patch did contain a food item, the time at which pecking the key produced this food item was determined by a parameter (λ) that specified a probability per second. Once this food item was obtained, access to that patch was terminated and a 1-s blackout occurred before the alternate patch was presented. In order that the two patches could differ with respect to p and λ , without subjects responding exclusively to the richer patch, food availability in a patch was dependently scheduled (Stubbs & Pliskoff, 1969). That is, a food item remained available in a patch (and no food item could be arranged in the alternate patch) until the arranged item was obtained. However, unlike standard concurrent variable-interval (VI) VI schedules, an arranged food item was not always available on entry into the patch in which it had been scheduled. Rather, the availability of the arranged food item on each entry into the patch was always determined by the value of p .

Behavior on concurrent schedules has received considerable attention in the experimental analysis of behavior (Davison & McCarthy, 1988), and quantitative relations between response or time allocation and reinforcer parameters in such procedures have been researched thoroughly. For example, the distribution of responses and time between two alternatives in concurrent VI VI schedules is clearly controlled by the relative frequency of reinforcers obtained from those alternatives (e.g., Davison & McCarthy, 1988). However, at least two other potential sources of control often covary when relative rates of reinforcement are varied in concurrent schedules. First, the number of successive reinforcers obtained per changeover to the richer alternative generally increases as the reinforcer ratios on the two alternatives become more disparate. Second, the time that it takes to obtain the first reinforcer after a change to an alternative may correlate with the rate of reinforcement arranged on that alternative. The effect of changing relative frequencies of reinforcers on both of these factors was investigated by Dreyfus, Dorman, Fetterman, and Stubbs (1982). They showed

that, when concurrent VI VI schedules were unequal, more reinforcers on the higher reinforcer-rate alternative were arranged when the subject was responding to this alternative than when it was responding to the lower rate alternative. On the other hand, more reinforcers were arranged on the lower reinforcer-rate alternative when the subject was responding on the higher reinforcer-rate alternative than were arranged when the subject was responding on the lower rate alternative (see their Figure 3). Consequently, on concurrent VI VI schedules that arranged a three-to-one reinforcer ratio, for example, about the same number of reinforcers on each schedule would be gained immediately following a changeover, but about five to six times as many reinforcers would be gained while the subject was responding on the higher reinforcer-rate alternative than while it was responding on the lower reinforcer-rate alternative. Thus, mean times to the first reinforcer after changeovers could be approximately equal between the alternatives even though the overall reinforcer rates on the alternatives differed. Dreyfus et al. identified this latter feature of their procedure as a possible factor contributing to the undermatching they observed.

The procedure arranged in the present experiment potentially dissociates the three sources of control described above by arranging contingencies that are quite different from those operating in standard concurrent VI VI schedules. An analysis of the effects of the relative frequency with which an alternative provides reinforcement, independent of both differences in the times between changing to an alternative and obtaining a reinforcer and the number of successive reinforcers per changeover, ought to be possible by varying, across a set of conditions, the probability that a reinforcer will be obtained after entry into an alternative (p), while keeping the probability per second that an arranged reinforcer will be delivered (λ) constant and equal for the two alternatives. This manipulation will change the relative frequency of reinforcers across the two patches, but, unlike concurrent VI VI schedules, the arranged average times from patch entry until reinforcement will remain relatively equal between the alternatives. (However, as a result of possible unequal time allocations between the two

patches, the obtained times could vary.) If relative reinforcer frequency for the alternatives alone controls time allocation in this procedure, then as p is varied, time-allocation ratios should covary with obtained relative-reinforcer frequencies. If, on the other hand, the average time between patch entry and reinforcement delivery controls choice, as suggested by the "some patches are empty" research mentioned above, then behavior-allocation ratios might not change as p is varied.

Similarly, in another set of conditions, the relative contribution of differences between the times to reinforcement after changing to an alternative, independent of both the probability of reinforcement following changing to that alternative and the number of successive reinforcers per changeover, ought to be revealed in the effects of varying the difference between λ values for the two alternatives while keeping p constant across conditions and equal for the two alternatives. If residence times increased with lengthening reinforcer-arrival times, time-allocation ratios would decrease as the ratio of reinforcer delivery rates in patches increased. In other words, subjects would enter each patch equally often but spend more time on leaner patches, thus obtaining reinforcers more efficiently. On the other hand, if only overall reinforcer rate on the alternatives controls choice, residence times would not change with changes in λ , time-allocation ratios would remain constant, and overall rates of obtaining food would decrease.

Previous research provides some predictions of the results. First, we would expect from Kamil et al. (1993), Davison and McCarthy (1994), and McCarthy et al. (1994) that mean residence times will increase with lengthening mean times to reinforcers in patches (decreasing values of λ), and that residence times will be longer than the optimal residence times that are predicted by McNamara and Houston's (1985) model. However, our expectations for changes in residence-time ratios are less clear from a concurrent-schedule perspective. The lengthening of residence times by increased reinforcer-arrival times reported in the above studies predicts that residence-time ratios should fall as the arranged reinforcer-arrival time ratios are increased. Initially, this prediction seems at

