UC San Diego

UC San Diego Previously Published Works

Title

Economic context and pigeons' risk-taking: an integrative approach

Permalink

<https://escholarship.org/uc/item/44w554g9>

Journal

Behavioural Processes, 65(2)

ISSN

0376-6357

Authors

Goldshmidt, J N
Fantino, Edmund

Publication Date

2004-02-01

Peer reviewed

Economic Context and Pigeons' Risk-Taking: An Integrative Approach

J. N. Goldshmidt and E. Fantino

University of California, San Diego

Address Correspondence to:

Edmund Fantino

Department of Psychology, 0109

U.C. San Diego

La Jolla, CA 92093-0109

(858)-534-3927

e-mail: efantino@ucsd.edu

Inclusive word count: 13,393

Abstract

The present work tested pigeons' (*Columba livia*) risk sensitivity to changes in resource availability in the concurrent-chains choice procedure. Subjects were provided choices, generally between variable-ratio (VR) and fixed-ratio (FR) outcome schedules with equal or different mean values. Predictions from ecology's risk sensitivity, behavioral economic's rate maximization, and psychology's delay-reduction theory were contrasted under settings where budget was adversely affected by one of three manipulations in seven experiments: (1) session length was dramatically reduced; (2) choice-phase duration was substantially increased by increasing the response requirements in the choice phase or (3) outcome duration was significantly increased by increasing the response requirements in the outcome phase while holding session length constant. Although preference measures were sensitive to every budget manipulation, the nature of the changes observed were dependent upon the manner in which resource availability was manipulated and the choice alternatives offered. For example, choice was affected in an opposite manner when budget was adversely altered by lengthening choice duration ("search time") as opposed to lengthening outcome duration ("handling time"). Findings revealed partial support for pigeons' sensitivity both to changes in budget and to changes in conditioned reinforcer value. The overall pattern of results thus favors an integrative approach to describing the effect of economic context on general risk sensitivity.

Key Words: budget; choice; delay-reduction; pigeons; rate-maximization; risk.

The problem of how organisms choose between different routes to reward or among different prey items has been a central concern to behavioral ecologists (e.g. Stephens & Krebs 1986; Bateson & Kacelnik 1995), behavioral economists (e.g. Hursh 1980; Hastjarjo & Silberberg 1992; Silberberg, Bauman & Hursh 1993) and psychologists in animal learning (e.g., Fantino & Abarca, 1985; Herrnstein 1970; Rachlin & Green 1972). For example, from the perspective of the behavioral ecologist, in a prey-selection task foragers encounter (mutually exclusive) items that differ in their associated profitability ratios (ratio of net energy yield to handling time of the prey item $[E/h]$). Optimal foraging theory (OFT) represents a general attempt at understanding the decision rules of foraging animals from a functional, or adaptive, standpoint (Pyke, Pulliam & Charnov 1977; Krebs 1978). Most foraging models presume that animals have evolved through natural selection to maximize this net rate of energy gain (although alternative currencies may exist. See McNamara & Houston 1986; Schrader & Green 1990; Williams & Fantino 1994). Thus, traditional theories have been concerned primarily with the mean rate of food intake.

However, within the last two decades, research has slowly accumulated suggesting that foragers' choices between alternative sources of a particular resource depend not only on the average level of that resource, but also on the variability of the rate and amount of that resource (Oaten 1977; Caraco 1981, 1982; McNamara & Houston 1992; Bateson & Kacelnik 1995). Foragers are not solely sensitive to differences in mean gain, but may be additionally sensitive to differences in the variance of the rate and amount of the prey items, findings which mirror psychological studies of schedules of reinforcement.

Caraco (1980, 1981, 1982) and others (Barnard and Brown 1985a, 1985b; Houston & McNamara 1985) have proposed that organisms forage so as to minimize the risk of starvation (Caraco and Lima 1987; McNamara and Houston 1992). To accomplish this, some foraging organisms follow a simple decision rule concerning risk: if expected mean rate of energetic gain is sufficient to obtain the amount of energy that the organism requires to survive (known as a positive energy budget) then foragers should be risk averse, characterized by preference for a lower-variance outcome. If, however, the mean rate is insufficient to meet energy requirements (a negative energy budget), then foragers should adopt a risk-prone strategy (Houston 1991). By favoring risk, the foraging animal accepts the chance of doing poorly in order to capitalize on the possibility of obtaining a relatively higher rate of energetic gain necessary to avoid starvation.

