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ASSESSMENT AND CHOICE: AN OPERANT SIMULATION OF FORAGING IN PATCHES

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Pigeons were presented with an operant simulation of two prey patches using concurrent random-ratio schedules of reinforcement. An unstable patch offered a higher initial reinforcement probability, which then declined unpredictably to a zero reinforcement probability in each session. A stable patch offered a low but unvarying reinforcement probability. When the reinforcement probability declined to zero in a single step, the birds displayed shorter giving-up times in the unstable patch when the ratio between the initial reinforcement probabilities in the unstable and stable patches was greater and when the combined magnitude of the reinforcement probabilities in the two patches was greater. When the unstable patch declined in two steps, the birds behaved as if their giving-up times were influenced heavily by events encountered during the most recent step of the double-step change. This effect was observed, however, only when the reinforcement probability in that step was .04, not when it was .06. All of these data agree with the predictions of a capture-probability model based on a comparison of the estimated probability of receiving a reinforcer in the current patch with that in alternative patches.

Key words: foraging, patch-leaving decisions, patch selection, choice, concurrent schedules of reinforcement, statistical decision theory, pigeons

An important question in behavioral ecology is the following: When a foraging animal encounters food items that are clumped in patches, how does it decide when to leave one patch to move on to another? This question is critical, because patch-leaving mechanisms, or what behavioral ecologists call *rules of thumb* (Houston, 1987; Stephens & Krebs, 1986), determine how efficiently animals can gather energy, a currency that is important to survival and reproductive success (MacArthur & Pianka, 1966; Schoener, 1971). Patch-leaving mechanisms are also of great interest to investigators of animal learning because such mechanisms are influenced by how well an animal can gather and remember information from its environment. This common interest in patch selection has stimulated a growing synthesis of ideas between behavioral ecologists and psychologists (Baum, 1987; Kamil & Roitblat, 1985; Shettleworth, 1988, 1994; Stephens, 1990, 1993).

Patch selection can be examined with tests of the predictions of optimization models, which can lead to insights into the types of currencies used by foraging animals, but determining the actual criteria used by a forager requires investigators to generate hypotheses that are derived from mechanistic (rule-of-thumb) models and subject those hypotheses to critical tests (Stephens & Krebs, 1986). A patch-leaving mechanism may consist of a process for assessing information about patch quality and a process for making decisions based upon that information. Therefore, a patch-leaving model can be viewed as consisting of an assessment model and a decision model (Dow & Lea, 1987).

The most commonly suggested assessment models are an arithmetic mean, a simple moving average, and an exponentially weighted moving average or *integrator* (see Davis, Staddon, Machado, & Palmer, 1993; McNamara & Houston, 1987a). An arithmetic mean model assumes that an animal assesses the mean rate of prey capture from the time of patch entry. A simple moving-average model assumes that an animal forms a mean over a limited memory window (Cowie, 1977) that moves forward in time as the animal forages.

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An integrator model assumes that the influence of past information on the animal's estimate of patch quality exponentially declines (Kacelnik, Krebs, & Ens, 1987; Killeen, 1981, 1991).

Proposed decision models include the following: (a) Leave the patch after *x* seconds (a fixed-time model); (b) leave the patch after capturing *y* prey (a fixed-number model); (c) leave the patch when the time since the last prey capture (or reinforcer) equals the estimated mean interval between captures for the whole environment (a giving-up time model; see Brunner, 1990; Krebs, Ryan, & Charnov, 1974; Roche, in press); and (d) leave the patch when the estimate of the rate of energy intake in the current patch falls to the estimated rate of energy intake in the whole environment, inclusive of estimated travel time (an estimated-rate model) (for reviews, see Gallistel, 1990; Green, 1984; Iwasa, Higashi, & Yamamura, 1981; McNair, 1983; McNamara & Houston, 1985, 1987a, 1987b; Roche, 1995). In addition, Kacelnik et al. (1987) presented a two-process model that compares the attractiveness of the current patch and alternative patches with two processes: One process measures intake rates, and a second process assesses whether or not there has been a sudden decline in the intake rate in the current patch (see also McNamara & Houston, 1980; Stephens & Krebs, 1986). We propose the following revised version of the two-process model, which incorporates a bias factor that accounts for the discounting of alternative patches due to changeover delay, travel time, or other factors (see Roche, in press):

$$\text{leave when } (P_p)(1 - P_p)^n < b(P_E)(1 - P_E)^n, \qquad (1)$$

where P_p is the estimated probability of reinforcement (or prey capture) in the current patch immediately after the last reinforcer, n is the number of iterations since the last reinforcer, b is a biasing factor that determines how heavily the value of alternative patches is discounted ($0 < b \leq 1$), and P_E is the estimated probability of reinforcement in alternative patches. P_p and P_E are estimated probabilities, n is iterated with each response (peck), and b decreases with an increase in the changeover delay (or travel time) to alternative patches. Note that the values of $[(P_p)(1 - P_p)^n]$ and $[b(P_E)(1 - P_E)^n]$ are updated after each response, whereas the value of P_p is updated after each reinforcer. In other words, this model states the following: Leave the current patch when the estimated probability of reinforcement in the next iteration in the current patch falls to that estimated for alternative patches.

Animals do not use the equations of learning theorists to decide when to leave patches, of course, but the predictions of the above models can be used to test hypotheses about their patch-leaving mechanisms. In the present study, we tested the predictions of patch-leaving models in pigeons by addressing the following questions: (a) Are giving-up times affected by the probability of reinforcement in the current patch or alternative patches, and if so, how? (b) To what extent do recent events influence giving-up times?

To examine the relationship between the reinforcement probability in patches experienced by the pigeons and patch persistence, we conducted a single-step change procedure in which the birds were presented with a low-quality but unvarying stable patch and a "sudden death" unstable patch in which the probability of reinforcement declined to zero in one step. Patches were simulated with concurrent random-ratio schedules of reinforcement in operant chambers. Possibilities for how the quality of the unstable and the stable patches might influence persistence in the unstable patch include the following: (a) There might be no effect of the reinforcement probability in either patch on persistence; (b) persistence might be affected by the reinforcement probability in the unstable patch (if this relationship were negative, it would be a phenomenon akin to the partial-reinforcement effect, see Kacelnik et al., 1987; Nevin, 1979, 1988; Staddon, 1983); (c) persistence might be influenced by the ratio of reinforcement probabilities between the unstable and stable patches; (d) persistence might be influenced by the absolute combined reinforcement magnitude of the two patches; or (e) persistence might be influenced by the magnitude of the difference between the two patches. We assessed persistence in the unstable patch by measuring the interval from the last reinforcer received in the unstable patch to the exit from the unstable patch (the giving-up time) and by the number of pecks (responses) between the last reinforcer in the unstable patch and patch exit.

To examine the length of the pigeons' window on the past, we conducted a double-step change procedure in which the probability of reinforcement declined to zero in two steps in one patch but remained low and unchanging in a second patch. This procedure tested how heavily encounters during the most recent step of the double-step change influenced the birds' giving-up times. To determine how heavily information from the second step of the double-step change influenced giving-up time, we compared the mean giving-up times from the double-step and single-step change conditions. For example, consider a double-step condition with an unstable patch in which reinforcement probabilities begin at .08, drop to .04, and then drop to 0 compared to single-step conditions with unstable patches in which initial reinforcement probabilities are .04 or .08. If the mean giving-up time in the double-step condition was similar to the mean giving-up time in the .08 single-step condition, the birds' giving-up times would not appear to have been strongly influenced by events from the .04 second step. If the giving-up time in the double-step change were similar to the giving-up time in the .04 single-step condition, however, the birds' giving-up times would appear to have been strongly influenced by events from the .04 second step.

METHOD

Subjects

We used 5 White Carneau pigeons (*Columba livia*), 5 to 6 years of age, that had been obtained from the Palmetto Pigeon Plant. Each bird had prior experience on temporal bisection procedures like those described by Stubbs (1976) and on concurrent variable-interval and concurrent variable-ratio schedules of reinforcement that permitted switching between schedules by pecking a changeover key. We maintained the birds at approximately 85% of their free-feeding weights from the beginning of the familiarization trials onward. The birds had been kept at their free-feeding weights for several months prior to these experiments; their free-feeding weights were measured on one day prior to the shift from ad libitum food. The 85% weights of individual birds ranged from 410 g to 470 g. Throughout the experiments, supplemental food was provided in the home cages, if necessary, to maintain these weights. The birds were housed individually in mesh cages in which water and grit were always available; the colony room was kept in constant light.

Apparatus

The birds worked in sound-insulated, ice-cooler style, three-key operant chambers. Three chambers were used; each individual bird used the same chamber throughout the experiments. The interior chamber measured approximately 1,156 cm^3. The Plexiglas keys (Gerbrands) were 8 cm apart and 25 cm above the floor. A force of 0.15 N was required to operate the microswitch behind the key and be counted as a response. Only the center key, which could be transilluminated with either green or red light, and the right key, which could be transilluminated with yellow light, were used. The food-access bay, which measured 5.5 cm by 5 cm, was 10.5 cm from the floor and 14.5 cm below the center key. The chamber could be lit with a white houselight located above the center key. Food was delivered by raising a solenoid-operated grain hopper (Lehigh Valley Electronics) to within reach of the access bay; a light behind the access bay illuminated the hopper. Background noise was provided by a fan in each chamber. Each chamber was connected to an Apple IIe® microcomputer with MED Associates interfaces. A computer program written in ZBasic controlled the experimental contingencies and recorded data.

Procedure

At the beginning of each session, the center key was green. The bird could then peck the green key to obtain food or it could switch to the red key by pecking the right changeover key twice. Pecks on the center key were reinforced with grain according to independent random-ratio (RR) schedules, under which reinforcers were delivered after a variable number of responses, with a predetermined mean probability. For example, an RR 25 condition provides a reinforcer after an average of 25 pecks, with a probability of .04 for each peck. Reinforcers consisted of

2-s access to mixed grain. When the grain hopper was raised, the feeder light was turned on and the houselight and keylights were turned off. Thus, the green and the red keys simulated prey patches; pecks on these keys simulated search; pecks on the changeover key simulated travel; and reinforcers simulated prey.