odds with the usual result obtained in research on concurrent VI VI schedules: Time-allocation ratios increase as overall relative reinforcer frequencies increase. This finding apparently predicts that residence-time ratios will increase as the arranged reinforcer-arrival time ratios are increased. However, these conflicting predictions arise from failing to consider concurrent VI VI schedules in the terms adopted for describing the present procedure. The equivalent of λ in a concurrent VI VI schedule is the number of reinforcers obtained in the time spent responding to an alternative, or the local rate of reinforcement for that alternative. The equivalent of p , on the other hand, is the overall relative rate of reinforcement for an alternative. When strict matching of time-allocation ratios to relative frequencies occurs in concurrent VI VI schedules, the local rates of reinforcement for each alternative must be equal. Therefore, evidence for matching in these procedures cannot be used to generate predictions about the likely effects of λ in the present experiment. Rather, matching in concurrent VI VI schedules might be taken to imply only that increasing p in the present study ought to increase patch residence times and therefore time-allocation ratios. This prediction seems consistent with the results of Davison and McCarthy, who showed that residence times in the "some patches are empty" procedure increased with increasing values of p . Thus, predictions derived from the "some patches are empty" literature seem not to conflict with those derived from concurrent VI VI schedule research after all.

The data from the present experiment will be analyzed in two ways. In order to make contact with the literature on concurrent-schedule performance, the ratio of total responses and times allocated to the two alternatives will be plotted as a function of the ratios of obtained reinforcer frequencies and mean reinforcer-arrival times. To make contact with the foraging literature, residence times on nonreinforced visits to the two alternatives will be analyzed as a function of the respective values of p and λ . Both approaches need to be taken here because the procedure we used (a maximum of one reinforcer per changeover to an alternative, and forced exit from an alternative after a reinforcer) is clearly different from the standard concur-

rent VI VI procedure, and these two aspects of the procedure combine to force some relation between the independent variables and the total response and time measures on reinforced patch visits. In contrast, there is no such forcing of behavior on occasions when responding in a patch is not reinforced.

METHOD

Subjects

Six homing pigeons, numbered 111 to 116, were maintained at $85\% \pm 15$ g of their free-feeding body weights by supplementary feeding immediately after the daily experimental sessions. Bird 114 died early in the experiment, and no data are reported for this subject. All subjects were experimentally naive at the start of the experiment.

Apparatus

All experimental contingencies were arranged on an IBM®-compatible computer running MED-PC® software situated remote from the experimental chamber. The chamber was 330 mm high, 330 mm wide, and 310 mm deep, was lightproof, and was fitted with an exhaust fan to provide ventilation and to help mask external noise. Three 20-mm circular response keys were set 110 mm apart and 250 mm from the grid floor on one wall of the chamber. Only the left and right side keys were used in this experiment. The left key could be illuminated yellow, and the right key could be illuminated red or green. When lit, the keys could be operated by pecks exceeding about 0.1 N. An aperture, 50 mm wide by 50 mm high, was located directly below the center key and 120 mm from the floor. A solenoid-operated hopper delivered wheat through this aperture. Each presentation of the hopper lasted for 3 s and was accompanied by the illumination of the aperture and the extinction of all key stimuli. Key and hopper illumination were the only light sources in the chamber.

Procedure

Initially, the subjects were slowly deprived of food, and when they had reached their designated body weights, they were trained to eat from the illuminated food magazine when it was presented. When all were eating reliably,

they were autoshaped to peck all keys and key colors, and were then trained on a variety of single VI schedules on each key and color. When all were pecking reliably, they were placed on the first condition of the experiment.

At the start of each session, the right switching key was lit yellow, and the left main key was lit either red or green randomly. At any time during the session, a response to the switching key caused a 1-s blackout of both keys and subsequently alternated the main-key color and patch parameters. Whether or not a reinforcer was available on any particular entry to a patch was dependent upon both which patch was next to contain a reinforcer (the dependent scheduling contingencies) and the separate probabilities that a reinforcer would be available on the current visit to a patch, p_{red} or p_{green} . That is, after a reinforcer had been obtained from either patch, the patch at which the next reinforcer would be obtained was determined probabilistically by $p_{\text{red}}/(p_{\text{red}} + p_{\text{green}})$. In addition, switching to the patch that was next to contain a reinforcer, determined, according to the values of p_{red} or p_{green} , whether a reinforcer was available on this particular entry to the patch. Thus, although a reinforcer may have been allocated to the patch being switched to, this reinforcer might not be available on a particular instance of patch residence.

Each time a patch containing a reinforcer was entered, a probability gate clocked at one per second determined whether the next main-key response would be reinforced according to the arranged values of λ_{red} or λ_{green} . If λ_{red} or λ_{green} arranged a reinforcer for the next response but the subject switched before obtaining that reinforcer, this reinforcer might not be available again on the next entry into that patch. Rather, although the reinforcer remained allocated to the same patch, each time this patch was reentered, p_{red} or p_{green} defined whether the current entry was to a patch containing food (a prey trial) or to a patch containing no food (a no-prey trial). If the reentry was to a patch containing food, the arrival time of the reinforcer was again determined by the appropriate value of λ .