At the same time, there has been a growing movement in economics to adopt animal models to simulate and empirically validate economic principles (Battalio, Kagel and MacDonald 1985; Hastjarjo, Silberberg and Hursh 1990). Hursh (1980) has argued that the large number of correspondences between decisions in the human economy and schedule-maintained behavior in non-humans indicate common processes that may underlie economic and operant behavior

Foraging animals confront problems conceptually similar to those facing an economically-minded consumer (MacArthur and Pianka 1966). Indeed, the last two decades have seen a broad application of economic models and principles in biological and psychological studies of risk and decision making (Hursh 1980; Kagel, Green and Caraco 1986; Kagel, MacDonald, Battalio, White & Green 1986). A growing consensus

suggests that ecological and economic theories may be largely indistinguishable (Real and Caraco 1986). Decision theorists (Hursh 1978; Caraco 1980) argue that maximization of expected utility is the appropriate optimization criterion for a wide variety of problems involving uncertainty. Both the assumptions and predictions of a rate-optimization approach to utility theory can be tested within a foraging context (e.g., Caraco, Martindale and Wittam 1980).

Finally, there is a rich literature on choice behavior, largely with pigeons as subjects, which has explored preference for different alternatives to reward (or schedules of reinforcement) often utilizing the concurrent-chains procedure (see Fantino & Logan 1979, pages 227-234, for history and rationale). These studies have included many investigations related to risk as studied by preference for variable- vs. fixed schedules of reinforcement with comparable mean values (e.g., Herrnstein 1964; Fantino 1967; see Bateson & Kacelnik 1995 and Case, Nichols & Fantino 1995, for recent reviews). For example, pigeons prefer a variable-interval schedule over a fixed-interval schedule with the same mean value (Herrnstein 1964).

Little has been done to explore how preference for risk in the concurrent-chains procedure (to be described below) is affected by economic context, perhaps because theories developed to describe choice in concurrent-chains schedules such as delay-reduction theory (or DRT, e.g., Fantino 1969a,b) do not make provisions for broader economic variables such as deprivation. Delay-reduction theory was designed to account for choice between two different variable-interval schedules using a concurrent-chains procedure. The theory states that the ability of a stimulus to act as a conditioned reinforcer can be determined by comparing the reduction in time to primary

reinforcement correlated with the onset of that stimulus, relative to the average delay to primary reinforcement (Fantino, 1969b, 1977; Squires & Fantino 1971). Simply put, those stimuli which signal a greater reduction in wait time to food should be preferred to those that signal lesser improvements. The following equation (after Squires & Fantino 1971) describes choice in the concurrent-chains procedure:

$$\frac{B1}{B1 + B2} = \frac{1/r1(T-t1)}{1/r1(T-t1) + 1/r2(T-t2)} \quad (1)$$

where B1 and B2 are the number of responses on each of the two initial links (the choice phase), T represents the overall average delay to primary reinforcement from the onset of the initial-links, t1 and t2 represent the average time spent in the terminal links (the outcomes being chosen), and 1/r1 and 1/r2 respectively represent the overall rate of primary reinforcement (number of primary reinforcers on one schedule divided by the sum of the initial-link and terminal-link times on that schedule). This equation reduces to Herrnstein's (1970) matching law when the terminal links are zero (t1= 0 and t2= 0). In several of the present experiments, terminal links are kept constant across conditions while the duration of the initial links (search time) is varied. Lengthening the initial links increases T and decreases the overall rates of primary reinforcement. This has the effect of decreasing the choice proportions predicted by Equation (1) towards indifference, an effect confirmed in many studies beginning with Fantino (1969a). Delay-reduction has successfully been extended to such areas as observing (Case & Fantino 1981; Fantino & Case 1983), self-control (Navarick & Fantino 1976; Ito & Asaki 1982), probabilistic reinforcement (Spetch & Dunn 1987) and foraging (Abarca & Fantino 1982; Fantino & Abarca 1985; Fantino 1987; Fantino & Preston 1988). However, it should be noted that

DRT loses its quantitative accuracy when applied to schedules other than variable-intervals, or to situations in which reinforcer magnitude differs between the two alternatives (but see Grace, 1994). Choice is more extreme than DRT would predict when fixed schedules are used (Duncan & Fantino 1970), and little work has been done examining choice in concurrent chains using ratio schedules (as the studies reported here have done). However, delay-reduction theory has been successfully applied to these "anomalous" situations on a qualitative, or ordinal, basis (Navarick and Fantino 1976; Williams and Fantino 1994). Williams and Fantino (1994) used variable-ratio schedules in the initial links of concurrent-chains schedules to contrast delay-reduction theory with a simple rate maximizing view from optimal foraging theory. Their work provided evidence that a qualitative analysis could distinguish the two theories on both a theoretical and empirical level. Thus, DRT may serve as a general framework on which to make predictions concerning choice behavior in concurrent chains with ratio schedules of reinforcement. However, Equation 1 makes no provision for global variables such as economic context or resource availability. Indeed, at least two studies with concurrent chains found no effect of economic context upon choice (LaFiette & Fantino 1989; Case et. al. 1995). That economic context would generally have no effect on choice seems implausible, however. Thus, one goal of the present series of experiments is to further explore the relation between economic context and choice in the concurrent-chains procedure.