In all conditions, the green key simulated an unstable patch in which reinforcement probability declined unpredictably, and the red key simulated a stable patch that offered an unvarying reinforcement probability within a session. In one set of conditions (the single-step change), pecks provided reinforcers at a higher probability in the unstable patch than in the stable patch, but the probability of reinforcement in the unstable patch declined unpredictably to zero (i.e., extinction) after either 20, 30, 40, 50, 60, or 70 reinforcers had been received. Each bird received all six transitions in a randomly selected order (determined by a random number generator) every 6 days. The order in which the transitions were presented was identical for each bird. Different transition points were used to mimic the unpredictability of natural foraging situations; in nature animals often do not display steady-state behavior because natural environments are often variable (Dreyfus, 1991; Kamil & Clements, 1990). Each session ended after a bird had received 80 reinforcers. Sessions were conducted 7 days per week between 9:00 a.m. and 1:00 p.m.

Table 1 lists the 13 experimental conditions chronologically, showing the sequence of reinforcement probabilities in each patch and the ratio of reinforcement probabilities between the unstable and stable patches. We conducted three single-step change conditions (Conditions 1, 2, and 3) in which the ratio of reinforcement probabilities between the unstable and stable patch varied and three single-step conditions (Conditions 1, 7, and 10) in which the ratio between the unstable and stable patches was 4:1. In addition, there was a final single-step condition (Condition 13) in which the ratio between the unstable and stable patches was 2:1, but the reinforcement probabilities were high (unstable patch = .16-0, stable patch = .08). The differences in the unstable:stable patch ratios among conditions enabled us to examine if this ratio had an influence on giving-up time. Comparisons across the .16-0/.04, the .16-0/.08, and the .04-0/.02 conditions enabled us to test whether the combined reinforcement probability of the two patches had an influence on giving-up time. To test the reliability of our results and to test for the presence of order effects, we conducted one redetermination of the .08-0/.02 condition (Condition 11) and two redeterminations of the .12-0/.03 condition (Conditions 9 and 12). Prior to the collection of data on the first single-step change condition, the birds were trained for 10 sessions with a procedure identical to the .08-0/.02 condition to familiarize them with the procedure.

Table 1

Chronological list of conditions (S^R = reinforcers in second step). All conditions consisted of 24 sessions except Condition 1, which consisted of 18 sessions. Replications are indicated by (#).

Condition	Reinforcement probability		Ratio of the two patches
	Unstable patch	Stable	
1	.08-0	.02	4:1
2	.04-0	.02	2:1
3	.06-0	.02	3:1
4	.08-.04-0:10S^R	.02	4:1-2:1
5	.08-.04-0:5S^R	.02	4:1-2:1
6	.08-.04-0:3S^R	.02	4:1-2:1
7[a]	.12-0	.03	4:1
8	.12-.06-0:3S^R	.03	4:1-2:1
9	.12-0(#2)	.03	4:1
10	.16-0	.04	4:1
11	.08-0(#2)	.02	4:1
12	.12-0(#3)	.03	4:1
13	.16-0	.08	2:1

[a] Condition 7 was preceded by a variable second step condition, not reported.

In the second type of conditions (the double-step change), pecks in the unstable patch initially provided reinforcers at a greater probability than did pecks in the stable patch. Then, at a preselected number of reinforcers before the transition to zero, the reinforcement probability in the unstable patch declined, but it still remained higher than in the stable patch. At the second transition point, which varied randomly between 20 and 70 reinforcers as in the single-step conditions, the reinforcement probability in the unstable patch declined the rest of the way to zero, thus creating a double-step change. We conducted three conditions (Table 1, Conditions 4, 5, and 6) in which the unstable patch began at .08, dropped to .04, and then dropped to 0, while the probability of reinforcement in the stable patch remained at .02. The number of reinforcers in the second step varied among these conditions from 10 reinforcers (.08-.04-0:10R), to five reinforcers (.08-.04-0:5R), to three reinforcers (.08-.04-0:3R). We varied the length of the second step to probe how heavily recent events during the second step influenced the birds' persistence in the unstable patch.

After the three .08-.04-0 double-step conditions were completed, a variable-second-step condition was conducted as a separate experiment (the data will not be reported here). In this condition the reinforcement probability in the unstable patch was .08 for 37 reinforcers, and a three-reinforcer-long second step was randomly varied among reinforcement probabilities of .04, .08, or .12 on 24 consecutive days. Subsequently, a double-step condition (Table 1, Condition 8), in which the probability of reinforcement in the unstable patch began at .12, dropped to .06 for three reinforcers, and then dropped to 0, was conducted (the .12-.06-0:3S^R condition). Condition 8 tested whether recent events influenced the pigeons more heavily when the pigeons experienced higher reinforcement rates than when they experienced low rates.

Data Analysis

Data recorded during each session included (a) the interval from delivery of the last reinforcer in the unstable patch until the first peck to the changeover key (the giving-up time) and (b) the number of responses from delivery of the last reinforcer in the unstable patch until the first peck on the changeover key (the giving-up responses). In double-step change sessions, giving-up times and giving-up responses were measured from the last reinforcer in the second step of the step change. Mean giving-up times and mean giving-up responses were calculated for each pigeon at each transition point for each condition.

In the first condition (.08-0/.02), transitions occurred after either 10, 20, 30, 40, 50, 60, or 70 reinforcers (on separate days). This series was conducted three times. In the other conditions, transitions occurred after either 20, 30, 40, 50, 60, or 70 reinforcers. This series was conducted four times. Only data from Transitions 20 through 70 were used from the first condition (18 sessions) to permit direct comparisons with other conditions.

Sometimes birds switched to the stable patch before the probability of reinforcement in the unstable patch had declined to zero. The data from these sessions were not used in order to standardize the number of reinforcers obtained before switching and in order to be consistent with the planned experimental design (a separate analysis of these sessions is provided in the Results). In addition, data were not used from sessions in the following situations: (a) when birds switched from the unstable patch to the stable patch at the beginning of the session before receiving any reinforcers (1% of the sessions); (b) when they did not finish a session (6% of the sessions); and (c) when more than 900 s passed between the last reinforcer in the unstable patch and exit from the unstable patch (less than 1% of the sessions).

Unless otherwise noted, comparisons among means were performed with a three-way block design analysis of variance (ANOVA) (Sokal & Rohlf, 1981; Zar, 1984) in which the dependent variable was the giving-up time (or giving-up responses) and the categorical variables were the subject (block), the point of transition, and the condition. Results were considered to be significant at an alpha level of .05.

RESULTS

Single-Step Change Conditions

Figure 1 shows that when the initial ratio of reinforcement probabilities between the unstable patch and the stable patch varied (i.e., 2:1, 3:1, and 4:1 in the .04-0/.02, .06-0/.02, and .08-0/.02 conditions, respectively), the birds displayed shorter mean giving-up times when the unstable patch had higher initial reinforcement probabilities, $F(2, 70) = 9.298$, $p < .001$. This general pattern was observed in 4 of the 5 pigeons and in 12 of the 15 conditions. Figure 2 shows that the pigeons also displayed a trend of fewer mean giving-up responses as the probability of reinforcement in the unstable patch increased from .04, to .06, to .08, $F(2, 70) = 10.415$, $p < .001$. This general pattern was observed in 4 of the 5 birds and 11 of the 15 individual comparisons.

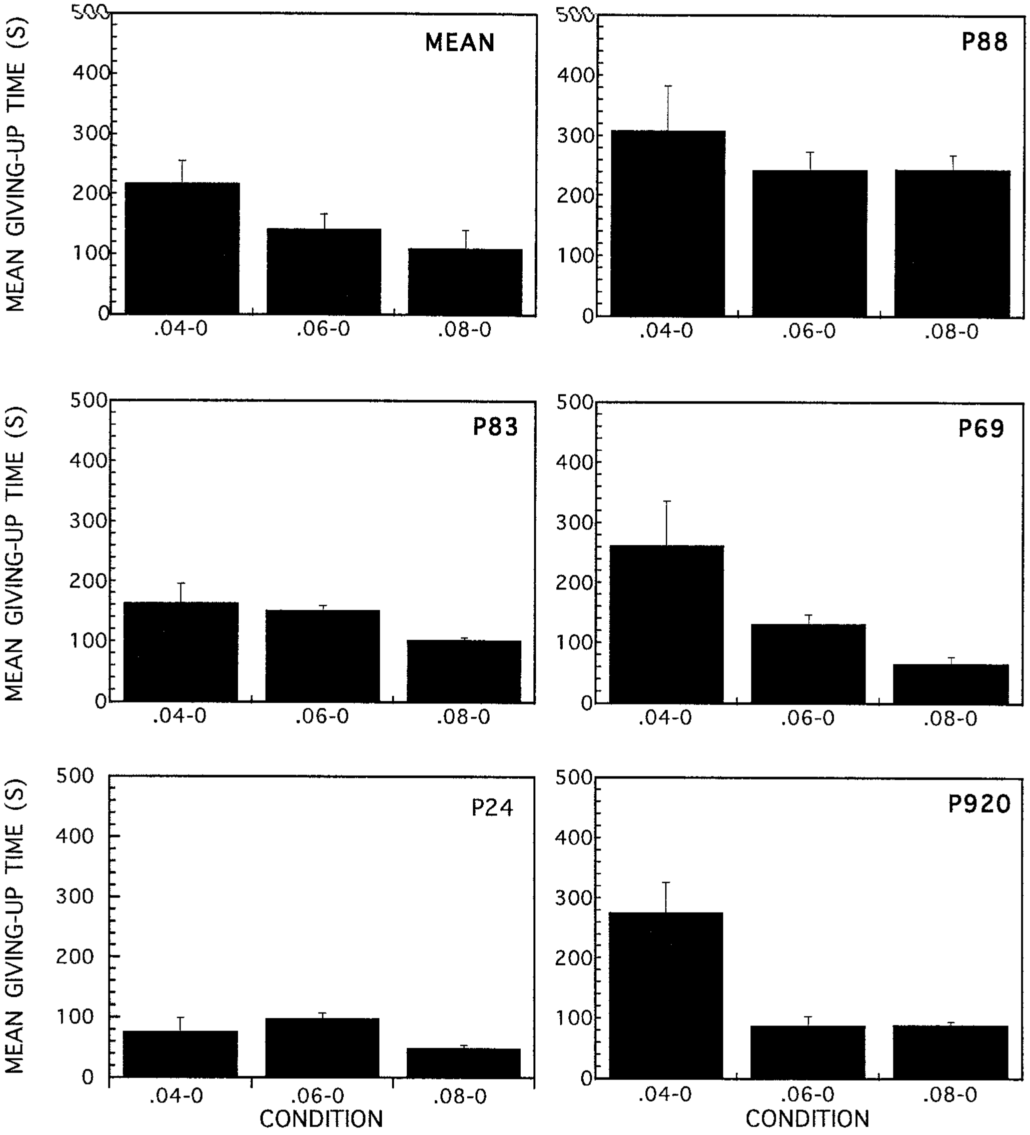

Fig. 1. Mean giving-up times (+1 *SE*) of pigeons in the .04-0/.02 condition, the .06-0/.02 condition, and the .08-0/.02 condition (unstable:stable patch ratios of 2:1, 3:1, and 4:1, respectively). Condition means for individual birds are the mean of the mean values from individual points of transition.