Consider, for example, a condition arranging $p_{\text{red}} = .9$, $p_{\text{green}} = .1$, $\lambda_{\text{red}} = .2$, and $\lambda_{\text{green}} = .2$. The probability that the first reinforcer in

the session will be allocated to the red alternative is .9, and the probability that it will be allocated to the green alternative is .1. Suppose that the reinforcer was allocated to the red alternative. Upon switching to the red alternative, the probability that this particular patch contains a reinforcer is again .9. If this patch does contain a reinforcer (i.e., the visit was defined as a prey trial), the probability that a response after 1 s of entering the patch will produce this reinforcer is .2. Therefore, on average, the subject will obtain reinforcers after 5 s of responding to the main key. However, if the subject switches out of this patch before it obtains the reinforcer, the red alternative remains the next to provide a reinforcer, but the probability that the next visit to a red patch will be a prey trial is again .9. Similarly, if the next visit to a red patch is defined as a prey trial, the probability that a response after 1 s of entering the patch will produce the reinforcer is again .2. Only after this reinforcer is obtained will the next reinforcer be allocated to the red or green alternative according to probabilities of .9 and .1, respectively. Clearly, by dependently scheduling reinforcers in this manner but reassessing p_{red} or p_{green} each time a patch is entered, the obtained probabilities of obtaining food per entry to a patch (assuming sufficiently long residence times on each visit) will be lower than those arranged. However, the ratio of obtained reinforcers will not deviate systematically from that arranged.

Sessions ended in blackout after 45 min had elapsed, or after 40 reinforcers had been obtained, whichever event occurred sooner.

Performance in a condition was deemed to be stable when the following criteria had been met. The first nine sessions of a condition were discarded. From the 10th session on, the relative frequency of responding on the red alternative (responses on red divided by total responses) in a session was calculated. A computer then searched over blocks of three sessions (starting at Sessions 10, 11, and 12) for monotonic trends in these relative response rates. After such a trend had not been found on five, not necessarily consecutive, sets of three sessions, the performance for that subject was taken as stable. When this criterion had been met by all the subjects, the data were collected and a new condition was implemented. The minimum number of ses-

Table 1

The λ values (probabilities of reinforcement per second), p values (probabilities of reinforcement per entry to an alternative), and the number of training sessions given in each experimental condition of Parts 1, 2, and 3.

Condi- tion	λ_{red}	λ_{green}	p_{red}	p_{green}	Ses- sions	Part
1	.20	.20	.50	.50	20	1, 2
2	.10	.30	.50	.50	23	1
3	.35	.05	.50	.50	23	1
4	.05	.35	.50	.50	24	1
5	.30	.10	.50	.50	26	1
6	.20	.20	.75	.25	22	2
7	.20	.20	.10	.90	23	2
8	.20	.20	.25	.75	19	2
9	.20	.20	.90	.10	24	2
10	.05	.35	.10	.90	28	
11	.05	.35	.90	.10	21	
12	.35	.05	.10	.90	26	3
13	.30	.10	.75	.25	22	3
14	.10	.30	.25	.75	21	3
15	.10	.30	.75	.25	22	3

sions before stability could be achieved was therefore 16. The actual numbers of sessions required to reach stability in each condition are shown in Table 1.

Table 1 shows, for each experimental condition, the arranged probabilities of obtaining a food item on each patch (p_{red} and p_{green}) and the arranged probabilities per second that a key peck would produce an arranged food item in a patch (λ_{red} or λ_{green}). In Part 1 of the experiment (Conditions 1 to 5), the arranged values of p were equal and constant across conditions (.5), and only the arranged values of λ varied. In all these conditions, the values of λ_{red} and λ_{green} totaled .4 per second and were varied from .05 (mean arrival time 20 s) to .35 (mean arrival time 2.86 s) on each key. In Part 2 (Conditions 1 and 6 to 9), both λ values were .2 per second (mean arrival time 5 s) while the prey-trial probabilities, which summed to 1.0, were varied between .1 and .9 on each key. Condition 1, in which equal λ and p values were arranged, was used in the analysis of both Parts 1 and 2. Finally, in Part 3, six conditions of combinations of values of λ and p were arranged. The first two of these (Conditions 10 and 11) failed to maintain consistent responding, so equivalent but less extreme conditions were arranged as Conditions 14 and 15.

RESULTS

The Appendix shows the number of main-key responses made, the time spent responding to the main key, the number of switching responses made, and the number of reinforcers obtained from each alternative for each subject in all experimental conditions. These data have been summed over the final five sessions of training.

Concurrent-Schedule Analyses

Figure 1 shows log response- and time-allocation ratios in Part 1 as a function of the log ratio of mean arranged times to reinforcers in the patches. This independent variable is, of course, the inverse of the log ratio of arranged λ values in the two patches, $\log(\lambda_{\text{red}}/\lambda_{\text{green}})$. Inspection of Table 2 shows that the fitted lines accounted for between 20% and 94% of the data variance. However, this measure of goodness of fit is influenced by the slope of the fitted lines, and all fitted lines had relatively low slopes. Nevertheless, for 8 of the 10 response and time fits, the slopes were more than two standard deviations greater than zero (the exceptions being the response and time fits for Bird 111). Response- and time-allocation slopes were not significantly different from each other on a sign test at $p = .05$. In addition, for both response and time allocation, the slopes of the lines for all subjects were positive, which is significant at $p < .05$ on a sign test. This indicates that subjects spent more time and emitted more responses in patches that arranged longer reinforcer-arrival times. However, because the slopes of these lines were not 1, it is also evident that response- and time-allocation ratios were not completely determined by the changing mean arranged arrival times of reinforcers. The intercepts were generally around 0, indicating only minor inherent biases to responding in or spending time in either patch. However, a small number of large biases were recorded.

Figure 2 presents an analysis of the response- and time-allocation data from Part 2 in which, for each patch, the λ values were kept equal and constant but the p values varied across conditions (see Table 1). Figure 2 shows log response- and time-allocation ratios as a function of the log ratio of the frequencies of reinforcers obtained in the patches.

