*DELAY REDUCTION AND OPTIMAL FORAGING:
VARIABLE-RATIO SEARCH IN A FORAGING ANALOGUE*

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The present study investigated conditions under which the conditioned reinforcement principles of delay-reduction theory and views based on simple maximization of reinforcement rate make ordinarily opposing predictions with respect to foraging-related choice behavior. The use of variable-ratio schedules in the choice phase also represents an extension of delay-reduction theory to schedules that may better mimic the effort involved in searching. Pigeons responded on modified concurrent-chains schedules in which equal variable-ratio schedules led to unequal variable-interval outcomes and unequal reinforcer amounts. All 4 subjects completed a minimum of two replications of conditions for which the predictions of delay-reduction theory and a simple rate-maximizing theory were opposed. Results were consistent with delay reduction's ordinal predictions in 11 of 11 replications of the divergent predictions favoring the smaller, more immediate alternative. The predictions of rate maximization were upheld only when they were consistent with those of delay reduction. Results are discussed in terms of conditioned reinforcement, sensitivity to reductions in delay to food, and possible rules of thumb that may be useful in characterizing foraging.

Key words: delay-reduction theory, rate maximization, evolutionary biology, choice, foraging, clustered encounter, concurrent chains, variable-ratio schedules, key peck, pigeons

Foraging organisms necessarily engage in various forms of decision making or choice. Every organism's ability to survive and reproduce is, in part, dependent upon its ability to effectively act upon environmental changes in prey density. This relation between forager and prey has been of intense interest to behavioral ecologists for several decades. Given the similarity between the instrumental response and its consequence in both naturally occurring foraging situations and in traditional conditioning experiments (Lea, 1982), the interdisciplinary convergence of theory and empirical assessment developing between evolutionary biology and behavior analysis has led to an increasingly productive partnership (Fantino, 1985, 1989). Operant analogues of foraging provide tests of the generality and external validity of behavior-analytic principles of choice while simultaneously testing predictions based on behavioral ecology's theories of optimal foraging.

Optimal foraging may be generally defined

as foraging behavior that maximizes fitness in terms of genotypic potential for inclusion in the gene pool. The mechanism by which an organism achieves this fitness has been the focus of much work in evolutionary biology (see Stephens & Krebs, 1986, for a review). At the heart of classical optimal foraging theory (MacArthur & Pianka, 1966) lies the notion of maximization of energy intake per unit time typically modified by particular constraints, tradeoffs, or rules of thumb. The constraints approach to optimality theory attempts to balance rate maximization with costs arising from other behavior required for survival, such as predator avoidance, territorial defense, or sensitivity to the variance in food supply (see Stephens & Krebs, 1986, for a review). Even increasingly complex constraint models, such as dynamic optimization (Houston & McNamara, 1988) in evolutionary biology and psychology's momentary-maximizing (Hinson & Staddon, 1983) and melioration models (Vaughan, 1981), grew out of optimization logic and retain a maximizing component. However, the important question of interest is: "What variables control the foraging choices that generally produce optimization?"

In behavioral psychology, the ongoing debate between matching and maximizing accounts of choice is relevant to the question of how animals optimize. Evidence suggests that an organism's concurrent-schedule choices tend

This research was supported in part by NSF Grant BNS 91-08719 and NIMH Grant MH 20752 to the University of California, San Diego. We would like to thank Alejandro Kacelnik for his comments on an earlier draft. We gratefully acknowledge Keith DeSonia, Gary Hardcastle, and Colleen Scherer for their assistance in the data collection. Reprints may be obtained from either author at the Department of Psychology, 0109, University of California-San Diego, La Jolla, California 92093-0109.

to match the relative rates of reinforcement rather than to maximize reinforcement (Herrnstein & Heyman, 1979; Heyman & Herrnstein, 1986). However, relative reductions in delay to reinforcement have been shown to be a more reliable predictor of choice behavior than the relative rate or immediacy of reinforcement in laboratory preparations that would better simulate the aspects of foraging (Dunn & Fantino, 1982; Fantino, 1969).

The delay-reduction theory from behavioral psychology and the optimal diet model (Charnov, 1976a, 1976b) from evolutionary biology have long been considered to be functionally equivalent with respect to their predictive accuracy in laboratory simulations of foraging-related choice (Fantino & Abarca, 1985). However, the question of whether foraging organisms rely primarily on rate maximization or on environmental cues that signal greater reductions in waiting time to food was not addressed in these investigations. The present study attempted to distinguish between these two potential primary determinants of foraging-related choice using a modified concurrent-chains analogue to foraging.