The .08-0/.02 condition, the redetermination of the .08-0/.02 condition, the .12-0/.03 condition, the redeterminations of the .12-0/.03 condition, and the .16-0/.04 condition all had equal ratios of reinforcement probabilities between the unstable patch and the stable patch (4:1). Although there was a significant difference in mean giving-up times among these conditions, $F(5, 161) = 12.093$, $p < .001$, Figure 3 shows that the mean giving-up times of pigeons in these conditions were similar with one exception: the .12-0/.03 condition. Tukey unplanned comparisons among these conditions found no significant difference among mean giving-up times in any of the comparisons, except for comparisons among the .12-0/.03 condition and all of the other conditions. Two redeterminations of the .12-0/.03 condition were conducted. Tukey unplanned comparisons

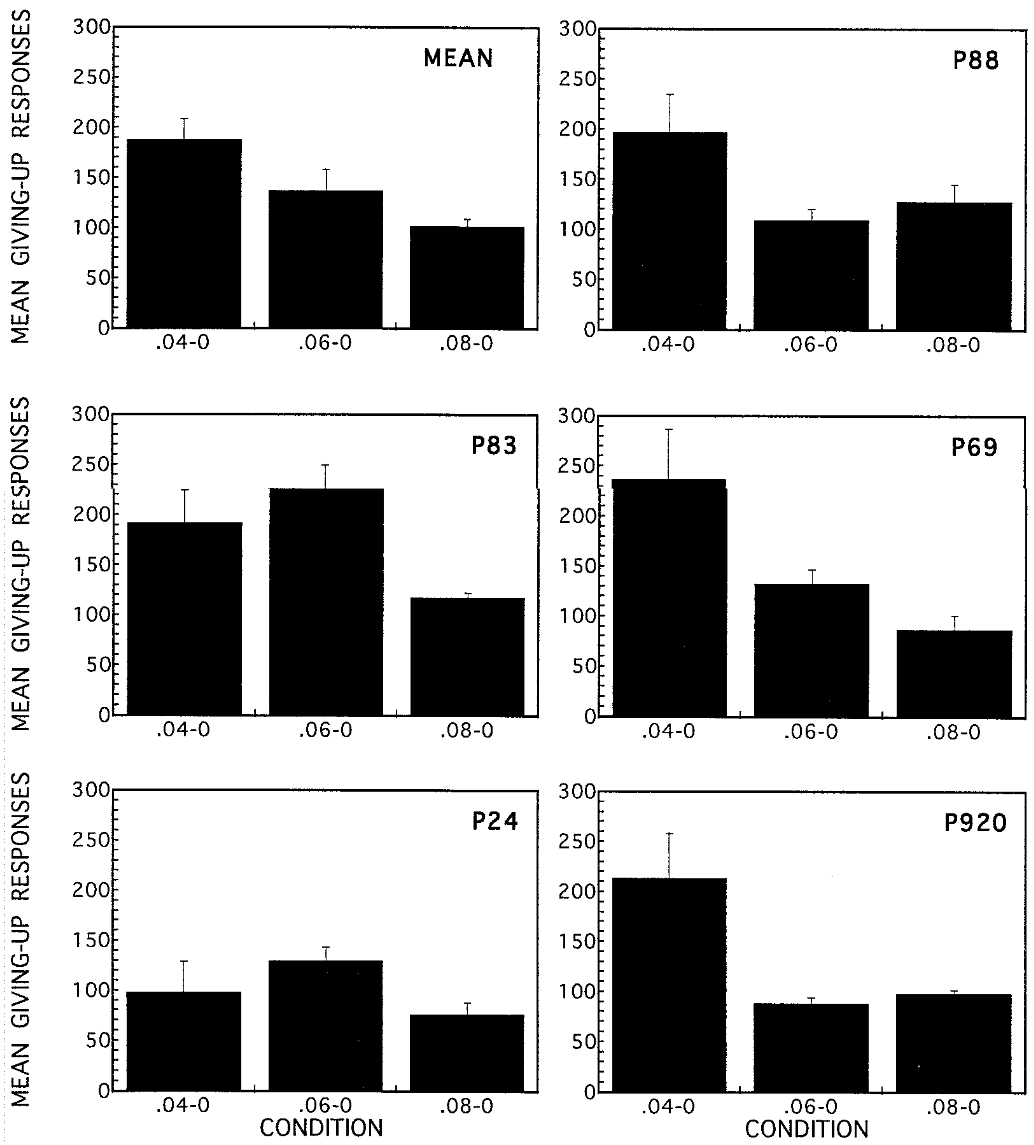

Fig. 2. Mean giving-up responses (+1 *SE*) of pigeons in the .04-0/.02 condition, the .06-0/.02 condition (3:1), and the .08-0/.02 condition (unstable:stable patch ratios of 2:1, 3:1, and 4:1, respectively). Condition means for individual birds are the mean of the mean values from individual points of transition.

showed no statistically significant difference in giving-up times between either of the .12-0/.03 redeterminations and either the .08-0/.02 condition or the .16-0/.04 condition. The giving-up times from the redeterminations of the .12-0/.03 condition also were not significantly different from each other (Tukey unplanned comparison, $p = .942$). These observations suggest that the data from the .12-0/.03 condition may have been anomalous. Two of the birds (P88 and P920) had relatively long mean giving-up times in this condition; the long giving-up times of these 2 birds had a large effect on the means from the.12-0/.03 condition.

There were no significant differences in giving-up times among the .08-0/.02 condition, the first .12-0/.03 redetermination, and the .16-0/.04 condition, $F(2, 79) = .929$, $p = .399$. However, there were significant differ-

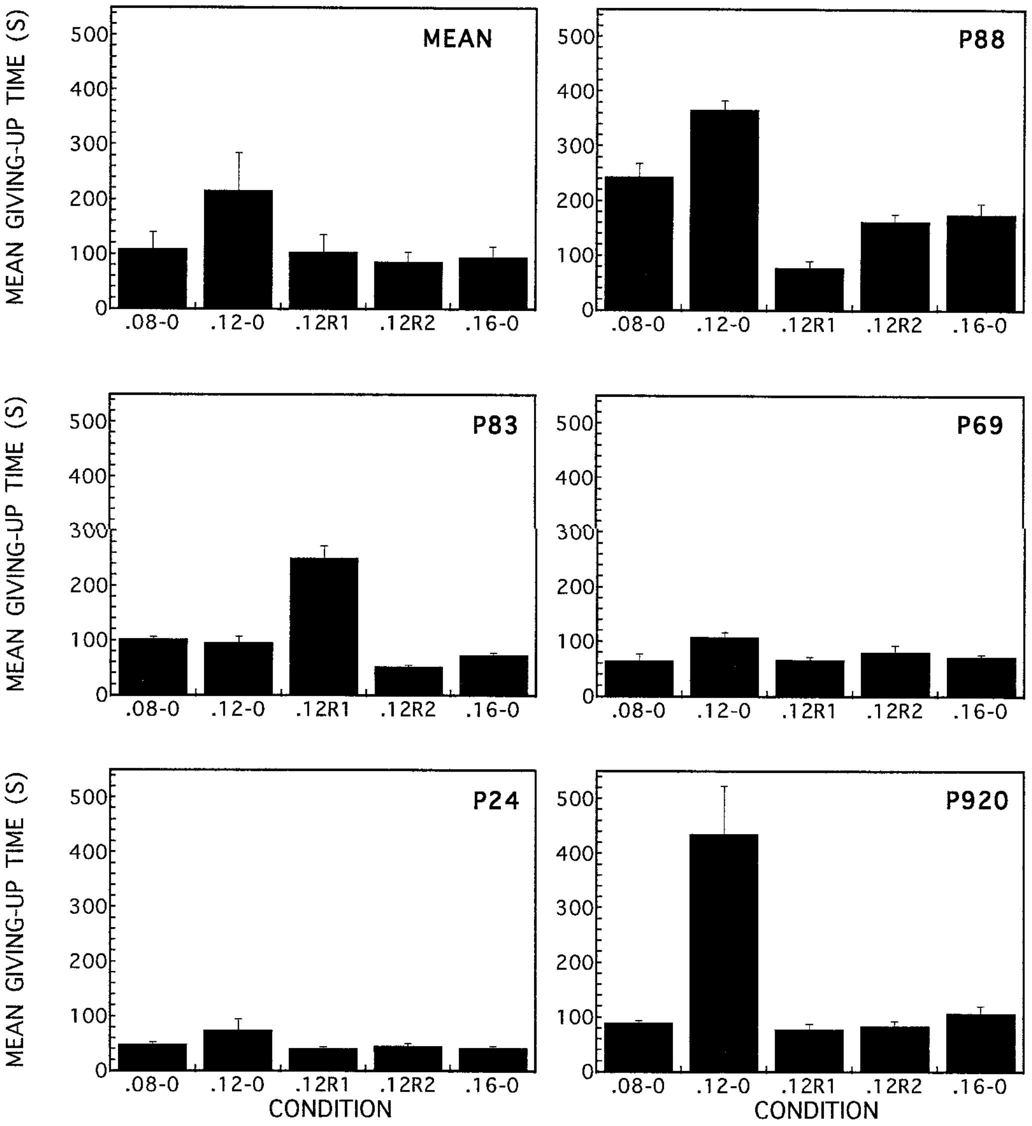

Fig. 3. Mean giving-up times (+1 *SE*) of the pigeons in the .12-0/.03 condition, the first .12-0/.03 redetermination (.12R1), and the second .12-0/.03 redetermination (.12R2) in comparison with the mean giving-up times of the .08-0/.02 condition and the .16-0/.04 condition (unstable:stable patch ratios of 4:1). Condition means for individual birds are the mean of the mean values from individual points of transition.