The obtained frequencies of reinforcers in the two patches, rather than the arranged probabilities of reinforcement in the patches (i.e., p_{red} and p_{green}), have been used in this analysis because the dependent scheduling of reinforcers ensured that the red:green ratio of these two measures would not be systematically different, and the former measure is that generally used in the analysis of concurrent VI VI performance. Again, straight lines were fitted to these data by the method of least squares, and the details of the fits are shown in Table 2. The fits of the straight lines were marginally worse in Part 2 compared with Part 1, but 9 of the 12 slopes were more than two standard deviations greater than 0. In Part 2, the slopes of all the fitted lines were positive, which is significant on a sign test at $p < .05$. This indicates that both response- and time-allocation ratios were controlled by the ratio of obtained reinforcer frequencies.

In Part 1, the dependent scheduling of reinforcers ensured that the obtained relative frequencies of reinforcers in the patches remained approximately equal when the mean reinforcer-arrival times were varied. However, in Part 2 we cannot be sure that the obtained mean arrival times of reinforcers in patches remained constant when p_{red} and p_{green} were varied. Given that residence times in a patch changed as a function of p in that patch (see Figure 2), the obtained mean food-arrival times will probably also have varied with p despite our arranging equal λ values. For example, if residence times on one alternative were very short because p for that alternative was low, the subject will often have switched out of trials containing a food item before obtaining that food, and, on reinforced trials, will have obtained food after shorter times than the arranged mean arrival times. Put another way, the subject will seldom have stayed in a patch containing food long enough to obtain those reinforcers that were scheduled to occur later than the mean arranged arrival time. As a result, the relative frequency of long obtained food-arrival times will be lower than that arranged, and the mean obtained food-arrival time will be less than the mean arrival time that was arranged. It thus follows that, in Figure 2, the arrival times implied by the arranged λ values may be quite different from the arrival times that the subjects experience. It is therefore worthwhile to rean-

Fig. 1. Log response- and log time-allocation ratios as a function of the log ratios of the arranged mean times to reinforcers in Part 1, in which λ values were varied. The straight lines were fitted by the method of least squares, and the parameters of the fits are shown in Table 2 (Part 1). The crosses in each panel denote the origin.

alyze the present data as a function of mean obtained arrival times. Further, overall performance measures, such as those shown in Figures 1 and 2, are to some extent forced by the present procedure, in that some vary-

ing proportion of the residence times making up these measures are determined by the food-arrival times that are in turn determined by the values of λ and p arranged in a condition.

Table 2

The results of least squares linear regression fits for both log response- and log time-allocation ratio data in Parts 1 and 2. The independent variable in the analyses labeled Part 1 was the log ratio of the mean arranged times to reinforcers ($1/\lambda$ values), and in those labeled Part 2 it was the log obtained reinforcer ratio. The data labeled Part 1b are the results of fitting lines to log residence-time ratios in Part 1 as a function of the log ratio of the mean obtained times to reinforcers in these conditions. The data labeled Part 2b are the results of fitting lines to log residence-time ratios in Part 2 as a function of the log obtained reinforcer ratio in these conditions (see text for further explanation). *SD* is the standard deviation of the slope, *SE* is the standard error of the fit, and %VAC is the percentage of data variance accounted for.

Subject	Slope	SD	Intercept	SE	%VAC
Part 1					
Group Response	0.208	0.034	-0.064	0.046	93
Group Time	0.202	0.030	0.039	0.041	94
111 Response	0.091	0.104	-0.175	0.142	20
111 Time	0.187	0.136	0.192	0.186	39
112 Response	0.225	0.032	0.069	0.043	94
112 Time	0.202	0.030	0.039	0.041	94
113 Response	0.206	0.028	-0.118	0.038	95
113 Time	0.155	0.052	0.030	0.072	74
115 Response	0.451	0.067	-0.253	0.092	94
115 Time	0.213	0.071	0.017	0.098	75
116 Response	0.221	0.058	-0.092	0.080	83
116 Time	0.213	0.028	-0.034	0.039	95
Part 2					
Group Response	0.272	0.055	-0.060	0.085	89
Group Time	0.152	0.048	-0.012	0.074	77
111 Response	0.304	0.079	0.012	0.122	83
111 Time	0.130	0.049	0.060	0.075	70
112 Response	0.268	0.137	-0.124	0.199	56
112 Time	0.263	0.063	0.018	0.091	85
113 Response	0.325	0.059	-0.099	0.092	91
113 Time	0.213	0.046	-0.010	0.072	88
115 Response	0.433	0.071	-0.236	0.127	93
115 Time	0.076	0.086	-0.084	0.154	21
116 Response	0.095	0.061	0.030	0.086	45
116 Time	0.045	0.051	0.036	0.072	21
Part 1b					
Group Time	0.341	0.057	0.032	0.050	92
111 Time	0.364	0.106	0.137	0.157	80
112 Time	0.519	0.047	0.049	0.023	98
113 Time	0.181	0.104	0.023	0.058	50
115 Time	0.402	0.118	-0.044	0.097	79
116 Time	0.415	0.023	-0.077	0.020	99
Part 2b					
Group Time	0.307	0.064	-0.053	0.098	89
111 Time	0.548	0.098	0.138	0.150	91
112 Time	0.353	0.104	-0.025	0.151	79
113 Time	0.235	0.105	-0.019	0.163	62
115 Time	0.197	0.077	-0.087	0.138	69
116 Time	0.598	0.142	-0.050	0.201	86