Delay-Reduction Theory

Delay-reduction theory states that the ability of a stimulus to serve as an effective conditioned reinforcer can be determined by comparing the reduction in time to primary reinforcement correlated with that stimulus, relative to the overall delay to primary reinforcement (Fantino, 1969, 1977; Fantino & Davison, 1983; Killeen & Fantino, 1990; Squires & Fantino, 1971). Put simply, given some overall average delay to food in general, those stimuli that signal greater improvements with respect to waiting time to food should serve as more effective conditioned reinforcers than those that signal lesser improvements.

Delay-reduction theory was originally formulated to account for choice in the concurrent-chains procedure (Autor, 1969; Herrnstein, 1964). In the standard concurrent-chains preparation, the subject chooses between two concurrently available initial-link alternatives that occasionally lead to one of two mutually exclusive terminal links and ultimately access to food. Completion of either initial-link variable-interval (VI) schedule results in the presentation of a distinctly colored terminal-link stimulus correlated with that initial link, lo-

cated on the same key. Upon entry into either terminal link (outcome phase), the other key becomes dark and inoperative. Terminal-link responses are reinforced according to the VI schedule correlated with either alternative. Completion of either terminal link leads to a single food presentation. Following food delivery, the subject reenters the initial-link phase in which the recently completed VI is reset with a new schedule value, and the other VI continues from its previous position. Fantino (1969) developed the following equation to describe initial-link choice within the paradigm:

$$\frac{R_1}{R_1 + R_2} = \frac{(T - t_1)}{(T - t_1) + (T - t_2)}, \quad (1)$$

where R_1 and R_2 are the number of responses on each of the two initial links. T stands for the average overall time to primary reinforcement from the onset of the initial-link stimuli and is determined by taking the sum of the average time spent in the initial links and the average time spent in the terminal links. t_1 and t_2 stand for the average time in the left and right terminal links, respectively. Equation 1 requires exclusive preference for Alternative 1 when $(T - t_2) > T$ and for Alternative 2 when $(T - t_1) > T$, a prediction confirmed by Fantino (1969) and Fantino and Davison (1983). Squires and Fantino (1971) expanded the basic delay-reduction theory formulation into a more general model of choice by including a parameter for the rate of primary reinforcement ($1/r$):

$$\frac{R_1}{R_1 + R_2} = \frac{1/r_1(T - t_1)}{1/r_1(T - t_1) + 1/r_2(T - t_2)}. \quad (2)$$

With the modification, the equation also reduces to Herrnstein's (1970) matching law when the terminal links are zero ($t_1 = 0$ and $t_2 = 0$). Over the course of nearly a quarter century, delay-reduction theory has been extended to such areas as observing, self-control, three-alternative choices, percentage reinforcement, and the serial position effect in studies of memory and foraging behavior (for a review, see Fantino, Preston, & Dunn, 1993).

Delay-reduction theory's ability to serve as a reliable predictor of foraging-related choice was successfully compared with the optimal diet model (Charnov, 1976a, 1976b) in a series

of investigations by Fantino and Abarca (1985). They showed that the two models are mathematically equivalent, using a straightforward application of the successive-encounters procedure developed by Lea (1979). Fantino and Abarca studied a range of conditions in which both delay-reduction theory and the optimal diet model made equivalent predictions about whether an item should be accepted or rejected in favor of further searching. Their results showed that they could account for the acceptance or rejection of a particular item when various parameters were manipulated using either model. However, the mathematical equivalence of the optimal diet model and delay-reduction theory does not necessarily imply equivalent or substitutable theoretical assumptions. For example, delay-reduction theory assumes a sensitivity to conditioned reinforcers (events signaling a reduction in waiting time to food) that the optimal diet model and other rate-maximizing theories do not. As a result of these differences, there are conditions under which the underlying assumptions of both delay-reduction theory and a rate-maximization version of optimal foraging theory logically lead to ordinally divergent predictions. These conditions provide the opportunity to distinguish between, as well as to test the generality of, delay-reduction theory and rate-maximization views, while investigating the efficacy of delay reduction as an alternative foraging-related currency. The present investigation was designed to juxtapose the underlying assumptions of conditioned reinforcement from delay-reduction theory and rate maximization from optimal foraging theory, in order to assess their independent influences on foraging-related choice.