ences in mean giving-up responses among these conditions, $F(2, 79) = 28.457$, $p < .001$. Figure 4 shows that the mean giving-up responses of the .12-0/.03 condition were similar to that of the two .12-0/.03 redeterminations and that this similarity was evident in all 5 pigeons. The mean giving-up time in the .12-0/.03 condition was significantly different from that in each of the .12-0/.03 redeterminations, but the mean giving-up responses in the .12-0/.03 condition were not significantly different from the mean giving-up responses in either of the .12-0/.03 redeterminations (Tukey unplanned comparisons). Therefore the anomalous nature of the initial .12-0/.03 condition was reflected in the mean giving-up time but not in the giving-up responses.

The mean giving-up times in the .08-0/.02 condition and its redetermination were simi-

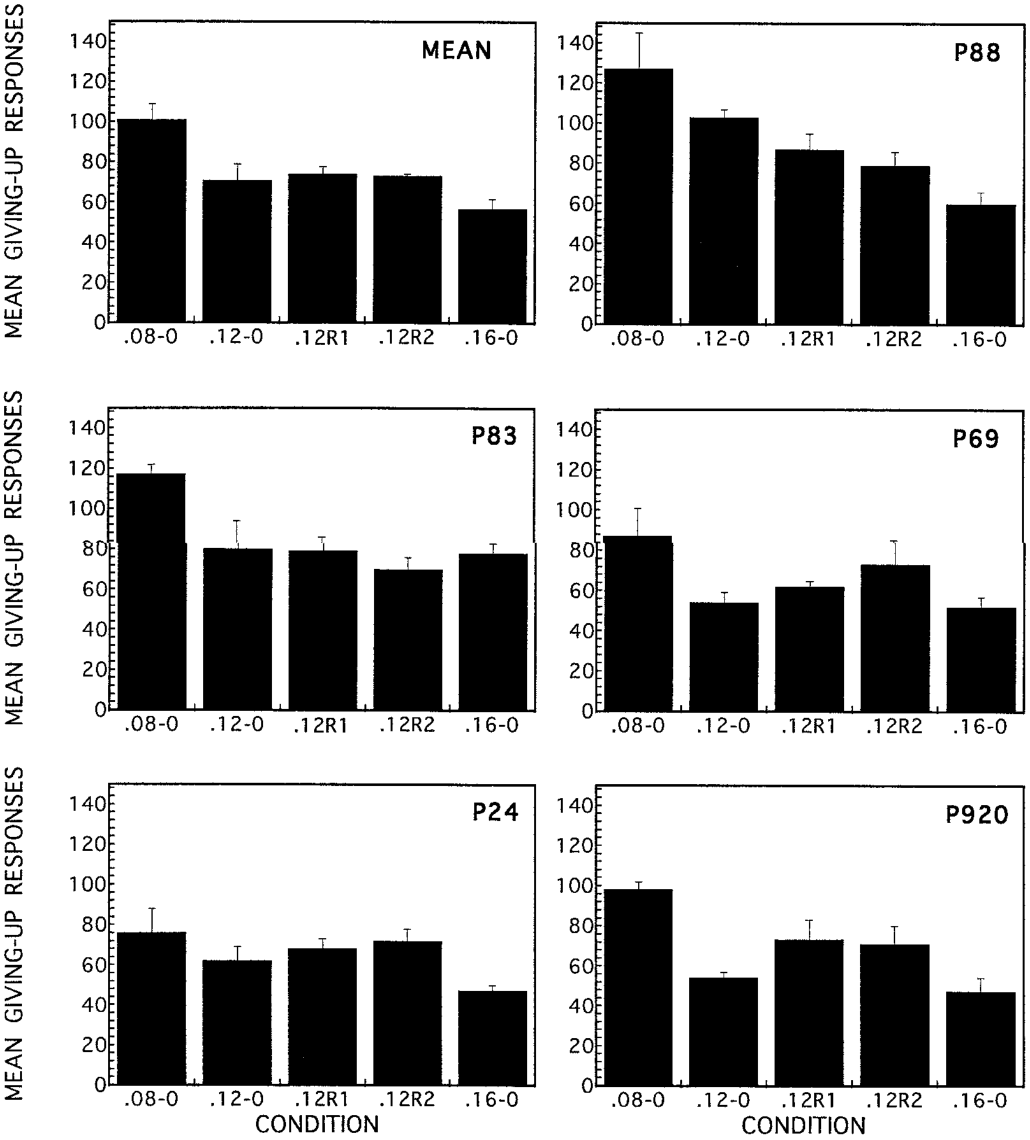

Fig. 4. Mean giving-up responses (+1 *SE*) of the pigeons in the .12-0/.03 condition, the first .12-0/.03 redetermination (.12R1), and the second .12-0/.03 redetermination (.12R2) in comparison with the mean giving-up responses in the .08-0/.02 condition and the .16-0/.04 condition (unstable:stable patch ratios of 4:1). Condition means for individual birds are the mean of the mean values from individual points of transition.

lar (Tukey unplanned comparison, $p = .999$). The mean number of giving-up responses was also similar in the .08-0/.02 condition and its redetermination (Tukey unplanned comparison, $p = 1.0$).

The mean giving-up time in the .16-0/.08 condition was 50.5 s (*SE* = 2.7), which was significantly lower than the mean giving-up time in the .16-0/.04 condition, $F(1, 49) = 27.877$, $p < .001$. Similarly, the mean number of giving-up responses in the .16-0/.08 condition was 42 (*SE* = 1.6), which was significantly lower than the mean giving-up responses in the .16-0/.04 condition, $F(1, 49) = 15.401$, $p < .001$. These differences indicate that the reinforcement probability in the stable patch influenced the pigeons' persistence. These data also indicate that the birds' persistence was not controlled entirely by either the ratio of the unstable patch to the stable patch or the difference in the reinforcement probabilities between the unstable and stable patches, but that they were sensitive to the combined magnitude of the reinforcement probabilities in the two patches. For example, although shorter giving-up times were observed with larger ratios between the unstable and stable patch in the .04-0/.02, .06-0/.02, and .08-0/.02 conditions, patch persistence was not solely a product of the unstable:stable patch ratio. Both the .04-0/.02 and the .16-0/.08 conditions had an unstable:stable patch ratio of 2:1, but the mean giving-up time was dramatically lower in the .16-0/.08 condition than in the .04-0/.02 condition.

To check if the difference in the mean giving-up times among the .04-0/.02, .06-0/.02, and .08-0/.02 conditions could have been due to an order effect, we examined the mean giving-up times in these treatments using only data from the second half of each condition. The mean giving-up times in the second half of the .04-0/.02, .06-0/.02, and .08-0/.02 conditions were 227.9 s, 144.0 s, and 109.4 s, respectively, $F(2, 67) = 15.401$, $p < .001$. Thus, the observed pattern across these conditions did not appear to be due to an order effect. Further indications that the trends in the data were not a result of order effects come from the fact that the mean giving-up time in the redetermination of the .08-0/.02 condition (117.8 s, $SE = 27.6$) was not significantly different from the mean in the .08-0/.02 condition (109.4 s, $SE = 31.0$); similarly, there was not a significant difference between the means of the giving-up times in the two redeterminations of the .12-0/.03 treatment.

Double-Step Change Conditions

Figure 5 shows that the mean giving-up times in the .08-.04-0 double-step conditions were closer to the giving-up times in the .04-0/.02 condition than to those in the .08-0/.02 condition. A weighted contrast test (Sokal & Rohlf, 1981) between the giving-up times in three .08-.04-0 double-step conditions and those in the .04-0/.02 condition showed no statistically significant difference, $F(1, 156) = 0.621$, $p = .432$. Conversely, a weighted contrast test between the giving-up times in the three .08-.04-0 double-step conditions and those in the .08-0/.02 condition was statistically significant, $F(1, 156) = 15.246$, $p < .001$. Also, a weighted contrast test between the giving-up times in the three double-step conditions and those in the .06-0/.02 condition was significant, $F(1, 156) = 5.143$, $p < .001$. Thus, the mean giving-up times in the .08-.04-0 conditions were closer to the mean giving-up time displayed in the single-step condition corresponding to the second step of the double-step condition than to the first step. In other words, the birds were behaving as if their patch-leaving decisions were based more on the probability of reinforcement in the second step than on that in the first step of the change. Figure 5 shows that this pattern was observed in 3 of the 5 individual pigeons and in 11 of the 15 individual conditions.

It is important to note that the birds experienced the first step for much longer than the second step in almost all of the sessions (the exception being the transition to a probability of zero after 20 reinforcers in the .08-.04-0:10R condition, in which the first and second steps were of equal length, i.e., 10 and 10 reinforcers). In the double-step change conditions, the second step was experienced an average of only 22%, 11%, and 7% of the time in the unstable patch when the second step was 10, five, and three reinforcers long, respectively. An arithmetic mean of the reinforcement probability experienced by pigeons in the unstable patch in these conditions would average .071, .076, and .077 when the second step was 10, 5, and 3 reinforcers long, respectively. Thus, the birds' behavior clearly did not agree with the predictions of an arithmetic mean model; if it did, their giving-up times would have been close to the giving-up times observed in the .08-0/.02 condition.