Foraging Analyses

Given the above considerations, we will now analyze the time spent responding on nonreinforced trials in each patch (residence times) as a function of the obtained mean food-arrival times and obtained probabilities of reinforcement in that patch. This aspect of

behavior has been the primary dependent variable in analyses of contingencies that are designed to simulate aspects of natural foraging. In addition, we need to consider obtained mean arrival times, rather than the arranged λ values, as the effective independent variable because, when the subject's behavior

PART 2: Reinforcer probability varied

Fig. 2. Log response and log time ratios as a function of the log obtained reinforcer ratios in Part 2, in which the probabilities of reinforcement per entry to a patch (p values) were varied. The straight lines were fitted by the method of least squares, and the parameters of the fits are shown in Table 2 (Part 2). The crosses in each panel denote the origin.

interacts with the present procedure, the distribution of obtained arrival times cannot be summarized by a single λ value because the obtained probability of reinforcement per second will not be constant over time. Thus,

Figure 3 shows log time-allocation ratios on nonreinforced trials (log residence-time ratios) as a function of the log ratio of mean obtained reinforcer-arrival times in the two alternatives in Part 1 in which λ values were

PART 1: Lambda varied

Fig. 3. Log time-allocation ratios on nonreinforced trials, or residence-time ratios, as a function of the log ratios of the obtained mean food-arrival times in Part 1, in which λ values were varied. The straight lines were fitted by the method of least squares, and the parameters of the fits are shown in Table 2 (Part 1b). The crosses in each panel denote the origin.

varied. Table 2 (Part 1b) shows the results of fitting straight lines to the data plotted in Figure 3. A comparison of Figures 1 and 3, and the data under Part 1 and Part 1b in Table 2,

reveals no systematic differences between measures of goodness of fit for the two analyses. Nevertheless, several other differences are apparent. First, in Figure 3, the obtained

arrival-time ratios generally varied over a much smaller range than did the arranged arrival-time ratios shown in Figure 1. This is particularly evident for Birds 112 and 113. This finding confirms that subjects were indeed sampling only a subset of the arrival-time distributions that were defined by the arranged values of λ . Second, the slopes of the lines describing how residence-time ratios changed with obtained arrival-time ratios (Table 2, Part 1b) were steeper than the slopes of the lines relating overall time-allocation ratios to arranged arrival-time ratios (Table 2, Part 1) for all 5 birds. This difference was significant on a sign test ($p < .05$) and suggests that residence-time ratios were controlled by obtained arrival-time ratios to a greater extent than were overall time-allocation ratios controlled by the arranged arrival-time ratios. However, it is worth noting that this difference may be entirely due to less variation in the x values in Figure 3 than in Figure 1.

Figure 4 shows log time-allocation ratios on nonreinforced trials (log residence-time ratios) as a function of log obtained reinforcer-frequency ratios (the same x -axis variable as in Figure 2) in Part 2 in which p values were varied. The results of fitting lines to these data are shown in Table 2 (Part 2b). These results should be compared with those obtained when linear regressions were performed on time-allocation ratios on all trials (Table 2, Part 2). A comparison of measures of goodness of fit between these two analyses indicates no systematic differences in how well the lines described the two sets of data. Furthermore, small and nonsystematic differences between the intercepts of lines fitted in the two analyses provide further evidence for the absence of significant inherent biases for responding to or spending time in either patch. However, for all subjects, the functions relating residence-time ratios to obtained reinforcer-frequency ratios (Part 2b in Table 2) were steeper than the functions relating overall time allocation to the same independent variable (Part 2 in Table 2). This difference was significant on a sign test ($p < .05$) and indicates that changes in residence-time ratios were more sensitive to changes in the distribution of reinforcers across the two patches than were changes in overall time-allocation ratios. This result is likely to have arisen because overall time-allocation ratios are partly

composed of residence times on reinforced trials (i.e., obtained food-arrival times).

Absolute Residence Times

The primary analysis of absolute residence times in either patch investigated the degree to which these times were controlled by the mean obtained times to food in a patch. Figure 5 shows the mean residence times per entry on nonreinforced red and green patches as a function of the mean obtained time to reinforcement on reinforced patches in Part 1 in which λ values were varied. Figure 6 presents an identical analysis of mean residence times in Part 2 in which p values were varied. Several effects are apparent in Figures 5 and 6. First, both figures show that the obtained mean times to reinforcers varied considerably in both Parts 1 and 2. In addition, a comparison of the range of mean obtained times to food in Figures 5 and 6 reveals that the variation in Part 2 was as great as it was in Part 1, despite arranged λ values being constant and equal in Part 2. Second, in both figures, data points generally fell above the line of equality, indicating that mean residence times were longer than mean reinforcer-arrival times. This was true in all except 3 of 90 cases (significant at $p < .05$ on a binomial test). Third, in both figures, residence times generally increased as reinforcer-arrival times increased, and there seemed to be no obvious difference between the functions for Part 1 (in which overall patch reinforcer rates were equal) and Part 2 (in which they were systematically varied). The failure to find any differences between these functions suggests that the mean times to reinforcement in each patch, rather than the relative reinforcer rates between patches, were the major variable controlling patch residence times.

The data from Part 3, in which the values of λ and p for each patch could both differ within a condition, will be addressed in the Discussion.

