*PIGEONS' CHOICES IN SITUATIONS OF DIMINISHING RETURNS:
FIXED- VERSUS PROGRESSIVE-RATIO SCHEDULES*

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In two different discrete-trial procedures, pigeons were faced with choices between fixed-ratio and progressive-ratio schedules. The latter schedules entail diminishing returns, a feature analogous to foraging situations in the wild. In the first condition (no reset), subjects chose between a progressive-ratio schedule that increased in increments of 20 throughout a session and a fixed-ratio schedule that was constant across blocks of sessions. The size of the fixed ratio was varied parametrically through an ascending and then a descending series. In the reset condition, the same fixed-ratio values were used, but each selection (and completion) of the fixed ratio reset the progressive-ratio schedule back to its minimal value. In the no-reset procedure, the pigeons tended to cease selecting the progressive ratio when it equaled or slightly exceeded the fixed-ratio value, whereas in reset, they chose the fixed ratio well in advance of that equality point. These results indicate sensitivity to molar as well as to molecular reinforcement rates, and those molar relationships are similar to predictions based on the marginal value theorem of optimal foraging theory (e.g., Charnov, 1976). However, although previous results with monkeys (Hineline & Sodetz, 1987) appeared to minimize responses per reinforcement, the present results corresponded more closely to predictions based on sums-of-reciprocals of distance from point of choice to each of the next four reinforcers. Results obtained by Hodos and Trumbule (1967) with chimpanzees in a similar procedure were intermediate between these two relationships. Variability of choices, as well as median choice points, differed between the reset and no-reset conditions. Although these differences are consistent with the relative costs (in responses per reinforcement) in the two procedures, the differing dispersions of choice probably arise mainly from differing structural constraints of the two procedures.

Key words: foraging, choice, fixed ratio, progressive ratio, molar/molecular reinforcement, variability, key peck, pigeons

In the fields of biology and psychology, there seem to be at least three approaches to the study of foraging. Ecologists conduct naturalistic studies (e.g., Davies, 1977; Smith & Sweatman, 1974) directly observing the behavior that, by definition, constitutes foraging. In the interest of improving internal validity, some researchers have attempted to simulate "real" environmental conditions in the laboratory, for example, by constructing artificial trees with varying amounts of prey (Krebs, Ryan, & Charnov, 1974) or burying food in sand (Mellgren, 1982). A third approach, often adopted by experimental psychologists, involves modeling particular features of foraging

through the use of schedules of reinforcement in operant conditioning chambers (e.g., Abarca & Fantino, 1982; Mazur & Vaughan, 1987; for a review of the research in these areas, see Fantino & Abarca, 1985; Lea, 1981).

An especially interesting type of foraging situation, addressed by all three types of research, is a "patchy" one in which prey density within a given patch decreases as a function of consumption. At some point, the rate of net gain (sometimes construed as energy intake) that results from continuing to forage within a patch falls below the net gain that would result from changing to a fresh, nondepleted patch. Although much theorizing has addressed this issue, most notably Charnov (1976), most models that have been proposed to account for behavior in such situations have proved unsatisfactory (Lea, 1981, pp. 395-397).

Empirically, the feature of depletion can be modeled through use of progressive-ratio schedules, because their reinforcement density declines much as the reinforcement density of a patch might decline. Hodos and Trumbule

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(1967) described such a procedure as an extension of Findley's (1958) study involving preference with progressive schedules, but they did not identify it as a foraging analogue. In their design, chimpanzees were faced with the choice of a fixed-ratio schedule (FR) versus a progressive-ratio schedule (PR); the FR values in their first experiment were varied parametrically, in irregular order, between 100 and 1,000. Their first experiment was called the reset condition, because every selection of the FR, after reinforcement, reset the PR to its initial value of 20. As the FR requirement increased, the animals switched from responding on the PR to responding on the FR well before the two schedules reached equal response requirements. Hodos and Trumbule showed that, by doing so, subjects minimized responses per reinforcement. In Hodos and Trumbule's second experiment, completion of the FR did not reset the PR, and thus responses per reinforcement could be minimized by switching from the PR to the FR when the two response requirements were equal. In this procedure, the chimpanzees typically drove the PR up to that equality point and then switched to responding on the FR.

In reporting a similar pair of experiments, Hineline and Sodetz (1987) identified this procedure as a foraging analogue. In their experiment, the increments of the PR were also 20, but the reset version of their procedure differed in that it could be reset to a value of zero, whereby the single response of choosing the schedule produced the reinforcer. For higher PR values, as for the FR, the single choice response disabled the alternative schedule until reinforcement on the chosen schedule. Thus, when the PR was at its initial value, the response requirement was actually $1 + 0$ or 1, the next value was $1 + 20$, then $1 + 40$, and so on. The same was true for the FR in that, given an FR value of 80, the response requirement was $1 + 80$ throughout the session. The FR values used in that experiment were varied parametrically in a geometric, ascending and then descending, series that ranged between 20 and 640 responses per reinforcer. A red lamp corresponded with the FR and a yellow with the PR. Additionally, the yellow lamp (correlated with the PR) flashed when the PR was reset to its minimal value. Hineline and Sodetz's (1987) procedure also differed in that Hodos and Trumbule (1967) began with the

reset condition followed by no reset, whereas Hineline and Sodetz first exposed their subjects to the no-reset procedure. In spite of these differences, Hineline and Sodetz also found that the animals switched to the FR in advance of the equality point in the reset condition, and switched at equality in no reset. At all but the highest FR value (640), Hineline and Sodetz's monkeys consistently switched from the PR to the FR schedule at points that minimized the overall number of responses per reinforcer, whereas Hodos and Trumbule's chimpanzees consistently exceeded that value to a moderate degree.