Figure 6 reveals that the mean giving-up responses for the .08-.04-0:10R and .08-.04-0:3R conditions were close to that for the .06-0/.02 condition, and the mean giving-up responses for the .08-.04-0:5R condition was intermediate between those for the .06-0/.02 and .04-0/.02 conditions. These impressions are supported by statistical analyses. A weighted contrast test of the mean giving-up responses between the three .08-.04-0 conditions and the .06-0/.02 condition was not significantly dif-

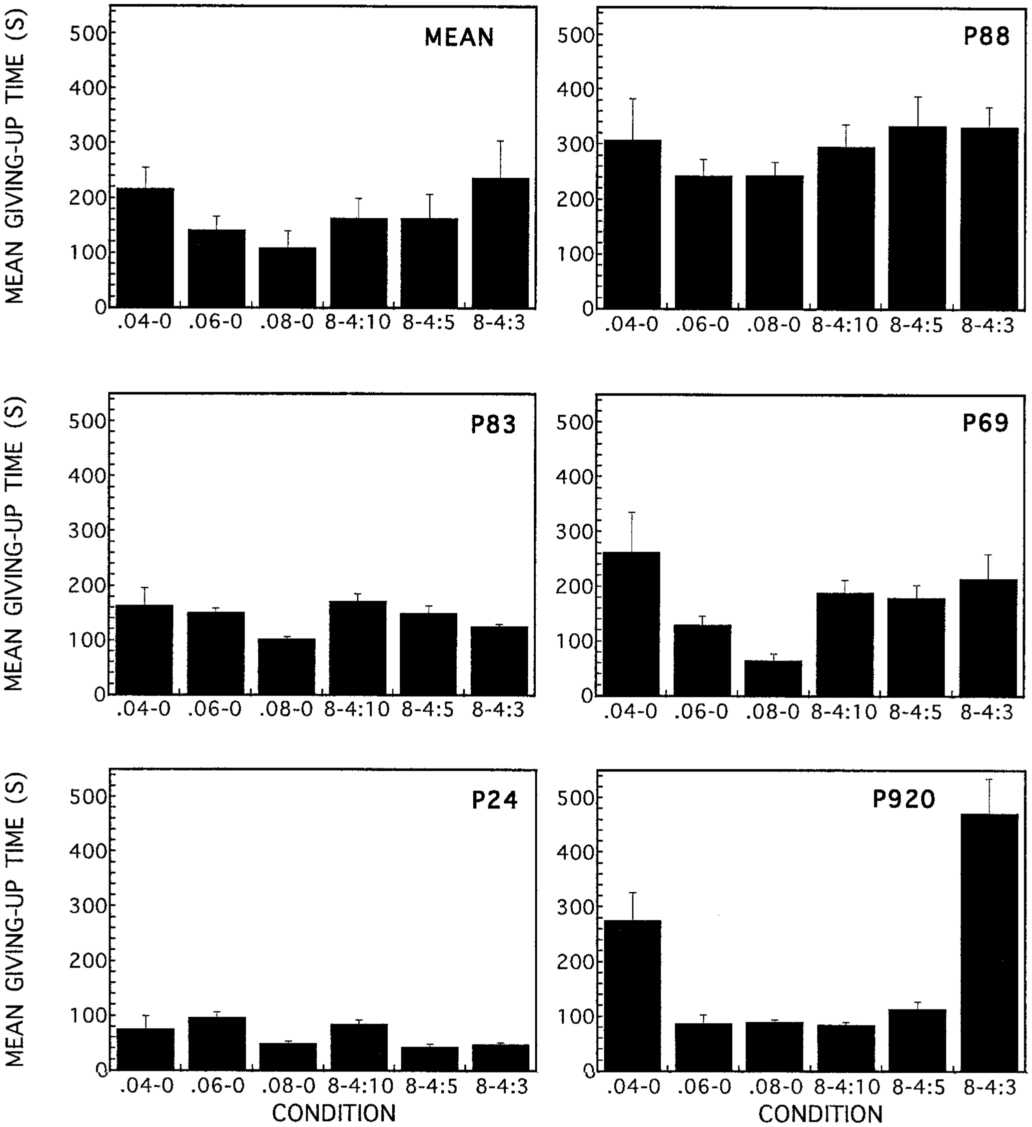

Fig. 5. Mean giving-up times (+1 *SE*) of pigeons in the .08-.04-0/:10R (8-4:10), .08-.04-0:5R (8-4:5), and .08-.04-0:3R (8-4:3) double-step change conditions in comparison with those of the .04-0/.02, .06-0/.02, and .08-0/.02 single-step change conditions (unstable:stable patch ratios of 4:1-2:1, 4:1-2:1, 4:1-2:1, 2:1, 3:1, and 4:1, respectively). Condition means for individual birds are the mean of the mean values from individual points of transition.

ferent, $F(1, 156) = 0.258$, $p = .612$. A weighted contrast test of the mean giving-up responses between the three .08-.04-0 conditions and the .08-0/.02 condition was significant, $F(1, 156) = 7.145$, $p < .001$. In addition, a weighted contrast test between the three .08-.04-0 conditions and the .04-0/.02 condition was also significant, $F(1, 156) = 12.521$, $p < .001$. Thus, the mean giving-up responses in the .08-.04-0 double-step conditions were closer to the giving-up responses in the .06-0/.02 single-step condition (which is equal to a mean of .08 and .04) than to the giving-up responses in the .08 or .04 conditions. An examination of the individual subject data reveals, however, that a pattern of intermediate giving-up responses was evident in only 2 of 5 birds and in 7 of 15 individual conditions.

The mean giving-up time in the .12-.06-0 condition was not significantly different from

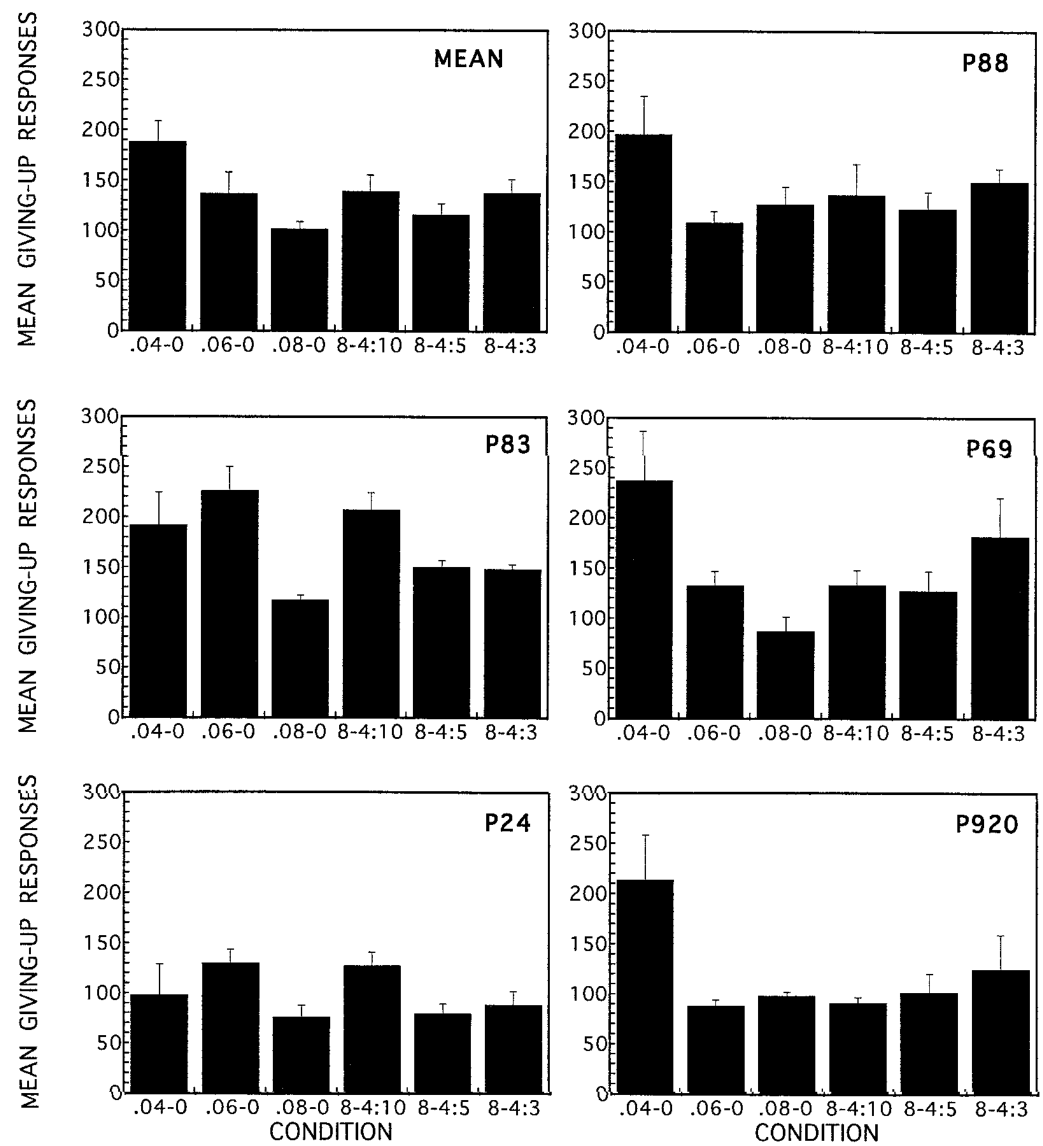

Fig. 6. Mean giving-up responses (+1 *SE*) of pigeons in the .08-.04-0:10R (8-4:10), .08-.04-0:5R (8-4:5), and .08-.04-0:3R (8-4:3) double-step change conditions in comparison with those of the .04-0/.02, .06-0/.02, and .08-0/.02 single-step change conditions (unstable:stable patch ratios of 4:1-2:1, 4:1-2:1, 4:1-2:1, 2:1, 3:1, and 4:1, respectively). Condition means for individual birds are the mean of the mean values from individual points of transition.

that in the .06-0/.02 condition, $F(1, 106) = 0.057$, $p = .813$ (contrast test) (Figure 7) and was significantly different from those in the .12-0/.03 redeterminations, $F(1, 106) = 13.003$, $p < .001$ (weighted contrast test). Thus, the mean giving-up time data appear to support the hypothesis that, on average, events during the second step of the .12-.06-0 condition heavily influenced the birds' patch persistence. The data from the individual subjects do not support this hypothesis, however.