While DRT does not predict that overall resource availability should affect choice, the risk-sensitivity view of behavioral ecology and the rate maximization view of behavioral economics often make explicit predictions of a relation between choice and

overall availability of resources. We present three sets of manipulations that explore the effects of economic context on choice and which, at the same time, assess various predictions made by the three types of approaches to choice (behavioral economics, behavioral ecology, and delay-reduction theory). It should be noted that other interpretations of these approaches are no doubt possible. Additionally, Grace's (1994) contextual choice theory would make predictions comparable to delay reduction in these experiments. The hope was that the results of these experiments would give some sense of the strengths and weaknesses of the three general approaches to risky choice as a function of budget.

In the first series of experiments, economic context was altered by varying the length of the experimental session. As session length shortened, food intake was compromised. In the second pair of experiments we manipulated economic context by varying the response requirements in the search phase of the concurrent-chains schedule. By increasing search effort while holding session length constant, food intake was again compromised. Finally, a third pair of experiments manipulated economic context by increasing the schedule requirements in the outcome (or handling) phase of the concurrent-chains procedure. As these requirements increased, so again was food intake compromised. In each case we examined how choice for a variable-schedule alternative is affected relative to a fixed-schedule counterpart. For each manipulation, subjects were offered choices between alternatives with identical means that differed in variance, or outcomes that differed in both mean and variance.

EXPERIMENT 1A: MANIPULATION OF TIME HORIZON

The first study manipulated the time horizon, or the time in which subjects were allowed to work for food. All experiments included baseline measures of preference when subjects were allowed to earn an unlimited number of reinforcers within a two-hour time frame. The critical manipulation was the decrease in the time allowed to work for food, from two hours to one-half hour. Few studies have examined the effects of session length on relative measures such as choice. The current literature base has focused primarily on session length effects upon within-session responding using multiple variable-interval schedules (McSweeney 1992; McSweeney, Roll & Cannon 1994), and has indicated systematic decreases in responding with longer session lengths, although response peaks were found to be independent of the session length. Although some experiments have suggested that choice appears unaffected by variations in session arrangement (e.g. Lafiette & Fantino 1989), other research has indicated that relative performance measures may indeed be sensitive to changes in session length (Plowright and Shettleworth 1991). Plowright and Shettleworth decreased session length from twenty minutes to ten minutes in a successive-encounters procedure (which measures acceptance or rejection of an alternative, rather than relative response rates) and found that pigeons were significantly more likely to accept a poorer outcome (in terms of profitability ratio) when the session length was shortened. They argued that a decrease in food intake prompted a switch in strategies from specialist to generalist (e.g., subjects were more likely to accept any outcome proffered when session length decreased).

Subjects in the present experiments were not fed outside the experimental setting unless their body weights dropped to or below 75%. Even with an increase in absolute

level of responding, subjects would be unable to maintain their body weights in the one-half hour condition, simulating a negative energy budget.

Experiment 1A varied the session length under conditions in which subjects were offered choices between two alternatives with identical expected values of responding that differed in variance. Subjects chose between a variable-ratio (VR) 20 and a fixed-ratio (FR) 20 outcome in the terminal links of the concurrent chain. The response requirement is identical across reinforcers for a fixed-ratio schedule; in a variable-ratio schedule, the response requirement varies from reinforcer to reinforcer but averages to some predetermined mean. Delay-reduction does not account for session length manipulations, and predicted no change in relative preference as session length decreases. Similarly, there is no obvious change in food maximizing as a function of session length. Thus, in this comparison, economic theories stressing rate maximization are also silent. However, according to risk sensitivity, as session length decreases to one-half hour, subjects should show a greater preference for the VR 20 schedule (become more risk-prone, assuming a shift from a positive to a relatively more negative energy budget).

General Method

To simplify the descriptions of the following seven experiments, basic commonalities across all experimental methodologies are described below.

Methodological details that differed from the general procedure are described in their respective experimental sections.

Subjects

Four White Carneaux pigeons (*Columba livia*) served as subjects. All birds within an experiment possessed equivalent experience with the concurrent-chains

methodology using variable-interval (VI) schedules in the initial and terminal links. Body weights varied dependent upon the experimental condition; supplemental feeding occurred only if birds' weights dropped to 75% of their free-feeding body weights. At that point, enough additional food was supplied to maintain them at that weight. Water and grit were made freely available in the home cage, in a room with regular day/night cycles. Sessions were typically conducted seven days a week at the same time each morning.

Apparatus

The experimental chambers were 32-cm long, 28-cm wide and 32-cm high. Three plastic response keys, each approximately 2.5 cm in diameter, were mounted on the front wall, 23 cm above the wire-mesh floor. A force of 0.1 N was required to operate each key, and produced audible feedback when the microswitch was operated. Visual stimuli were projected onto each key by an IEE 12-bulb projector mounted behind the front wall. A hopper, located approximately 11 cm above the wire floor and directly below the center key, provided access to mixed grain. During reinforcement presentations, all stimuli were turned off save for a 6-W white light illuminating the hopper. Another 6-W white light was located on the ceiling and provided diffuse lighting when grain was not available. Each chamber was enclosed in a sound- and light-attenuating wooden box that contained a small ventilation fan that masked extraneous sounds. An IBM-compatible computer in an adjacent room used a Turbo Pascal program via custom-made interfacing to control stimuli and record responses.