Hineline and Sodetz (1987) discussed their procedure and that of Hodos and Trumbule (1967) in terms of characteristics analogous to those of foraging environments, considering the PR as corresponding to a patch that becomes leaner as the animal eats within it, and the FR as corresponding to the cost of travel to the next nondepleted patch. The present study used similar procedures with pigeons as subjects to enable a comparison of avian behavior with that of primates in comparable situations, with features that are likely to have been relevant in the evolutionary history of each species.

These procedures also enable us to address some theoretical concerns that have arisen, irrespective of the foraging analogues, in laboratory studies of pigeons' choices between schedules of reinforcement. Both the no-reset and the reset conditions can be viewed on a molecular level (i.e., does the animal choose a greater rather than a lesser number of responses in the shorter term?) and on a molar level (i.e., what is the overall cost of these choices, in the number of responses per reinforcer?). In the no-reset procedure, both molecular and molar relationships lead us to predict switching from the PR to the FR schedule at the point in the PR progression at which the two schedule values are equal. In the reset condition, short-term consequences continue to support switching at that same point. However, in that condition, the overall (molar) cost of reinforcement can be minimized only if the FR is chosen while the PR value is substantially smaller—that is, when an "easier" immediate PR requirement could be selected.

The relevance of molar and molecular relationships has been a lively issue in behavior analysis, with some theorists favoring the molecular (e.g., Navarick, 1979), others favoring

the molar (e.g., Baum, 1981), and still others offering formulations that evaluate immediate, molecular consequences in a molar context (e.g., Fantino, 1969—the delay-reduction hypothesis). As Hineline and Sodetz (1987), Mazur and Vaughan (1987), and Shull and Spear (1987) all have pointed out, the present procedures are clearly relevant to these issues. Hence, comparisons between molar and molecular relationships will be explored here, as they pertain to behavior theory and the operative principles of behavior in environments that involve foraging.

EXPERIMENT 1

In this experiment, pigeons' choices between FR and PR schedules were examined with a procedure in which short-term and long-term consequences of choice were not in conflict. It was a systematic replication of a procedure that Hineline and Sodetz (1987) used with monkeys as subjects. The FR values were manipulated systematically across conditions.

Method

Subjects. Four White Carneau pigeons (P1, P2, P3, and P4) with prior histories of auto-shaping served as subjects. Because the birds showed some ratio strain during their preliminary training, they were maintained at 75% of their free-feeding weights rather than the usual 80%. P1's data are not presented due to ratio strain throughout the experiment, resulting in exposure to only the lower ratio values. Sessions were conducted daily.

Apparatus. Electromechanical recording and control equipment was connected to a Gerbrands (model G7105) operant conditioning chamber in a separate room. The chamber was equipped with two response keys, symmetrically placed in the back wall, 14.3 cm apart (center-to-center) and 22.5 cm from the floor. Each translucent key could be illuminated either yellow or red, with 28-V lamps (1829) with plastic covers. A grain hopper, accessible through a circular opening (50 cm diameter) in the lower center of the same wall, provided 3-s access to grain as reinforcement; during food delivery, both keys were dark and the hopper was illuminated achromatically.

Preliminary training. The subjects initially were exposed to a series of FR schedules. The FR was pseudorandomly switched between

keys to discourage side preferences; the key with the schedule was lighted red and the alternative key was dark. The FR requirement was increased gradually over a period of several weeks through the sequence: 1, 5, 10, 15, 25, 40, 60, and 80.

Procedure. Although a free-operant procedure was used, it involved discrete choice points, dividing the procedure into episodes that are appropriately designated as "trials." (Technically, it was a concurrent-chains procedure with FR 1 in the initial links and FR versus PR in the terminal links.) At the beginning of each trial, the subject chose either an FR, requiring a constant number of responses per reinforcement, or a PR whose value increased each time it was selected. FR values were 20, 40, 60, 80, 100, and 120; a given value was held constant across sessions until stability criteria were met, as described below. On the other hand, the PR was set to a requirement of 0 at the beginning of each session and incremented by 20 additional responses each time it was chosen. Thus it had a value of 0, then 20, 40, 60, and so on, depending on how many times it had been chosen. A choice response of 1 was required for the selection of either ratio, so the total ratio requirements were $1 + \text{ratio}$, resulting in the lowest PR value of $1 + 0 = 1$, followed by $1 + 20 = 21$, then 41, and so on. Likewise, the FR required a $1 + \text{ratio}$ value.

The stimulus lamps (yellow was correlated with PR and red with FR) were switched pseudorandomly between the left and right sides on successive trials. Once a schedule was selected, its corresponding stimulus light remained on until the next food delivery, and the light for the other schedule was turned off. Pecks on the unlit key had no programmed consequences. When the trial ended (i.e., when the required number of responses was completed for the selected schedule) the keylight was turned off during food delivery; the next trial followed immediately thereafter. A session ended after 40 reinforcers were delivered.

Each choice of the PR incremented that schedule by 20 responses throughout each session, starting over only with the next day's session. Across blocks of sessions, subjects were exposed to an ascending, and then a descending, series of FR values: 20, 40, 60, 80, 100, and 120 followed by 100, 80, 60, 40, and 20. (This procedure was called no reset because

completions of the FR schedule did not reset the PR to its starting value of 0.)

Assessments of stability were based on conditional probabilities computed over successive five-session blocks, as follows: At a given PR value, the probability of choosing the FR was computed as the number of FR choices at a given step in the PR schedule, divided by the number of opportunities to choose at that PR value. Thus, choice probabilities were assessed separately for trials with each size of PR momentarily in effect. We defined the "probabilistic switch point" as the lowest step in the PR schedule at which the probability value exceeded .80 without subsequently dropping below .80. (The probability value was set at .80, the smallest whole-integer value exceeding .75, which is midway between indifference and exclusive preference.) PR values at which the bird had fewer than 10 opportunities to choose the FR did not figure in the determination of the switch points. When the probabilistic switch point remained the same for two consecutive five-session blocks, data from the *subsequent* five-session block were reported as the final data for the condition. In addition, data from the first five sessions of a new condition were considered transition data and were not used to assess stability. Therefore, the minimum exposure to any one condition was 20 days (i.e., the first block as transition, two blocks criterion, and the final block as reported data). Whenever a bird's behavior did not meet criterion, the subject was studied for 50 days (10 five-session blocks) and then was moved to the next condition.