Figure 7 shows that the mean giving-up time from the .12-.06-0 condition was elevated by the high mean value from P88 and that individual-subject data from only 1 bird (P88) agreed with the hypothesis that events from the .06 probability second step heavily influenced patch persistence. In addition, the giv-

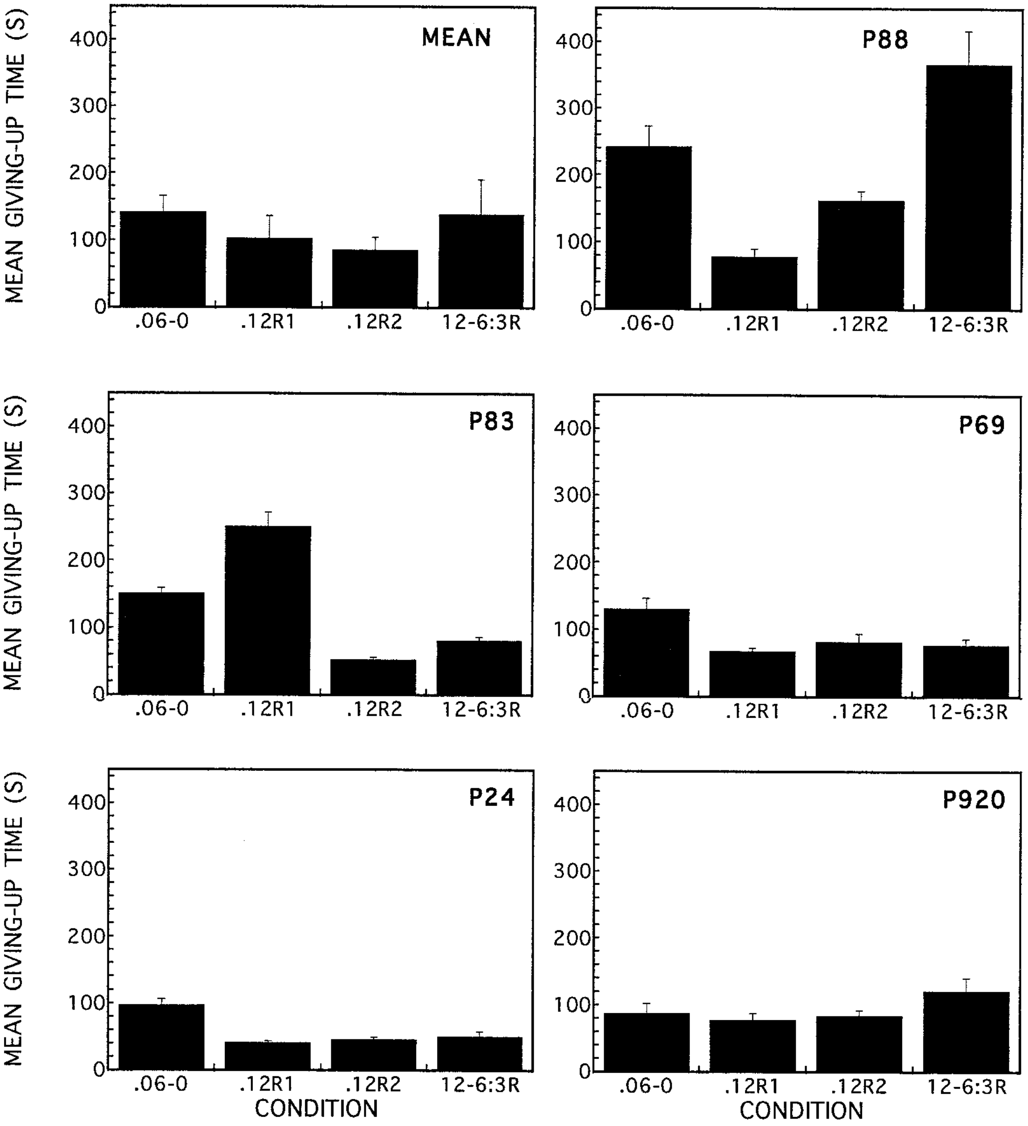

Fig. 7. Mean giving-up times of pigeons (+1 *SE*) in the .12-.06-0:3R double-step change condition (12-6:3R) in comparison with the mean giving-up times of the .06-0/.02 condition, the first redetermination of the .12-0/.03 condition (.12R1), and the second redetermination of the .12-0/.03 condition (.12R2) (unstable:stable patch ratios of 4:1-2:1, 3:1, 4:1, and 4:1, respectively). Condition means for individual birds are the mean of the mean values from individual points of transition.

ing-up responses data did not support this hypothesis either. Figure 8 shows that the mean giving-up responses in the .12-.06-0 condition were lower than the mean giving-up responses in the .06-0/.02 condition, $F(1, 106) = 54.230$, $p < .001$ (contrast test) and was similar to those in the .12-0/.03 redeterminations, $F(1, 106) = 0.3287$, $p = .568$ (weighted contrast test) (Figure 8). Also, the giving-up responses data from individual birds in Figure 8 do not suggest that events from the second step of the .12-.06-0 step change were heavily influencing patch persistence. The giving-up responses data from the .08-.04-0 conditions and the giving-up time and giving-up responses data from the .12-.06-0:3R condition emphasize the importance of individual-subject data in behavioral analyses.

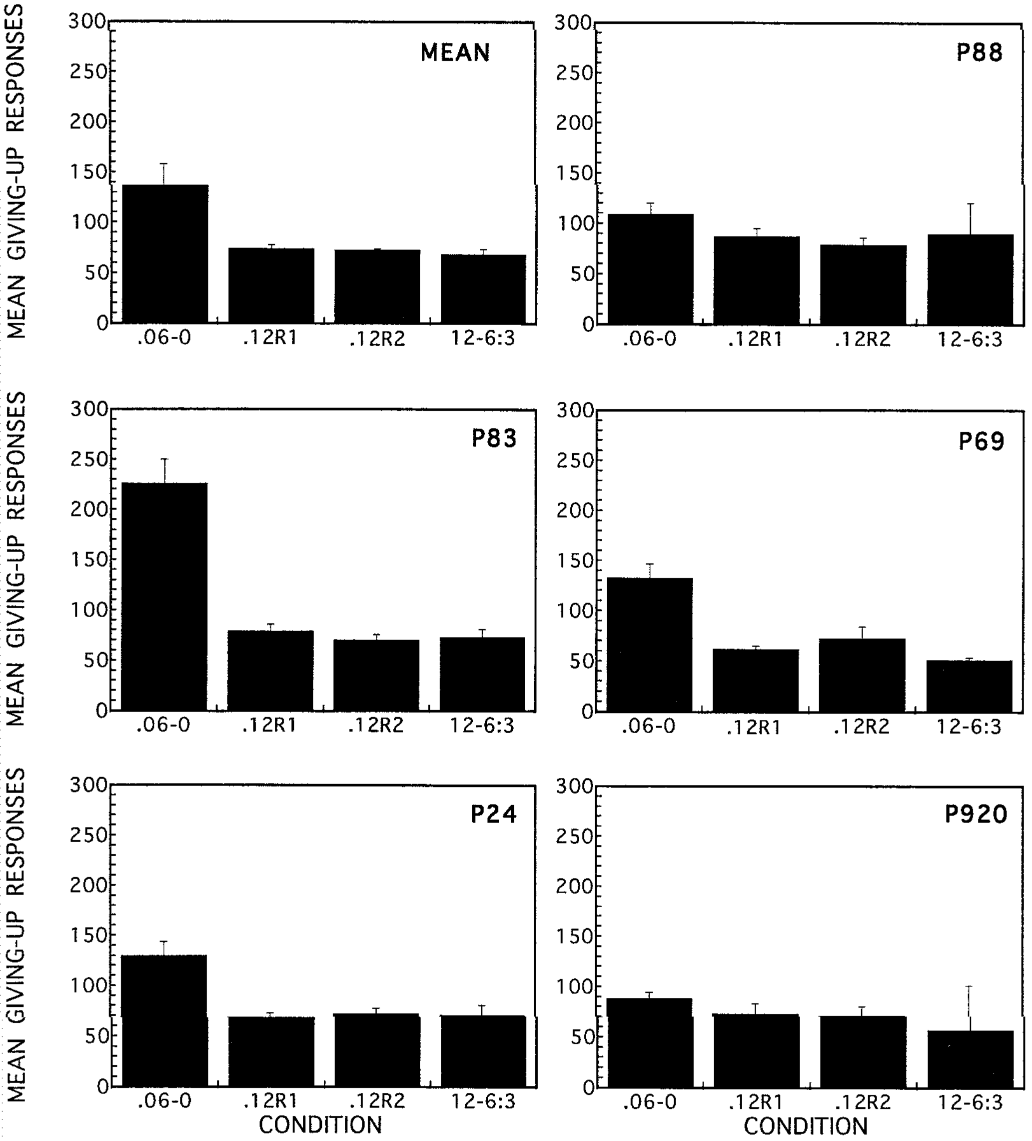

Fig. 8. Mean giving-up responses (+1 *SE*) of pigeons in the .12-.06-0:3R double-step change condition (12-6:3) in comparison with the mean giving-up times of the .06-0/.02 condition, the first redetermination of the .12-0/.03 condition (.12R1), and the second redetermination of the .12-0/.03 condition (.12R2) (unstable:stable patch ratios of 4:1-2:1, 3:1, 4:1, and 4:1, respectively). Condition means for individual birds are the mean of the mean values from individual points of transition.