Optimal Foraging Theory

Based on the early work of MacArthur and Pianka (1966), bouts of foraging have been typically divided into two distinct phases: search and handling (h). In classic operant analogues of foraging, the various links in each chain simulate these periods of search and handling, and are followed by a consumption phase during which food is presented (Fantino & Abarca, 1985; Lea, 1979, 1982). In concurrent-chains procedures, the initial links are analogous to the search phase, and terminal links simulate independent handling times correlated with the different prey items. (For details regarding

preferred procedures, see Fantino & Abarca, 1985; Kacelnik & Krebs, 1985; Killeen, 1985.)

Optimal foraging theory traditionally predicts exclusive preference (1.0) for the prey item correlated with the greater local profitability ratio (E/h ; where E = energy intake) relative to the total, T , of search and handling times (E/T) combined (Lea, 1982). Put simply, only when the addition of a prey item represents an improvement in the global profitability ratio should that item be included in the diet. In a choice test between two mutually exclusive prey items of equal magnitude, where search time is equal but total handling time is not, ordinal preference for one alternative over another should be a function of the local profitability ratios of the two alternatives. However, when prey items follow unequal handling delays and are not of equal magnitude, profitability ratios can reverse as a function of equal increases in search duration. With sufficiently long search times, the ordinal predictions of delay-reduction theory and rate maximizing will diverge, with delay reduction predicting continued preference for the leaner, more immediate reward beyond the point at which rate maximization requires a reversal of preference.

Given the nature of the typical foraging experience, sensitivity to the environmental cues that signal improvements with respect to waiting time to food would appear to be inexorably linked with choice. But are foragers sufficiently sensitive to these cues that they would override rate maximization? By using unequal reinforcer amounts or multiple reinforcers in a concurrent-chains procedure, circumstances can be produced in which optimal foraging theory's profitability ratios will require a reversal of preference whereas delay-reduction theory will not. The question is whether pigeons will prefer greater reductions in the delays to leaner prey items over a richer, more delayed alternative considered to be optimal according to rate-maximizing assumptions.

One way to address this question involves the use of a sort of "clustered-encounters" procedure. These encounters may be characterized by a single search resulting in a cluster of prey items, each requiring an independent handling period. In a concurrent-chains procedure, the encounter may be simulated through the use of recycling terminal links, in which repeated presentations of a terminal link

(handling phase) and its associated reinforcer (prey item) follow the completion of the initial link (search phase).

Delay-reduction theory, as currently formulated, neglects all terminal links subsequent to the first, basing its predictions entirely on the delay reduction signaled by the first item encountered in each chain or cluster. Although this systematic neglect has been noted as a serious problem regarding the quantitative accuracy of the model (Navarick & Fantino, 1976), the degree to which it represents a shortcoming for delay reduction's *ordinal* predictions remains an empirical question.

Simulation of Renewable Resources

Traditionally, VI schedules have been used to simulate searching and handling delays associated with resources that renew themselves over time (Abarca & Fantino, 1982; Fantino, 1987; Fantino & Abarca, 1985; Fantino & Preston, 1988; Ito & Fantino, 1986). Concurrent VI schedules generally provide good experimental control over initial-link durations and facilitate sampling of both alternatives. However, not all searching delays are determined by temporal contingencies alone. In order to better simulate delays contingent upon the forager's search effort, the present investigation employed variable-ratio (VR) initial-link schedules to determine the rate and frequency with which prey items are encountered. Unlike concurrent VI schedules, in which either alternative has a progressively increased likelihood of leading to a terminal-link entry, concurrent VR schedules rely on responses to advance each VR counter independently. Based on investigations using simple concurrent VR schedules (Herrnstein & Loveland, 1975), extreme or exclusive preference should be enhanced, and as such, should facilitate assessment of obtained choice proportions when the ordinal predictions of delay reduction and rate maximizing diverge.

Consider the following illustration relevant to the present study. Assume that a pigeon responds at an average rate of one response per second. A VR 90 initial link leading to a VI 30-s terminal link and 3 s of access to grain could provide 6 s of grain every 240 s. Meanwhile on the other alternative, the same VR 90 leading to two successive terminal links, each consisting of a VI 60-s terminal-link schedule and 3 s of grain, could produce the

same 6 s of grain in only 210 s. According to a strict rate-maximization analysis, the optimal response pattern would be preference for the longer, richer terminal-link alternative. Delay reduction, however, predicts preference for the shorter, leaner alternative when calculated at the same rate.