The probabilistic measures of switching, although used to determine stability, are not presented as primary data for several reasons. At times the subjects did not meet the probabilistic stability criterion and consequently conditions were changed after 50 sessions. Additionally, it was not uncommon for subjects to switch with a probability of .80 at a given PR value, but then switch at less than .80 at a higher PR increment, then again switch reliably. For example, at PR values of 20, 40, 60, 80, and 100, if the probability values were .95, .90, .83, .75, and .85, respectively, the switching point was assessed as 100, even though switching was occurring with high probability at lower values. Such fluctuations had not been anticipated, because in earlier work using these procedures with monkeys (Hineline & Sodetz,

1987), subjects' switching had entailed precipitous and consistent shifts to a high probability of choosing the FR schedule. Hence, the median switching point, which is less affected by such vicissitudes, is used as our primary measure for presentation of results.

Results

Median switch points. For the final five sessions with a given FR value, the PR value above which (and below which) half of all FR choices occurred was designated as the median switch point. (Accordingly, a median value can be reported which is between two actual PR values, e.g., 70, even though the subject could not "truly" switch at a PR of 70.) Stating, for example, that a bird "switched at PR 60" means that, more often than not, the PR was selected when it had values through 40, but, when the PR was 60 or greater, the FR was chosen more frequently than the PR. A summary of 3 subjects' median switch points, as a function of FR value, is shown in Figure 1. On each part of the figure there are two lines labeled "optimal/equality," denoting that equal cost (responses per reinforcement) is incurred by switching to the FR when the PR is either equal to, or one increment in excess of, the FR value. (By convention, switching points are defined in terms of the PR value confronting the subject, not the last PR value completed.) For example, with an FR value of 60, switching to the FR after completing PR 40 or after completing PR 60 would result in the same overall number of responses per reinforcement, differing only in whether one of the 60-response ratios came via the PR schedule. If the subject completed the PR 60 before switching, the switching point would be recorded as 80.

Data from ascending and descending sequences of FR values are presented separately, but there appear to be no consistent differences in performance between the ascending and descending series. For all birds, the median switch point increased systematically with the size of the FR schedule. Birds P3 and P4 frequently switched at the higher of the two optimality points (points of minimal overall responses per reinforcement) particularly at the lower FR values. However, subjects did not exclusively select the PR prior to switching to the FR; in many instances, FR selections were interspersed with PR selections.

Interquartile ranges. To assess variability in switching, the distributions of FR choices were divided into quartiles along the PR increment scale. Figure 2 shows the interquartile ranges for successive five-session blocks of every FR condition, drawn from the descending series, for each bird. The filled circles indicate median switch points; in those cases in which the interquartile range was the same as the median switch point, the plot falls on the same point in the graph, denoting an interquartile range of zero. In addition, parallel horizontal lines indicate the optimal switch points for each condition.

Across conditions, the degree of fluctuation in the median switching point and the width of the interquartile ranges tended to increase as a function of increasing FR value. Consequently, the stability criterion (which had been selected early in the experiment) often was not satisfied, and subjects remained on these higher values in excess of eight 5-day blocks, very often reaching the ten 5-day block maximum before being moved arbitrarily to the next condition. Consistent with the data in Figure 1, median switching points often exceeded the optimal switch points, with switching beyond equality more prevalent and more extreme at higher FR values. Within conditions, the median switch point tended to approach optimality and become less variable from block to block as a function of extended exposure to a given condition (with P2 and P3 on FR 120 being notable exceptions).

Cost. Figure 3 shows cost functions (in responses per reinforcement, calculated by dividing total responses by total reinforcers) for the no-reset condition, with each point based on the final 5-day block of sessions on a given FR value, for each subject. The optimal line (minimum possible cost or "mpc") represents the minimal number of responses per reinforcer (cost) that could be incurred at each FR value. Actual numbers of responses per reinforcer on the ascending and descending series are plotted on the same graph. Obtained cost was not substantially in excess of the minimum possible even though, as detailed above, median switch points were not always close to optimal. Although counterintuitive, this is not a logically inconsistent outcome, as will be discussed below.

Dispersion of FR choices and efficiency. Figure 4 presents the frequency of choosing the FR

Fig. 1. Choices between the FR and a nonresetting PR schedule, as a function of FR value, for each of 3 pigeons. The results from both ascending and descending sequences of FR values are shown separately; with the median PR value at which subjects switched from the PR to the FR schedule computed over the last five sessions of each condition. The parallel dotted lines indicate the points of equality between the schedules, allowing for the fact that switching either just before or just after the PR that equaled the FR resulted in the same number of responses per reinforcer. (A data storage malfunction resulted in the loss of FR 100 data for P3 and P4.)

Fig. 2. Variability in switching, within and across conditions, for each of 3 pigeons given choices between FR and nonresetting PR schedules. The interquartile range of PR values at which switching to the FR occurred is shown as a function of successive 5-day blocks, shown separately for each condition in the descending series of FR values. Each graph is from one FR value, with the lowest FR value at the top of the figure. The parallel lines indicate the points of equality between the FR and PR schedules. Filled circles indicate the median switching point. Circles without lines indicate that the interquartile range fell entirely within the median value. (FR 20 data for P3 are missing due to a computer malfunction.) Note also that the number of 5-day blocks to criterion can be seen here.

schedule as a function of successive steps in the PR sequence for 3 birds' final-block performance on all conditions (with the exception of FR 20 for P3, due to a data storage problem). Also shown in these graphs are derived efficiency functions (the inverse of cost) showing the relative number of reinforcers per response that would result from always choosing the FR at the same given PR value. These theoretical functions were normalized to the highest number of actual FR choices, and then displaced upward by a constant distance.