Note that the average interval of the second step would be shorter in a .12-.06-0:3R condition than in a .08-.04-0:3R condition, because it takes less time to receive three reinforcers when the probability of reinforcement is .06 than when it is .04. Therefore, the results of the .12-.06-0:3R condition do not necessarily contradict the results of the .08-.04-0:3R condition; they merely suggest the possibility that if the temporal length of the second step is too short, the reinforcement probability in the second step will no longer heavily influence patch persistence.

Sessions in Which Pigeons Switched Early

In some sessions, birds switched from the unstable patch to the stable patch before the transition was reached. The birds left the un-

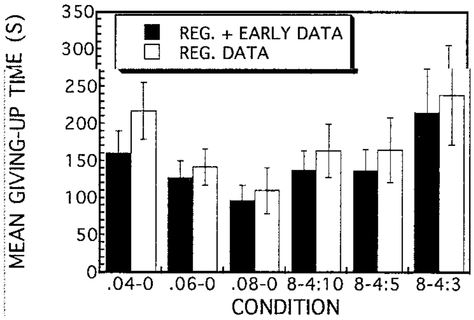

Fig. 9. Mean giving-up times (+1 *SE*) of pigeons in the .04-0/.02, .06-0/.02, .08-0/.02, .08-.04-0:10R, .08-.04-0:5R, and .08-.04-0:3R conditions showing the data from when the pigeons reached the transition point (reg. data) as well as the combined data from when the pigeons reached the transition point and when they switched patches before the transition point (reg. + early data).

stable patch before the transition during approximately 20% of the sessions, on average, over all of the conditions. The percentage of instances of leaving early in individual sessions ranged from a low of about 6% in the second .12-0/.03 redetermination to a high of 38% in the .04-0/.02 condition, the condition in which the reinforcement probabilities in the unstable and stable patches were the most similar. The proportion of trials in which pigeons left the unstable patch before its reinforcement probability had declined to zero was correlated with the reinforcement probability in the unstable patch, r (n = 13) = .604, p = .029.

To examine whether or not the data from the sessions in which birds switched early would have affected our results, we calculated the combined mean giving-up times for the sessions in which pigeons reached the transition point and for switch-early sessions by taking means of similar switching points (e.g., a mean of sessions in which one to nine reinforcers were received in the unstable patch before switching, after 10 to 19 were received, after 20 to 29 were received, etc.) for each bird and then taking a grand mean. For example, Figure 9 shows that the combined regular and switch-early data from the .04-0/.02, .06-0/.02, and .08-0/.02 conditions reveal the same trend of shorter giving-up times with higher initial reinforcement probabilities, F(2, 84) = 6.71, p = .002. Figure 9 also shows that the combined data from the .08-.04-0 conditions were closer to the combined giving-up time data from the .04-0/.02 condition than the .08-0/.02 condition. This pattern was consistent in 4 of the 5 animals. Contrast tests among the combined regular and switch-early values of the single-step and double-step conditions revealed the same trends as were seen in the regular data. A weighted contrast test between the .08 condition and the three .08-.04-0 conditions was significantly different, F(1, 179) = 14.187, p = .001. On the other hand, a weighted contrast test between the three .08-.04-0 conditions and the .04-0/.02 condition did not reveal a significant difference, F(1, 179) = 0.282, p = .596. In other words, the data from the sessions in which birds switched early did not change the trends in the results. Comparisons of the regular data and the combined regular plus switch-early data in Figure 9 do show that the mean giving-up times from the combined data were consistently lower than those from the regular data.

DISCUSSION

The Influence of Recent Information

In the .08-.04-0 double-step change procedure, the birds' giving-up times appeared to be heavily influenced by the second step of the step change. That is, the more heavily recent events influenced giving-up times in the .08-.04-0 conditions, the closer the mean giving-up times would be expected to be to the mean giving-up time in the .04-0/.02 condition. The mean giving-up times in the .08-.04-0 conditions were all closer to the mean giving-up time in the .04-0/.02 condition than they were to the mean giving-up time in the .08-0/.02 condition. The data from the .08-.04-0 conditions do not agree with the predictions of an arithmetic mean calculated over the entire time the birds were in a patch; an arithmetic mean model would predict that the birds' mean giving-up times in the .08-.04-0 conditions would have been very close to those in the .08-0/.02 single-step change condition.

These findings build upon observations in other studies that indicate that recent events sometimes heavily influence the behavior of animals. In an aviary experiment with black-capped chickadees (*Parus atricapillus*), birds were presented with a single-step change procedure and a double-step change procedure (Roche, in press). The chickadees' pattern of patch-leaving behavior agreed closely with that of the pigeons in the present study. In the single-step change experiment, the chickadees displayed significantly shorter giving-up times as the ratio of capture probabilities between the unstable and stable patches became higher; in the double-step change experiment, the birds' giving-up times were influenced by the capture probabilities in the second step of the double-step change.

In an operant simulation of foraging in which pigeons encountered simulations of high- and low-quality prey, Shettleworth and Plowright (1992) found that the birds' tendency to accept low-quality prey was heavily influenced by the duration of the last period of search. Other studies have shown that pigeons often display a pause in pecking after receiving a reinforcer under certain kinds of variable-interval schedules. The duration of this pause has been observed to correlate closely with the last interval between food deliveries, a process called *linear waiting* (Higa, Wynne, & Staddon, 1991; Staddon, Wynne, & Higa, 1991). Linear waiting suggests a heavy influence of recent events. Cuthill, Kacelnik, Krebs, Haccou, and Iwasa (1990), in an operant simulation of foraging using starlings (*Sturnus vulgaris*), also observed a strong influence of recent events; they found that the birds' patch residence times were determined by the last travel time they had experienced.

There are clear advantages to weighing recent events heavily; to do so allows animals to track environmental changes in food availability more quickly. Yet if recent information is weighed too heavily, an animal will be subject to making mistakes such as leaving a patch after a run of bad luck before patch quality has declined (Killeen, 1981; Shettleworth, 1994; Shettleworth & Plowright, 1992). Therefore, the evolution of a memory window for foraging decisions presumably is subject to a balance between the benefits from tracking the environment and those from avoiding mistakes. It is important to note that although the pigeons' giving-up times in the present study were heavily influenced by recent events experienced within a patch, a comparison of the giving-up times in the .16-0/.04 and .16-0/.08 conditions suggests that their tendencies to switch patches were influenced by events experienced in the alternative patch at least 24 hr before.

Predictions of the Giving-Up Time Model

The data collected in this study rule out the fixed-time and the fixed-number hypotheses: the residence time (the interval from patch entry to patch exit) within patches and the number of reinforcers received in patches varied among sessions. However, do the observations from the single-step and double-step change conditions agree with the predictions of the giving-up time model, the estimated-rate model, or the capture-probability model? In the single-step change procedure, the birds' giving-up times and giving-up responses showed a general trend of shorter giving-up times and fewer giving-up responses as the ratio of reinforcement probabilities between the unstable patch and the stable patch became higher. However, the mean giving-up time in the .16-0/.08 condition, which had a ratio between the unstable patch and the stable patch equal to that in the .04-0/.02 condition, had a mean giving-up time considerably below that from the .04-0/.02 condition. This difference indicates that giving-up time is influenced by both the ratio of reinforcement probabilities between the unstable patch and the stable patch and by the combined magnitudes of the reinforcement probabilities in the two patches. Any realistic model of patch persistence will therefore have to account for these observations.

The giving-up time model predicts that the giving-up time is set by the estimated average intercapture interval for the whole environment. The giving-up time model therefore may be interpreted as requiring an animal to display the same giving-up time in all patches in an environment (see Krebs et al., 1974). If an animal were assessing the mean intercapture interval for the whole environment, however, this estimate would be influenced by the mean intercapture interval in the current patch. Thus, the estimated intercapture interval for the whole environment would be decreased when a patch had a high initial reinforcement rate. For example, the mean overall reinforcement probability experienced in the .08-0/.02 condition was about .05, and the mean in the .04-0/.02 condition was about .03. Thus, a giving-up time model would predict shorter giving-up times in initially richer patches due to the influence of experience in the current patch on the environmental average. The giving-up time model could also explain why animals often display shorter giving-up times when alternative patches are richer or when travel times are shorter (see Stephens & Krebs, 1986): Richer patches and shorter travel times would reduce the overall mean intercapture interval.

The data from the present study agree qualitatively with the predictions of the giving-up time model, but the data from the .08-.04-0 conditions raise some doubts. For example, the mean overall probability of reinforcement in the .08-.04-0:3R condition was about .05. This probability was close to the overall probability in the .08-0/.02 condition (.05) and was higher than the overall probability in the .04-0/.02 condition (.03). However, the mean giving-up time in the .08-.04-0:3R condition was closer to the mean giving-up time in the .04-0/.02 condition than to that in the .08-0/.02 condition. This finding does not support a giving-up time hypothesis.

Predictions of the Estimated-Rate Model

The estimated-rate model, which is a rule-of-thumb version of Charnov's (1976) marginal value theorem, can explain some experimental trends, such as the tendency for animals to leave a patch more readily when alternative patches offer higher reinforcement rates. However, it does not easily explain shorter giving-up times in patches with higher ratios of reinforcement probability between the unstable and stable patches. The estimate of the current patch provided by an estimated-rate model would be higher when the reinforcement rate in that patch is high than when it is low. That estimate would therefore have farther to fall to reach the patch-leaving threshold when the difference in magnitude between the unstable and stable patches is greater. For example, the difference between the initial reinforcement rate in the unstable and the stable patches was greater in the .08-0/.02 condition (.06) than in the .04-0/.02 condition (.02) (see Bailey & Mazur, 1990; Mazur & Ratti, 1991; Staddon, 1983; see also Mazur, 1992). An estimated-rate model with an unchanging weighing of recent events would therefore predict longer giving-up times in patches with higher initial reinforcement probabilities, a prediction contradicted by our results.