According to Equation 2, the delay-reduction prediction would be as follows:

$$T = 90 + [(30 + 60)/2] = 135.$$

$$\frac{R_1}{R_1 + R_2}$$

$$\begin{aligned} &= \frac{1/120(135 - 30)}{1/120(135 - 30) + 2/210(135 - 60)} \\ &= \frac{.875}{.875 + .714} \\ &= .55. \end{aligned}$$

Although the quantitative accuracy of the prediction (.55) may not be accurate, preference should at least favor the shorter chain. As long as the average time spent searching is 60 s or less, both delay reduction and rate maximization predict preference for the shorter chain. As search times extend beyond the 60-s point, rate maximization predicts a reversal of preference. However, delay-reduction theory does not predict a preference reversal until the average initial-link durations reach 132 s. As long as the search duration is greater than 60 s and less than 132 s, optimality (in terms of rate maximization) requires preference for the richer, more delayed alternative, whereas delay reduction continues to require a slight preference for the smaller, more immediate reward. Sufficient increases in searching delays (beyond 132 s) again result in convergent predictions of preference for the richer, longer chain by both theories. Put simply, the point at which subjects' preferences should reverse differs depending upon the accepted set of underlying assumptions and the duration of the search. The range of search-duration values for which divergent predictions are produced can be expressed graphically, as seen in Figure 1.

In real foraging situations, it is likely that most powerful conditioned reinforcers are correlated with greater prey density. Although foraging organisms are rarely forced to choose between primary and conditioned reinforcers

Fig. 1. The two axes are the classical axes in foraging theory: time and rewards. The search times (initial links) lie to the left of the origin, and the handling times (terminal links) lie to the right. The small black circle represents the smaller prey item correlated with the shorter handling time. The two open circles are the two sequentially handled prey items correlated with the two independent, recycling terminal links. "a" represents the handling time in the single-reward option (VI 30 s), and "b" is the handling time for each item in the two-reward option. Line 1 shows that for very short search times, it pays to take the immediate single prey item. Line 2 shows that for some intermediate search time, t (61 s in the present experiment), a single slope intersects both alternatives, suggesting that a rate maximizer should be indifferent. For all search times less than t (left of t) should produce a bias in favor of the two-reward option. Line 3 represents the point at which delay-reduction theory predicts a reversal of preference for the single-reward option to the two-item alternative. The search times of interest in the present investigation are those which lie between the two predicted switch points: 132 s and 61 s (the shaded area) (contributed by A. Kacelnik, personal communication, April 1993).

in the real world, our primary purpose was to determine whether optimal foragers' choices (particularly when encounter rate is determined by effort rather than time) depend primarily on simple profitability ratios or on environmental cues that signal a reduction in delay to food. By placing these two putative determinants of choice in opposition to each other, we attempted to determine whether sensitivity to temporal improvements with respect to reward may provide an alternative currency or mechanism by which animals more generally optimize.

METHOD

Subjects

Four pigeons, with equivalent experimental experience in concurrent-chains procedures, were maintained at 80% of their free-feeding weights. Following experimental sessions,

subjects were weighed and fed accordingly. Water and grit were available continuously in the home cage.

Apparatus

Subjects were randomly assigned to one of four standard experimental operant conditioning chambers. Experimental chambers were cubes, approximately 32 cm on each side, located inside ventilated wooden enclosures. The front panel was aluminum and was equipped with three translucent response keys that could be transilluminated from behind with a variety of shapes, colors, and line orientations. The keys (2.5 cm in diameter) were evenly spaced 23.5 cm above the grated floor. Keys required a minimum force of 0.16 N for operation. Following each individual response, a 50-ms blackout provided feedback.

The hopper was located 9.0 cm beneath the center key. When activated, the solenoid-operated hopper, illuminated by a white light,

allowed access to mixed grain for a predetermined length of time. A houselight mounted in the ceiling provided general illumination throughout the session, except during hopper operation. Ventilation fans provided white noise continuously. Scheduling of events and data collection were maintained by IBM-compatible personal computers.