Procedure

Figure 1 diagrams a concurrent-chains procedure employing variable-ratio and fixed-ratio schedules. A session began with the onset of the white-illuminated side keys, signaling the operation of the concurrent initial-link schedules. Equal, independent VR schedules operated during the initial links. A change-over delay (COD) of 2 s was in effect; i.e., a minimum of 2 s had to elapse between a changeover response and entry into a terminal link. This contingency is employed to discourage frequent key switching. Completion of either initial link produced a terminal-link stimulus on the same key and initiated a corresponding terminal-link schedule. The alternative not chosen was darkened and inoperative. Completion of the terminal link was reinforced by four seconds of access to grain, following which the initial-link timers resumed operation and the cycle repeated. Session length was manipulated in the first three experiments, but was held constant at one hour in the remaining four studies. There was no limit placed on the number of reinforcers that a subject could obtain during a session. Schedules employed for all experiments were ratio schedules (see Experiment 1C for the sole exception). The VR-schedule distributions consisted of Fleschler and Hoffman (1962) progressions of 10 values. Array values were selected randomly until all values had been used, at which time all values again became available for selection in a new, random order.

Pretraining

Because all subjects had prior experience with concurrent chains (using VI schedules), preliminary training consisted of exposing subjects to the concurrent-chains procedure using small VR schedule values in both the initial and terminal links. If responding was reliably maintained, the schedule values for both the initial and terminal

links were increased by 10 (from VR 10 to VR 20, etc.) until schedule values reached their terminal experimental arrangement. Under most circumstances, one terminal-link schedule operated as a variable ratio, and was signaled by either a red (or green) key color; the other terminal-link schedule operated as a fixed ratio, and was signaled by either a green (or red) key color. The position of the variable schedule, and the key color associated with it, was counterbalanced across subjects to control for side or color biases.

Conditions

All subjects started the experimental conditions with the positive budget condition. The positive budget condition was defined as the experimental context that would allow for maximal reinforcement opportunity within the experimental constraints (either longer session length or smaller schedule values) and which maintained body weights at approximately 90% of free-feeding weights. Upon completion of the positive budget condition, experimental values were altered to effect a relatively negative budget (decreased session length or increased schedule values) by decreasing reinforcement opportunities. The positive and negative budget conditions were then replicated, but the locations of the variable and fixed terminal-link alternatives were reversed. The reversal conditions provided a means of testing the replicability of the results, as well as providing evidence for potential side bias. The first four sessions of every condition were conducted using a forced-sampling procedure: while both initial-link keys were illuminated, only one was functional on any given trial. The operative key was chosen at random, and never for more than three consecutive trials, at which time the other initial link was chosen. This procedure ensured that subjects had adequate sampling of both terminal-link schedules. All other sessions were conducted as free-choice sessions, with

no experimental constraints on the initial links. Conditions lasted for a minimum of ten sessions (not including the first four forced-sampling sessions).

Data

Choice proportions (responses on the initial link leading to the variable-ratio schedule divided by total responses towards both initial-link schedules) were regularly checked for stability from the tenth session onward. Performance was judged stable by one of two methods: 1) if the means of each three-session block from the preceding nine sessions did not differ by more than 0.05 and revealed neither an upward ($M1 < M2 < M3$) nor a downward ($M1 > M2 > M3$) trend; or 2) if preference for either alternative in the last three sessions was above 90%. The latter criterion was implemented to decrease the probability of response perseveration known to produce side biases in pigeons. Time allocation, which may serve as a complementary measure of choice (Baum and Rachlin 1969), was measured from onset of the first response to an initial-link key until a response on the other initial-link key: time was not counted before a response, but continued to accrue after the first response to an initial-link alternative even if a pause occurred. Since, in all cases, time allocation closely matched choice proportions, statistics are reported only for the more common choice measure (relative responding). Statistical analyses consisted of 1) ANOVAs on the choice proportions and 2) converting correlation values into t-values for repeated-measures t-tests on the significance of the correlations obtained. In all cases the means for the data presentations and statistics were taken from the final nine sessions of each condition, except when the final three sessions (after a minimum of 10 sessions) were above .90 preference. Under these circumstances, mean preference was obtained from the final three sessions only.

EXPERIMENT 1A

Subjects S1, S2, S3 and S4 began Experiment 1A in the positive budget condition, with session length of 2 hours. Initial-link values were concurrent VR 60 schedules; terminal links consisted of a comparison between VR 20 and FR 20 schedules. As the terminal-link schedules had identical means, they differed only in their variances.

Negative Budget

The negative budget condition was identical to the positive budget condition save that session length was now decreased to one-half hour, reducing the opportunity to earn food sufficiently to drop body weights in all subjects.