DISCUSSION

The present experiment investigated an extension of the standard "some patches are empty" procedure (Davison & McCarthy, 1994; Kamil et al., 1993; McCarthy et al., 1994) by presenting subjects with a choice between two concurrently available and descri-

PART 2: Reinforcer probability varied

Fig. 4. Log time-allocation ratios on nonreinforced trials, or residence-time ratios, as a function of the log ratios of the obtained relative frequencies of reinforcers in Part 2, in which p values were varied. The straight lines were fitted by the method of least squares, and the parameters of the fits are shown in Table 2 (Part 2b). The crosses in each panel denote the origin.

minable patches. Only one food item could be obtained per entry into either patch, but each patch could differ with respect to both the probability that it contained food (p) and the probability per second that a response would produce this food (λ). Despite each

patch being in the context of an alternative patch that also provided food, the present results fully replicate those from the standard one-patch procedure. The average time between entering a patch and switching to the alternative (residence time) increased with

PART 1: Lambda varied

Fig. 5. Mean residence times (in seconds) on nonreinforced red- and green-patch entries in Part 1 as a function of mean times to the delivery of reinforcers on reinforced red- and green-patch entries. The straight line depicts equality between the two measures. Note that the x axis for Bird 111 differs from those of the other subjects, but that the intervals between ticks are 5 s in all cases.

decreasing λ values (Figures 1, 5, and 6) and as p values increased (Figure 2), as previously reported. In addition, residence times in both patches were consistently longer than

the obtained mean arrival times of food in those patches (Figures 5 and 6). Together, these findings suggest that the reinforcement parameters of an alternative patch contribute

PART 2: Reinforcer probability varied

Fig. 6. Mean residence times (in seconds) on nonreinforced red- and green-patch entries in Part 2 as a function of mean times to the delivery of reinforcers on reinforced red- and green-patch entries. The straight line depicts equality between the two measures.

little to the qualitative effects of p and λ in a patch on residence times in that patch. Given the degree to which the present results replicate those from the standard “some patches are empty” procedure, it is of some

theoretical interest to establish whether the residence times produced by the present procedure were also longer than the residence times predicted by the maximization approach of McNamara and Houston (1985).

Figures 7 and 8 show the residence times obtained on the red (Figure 7) and green (Figure 8) alternatives in every condition of the present experiment as a function of the optimal residence times predicted by McNamara and Houston's model. The predicted residence times used in these figures were calculated separately for each alternative (because we arranged dependent scheduling) and assumed a travel time of 1 s in each condition (the duration of the blackout following switching). When Figures 7 and 8 are considered together, obtained residence times were longer than predicted residence times in 123 of 130 cases, a finding that is significant on a binomial test ($p < .05$). Therefore, in addition to replicating the effects of p and λ , the present procedure also replicated the "overstaying" beyond optimal residence times that has been reported in the standard procedure by Kamil et al. (1993), Davison and McCarthy (1994), and McCarthy et al. (1994).

Although the reasons why McNamara and Houston's (1985) model consistently underestimates obtained residence times are not yet altogether clear, one factor that is likely to contribute to this systematic error concerns the nature of the equation proposed in their model. Specifically, this equation is static and predicts, given various procedural parameters, *fixed* patch residence times with no variance. Brunner, Kacelnik, and Gibbon (1992) have shown that allowing variance in residence times in such formulations will result in predicting longer optimal residence times. Thus, it is quite possible that alternative models that are also based on the maximization of overall reinforcer rates, but attempt to predict the defining characteristics of residence-time *distributions*, might better describe obtained residence times in both the standard procedure and the concurrent analogue of that procedure arranged here.

Joint Control of Residence Time

Given that we obtained reasonable fits of log residence-time ratios to both the log obtained reinforcer-arrival-time ratios and the log obtained reinforcer-frequency ratios (see Table 2, Parts 1b and 2b), we can now ask whether these two independent variables jointly controlled residence-time ratios in a linear fashion. The appropriate equation for describing how a simple linear combination

of arrival-time ratios and obtained reinforcer-frequency ratios controls residence-time ratios is as follows:

$$\log\left(\frac{T_r}{T_g}\right) = a_s \log\left(\frac{A_r}{A_g}\right) + a_f \log\left(\frac{R_r}{R_g}\right) + \log c, \quad (1)$$

where T_r and T_g represent the times spent responding on nonreinforced trials, A_r and A_g represent the obtained mean arrival times of reinforcers, and R_r and R_g represent the frequencies of reinforcers for the red and green alternatives, respectively. The parameters a_s and a_f are sensitivity parameters as in the generalized matching law (Baum, 1974, 1979), and $\log c$ is inherent bias, or a constant proportional preference for one alternative over the other as the independent variables (here, relative reinforcer-arrival times and relative reinforcer frequencies) are varied. Equation 1 was fitted to individual subject data from all three parts of the experiment by the method of least squares. The estimates of the sensitivity of log residence-time ratios jointly to the log ratio of mean food-arrival times (a_s) and to the log ratio of obtained reinforcer frequencies (a_f) and the estimates of inherent bias ($\log c$) obtained in this analysis are shown in Table 3. In addition, Figure 9 shows the log obtained residence-time ratios for all three parts of the experiment, plotted as a function of the predictions of Equation 1.