Design and Procedure

Pretraining consisted of a series of equal concurrent VR schedules in which the mean interreinforcement ratios were gradually increased. When responding was reliably maintained on concurrent VR 90 VR 90 schedules in the presence of a red and green keylight, the procedure was changed from simple concurrent schedules to a modified concurrent-chains procedure. In the standard concurrent-chains procedure, equal VI initial links lead to unequal VI terminal links. Modifications for the present investigation included concurrent VR initial-link schedules leading to a single VI terminal link on one alternative and a recycling VI terminal link on the other. Each cycle included a VI requirement followed by its associated reinforcer.

A diagram of the procedure is presented in Figure 2, along with the schedule values and reinforcer durations. During the initial-link (search) phase, the red and green keylights were presented simultaneously on the two side keys on equal concurrent VR schedules. Each color was consistently correlated with a particular side key and was counterbalanced across subjects. Fulfillment of either VR requirement resulted in the presentation of a terminal-link stimulus (handling phase) on the same key (green leading to yellow; red leading to blue). Terminal-link responses were reinforced according to the VI schedule correlated with each terminal-link stimulus—either a single VI 30-s schedule followed by 3-s grain access on one alternative, or a pair of VI 60-s schedules, each followed by 3-s grain access, on the other. Upon entry into one terminal link, the other key became dark and inoperative. The subject was required to complete all terminal-link cycles and earn the reinforcers before the concurrent VR initial links were reinstated; at this point, the recently completed VR was reset with a new value and the other VR continued from its previous position.

The upper and lower search durations re-

quired to produce divergent predictions were determined a priori for the present investigation. A minimum of 61 s and a maximum of 132 s were necessary to produce divergent predictions by the two theories. Due to the unique nature of ratio schedules, it was necessary to titrate scheduled initial-link VR values both across the various birds and across reversals for individual birds. With very short initial-link delays, both rate maximization and delay-reduction theory predict preference for the shorter chain. At 61 s, profitability ratios based on rate maximization are 9/273.0 for the 30-s alternative, 9/272.0 for responding to both alternatives, and 9/271.5 for the recycling VI 60-s VI 60-s alternative. The better alternative, although only slightly better, is the longer, richer chain. This superiority increases as the initial-link delays increase beyond 61 s.

According to delay-reduction theory, initial-link delays ranging from 61 s to 122 s produce predictions of preference for the shorter chain alternative. At 122 s, the prediction drops to relative indifference and remains there until finally reversing to preference for the longer alternative at 132 s. (Predictions are determined as per calculations above. Recall that the second terminal link is disregarded for calculation purposes.)

To ensure sampling of both alternatives, a forced-choice procedure was implemented during the first 4 days of each condition, with equal exposures to both outcomes across each of the four sessions. Following the fourth session of forced choice, the standard free-operant method was reinstated for the remainder of the condition. The subsequent free-operant sessions allowed preference to range from 0 to 1.0 for either alternative. Forced-choice sessions were not included in the final analyses.

Each session lasted a maximum of 50 min or until the subject earned 40 reinforcers. Conditions continued for a minimum of 15 sessions and until the following stability criterion had been satisfied. Following the 15th session, and daily thereafter, the choice proportions based on the initial-link responses during the last nine sessions were divided into blocks of three consecutive sessions. Preference was considered stable when the mean choice proportion in each of the three blocks differed by no more than .05 and exhibited no directional trend (neither $M1 > M2 > M3$ nor $M1 < M2 < M3$). Each subject received an average choice-

Fig. 2. The modified concurrent-chains procedure used in the present investigation. Panel A shows the sequence of events leading to reinforcement on the left key; Panel B shows the analogous sequence for the right key. Equal concurrent VR initial links (search phase) lead to terminal links (handling phase) consisting of either a single VI 30-s schedule followed by 3-s grain access or a pair of recycling VI 60-s schedules (clustered encounter), each followed by 3-s grain access.

proportion score representing preference for the short-chain alternative across the final nine sessions.

Following stability, the VI values in the terminal links were reversed to assess side or color bias and to confirm stimulus control. Subjects were required to complete a minimum of two tests of the divergent predictions. However, although the terminal-link contingencies alternated on the left and right across subsequent reversals, there were no guarantees that a particular condition would result in a test of the divergent predictions. Therefore, there were

no requirements that the two divergent tests be contiguous or that they occur on opposing side keys (i.e., one on the left and one on the right), as long as stimulus control via the contingencies could be established.