The birds' distributions of FR choices show some correspondence to the flatness of the corresponding efficiency function. At FR 20, choices were distributed across three PR values: 20, 40, and 60. However, the greatest numbers of FRs were chosen when the PR was at 20 and 40; that is, at the equality points. The drop-off in the frequency of switches occurred at roughly the same point at which there was an appreciable decrease in the efficiency function. In contrast, in FR 120, the birds tended to drive the PR well past the equality point, resulting in substantial dispersion of FR choices. Note, however, that the theoretical efficiency curve flattens as the FR value is increased. The determinants of these efficiency functions will be considered in the General Discussion.

Discussion

While on this procedure, both the immediate consequences of choice (responses to next reinforcer) and the longer term consequences of choice—indeed, virtually all theories of choice—could be said to favor switching at the equality point. This experiment found that the FR schedule tended to be chosen at PR values in excess of the point of equality between the FR and PR schedules; overshooting equality was more frequent and extreme at higher than at lower FR values. The reason for greater overshooting at higher values may be that overshooting at higher FR values is less costly, averaged over entire sessions, than is overshooting when the FR value is low. Thus, although we did not initially view this procedure as assessing long-term versus short-term consequences (molecular vs. molar optimizing), the degree of departure from optimal performance suggests that the birds were more sensitive to long-term than to short-term cost in responses per reinforcement. Additional

Fig. 3. Cost functions, defined in terms of responses per reinforcer, as a function of FR value for choices between an FR and a nonresetting PR schedule. The dotted line without symbols represents cost that would result from always switching to the FR when it was equaled by the PR schedule (or the minimal cost requirement). The other lines show the costs resulting from the 3 birds' actual choices, averaged over the final five sessions of each condition in the descending series of FR values.

Fig. 4. Bars display the frequency of FR choices (uncorrected for opportunity) as a function of PR value at which each FR choice occurred based on data pooled over the final five sessions of each condition in the descending sequence of FR values. The curves over the bars, normalized to the height of the highest bar and displaced vertically by a constant amount, indicate efficiency (reinforcers per response) that would result from exclusively switching to the FR at the PR values indicated on the abscissa. Data for P3, FR 20, are unavailable. Note that this figure shows how the subjects occasionally switched back and forth from FR to PR.

Table 1

The number of responses and resulting cost, in each possible Reset switching condition, given an FR 120 and PR 20 with an FR 1 initial link.

PR total	FR	Total responses	Total reinforcers	Responses per reinforcement
(1×1)+0	1+120	122	2	61.00
(2×1)+0+20	1+120	143	3	47.67
(3×1)+0+20+40	1+120	184	4	46.00 ^a
(4×1)+0+20+40+60	1+120	245	5	49.00
(5×1)+0+20+40+60+80	1+120	326	6	54.33
(6×1)+0+20+40+60+80+100	1+120	427	7	61.00

^a Note that, on a molar level, subjects can optimize cost by switching to the FR 120 when faced with a PR value of 60. (In calculating the total number of responses on the PR, the commitment response for each selection is included by multiplying it by the number of successive PR choices in the hypothetical "run.")

considerations arising from the structural characteristics of the procedures will be considered in the General Discussion.

EXPERIMENT 2

The contingencies of Experiment 1 resembled those of a foraging environment in which subjects may travel (back and forth) between a depleting patch (the PR schedule) and one of fixed density (the FR). A laboratory situation more analogous to a depleting-patch foraging environment is one in which the PR becomes progressively leaner as it is repeatedly selected (a depleting patch) but can be replenished by selecting the FR, as in the present experiments. This, of course, assumes that the FR is substantially larger than the increments within the PR schedule, making the between-patch density of prey lower than the (undepleted) within-patch density. The replenishment is achieved by resetting the PR schedule to its minimal value upon completion of the FR schedule requirement. In the present experiment, selecting the FR schedule resulted in both a reinforcer and the resetting of the PR to its initial value of 0, from which it again incremented with subsequent PR selections. (Although one might wonder whether this is an appropriate analogy to travel, given that the FR schedule arranges its own reinforcer, it should be noted that, in some foraging situations, arrival at the new patch coincides with, and becomes discriminable through, capture of the first prey from that patch.)

This procedure also placed long-term and short-term consequences into opposition. Whereas minimization of responses per reinforcer (cost) was possible in Experiment 1 by

switching to the FR when the PR and FR requirements were equal, in most conditions of the present experiment responses per reinforcement could be minimized only by switching well in advance of that equality point. The same FR values, presented in the same order, were used as in Experiment 1, but FR completions also reset the PR schedule requirement to 0.

Method

Subjects and apparatus. The birds were the same as in Experiment 1, and the same electromechanical equipment described in Experiment 1 was used.

Procedure. The procedure was identical to that of Experiment 1, except that no pretraining was conducted and FR completions reset the PR requirement to 0, from which the PR again incremented following consecutive PR completions. Stability criteria also were the same as before, with computation of conditional probabilities adjusted for the change in procedure. (The number of opportunities for choice at a given step in the PR schedule equaled the number of PR choices at that and at all higher steps.)

Results

Some implications of switching in advance of the equality point in the reset condition can be examined by referring to Table 1, which shows each possible switching scenario with an FR value of 120. Entries include the total number of responses emitted on the PR, those on the FR, and the resulting costs in responses per reinforcer. For example, note that the top row indicates the cost incurred (in total responses per reinforcement) if a subject switches

Fig. 5. Individual data for 3 pigeons, showing the median PR value at which subjects switched from the PR to the FR schedule, as a function of FR value. Each data point is based on the last five sessions of a given condition, with the ascending and descending sequence of FR values presented separately. The dotted line indicates the lower point of equality between the schedules (corresponding to the lower of the two parallel lines in Figure 1).

to the FR when faced with a PR 20; the second row shows the same when faced with the FR versus PR 40, and so forth. Given an FR value of 120 and PR increments of 20, the cost, in responses per reinforcement, is minimized if the subject switches from responding on the PR to responding on the FR when the next PR would be 60, yielding 46 responses per reinforcer. Continuing to select the PR sched-

ule past (or before) that point results in a greater response requirement per reinforcer. This is a representative example for the Reset condition—most often, minimizing the overall number of responses per reinforcement requires choice of the FR at a point well before the PR equals it.