Table 3 shows that the percentages of the data variance accounted for by Equation 1 fell between 60% and 90% for the individual subjects. In addition, Figure 9 shows that Equation 1 predicted log residence-time ratios that often differed substantially from obtained ratios, although we can discern no systematic deviations from the line of perfect fit for any particular part of the experiment. Table 3 also shows that estimates of inherent bias ($\log c$) were generally small and, across individual subjects, not systematically different from zero. More important, estimates of a_s and a_f were greater than zero for all 5 subjects, a result that was significant on a one-tailed sign test ($p < .05$). This finding indicates that residence-time ratios were positively related to arrival-time ratios and to reinforcer-frequency ratios. However, insofar as a_s and a_f were not systematically different across subjects, there were no clear differences in the degree to

Fig. 7. Absolute residence times on nonreinforced entries to the red alternative as a function of residence times predicted by the model of McNamara and Houston (1985). The solid diagonal lines depict equality between predicted and obtained residence times.

Fig. 8. Absolute residence times on nonreinforced entries to the green alternative as a function of residence times predicted by the model of McNamara and Houston (1985). The solid diagonal lines depict equality between predicted and obtained residence times.

Table 3

Estimates of the sensitivity of log residence-time ratios jointly to the log obtained arrival-time ratio (a_t) and the log obtained reinforcer-frequency ratio (f_t), and estimates of inherent bias ($\log c$) obtained when Equation 1 was fitted by the method of least squares to individual subject data from Parts 1, 2, and 3. %VAC is the percentage of data variance accounted for by Equation 1.

Subject	Sensitivity to ar- rival time (a_t)	Sensitivity to reinforcer frequency (f_t)	Bias	%VAC
Group	0.344	0.272	0.008	93
111	0.388	0.389	0.108	78
112	0.621	0.191	-0.022	90
113	0.356	0.267	0.002	78
115	0.151	0.190	-0.032	60
116	0.229	0.501	-0.036	78

which either variable controlled behavior. Thus, although it is unlikely that Equation 1 represents the ideal combination of obtained reinforcer-arrival time and obtained reinforcer-frequency ratios, the above analysis at least indicates clearly that the average time between changing over and gaining a reinforcer does, either directly or indirectly, affect the time spent on an alternative.

The contingencies of reinforcement that define the present procedure are somewhat different from those that operate in concurrent VI VI schedules. In addition to the differences described in the introduction, the two procedures also differ with respect to the control of reinforcer-arrival times following a changeover to an alternative. This variable was explicitly controlled and varied in the present experiment. However, in a standard concurrent VI VI schedule, the times to the first reinforcer after switching into an alternative are undefined, but are dynamically produced by an interaction between the subject's relative and absolute time allocation and the reinforcer schedules arranged on either alternative. The analysis reported by Dreyfus et al. (1982) suggests that a substantial proportion of the reinforcers obtained from either the richer or the leaner alternative is obtained immediately following a changeover to that alternative and, usually, a subsequent changeover delay. Dreyfus et al. suggested that this effect could contribute to the undermatching (Baum, 1974) so often

observed in concurrent VI VI performance. The effects of λ on time allocation observed in the present experiment lend some support to this suggestion. When reinforcers from both alternatives in a concurrent VI VI schedule are frequently obtained immediately after switching to an alternative, the distributions of times from changeover to reinforcement on the two alternatives will tend to be equalized. If one assumes that other variables operating in a concurrent VI VI schedule do not eliminate the effects of arrival times of the first reinforcer, then similar arrival times on both alternatives, despite differences in the frequencies with which the two alternatives provide reinforcement, may function to reduce differences between the times allocated to the two alternatives per changeover and, thus, decrease the overall time-allocation ratio.

The procedure arranged in the present experiment raises other questions that are pertinent to understanding performance in generic concurrent schedules of reinforcement. For example, we could ask: What are the effects of entering alternatives, and then exiting without having gained a reinforcer? Similarly, given that choice is our primary dependent variable, what are the effects of the relative frequency with which this happens on an alternative? In the present experiment, the frequency with which an entered alternative provided a reinforcer (simply the inverse of the frequency with which it did not) was determined not only by p but also by the subject's distribution of residence times for that alternative. This seems to imply a need for further analysis. However, this analysis has already been done (Figures 2 and 4), because the ratio of the obtained probabilities with which visits to the two alternatives were reinforced is identical to the ratio of obtained reinforcers in the two alternatives. Alternatively, we could ask whether the *local* rates of reinforcement in either patch controlled time allocation to that patch. This analysis has also been done. Because the values of p and λ jointly control the local reinforcer rates in patches, Figure 9 shows the effects. Finally, the effect of the relative frequency of nonreinforced entries into a patch on *absolute* residence times in that patch has been shown in Figures 7 and 8 (Part 2 data)

Fig. 9. Obtained log time-allocation ratios on nonreinforced entries as a function of log time-allocation ratios predicted from the fits of Equation 1. The solid diagonal line depicts perfect equality between obtained and predicted ratios.

via an analysis of the effects of reinforcer probability (p).

This experiment investigated response and time allocation when subjects were presented with a choice between concurrently available and signaled response alternatives in which only one reinforcer was available per change-over to an alternative. The major results of this experiment have shown that the relative period of time spent responding to an alternative (and, hence, presumably the relative number of responses made to that alternative) in this procedure can be increased both by increasing the relative frequency with which responding to that alternative is reinforced and by increasing the relative times to reinforcers following a changeover to that alternative. Both of these effects seem to be consistent with the results of other foraging studies that have investigated time allocation in a single patch (Davison & McCarthy, 1994; Kamil et al., 1993; McCarthy et al., 1994). In addition, the present experiment begins to identify some of the variables that may contribute to the control of relative time allocation in standard concurrent VI VI schedules. For instance, it is clear that the availability of more than one reinforcer per entry into an alternative on standard concurrent schedules is a further strong controller of response and time allocation, and that this independent variable on its own may well strongly control choice. Relatively minor modifications to the procedure arranged in the present experiment would accommodate the dynamic interactions that are possible between a subject's absolute and relative time allocation and the various reinforcement parameters of interest.