RESULTS

Tests were divided into two subcategories according to whether the conditions resulted in predictions that differed for delay-reduction theory and optimal foraging theory (tests of divergence) or whether the predictions of de-

Table 1

Average obtained initial-link durations and choice proportions for conditions providing divergent predictions for delay-reduction theory and a simple rate-maximizing approach to optimal foraging theory.

Subject	Obtained initial-link VR values	Average obtained initial-link duration (s)	Scheduled terminal-link VI values (s)	Obtained choice proportion (short terminal link)	Obtained time allocation (short terminal link)	Sessions to criterion
R1	78	90	VI 30; VI 60 VI 60	.99	.98	15
	78	69	VI 60 VI 60; VI 30	1.00	1.00	15
	100	62	VI 60 VI 60; VI 30	.69	.74	19
	100	67	VI 30; VI 60 VI 60	.80	.82	41
R2	82	88	VI 30; VI 60 VI 60	.97	.98	18
	85	77	VI 30; VI 60 VI 60	.51	.44	26
R3	118	62	VI 60 VI 60; VI 30	.64	.70	18
	116	70	VI 30; VI 60 VI 60	.69	.65	18
	121	73	VI 60 VI 60; VI 30	.96	.96	21
R4	125	74	VI 60 VI 60; VI 30	.76	.76	16
	120	63	VI 60 VI 60; VI 30	.60	.70	34

lay-reduction theory and a rate-maximizing version of optimal foraging theory were comparable (tests of convergence).

Tests of Divergent Predictions

The requirement for divergent predictions depended upon obtained initial-link durations between 61 and 132 s. Table 1 shows the obtained average initial-link durations for those conditions in which those initial-link durations were met by each of the 4 subjects. Obtained initial-link durations were calculated using the last 9 days of stable data for each test. Table 1 also shows the obtained values for the VR initial links, the allocation of initial-link times, and average choice proportions, all calculated using stable data from the last 9 days.

Overall average initial-link durations ranged from 62 s to 88 s ($M = 72$ s). Choice proportions for each test of divergence obtained for the 4 subjects are presented in Figure 3. Obtained choice proportions are plotted in terms of the initial link leading to the single VI 30-s terminal link. Delay-reduction theory predicted preference for the shorter chain (above .50), whereas the rate-maximizing version of optimal foraging theory predicted preference for the longer, recycling terminal-link alternative (below .50). In all 11 divergence tests, subjects showed preference for the alternative required by delay-reduction theory (i.e., the

initial link leading to the VI 30-s schedule). According to simple binomial probabilities, the likelihood of obtaining 11 choice proportions greater than .50 across 11 independent tests due to chance is less than .01. Obtained choice proportions ranged from .51 to 1.0 ($M = .86$) for the initial link leading to the shorter, leaner terminal link.

Time-allocation data (also seen in Table 1) were similar to the choice data, clearly favoring the short-chain alternative in 10 of the 11 cases ($M = .80$). In general, subjects required fewer than 26 sessions to reach stability (except for R1 and R4, who required 41 and 34 sessions, respectively, before reaching stability on one occasion).

Tests of Convergent Predictions

Table 2 shows the obtained average initial-link durations for those conditions in which the search times produced ordinally identical predictions for each of the 4 subjects (less than 61 s or greater than 132 s). According to both theories, the short terminal-link alternative (VI 30 s) should have been preferred when the initial-link durations fell below 61 s; when the initial-link durations were 132 s or more, the larger, more delayed terminal link (recycling VI 60 VI 60) should have been preferred.

Figure 4 shows the obtained choice proportions for the conditions in which the initial-

Fig. 3. Obtained choice proportions for the conditions resulting in tests of the divergent predictions of delay-reduction theory (DRT) and optimal foraging theory (OFT). Relative response ratios are graphed in terms of preference for the initial link leading to the VI 30-s terminal-link alternative. Independent test conditions (replications) are identified according to obtained initial-link durations.

Table 2

Average obtained initial-link durations and choice proportions for conditions providing comparable predictions for delay-reduction theory (DRT) and a rate-maximization view of optimal foraging theory (OFT).