Longer Initial-link Schedule Values

The positive and negative budget conditions were replicated using larger initial-link schedule values. Due to the extreme preferences observed in the first positive budget condition, it was considered prudent to increase the initial link values to concurrent VR 120 in hopes of decreasing preference in the positive budget condition. Although the overall effects were as predicted (a general decrease in preferences), this manipulation had the additional side effect of increasing variability across subjects. Subjects were lastly returned to the positive budget condition with concurrent VR 120 initial links following the negative budget condition utilizing the longer initial links, for an ABA design.

Results and Discussion

Figure 2 displays the mean obtained time allocation and choice proportions averaged across sessions and subjects as a function of budget condition and initial-link value change. Time allocations and choice proportions above .50 represent preference for

the variable-ratio 20 schedule. As can be seen, time allocation closely matched choice proportions.

Examination of preference for the first two conditions that employed concurrent VR 60 initial links demonstrates that subjects showed a strong initial preference for the VR 20, corresponding to risk-prone behavior, with a consistent increase in preference as budget decreased in the one-half hour condition. Preference for the VR 20 relative to the FR 20 increased from .93 to exclusive preference for the variable schedule at 1.0. Although such an increase appears to be only moderate in form because of natural ceiling effects, it was significant ($F(1,3) = 101.4$, $p < 0.002$) due to the low variance across subjects, and proved a reliable trend across all subjects. Subjects completed both conditions in a relatively short number of sessions (typically the minimum, 10) as a result of the extreme preferences involved.

Percent of body weight was used as an index of both the effectiveness of the budget manipulation as well as an indicator of "internal reserves." To claim that decreasing session length functionally simulated a negative budget, it would be necessary to demonstrate two effects: 1) that a substantial energy deficit was produced, and 2) overall food intake was compromised. Subjects' body weights declined from a mean of 90% in the positive budget condition to an average of 83 % in the negative budget condition, indicating that the session-length manipulation had the desired effect on body reserves. In most operant studies with pigeons, subjects are kept at 80% of their free-feeding body weights. Although subjects in the current study had greater percent body weights in the positive budget condition, their body weights did not fall below 80% in the

negative budget condition, because subjects satisfied the stability criterion before such weights were reached.

Due to the ceiling effects obtained in the first two conditions, the study was replicated using initial-link values doubled from their previous values (from VR 60 to VR 120). In the conditions that employed concurrent VR 120 initial links, subjects' preference for the VR 20 in the positive budget condition decreased an average of .29 (relative to the positive budget condition with VR 60 initial links). There was substantial individual variation in choice proportions (ranging from .38 to .90 preference for the VR 20). Although all subjects demonstrated an increased preference for the VR 20 in the second negative budget condition, the change was not statistically significant ($F(1,3) = 4.8$, $p = 0.12$) due to the high variability across subjects. Despite the lack of statistical significance, the qualitative changes were robust (range of .08 increase for subject 2 to .58 increase for subject 1). Thus, a logistic regression analysis using a Gaussian family value descriptor was performed given the greater sensitivity of a regression model to the standard error relative to an ANOVA. When both positive budget conditions (2 hr) were contrasted with the negative budget (1/2 hr) condition, coefficient values proved to be statistically significant. A Chi-Square test on both coefficient values, representing the comprehensive effects of session length on choice, yielded a Chi-Square (2 df) = 16.04, $p < .001$. Only subject 4 returned to near-baseline levels when the positive condition was reinstated. It is most probable that subjects developed side biases, a common problem with pigeons as subjects, that was likely exacerbated by the extreme preferences generated. Subjects generally took longer to complete all three long conditions. Subjects' body weights declined steadily from a mean of 88% in the positive condition to

an average of 78% in the negative budget condition, and increased to a mean of 85% in the last condition, indicating that the session-length manipulation had the expected impact on body reserves. Subjects were more likely to reach lower body weights in these conditions (subjects 1 and 4 both reached the 75% minimum), probably due to the longer exposure to each condition.

Given that schedules were not changed between the positive and negative budget conditions, delay-reduction theory predicted no change in behavior as a function of budget manipulation. Risk sensitivity predicted that subjects would be risk-averse in the positive budget condition, and switch to a risk-prone strategy in the negative condition. Only two of the four subjects demonstrated preferences for the FR schedule (subject S1 positive budget condition with VR 120 initial links and subject S4 positive budget Replication with VR 120 initial links). This finding mirrors the general lack of evidence for risk aversion when variable versus constant delays are tested (Zabludoff, Wecker and Caraco 1988). However, the qualitative description of increasing risk-prone behavior with decreasing resources was supported for all subjects under all conditions. The results from Experiment 1A offer general support that subjects were indeed sensitive to changes in budget or resource scarcity; preference for the variable schedule reliably increased as resource availability decreased. There was a significant negative correlation between preference for the variable schedule and percent body weight [$r = -.69$, $t(.025, 6df) = -2.33$, $p < .025$]; indicating that as body weight decreased, risk-prone behavior was more likely to increase. Body weight (a measure of the effectiveness of budget) was related to risk behavior in the fashion predicted by Caraco's risk-sensitivity. As the environmental budgetary context shifts from rich to lean (positive to negative), foragers should alter

food-seeking strategies from avoiding risk under rich conditions to accepting riskier alternatives under negative budget conditions. Kacelnik and Bateson (1996) reviewed the effects of budget manipulation on risky choice in studies in which the variable dimension was amount or delay. They found that when risky choice involved variable vs. fixed delay, in four of six studies no effect was found. The present results, however, show a clear effect of budget manipulation (the significant negative correlation between risk preference and percent body weight), and in the direction required by risk sensitivity.