The birds' behavior could be explained by an estimated-rate model, however, if recent events had more of an influence on patch persistence when reinforcement rates were higher. Two proposed processes that could increase the influence of recent events on estimates of patch quality in higher quality patches are the following: (a) The rate of an internal timer could increase with higher rates of reinforcement, causing a faster rate of iteration of the estimate; and (b) the value of the currency parameter in an integrator model could change with reinforcement rate (see Bizo & White, 1994; Fetterman & Killeen, 1995; Killeen 1984, 1991; Killeen & Fetterman, 1988, 1993; MacEwen & Killeen, 1991). These predictions were illustrated by simulations of two estimated-rate models conducted by Kacelnik et al. (1987). They found that although estimated-rate models with unchanging memory windows did not predict shorter giving-up times in initially richer patches, shorter giving-up times were predicted by Killeen's (1984) integrator-based estimated-rate model in which the influence of recent events changes with reinforcement rate. Shorter giving-up times were also predicted by Kacelnik et al.'s two-process model.

Although the giving-up times of the pigeons in the .08-.04-0 conditions suggested that events experienced during the second (.04) step heavily influenced their behavior, the data from the .12-.06-0:3R condition did not indicate that the birds in that condition were heavily influenced by events experienced during the second (.06) step. If recent events influence patch persistence more heavily in patches of higher quality, we would predict that events experienced during the second step of the double-step change would influence patch persistence 1.5 times (.06/.04) more in the .12-.06-0:3R condition than in the .08-.04-0 condition. Data from 4 of the 5 pigeons in the .12-.06-0:3R condition did not agree with this prediction. Thus, the data from the .12-.06-0:3R condition do not support the hypothesis that the influence of recent events was proportional to the experienced reinforcement rate. Note that, as was mentioned in the Results, if the influence of recent experience does not change with reinforcement rate, the influence of the second step would be less in the .12-.06-0:3R condition than in the .08-.04-0:3R condition because the second step would be experienced for a shorter duration.

Predictions of the Capture-Probability Model

The capture-probability model proposes a signal detection (see Egan, 1975) interpretation of patch persistence. When the rate of reinforcement is higher, the mean interval between reinforcers is shorter, and thus changes in reinforcement rate may be more detectable. It takes about 25, 16.7, and 12.5 pecks, on average, to receive a reinforcer in random-ratio schedules with reinforcement probabilities of .04, .06, and .08, respectively. Therefore, it should be easier to discern a decline in reinforcement probability when reinforcers are received after an average of 12.5 pecks than when they are received after an average of 25 pecks. However, the giving-up times observed in the pigeons were not only influenced by the initial reinforcement probability in the unstable patch; they were also influenced by the ratio between the unstable and stable patches and the overall probability magnitude within the two patches. The capture-probability model, which compares the estimated probability of receiving a reinforcer in the current patch after a given number of iterations with the estimated probability of reinforcement in the alternative patch, can account for all of the patterns observed in this study.

The capture-probability model can be explored by examining the following function P_n (see Fetterman, Dreyfus, & Stubbs, 1989):

$$P_n = P_p(1 - P_p)^{n-1}, \qquad (2)$$

where P_p is the estimated quality of the patch immediately after the last reinforcer and n is the number of iterations (responses). Figure 10 plots the function P_n for a patch that has an initial reinforcement probability of .08, a patch that has an initial reinforcement probability of .04, and a patch that has an initial reinforcement probability of .02. The estimated probability of the animal's receiving a reinforcer on the iteration is represented by the y axis, and the number of iterations is represented by the x axis. Note that a given number on the x axis represents the number of iterations (n), whereas the exponent in Equation 2 is $n - 1$; this explains why the curves in Figure 10 begin at $x = 1$. The y values of these curves decrease as the x values increase. This decline represents the decrease in the probability of receiving a reinforcer with increased durations of unsuccessful search. The crossover point between the function for the .08 patch and that for the .02 patch is between Iterations 22 and 23. Thus 23 iterations represents the best changeover point from a .08 patch to a .02 patch, in the absence of a bias to stay long. The best changeover component of the capture-probability model bears a similarity to optimization models, but the initial probabilities are based on estimates made by the animal rather than absolute values from the environment.

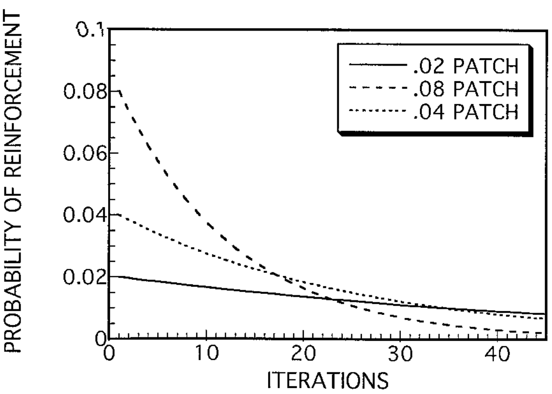

Fig. 10. A plot of the probability distributions produced by the function $P_n = P_{n-1}(1 - P_{n-1})^{n-1}$ (see text) in patches with initial probabilities of reinforcement of .08, .04, and .02.

Figure 11 shows the predicted best changeover points calculated from Equation 2 plotted against observed data. Figure 11A compares the predictions of the response-based capture-probability model with the pigeons' mean giving-up responses. To explore whether time may be a more appropriate measure than responses, Figure 11B compares the predictions of a capture-probability model that is iterated after x time units (where $x = 1$ s) with the pigeons' mean giving-up times. The response-based model explained 97.1% of the variance in the observed giving-up responses, whereas the time-based model ex-

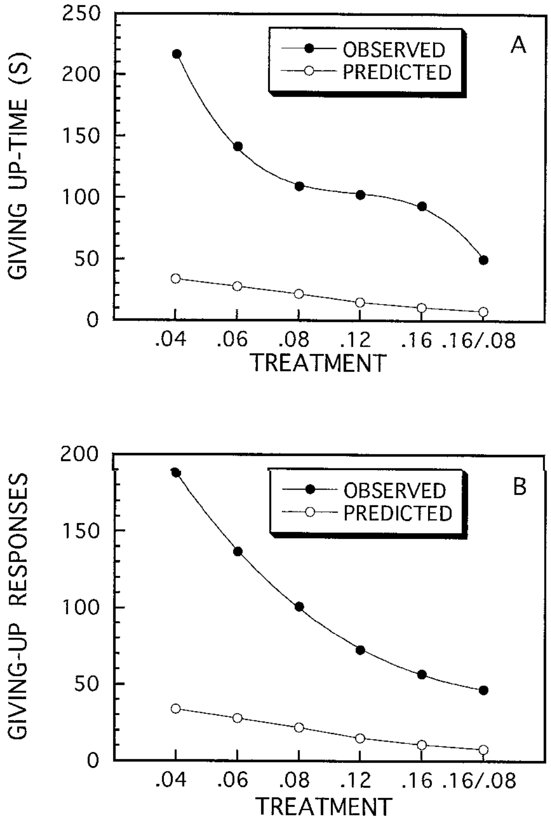

Fig. 11. (A) Comparison of the predictions of a capture-probability model that is based on responses and the mean giving-up responses observed in the single-step conditions (R^2 of regression of predicted vs. observed giving-up responses = .971). (B) Comparison of the predictions of a capture-probability model that is based on time and the mean giving-up time observed in the single-step conditions (R^2 of regression of predicted vs. observed giving-up times = .876).

plained 87.6% of the variance in the observed giving-up times.

Figure 11 shows that the predictions of the capture-probability model agree with the observed fewer number of giving-up responses (and shorter giving-up times) with higher reinforcement probability ratios between the unstable and stable patch (.08-0/.02, .06-0/.02, and .04-0/.02 conditions) and that they also agree with the observed data from the .16-0/.08 condition, in which the ratio of reinforcement probabilities in the unstable versus the stable patch was 2:1 but in which the absolute probability of reinforcement in the patches was high. A significant difference was observed among the mean giving-up times across the .04-0/.02, .06-0/.02, and .08-0/.02 conditions, but not among the .08-0/.02 and .12-0/.03 redeterminations and the .16-0/.04 conditions. Note that the capture-probability model predicts a large difference between the .04-0/.02 and the .08-0/.02 conditions, a somewhat smaller difference between the .08-0/.02 and .12-0/.03 conditions, and an even smaller difference between the .12-0/.03 and .16-0/.04 conditions.

There was a good fit between the model's predictions of trends and the data, but the pigeons stayed in the unstable patch about five times longer than predicted. This bias to stay long may be a result of limitations on the birds' ability to estimate mean interreinforcement responses or interreinforcement intervals; in other words, they may need to stay longer than predicted to successfully detect a difference in probability between the two patches. The ability to detect a difference would be affected by the type of distribution of the responses or the intervals between reinforcers. When the number of responses between reinforcers is random around a given mean, as in this study, animals would be expected to show more of a bias to stay long than when the distribution was even (i.e., a fixed-ratio schedule). Changeover delay (simulated travel time) was unlikely to contribute greatly to a bias to stay long in these experiments; the changeover delay was usually under 2 s, a small proportion of the giving-up time in all of the conditions.

The present study provided several insights into the patch-leaving behavior of pigeons. In summary, our data do not agree with the predictions of a giving-up time model or with an estimated-rate model. Our data do agree with the predictions of a capture-probability model. Many important questions remain to be answered in future studies, however. First, does the patch-leaving behavior of pigeons agree more closely with a simple moving-average model of patch assessment or an integrator model? Second, are updates of estimates of patch quality time based or response based (see Church & Meck, 1984; Fetterman, 1993)? Third, do the characteristics of the patch-assessment mechanism of pigeons seem to change in different conditions? For example, Kamil, Yoerg, and Clements (1988) found that blue jays (*Cyanocitta cristata*) used both number cues and temporal cues in their patch-leaving decisions in an operant simulation of foraging and that the relative influence these cues had on the bird's behavior changed in different situations. Can pigeons display similar flexibility? Finally, what are the similarities, and differences, in the patch-leaving behavior of pigeons and other species? A continued synthesis of ideas between animal learning and behavioral ecology promises to provide exciting answers to these questions.

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