Subject	Obtained initial-link VR values	Average obtained initial-link duration (s)	Scheduled terminal-link VI values (s)	Obtained choice proportion (short terminal link)	Obtained time allocation (short terminal link)	Ordinal prediction OFT and DRT	Sessions to criterion
R1	80	51	VI 30; VI 60 VI 60	.54	.47	short	28
R2	157	132	VI 60 VI 60; VI 30	.49	.50	long	24
R3	79	41	VI 30; VI 60 VI 60	.96	.96	short	22
	81	46	VI 60 VI 60; VI 30	.96	.96	short	26
	100	44	VI 30; VI 60 VI 60	.85	.79	short	30
	97	49	VI 60 VI 60; VI 30	.74	.76	short	31
	114	56	VI 30; VI 60 VI 60	.60	.56	short	15
R4	77	50	VI 60 VI 60; VI 30	.98	.94	short	15
	80	47	VI 30; VI 60 VI 60	.69	.62	short	15
	102	46	VI 60 VI 60; VI 30	.83	.89	short	48
	107	53	VI 60 VI 60; VI 30	.98	.97	short	20
	103	57	VI 30; VI 60 VI 60	.54	.58	short	15
	120	56	VI 30; VI 60 VI 60	.50	.47	short	21

Fig. 4. Obtained choice proportions for the conditions resulting in tests of the divergent predictions of delay-reduction theory (DRT) and optimal foraging theory (OFT). Relative response ratios are graphed in terms of preference for the initial link leading to the VI 30-s terminal-link alternative. Independent test conditions (replications) are identified according to obtained initial-link durations.

link durations were either less than 61 s or 132 s or greater. Again, the choice proportions are plotted in terms of preference for the initial link leading to the single VI 30-s terminal link. In all 13 convergent conditions, subjects' ordinal preferences ($M = .74$) were accurately predicted by both theories, with an accuracy that was significantly greater than predicted by chance alone ($p < .01$). In 12 of these tests, the initial-link durations fell below 61 s and are characterized by choice proportions above .50 on Figure 4. The mean obtained choice proportion for these 12 conditions was .72, and the average proportion of time spent searching on the alternative leading to the short VI was .77. The initial-link durations reached 132 s in only one case (R2), and the data conformed to the convergent prediction of preference for the longer alternative, shown in Figure 4 as the choice proportion of .49 for the short-chain alternative.

DISCUSSION

When the predictions of delay-reduction theory and rate maximization diverged, choices were consistent with the ordinal predictions of delay-reduction theory in all 11 cases. On all but one occasion, subjects spent a greater proportion of their search time in the initial link leading to the shorter VI. Based on simple binomial probabilities, the likelihood of these results occurring by chance is less than .01. Thus, it appears that choice in this procedure appears to track environmental cues that signal a greater reduction in delay to reinforcement and not simple prey density ratios.

Although the obtained choice proportions ordinally supported the predictions of delay reduction (Figure 3), the average choice proportion (.86) was higher than the range of quantitative predictions provided by the theory (i.e., .50 to .58). These inflated choice pro-

portions may be due to the unique tendencies for VR schedules to enhance preferences in choice procedures (Herrnstein & Loveland, 1975). Replications of the present investigation utilizing VI schedules instead of VRs could prove to be useful in determining whether VR initial-link schedules are responsible for the observed inflation in choice proportions. In any event, the deviations from the predictions made by delay-reduction theory in the present investigation are in direct opposition to, and therefore offer no support for, a rate-maximizing version of optimal foraging theory. Furthermore, although there is considerable variability among the obtained choice proportions, we should note that as the initial-link durations increase, the variability also increases. This may be due to the tendency of choice behavior to be increasingly influenced by alternative sources of reinforcement as preference approaches indifference. These alternative stimuli might include a color or side bias or simply a tendency to favor immediacy of reinforcement.

The conditions in which the predictions of delay-reduction theory and a rate-maximization view of optimal foraging theory converged are, in a sense, similar to those formally addressed by Fantino and Abarca (1985), because the more profitable outcome is also the outcome correlated with greater delay reduction. For obtained initial-link durations below 61 s, both theories predicted preference for the initial link leading to the shorter terminal link (VI 30 s). In terms of profitability ratios, this alternative represents the optimal choice, whereas in delay-reduction terms it provides the stimulus correlated with the greater reduction in delay to food. Both the choice-proportion and time-allocation data provide support for both models under these convergence conditions, and they serve to extend previous findings to procedures varying search effort (VR schedules) and to the clustered-encounters procedure (recycling terminal links). It should also be noted that delay-reduction theory's predictions were upheld in all 24 independent tests across both convergence and divergence conditions. Furthermore, the predictions of a simple rate-maximization version of optimal foraging theory were supported only when its predictions conformed to those of delay reduction in the convergence conditions.