EXPERIMENT 1B: UNEQUAL TERMINAL-LINK ALTERNATIVES

In the prior experiment, subjects chose between alternatives with equal means but unequal variance. In Experiment 1B, subjects were offered a choice between two alternatives that differed in both mean and variance--a choice between VR 40 and FR 20. Given the robust nature of preference for variable delay, subjects sometimes prefer a variable schedule with a greater mean response requirement over a smaller, but fixed, schedule, even though the rate of reinforcement favors the constant alternative (Fantino 1967). Yet as resources become scarce, subjects may better defend against an energetic deficit by choosing the smaller fixed schedule over the variable schedule. Again, DRT does not predict changes in preference for the VR schedule as budget decreases with decreases in session length. Models in behavioral ecology such as optimal foraging theory (OFT) predict near absolute preferences for the FR 20 under most conditions. However, rate maximization predicts a shift in risk taking: as budget becomes increasingly negative (associated with a reduction in food intake and body weight), subjects should increasingly prefer the fixed schedule correlated with the higher rate of reinforcement unless they are already maximizing food intake. One may question,

however, why rate maximization doesn't predict that organisms should always maximize rate of food intake. As stated earlier, subjects often prefer a variable schedule with a higher mean value, and thus correlated lower rate of food intake, to a fixed alternative correlated with a lower schedule value and higher rate of reinforcement. One probable answer may lie in the fact that choice behavior is mediated by a number of [sometimes] competing sources of control. If food intake is sufficient to maintain a subject at a stable body weight, then other variables may influence choice responding, such as leisure time (Schrader & Green 1990) or conditioned reinforcement value (Fantino 1987, 1988; Williams & Fantino 1994). Thus, at sufficient levels of food intake, subjects may trade off increases in rate of reinforcement for increased leisure, conditioned reinforcement value, or some alternative currency. Only when food intake is severely compromised should subjects direct responding more intensely toward maintaining (or increasing) rate of consumption. According to this view of rate maximization, under severe budgetary constraints food maximization should dominate preference.

Method

Subjects

The same subjects from Experiment 1A served as subjects for Experiment 1B.

Apparatus and Procedure

The sole difference between this experiment and the prior one was that the mean value of the variable-ratio schedule was now twice that of the fixed-ratio schedule (a VR 40 vs. FR 20 comparison). No pretraining was necessary due to subjects' immediate prior experience. Initial-link values were chosen at concurrent VR 90 schedules. For each subject, the terminal-link VR schedule was arranged on the key light opposite from its

location in the previous experiment. If the VR schedule had been situated on the left key, it was now situated on the right. The position of the variable schedule, and the key color associated with it, were still counterbalanced across subjects to control for side or color biases.

Conditions

Only the positive budget condition was replicated in this study, employing identical schedule values as in the first positive budget condition (for an ABA design, where A is the positive, and B, the negative, budget condition).

Results and Discussion

Figure 3 displays the obtained time allocation and choice proportions for subject S1 (top graph) and the averaged time and choice measures for subjects S2 through S4 (bottom graph) as a function of budget condition. Time allocation closely matched choice proportions across conditions for all subjects. Mean choice proportion in the positive budget condition reflected a marginal preference for the VR 40 relative to the FR 20, which was strongest for subject S1. When session length was decreased, a clear preference emerged for the richer FR 20 outcome for subjects S2 through S4, consistent with the rate maximization view articulated above. Preference for the FR 20 was eliminated in a return to the longer session length. However, subject S1 showed an increase in preference for the VR 40 (from .68 to .89) in the negative budget condition. Subjects approximated baseline choice proportions in the Replication condition, again save for subject S1 (from .89 in the negative condition to only .84 in the Replication condition), although there was greater inter-subject variability in the Replication condition relative to the initial positive budget condition. Choice proportions were not

statistically significant between the positive and negative budget conditions ($F(1,3) = 1.8$, $p = 0.27$) but reached marginal significance when S1's data were removed ($F(1,2) = 13.4$, $p = 0.06$). Subjects generally took longer to complete a condition relative to prior performance.