With such modifications, an assessment of the relative degree to which these parameters of reinforcement control choice may also be possible.

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APPENDIX

Numbers of responses emitted (B), seconds spent responding (T), number of switches from the alternative (SW), and number of reinforcers obtained (R) for the red and green alternatives summed over the final five sessions of each experimental condition for each subject.

Condi- tion	Bird	B_{red}	T_{red}	SW_{red}	R_{red}	B_{green}	T_{green}	SW_{green}	R_{green}
1	111	6,049	5,373	484	85	4,061	4,344	479	93
	112	9,155	4,312	604	93	4,035	3,199	590	107
	113	3,978	2,889	461	93	3,380	3,441	445	107
	115	5,904	4,129	284	104	4,508	3,452	290	96
	116	9,946	3,434	407	96	5,650	3,352	399	104
2	111	2,518	6,670	264	69	1,721	3,157	267	67
	112	12,343	5,458	652	106	3,999	3,553	670	88
	113	5,863	4,863	556	90	3,157	3,449	535	110
	115	6,792	4,758	312	95	4,460	3,517	306	98
	116	10,884	4,873	445	97	6,516	4,019	442	100
3	111	1,087	2,704	94	22	865	1,553	104	13
	112	8,783	4,067	666	104	4,909	5,581	690	80
	113	4,959	4,864	490	72	5,426	5,553	483	79
	115	1,312	4,861	270	48	3,268	5,958	268	51
	116	8,643	3,611	450	69	11,508	6,342	445	72
4	111	2,393	6,679	377	45	1,894	2,580	347	76
	112	10,123	5,835	731	90	3,762	3,475	735	88
	113	7,445	5,812	571	90	3,407	3,848	578	83
	115	7,350	6,422	390	77	3,303	4,187	394	73
	116	14,549	5,593	551	80	7,647	4,353	542	89
5	111	1,957	4,502	336	54	2,757	5,807	332	57
	112	5,872	3,591	519	116	4,811	4,119	554	83
	113	5,137	4,200	556	99	4,707	4,637	566	92
	115	3,331	3,496	339	85	6,640	5,835	313	108
	116	9,616	3,369	445	103	7,978	4,541	451	97
6	111	9,218	5,354	394	127	3,793	3,813	469	50
	112	5,978	4,096	548	144	3,615	2,797	641	49
	113	5,607	3,967	327	154	2,964	2,591	433	46
	115	9,489	4,858	391	139	6,977	4,257	473	56
	116	15,622	4,428	332	143	10,367	3,422	418	57
7	111	2,346	3,470	431	18	611	3,531	295	155
	112	3,447	2,056	590	21	925	3,857	432	179
	113	2,707	2,245	449	19	1,119	3,316	289	181
	115	686	1,599	245	6	1,411	2,726	86	167
	116	7,321	3,047	447	20	1,093	2,705	286	180
8	111	4,340	3,559	422	37	2,802	4,722	309	151
	112	3,132	3,253	782	56	2,319	4,361	694	144
	113	3,532	2,621	483	44	2,482	3,928	374	154
	115	3,309	3,338	385	43	3,770	5,251	273	155
	116	8,969	3,550	423	58	3,960	4,193	340	142
9	111	7,428	5,041	312	153	3,983	3,469	449	16
	112	4,901	3,524	530	179	4,874	2,246	686	21
	113	6,354	4,108	350	179	4,337	2,840	505	21
	115	4,675	3,480	209	132	4,580	5,306	320	18
	116	8,890	2,949	223	177	6,401	2,496	376	23
12	111	1,415	3,075	305	12	1,690	6,712	242	74
	112	767	1,104	398	15	1,674	7,619	234	180
	113	2,744	2,305	448	17	1,958	7,565	315	149
	115	1,865	2,604	289	12	2,818	7,876	180	122
	116	5,426	2,465	433	23	2,963	7,507	297	160
13	111	7,233	4,246	369	128	7,588	5,373	450	45
	112	4,536	3,854	482	142	3,518	4,416	575	46
	113	3,972	2,911	403	145	4,656	3,329	493	53
	115	3,714	3,467	235	151	5,300	4,225	341	44
	116	11,346	3,917	437	148	10,374	4,187	532	50

APPENDIX

(Continued)

Condi- tion	Bird	B_{red}	T_{red}	SW_{red}	R_{red}	B_{green}	T_{green}	SW_{green}	R_{green}
14	111	3,228	4,914	355	39	2,683	4,019	289	104
	112	3,180	3,343	660	38	2,359	3,990	540	161
	113	6,295	3,600	532	46	1,844	3,594	426	154
	115	4,029	4,679	453	44	2,925	5,350	351	149
	116	8,480	3,481	452	50	3,745	3,631	353	150
15	111	9,683	5,659	457	116	3,807	3,503	516	54
	112	7,153	5,684	540	142	5,951	3,174	621	58
	113	10,723	5,801	375	145	3,211	2,655	473	46
	115	5,800	7,345	228	112	2,485	3,171	312	30
	116	18,335	5,551	423	135	6,591	2,909	503	54