Median switch points. The median switch points for the final five sessions of exposure to each FR value are shown in Figure 5. The short-term consequences of choosing the FR at various steps in the PR sequence are the same as in Experiment 1; if the birds switched to the FR at the equality point (which corresponds to never choosing the larger of the two alternatives available at the point of choice), their data points would lie along the diagonal, dotted lines shown in the figure. Each graph in the figure also shows an additional reference line that is useful for characterizing performances on this procedure, this line showing the locus of PR choices that would minimize responses per reinforcement as illustrated in Table 1. Note that for FR 40 and for FR 100 there are two optimal switch points, indicated by vertical connecting lines, with both ends of each line representing optimal performance.

Results from both the ascending and descending series of FR values are almost the same, showing that the birds' median switch points usually occurred at, or more typically, at one PR increment beyond the one that would minimize responses per reinforcement. The obtained median switch points never exceeded the equality line.

Interquartile ranges. Figure 6 portrays the variability of switching both within and across five-session blocks, showing interquartile ranges for the descending series of FR values, for all birds. On FR 20, the overwhelming majority of switches occurred when the FR and PR schedules were equal. That is, subjects tended to strictly alternate between the schedules. At FR 40, switching usually occurred at PR 40, even though switching at FR 20 would have incurred the same cost over the course of the experiment. Beyond FR 40, the width of the interquartile range was generally one to two PR increments (20 responses per increment), with no particular trend as a function of FR size. Within conditions, however, the width of the interquartile range most frequently declined as a function of successive blocks of sessions, as shown by comparing the

Fig. 6. The interquartile range (see text) of PR values at which switching to the FR occurred, as a function of successive 5-day blocks, descending series. Each graph is from one FR value, with the lowest FR value at the top of the figure. The parallel lines indicate the optimal switching point, filled circles indicate the median switching point, and circles without lines indicate that the interquartile range fell entirely within the median value. Note also that the number of 5-day blocks can be seen here.

Fig. 7. Cost functions, defined in terms of responses per reinforcer, as a function of FR value for the procedure in which choices and completion of the PR schedule reset the PR schedule to its minimal value, averaged over the final five sessions of each condition. The dotted line without symbols indicates the cost, for each FR value, of switching at the equality points. The minimum possible cost for each FR value is indicated by solid lines without data points. Each data point in the obtained functions is based on the final five sessions of a given condition, with ascending and descending series of FR values plotted separately.

width of the interquartile range of the first block to that of the last block.

Cost. Figure 7 depicts cost data for all subjects, summarizing final-block data for all FR values. The obtained number of responses per reinforcer most often fell between the minimum possible and that which would result from switching at the equality point. Cost in excess of the minimum was usually the result of switching in advance of the optimal switching point, rather than beyond.

Dispersion of FR choices and efficiency. The frequencies of FR choices as a function of PR value are presented in Figure 8 for each subject. These data have not been corrected for the decreasing number of opportunities to choose the FR as the PR increases (resulting from the fact that a choice of the FR when confronted with a PR value eliminates opportunities to select the FR at higher PR values). Included on each graph is an efficiency function, normalized to the height of the highest bar in each plot (and then displaced upward by a constant). The efficiency functions are based on the reinforcers per response (the inverse of cost) resulting from switches to the FR (computed as in Table 1) as a function of PR value. Note that, at FR 20, efficiency falls off rapidly to either side of the peak of each curve. At higher FR values, efficiency falls off more slowly and asymmetrically, decreasing more rapidly to the left of the peak than to the right. Stated differently, choosing the FR in advance of the peak results in greater decreases in efficiency than does switching beyond the peak. These costs of switching at PR values other than the optimal are more severe at lower FR values than at higher ones.

For all birds, the dispersion of FR choices roughly corresponds to the overlying envelope of the idealized efficiency curves, suggesting that the disproportional cost of switching prior to the optimal point is reflected in the distribution of choices; the preponderance of switches occurring off-peak were at PR values to the right of the peak. Similarly, the dispersion of switching points reflects the overall flatness of the efficiency curves, with very little off-peak switching at lower FR values.

Discussion

The patterns of switching in this experiment clearly suggest sensitivity to the reset contingency. Whereas the median switch points un-

Fig. 8. Bars display the frequency of FR choices, uncorrected for opportunity, as a function of PR value, with each graph portraying data averaged over the final five sessions of each descending FR value. Curves over the bars, normalized to the height of the highest bar and displaced vertically by a constant amount, indicate the theoretical efficiency reinforcers per response) associated with exclusively switching to the FR as a function of PR value. Note that this figure shows how the subjects occasionally switched back and forth from FR to PR.

der the no-reset contingency of Experiment 1 occurred at or beyond the equality point, those obtained under the reset contingency of Experiment 2 occurred in advance of or at the equality point. In terms of short-term consequences, faced with a choice between a lesser PR requirement and a greater FR requirement, subjects frequently selected the greater FR requirement.

GENERAL DISCUSSION

Viewed as a replication of prior experiments with monkeys and chimpanzees, our results indicate that pigeons' behavior is roughly similar to that of primates in comparable situations. Furthermore, the systematic changes in switching from the PR to the FR schedule, as a function of FR size, and the differences between median switch points on the no-reset versus the reset procedures for a given FR size, indicate at least approximate sensitivity to relationships that are identified by optimal foraging theory. Thus, we suggest that optimal foraging theory has relevance for behavior in operant conditioning situations; conversely, it appears that this laboratory arrangement of diminishing returns may successfully mimic a key feature of depleting-patch situations outside of the laboratory.