Within-session response patterns were examined in this and the prior study. Stephens (1981) has argued that a forager's risk sensitivity may be influenced by the number of decisions left to make (see also McNamara and Houston 1992). According to his formulation of risk sensitivity, foragers with only a few decisions left (at a higher energy reserve) should become more risk-prone than a forager with many decisions left to make. One might then expect to see a pattern of gradually increasing preference for the VR schedule as the session nears completion. There were no consistent trends across subjects; in fact, while the first two subjects demonstrated an initial increase in preference for the variable schedule in Experiment 1B, S4 demonstrated a sharp initial decline in preference for the VR 40 schedule. Subject S4's pattern of responding can be explained by assuming that organisms just beginning a foraging bout are at their lowest point with respect to internal body reserves. If internal reserves serve as a partial cue directing risk-prone strategies of foraging, then subjects should be more risk prone at the onset of the experimental session. However, this trend was only observed in S4.

Body weights were sensitive to budget manipulations, with a mean drop of 8% between the positive and negative budget condition, indicating that the session-length manipulation had the anticipated effect on body reserves. Three of the four subjects (excluding S1) dropped below 80% in the negative budget condition. There was a significant positive correlation between preference for the variable schedule and percent

body weight [$r = .62$, $t(.025, 10 \text{ df}) = 2.49$, $p < .025$]; eliminating subject S1's data increased the correlation [$r = .80$, $t(.025, 9 \text{ df}) = 4.0$, $p < .005$]. These findings indicate that as body weights dropped, preference for the VR 40 tended to drop. Absolute food intake also dropped significantly from the positive to negative budget condition for all birds, consistent with findings from Experiment 1A.

Subject S1's increased preference for the VR 40 in the negative budget condition could reflect either an increased preference for variability (increased risk-prone behavior) or a side bias that developed with continued exposure. This latter explanation is plausible given the failure to return to baseline levels in the positive Replication condition. Overall, though, the results from Experiment 1B (particularly the correlation between percent body weight and risk) offer some suggestion that subjects were sensitive to resource availability, and shifted risk-taking strategies to maximize rate of food intake given an energy deficit, as predicted by an economic view of consumer behavior (and in so doing, became less risk-prone).

EXPERIMENT 1C: RATIO VERSUS INTERVAL SCHEDULES

Subjects were offered a choice between a VR 50 and a VI 20 s schedule in Experiment 1C. As session length decreases, only on the ratio schedule can subjects increase rate of food intake (because only on ratio schedules does rate of responding dramatically affect rate of reinforcement). Although this does not represent a pure test of risk (since both schedules are associated with variance), these alternatives can provide a unique test of the economic theory of rate maximization, which received support in Experiment 1B. Will subjects increase their preference for the alternative that best aids in the defense against a

loss of consumption? In this experiment neither DRT nor risk sensitivity of behavioral ecology makes a clear prediction.

Method

Subjects, Apparatus and Procedure

The same subjects and experimental chambers from the prior experiments were utilized. A concurrent-chains procedure identical to Experiment 1B was employed. Session length was either two hours or one-half hour, depending upon the condition, and initial-link schedules were again arranged as concurrent VR 90. The sole difference between this experiment and the prior one was that subjects chose between a VR 50 and a VI 20s schedule. For each subject, the VR terminal-link schedule was arranged on the key light opposite from its location in Experiment 1B. The position of the VR schedule, and the key color associated with it, was still counterbalanced across subjects to control for side or color biases. Due to subject S1's strong preference for the VR 50, the ratio schedule value was increased to a VR 70, for this subject only, to lower initial preference.

Results and Discussion

Figure 4 displays the mean obtained time allocation and choice proportions as a function of budget condition. Mean choice proportion in the positive condition reflected a marginal preference for the VR 50 (or VR 70 for S1) relative to the VI 20 s. There was little variability across subjects; most subjects' preferences were just above the indifference point. Preference for the VR over the VI increased for all subjects (from a mean of .55 to a mean of .78) as budget decreased. The difference in preference was significant between the positive and negative budget conditions ($F(1,3) = 11.80, p < 0.05$).

Percent body weights differed by 11% between the positive and negative budget conditions, indicating that the session-length manipulation had the predicted effect on body reserves. All four subjects' weights dropped below 80% in the negative budget condition. There was a significant negative correlation between preference for the variable-ratio schedule and percent body weight [$r = -.73$, $t(.025, 10 \text{ df}) = -3.38$, $p < .005$] indicating that as body weight decreased, preference for the ratio schedule was likely to increase, supporting the predictions from the economic perspective. As budget became increasingly negative, subjects were more likely to choose the schedule that provided a potential opportunity to increase expected rate of food intake in favor of the alternative where the minimum expected rate was temporally bounded. Absolute food intake also dropped significantly from the positive to negative budget condition for all subjects, consistent with findings from Experiments 1A and 1B.

A rate maximizing view predicted that subjects would favor the ratio schedule more in the negative budget condition than in the positive condition. All subjects conformed to this pattern; as budget decreased, the VR schedule was more often favored over the VI schedule. The results from this experiment are consistent with the suggestive results from Experiment 1B in supporting a rate-maximization approach to changes in resource availability.