At this point, we should reiterate that the use of unequal reinforcer magnitudes and VR initial links prevents the extension of the present results to a quantitative comparison of the two models. Replications employing only VI schedules might facilitate a more detailed analysis of values at the longer end of the critical search-duration window. However, it is important to note that the divergent predictions produced by the two theories depend critically on discrepancies in reinforcer magnitude. Therefore, an extension to cases utilizing VI initial links would continue to be a qualitative one (Navarick & Fantino, 1976). However, continued investigations into a parameter for reinforcer magnitude might enhance the quantitative generality of the delay-reduction model.

General Conclusions

The conditions faced by the subjects in the present investigation represent only a subset of foraging-related dilemmas. It is likely that foragers do not usually choose between primary rates of reinforcement and conditioned reinforcers. Instead, in most cases, the conditioned reinforcer and the richer profitability ratio would likely be correlated with the same prey item, as in the Fantino and Abarca (1985) studies. However, the purpose of the present investigation was to determine whether foragers depend *primarily* on profitability ratios or on those environmental cues that signal a reduction in delay to food. By empirically placing these two putative determinants of choice in opposition to each other, we have demonstrated that sensitivity to temporal improvements with respect to reward may, in fact, be one possible mechanism by which organisms optimize reinforcement under more general foraging circumstances.

From a certain evolutionary-biological perspective, organisms do not, by definition, demonstrate "nonoptimal behavior." Instead, the present data suggest that a sensitivity to environmental cues that signal greater delay reductions may have been favored in the natural selection of foraging mechanisms. Although the present study represents the first attempt to make a distinction between delay reduction and long-term rate maximization with respect to foraging currencies, it is not the first attempt to identify the determinants of such ostensibly "suboptimal" foraging-related choice behavior. Attempts to provide a clearer picture of

the failure to maximize rate in foraging organisms have been repeatedly argued in a long-standing debate within evolutionary biology, specifically between environmental constraints and physiological design. Some researchers (Barnard & Brown, 1981, 1985; Janetos & Cole, 1981; Yoerg, 1988) suggest that organisms may come preequipped with suboptimal rules, from which they do not deviate. Such fixed rules become less than satisfying, however, when we look at the bigger evolutionary picture of natural selection and biodiversity, as well as the richness of ontogenic adaptability. Others (Caraco, 1981; Caraco & Lima, 1985; Caraco, Martindale, & Whittam, 1980; Galis, 1990; McNair, 1982; Stephens & Krebs, 1986) have suggested other currencies—rules of thumb—that retain a rate-maximization foundation at their core and provide various modifications based on physiological, developmental, or environmental constraints. Behavioral psychology may provide an alternative to this constrained-maximization approach. Foraging-related choices may be described as a subset of more generalized choice phenomena and may be governed by the same general principles that apply to other forms of choice behavior, just as self-control is considered to be a special case of choice (Rachlin & Green, 1972).

The present results, combined with previous delay-reduction studies in the areas of foraging and choice, suggest that the principles of conditioned reinforcement, or more specifically, the sensitivity to reductions in delay to reinforcement may be useful in providing a robust mechanism that can address important questions including accept/reject problems, time allocation, questions regarding relative preference and diet selection, and instances of choice behavior in which subjects fail to maximize overall rate of primary reinforcement. Because nearly every foraging experience carries with it some environmental cue that signals the transition from search time to handling time, in addition to energy costs and benefits, the question remains whether delay-reduction effects are sufficient to warrant their inclusion in a more fundamental definition of what qualifies as optimal. In other words, the inclusion of delay reduction or a more generalized conditioned reinforcement parameter in future models of foraging-related choice may produce more sensitive and flexible dynamic models of

optimization, as previously suggested by Fantino (1988). At the same time, this inclusion would serve to formalize the increasingly apparent relationship between primary and conditioned reinforcement with respect to foraging behavior and choice.

The present investigation not only serves as a first attempt to distinguish between the fundamental assumptions underlying delay-reduction theory and rate-maximization versions of optimal foraging theory, but also provides a starting point for identifying the role played by salient environmental cues in signaling temporal relations between choice and reinforcement in a foraging context.

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Received June 2, 1993

Final acceptance December 15, 1993