The variability of our pigeons' switching was greater than that observed with primates on comparable procedures. The conventional behavioral interpretation would consider this variability as indicating lack of experimental control (Sidman, 1960). However, from a biological viewpoint, variability is often seen as adaptive; variation around an optimal pattern of behavior, rather than stereotyped performance of that pattern, increases the likelihood of the organism's adaptation to unstable environmental circumstances. Furthermore, variability in operant behavior has been a dimension of interest in its own right—as a reinforceable dimension of operant behavior, as a feature arising from dynamic interaction between procedure and behavior, and sometimes as affected by structural constraints of environmental situations.

In discussing our results, we shall proceed on the assumption that specific relationships that have been of concern within behavioral theory are also relevant to behavioral processes within foraging situations. The background of

that theory includes extensive experimentation with a single species (pigeons) in fairly standardized procedures, which permits detailed examination of subtly differing relationships that may advance our understanding of behavioral processes that contribute to the relationships described by foraging theory. In this discussion, foraging theory will be represented most directly by the relationship we have identified as long-term optimizing, because in our experimental situation, this coincides with the marginal value theorem from that tradition (Charnov, 1976). We shall focus upon evaluation of immediate versus remote consequences as affecting choices in situations of diminishing returns and upon the possible sources of variability in such choices.

Immediate versus Remote Consequences

For the no-reset procedure, because most theories predict switching from PR to FR at the equality point (presumably with some variability), our results indicate sensitivity to the size of the FR option, but with the median switch points consistently occurring at or one step beyond the equality points. In initially characterizing our birds' performances on the reset procedure, we presented two reference functions that indicated possible points of switching from the PR to the FR schedule as functions of the size of the FR schedule. One, of course, is the function corresponding to equality points, where the size of the PR equals that of the FR schedule. The other corresponds to the switch points that, in the long term, minimize responses per reinforcer—in this sense, an "optimality function." These are also the values predicted from the marginal value theorem of optimal foraging theory (Charnov, 1976). Thus, in Figure 5, the upper reference line is that corresponding to units of behavior delineated by individual reinforcers, and the lower reference line corresponds to relatively unlimited aggregates of responses and reinforcers. In particular, the unit here is the "block" identified by Hodos and Trumbule (1967), which is the aggregate beyond which the response-reinforcement relation does not change appreciably. For the no-reset condition, these collapse onto a single reference function because both short-term and long-term reinforcement relations predict switching at the equality point, as shown by the dotted line in Figure 1.

Choice patterns in both procedures were systematically related to the size of the FR schedule. Thus, the differences between choice patterns on the reset and the no-reset procedures can be taken as indicating sensitivity to long-term consequences of choice; identical median choice points in the two procedures would indicate sensitivity only to short-term consequences. In addition, if on the reset procedure the subjects' choices between the two schedules were to correspond closely to one or the other of those two reference lines, that function could be taken as characterizing the operative relationship. With such outcomes, little more need be said, because both an appropriate scale of integration and an appropriate method of averaging are implied. Indeed, in the experiment that we have replicated here with pigeons, Hineline and Sodetz (1987) found that monkeys' responding corresponded closely to the long-term optimizing function on the reset procedure and to the differing combined function on the no-reset procedure. However, the performances of Hodos and Trumbles' (1967) chimpanzees on a similar procedure and those of our pigeons gave orderly data that clearly lay between these two reference lines. Thus, the results from these two experiments indicate either an intermediate scale of intergration, a different averaging principle, or both. (Note also that once the PR is driven past the equality point, determining whether the molecular or molar relationship is at work is impossible to assess.)

Shull and Spear (1987) reviewed studies of choice (mainly with pigeons as subjects) between differently distributed reinforcers and the various averaging principles that have been proposed. They noted that the harmonic mean has been favored as a principle that has the likely advantage of giving increased weight to short interreinforcement intervals (e.g., Killeen, 1968). However, they found that strict harmonic averaging of reinforcers over time, as well as arithmetic averaging, was inadequate for a reanalysis of data from an experiment by Shull, Spear, and Bryson (1981), which examined effects of "detention periods" after reinforcement in conjunction with delays between choice responses and primary reinforcers. Instead, Shull and Spear found a different combination of reciprocals to be applicable to those data. Following McDiarmid and Rilling's (1965) rule-of-thumb, they presented

an analysis suggesting that each of a few (e.g., three) delayed reinforcers contribute to a choice, each weighted according to the reciprocal of its remoteness from the point of that choice. Thus, each reinforcer is construed as having effects "in parallel" on more than one choice. The computations identify a reinforcement-based "value" for alternative sequences of reinforcers, with predicted choices of alternatives with greater value.

Shull and Spear (1987) also applied this averaging principle to procedures like the present one. For predicting choice at a particular point in the progressive schedule, they assumed that delay times are proportional to ratio requirements, and they measured all reinforcer-delay times from that choice point, rather than treating them as successive intervals between reinforcers as conventional rate measures do. They acknowledged that the close fit of the optimizing function, based on linear averaging, to the data from the Hineline and Sodetz (1987) experiment does not require the less conventional averaging based on sums of reciprocals. However, they noted that the data from Hodos and Trumbule's (1967) chimpanzees were more supportive of their approach, although they did not provide a precise evaluation of this.

Mazur and Vaughan (1987) recently provided data describing pigeons' behavior that give further support to Shull and Spear's (1987) formulation. Their basic procedure was similar to our reset procedure, providing choices between a fixed ratio of 80 and a progressive ratio that increased by increments of 10. Their major manipulation was to add time periods following food deliveries, thus providing timeout or intertrial intervals somewhat analogous to the "detention periods" of Shull et al.'s (1981) procedure. As Mazur and Vaughan point out, the addition of this constant time interval does not affect the points of minimal cost in the optimality functions—the switch point yielding minimal responses per reinforcer occurs at the same increment in the PR sequence, with or without the intertrial interval. Yet Mazur and Vaughan found that the timeout periods had the clear effect of increasing the degree to which the pigeons persevered in choosing the PR before switching to the FR schedule. To compute sums of reciprocals based on remoteness of reinforcers, it was necessary to make the timeout periods commensurate with

Fig. 9. A comparison of obtained Reset switch points to the switch points predicted by switching at equality, the optimal switching point, and the point predicted by the sums-of-reciprocals equation with an aggregate size of four and the maximum possible aggregate size. The equality and sums of reciprocals with aggregate size of one are identical functions.

the ratio contingencies of the procedure. Mazur and Vaughan accomplished this by assuming a constant one-per-second rate of responding, and then included both the timeouts and the ratio requirements in computing sums of reciprocals. With that computation, the effects of adding a timeout were readily handled, using aggregates of four reinforcers.

The median switch points for our pigeons are also very nicely fit by the sums-of-reciprocals formulation, as shown in Figure 9 for each bird, assuming delay as proportional to ratio requirements and assuming PR increments of 20. The straight line again presents the locus of switching that would result if only the most proximal reinforcer affected choice, illustrating the fact that averaging based on sums of reciprocals differs from linear averaging only when more than one reinforcer is included in the aggregate. The locus of linearly computed optimality points is also shown by the lowest line in the figure, revealing that (with PR increments of 20) at FR values of 20, 40, and 60, there is no difference between this and the predictions based on summed reciprocals of the delays to the next four reinforcers. However, at larger FR values, the pre-

dictions based on sums of reciprocals depart from the optimality function in a way that corresponds to most of our data: Of the 18 median switch points (six for each bird), all but two points lie on the line corresponding to sums of reciprocals of the delays to the next four reinforcers. This figure suggests that the aggregate size need not be extended beyond four to accommodate these relationships, because further increases in the aggregate size would produce no change in the predicted function for the range of FR values that we used. However, at FR values higher than those of the present experiment, larger aggregate sizes predict switching points above those predicted by the aggregate size of four, as shown in the figure by the divergence at FR values above 160, of the lines corresponding to $N = 4$ and $N = \text{maximum}$ (" $N = \text{maximum}$ " identifies the aggregate size beyond which still further increases in aggregate size would have no effect on the predicted switching point for a given FR value).

Hodos and Trumbule's (1967) experiment (as well as that of Hineline & Sodetz, 1987) included a wider range of fixed-ratio values, and hence their data have some bearing upon whether the effective aggregate sizes exceed four. First, it should be noted that the procedure of Hodos and Trumbule differed from that of the other experiments in that completions of the FR reset the PR to 20 rather than to 0. They also required 10 additional "start responses" whose consequence was to produce the FR 1 choice link. At small aggregate sizes, increases in that dimension produce increasing departures from the equality function in the direction of the long-term optimality function that is based on linear averaging (shown as the lowest curve in Figure 10). However, as Figure 10 shows, increasing the aggregate of summed reciprocals to maximal size results in a predicted curve that lies well above the optimality function, but below the function for an aggregate of three. The data from Hodos and Trumbule's experiment plainly fall between the optimality and sums-of-reciprocals functions. That is, even when the sums-of-reciprocals function is generalized to include unlimited integration over responses, the behavior of both subjects is intermediate between the resulting prediction and that of linearly averaged optimality.

Given that the data of Hineline and Sodetz

(1987) lie virtually on the optimality function, the data of the present experiment are remarkably well described by the sums-of-reciprocals function, and the data of Hodos and Trumbule (1967) lie in between, particular combinations of procedure and species may determine the degree of control represented by the two types of function. It seems odd that the behavior of pigeons should be intermediate between that of chimpanzees and monkeys, but we are unable to suggest any explanations for this outcome.

Variability of Choices

All behavior is describable, in part, by the degree to which it is variable. Variability in response location has been shown to be a function of increasing schedule requirement (Eckerman & Lanson, 1969; Tatham, 1987), whereas variability in response rate is functionally related to increasing variable-interval requirements and percentage of free-feeding body weight (McSweeney, 1974). Importantly, there is mounting evidence that the degree of variability is sensitive to its consequences, and, thus, that variability may be a defining feature of an operant class (Page & Neuringer, 1985).

Figures 2 and 6 showed that our birds' choices were characterized by decreasing variability in switching point within conditions but increasing variability as a function of FR value. Decreasing variability under extended exposure to a given condition, in the absence of explicit reinforcement of variability, is consistent with recent research (Page & Neuringer, 1985; Schwartz, 1980).

Figures 4 and 8 portrayed the variability in terms of relative switching distributions with overlaid efficiency curves; the dispersions of choices in the two experiments roughly corresponded to the curves showing relative efficiency of switching at particular PR values. Under the no-reset contingencies of Experiment 1, the dispersion of FR choices across PR values increased as the FR value was increased. The increases in dispersion appeared to parallel the decreasing loss of efficiency associated with nonoptimal switching as FR value increased, which suggests sensitivity to cost, or its reciprocal, efficiency. In Experiment 1, where the efficiency curves were more peaked, the birds' choices were less widely dispersed.

In addition, Figure 11 shows cost functions

Fig. 10. A comparison of data replotted from Hodos and Trumbule (1967) to the switch points predicted by switching at equality, the optimal switching point, the point predicted by the sums-of-reciprocals equation with an aggregate size of three and by sums of reciprocals with the maximum possible aggregate size. Chimpanzees Kenny and Penny chose between a progressive ratio that incremented by 20 and was reset to its minimal value of 20 by completion of a fixed ratio. The fixed ratio was varied across sessions from 40 to 1,000.

(reciprocally related to efficiency functions such as those of Figures 4 and 8) for Mazur and Vaughan's (1987) procedure in which pigeons chose between FR 80 and a PR that incremented from 0 by 10, with constant timeout periods of 0, 25, or 50 s inserted following the delivery of each reinforcer. Irrespective of timeout duration, the minimum cost is obtained by switching to the FR when the PR requirement is 30, with the cost of undershooting the optimal switching point rising more rapidly than the cost of overshooting. It can be seen that the cost function flattens as duration of the timeout is increased. Specifically, if variability in the birds' choices were sensitive to the costs of that variability, more variability in switching points should occur as timeout value is increased, and overshooting should be more prevalent than undershooting. This trend was shown in their data, except when added stimulus lights were correlated with PR steps (which may make some of their data noncomparable). Although comparable

Fig. 11. The percent increase in responses per reinforcer that would be incurred by switching from the PR to the FR for different PR values relative to the cost of switching to the FR at PR 30 in Mazur and Vaughan's (1987) procedure. In this procedure, pigeons chose between a PR that incremented by 10 following each PR completion and an FR (held constant at 80) that reset the PR to its minimum requirement of 0. Following each reinforcer, a timeout of 0, 25, or 50 was imposed.

predictions regarding variability presumably could be derived from the sums-of-reciprocals approach, expressed in terms of the value of schedule alternatives, a cost analysis may be more straightforward.

Structural Effects of the Progressive-Ratio Procedures

In our no-reset condition, the birds drove the PR up to very high values (Figure 4), whereas in reset (Figure 8) the birds did not extend their FR responses over as great a dispersion, yet the *obtained* cost curves (Figures

3 and 7) show that cost was about equal in either condition. The flatness of the no-reset efficiency curves indicates that this is a legitimate outcome but is one that we initially found counterintuitive. Hence, the source of this relationship bears examination. In the no-reset condition, the inclusion of 40 reinforcers per session meant that a relatively small proportion of the session's choices (reinforcers and responses) allocated to the PR sufficed to advance the PR schedule to the equality point. By implication, this means that with even rough sensitivity to the relative sizes of the two schedule requirements, the large majority of a session's reinforcers were produced on the FR schedule. Furthermore, whether the PR choices came early or late in the sequence was immaterial; even alternating between the two schedules (up to the equality point) would have no effect on overall responses per reinforcer. Furthermore, with the preponderance of responses allocated to the FR schedule (typically thousands were included within each 5-day block) overshooting the optimal switch point by a few steps is not necessarily very costly in the long term. Thus, variability in choice between the alternatives in the no-reset procedure is far more costly on a molecular, than on a molar, level.

The above considerations led us to look for more general implications of differing interaction between the variability and the structural constraints of the two procedures. For example, if the probability of switching from the PR to the FR rose stochastically as a single function, step-by-step, of increasing PR value (identical under both no-reset and reset conditions) would the structural differences of the two procedures result in different obtained median switch points with differing degrees of variability? We undertook a preliminary exploration of this in a series of simulations of data which would result on the two procedures, using a single, step-by-PR-step sequence of probabilities of selecting the FR.

The simulation was generated by initially eliminating data from the no-reset FR 80 condition and assigning probabilities of choosing the FR at each PR step. These probabilities were used in conjunction with a random number table to simulate 40 choices per session for five sessions, and the probabilities were adjusted until a range of distributions was obtained that roughly matched those of our data.

The frequency distributions of FR choices for no reset and reset were then tabulated separately, but using the *very same sequence* of table entries. Even though the same sequence of trial-by-trial probabilities was used to generate the left and right panels, it was clear that the reset procedure produced less variable distributions of choice than did the no-reset procedure. The median switching points also differed somewhat by being in excess of and in advance of equality in the no-reset and reset procedures, respectively. However, these differences were not sufficiently large to argue that our empirically obtained differences between medians for the reset and the no-reset conditions were simply a result of structural constraint in the procedures. Structural constraints in the environment have largely gone unnoticed in behavior analysis, although they sometimes have ubiquitous effects.

We also learned from examining simulations that the degree to which the median switching point on the no-reset procedure exceeded the equality point was at least partly a function of session length. If there was even a small probability of choosing the FR (irrespective of the PR value), as in a position or key-color preference, the median switching point would continue to increase somewhat as a function of session duration, because the PR never reset except at the beginning of sessions. Nevertheless, no-reset switching was at least partially controlled by FR value, because median switching points clearly changed as a function of schedule parameter while the session lengths were held constant.

Clearly, a thoroughgoing program of simulations could be instructive regarding the contribution of structural constraints to measured choices in situations of diminishing returns. However, such a program is beyond the scope of this paper.

Another important issue to consider is the fundamental asymmetry between the no-reset and reset procedures in that there are more opportunities to switch to the FR at lower PR values on the reset procedures. It can be argued that the lower median switching points obtained on the reset procedure are due to this constraint; however, there is evidence that this does not account for the results. If switching on reset occurs at lower PR values than on no reset because reset affords more opportunities to switch at lower values, then more switching

during reset should be seen at PR values lower than the median switching point. In fact, it should be very frequent at very low PR increments (e.g., 0 and 20), because they present the most opportunities to switch. A comparison of switching at PR 0 and PR 20 for reset (Figure 8) and no reset (Figure 4) clearly shows that this did not occur. FR 60 and FR 80 are particularly salient demonstrations that this did not happen; it is improbable that lower median switching points, under reset, were procedural artifacts.

Theories of Foraging and of Behavior Analysis

The environments involved in foraging situations are complex and subtle, as are the relationships addressed in the study of choice between schedules of reinforcement. Although they contribute to this complexity, we are hopeful that the "diminishing return" properties of the present procedures, and the orderly relationships they reveal, enable a legitimate linkage between these two areas of study. It seems especially worthwhile to focus on experiments that are relevant to more than one interpretive tradition, because interpretations from differing traditions may converge in providing a more thorough understanding of the experiments; the experiments may be informative to each of the traditions; and, through the experiment, each interpretive tradition may be made informative to another.

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