EXPERIMENT 2A: EFFECTS OF SEARCH COST WITH EQUAL OUTCOMES

Experiment 2A manipulated budget by changing the initial-link schedule values across conditions. Within behavioral economics, the initial links may be conceptualized as the flow or rate of income experienced. Within behavioral ecology, the initial links of a concurrent chain are analogous to the effort of searching for a prey item. As initial-link

values increase, both absolute rate of food intake and body weights should decline (as long as session length is held constant). All experiments took baseline measures of preference under conditions that employed relatively short initial links; initial-link values were then increased four-fold to decrease energetic intake.

Delay-reduction theory makes explicit predictions concerning increases in initial-link values: as initial links increase, the relative delay-reduction properties of both alternatives approach equivalence, and choice proportions should approach indifference (Fantino 1969a). Economic theories of utility maximization would suggest that, regardless of initial preferences, as budget worsens, subjects should favor alternatives that provide the best means of optimizing expected food intake. Two factors could influence behavior according to ecologists: search cost and budget. According to traditional OFT, as search cost increases, with increasing initial-link values, foragers should adopt a more generalist pattern of responding (corresponding to a response convergence towards indifference, similar to DRT's predictions). However, according to risk sensitivity, as search cost increases, budget is adversely affected, and foraging organisms should demonstrate greater preference for variability. Thus, one may anticipate either an increase in risk behavior, consistent with risk-sensitive foraging theories, or a decrease in risk, consistent with traditional theories of optimal foraging.

Experiment 2A varied the initial links under conditions where subjects were offered choices between two alternatives with identical mean requirements that differed in variance (VR 20 versus FR 20). Although delay-reduction theory does not predict preference for variability (VR 20 vs. FR 20), given that a preference does occur, delay reduction requires that it be modulated by search time. Thus, delay-reduction predicted a

decline in preference for the VR 20 towards indifference with higher initial-link values. According to risk sensitivity, subjects should show a greater preference for the VR 20 schedule (become more risk-prone) as initial links increase; according to traditional OFT, though, preference for the VR 20 should decrease as the initial links increase. No explicit predictions emerge from a behavioral economic orientation because mean expected intake is equivalent across alternatives.

Method

Subjects

Four different White Carneaux pigeons (*Columba livia*) served as subjects (I1, I2, I3, I4).

Apparatus and Procedure

The experimental chambers used in the prior studies were again employed for this experiment. The concurrent-chains procedure used in the prior studies was also utilized for this and the following studies.

Pretraining

Pretraining was conducted as described in experiment 1A until subjects were responding to the final condition values.

Positive Budget

Initial-link schedule values were concurrent VR 60 for all subjects; terminal-link values were VR 20 and FR 20. In this and all other studies, session length was held constant at one hour.

Negative Budget

The negative budget condition was identical to the positive budget condition save that initial-link schedule values were increased four-fold, to concurrent VR 240 schedules, reducing the opportunity to earn food sufficiently to lower body weights in all subjects.

Reversals

The positive and negative budget conditions were replicated, but locations of the VR 20 and FR 20 terminal-link alternatives were switched.

Results and Discussion

Figure 5 displays the time allocation and choice proportions averaged across subjects as a function of budget condition. Time allocations and choice proportions above .50 represent preference for the VR 20 schedule, and correspond to risk-prone preference. Subjects showed a strong initial preference for the VR 20, corresponding to extreme risk-prone behavior. These data match initial choice proportions from Experiment 1A, which used identical schedule values. Preference for the VR 20 relative to the FR 20 decreased from .95 preference for the variable schedule to .54 preference for the VR 20 in the first two conditions, and decreased from .73 to .45 preference for the VR 20 in the two reversal conditions. If choice proportions are averaged across the two positive budget conditions and the two negative budget conditions, there was a mean drop in risk-prone behavior from .84 to .50. Variability across subjects was much higher in the positive reversal condition than in the positive budget condition, but higher in the first negative budget condition relative to the negative reversal condition. Most subjects did not return to their previous levels of risk-prone preferences in the positive reversal condition (except for subject I1), indicating the development of a moderate side bias. The

drop in preference for the VR schedule across budget manipulations was statistically significant ($F(1,7) = 160, p < 0.005$) when comparing the aggregate data (averaged across subjects and reversal conditions). This finding is consistent even when comparing the two budget manipulations independently.

Body weight was again used as an index of both the effectiveness of the budget manipulation as well as an indicator of "internal reserves." Subjects' body weights declined steadily from a mean of 91% in the positive budget condition to an average of 78% in the negative budget condition, and from 88% in the positive reversal condition to 76% in the negative reversal condition, indicating that the initial-link manipulation had the expected effect on body reserves. The correlation between body weight and risk preferences was significant at [$r = .52, t(.025, 14 \text{ df}) = 2.28, p < .025$]. Absolute food intake dropped sharply from the positive to negative budget condition for all birds. There was as great as a 4:1 (positive:negative) decline in absolute number of reinforcers obtained (subject I3), indicating that birds were earning significantly fewer reinforcers in the negative budget condition than in the positive budget condition.

Delay-reduction theory predicted a decline in preference for the VR 20 schedule as initial-link values increased, consistent with the current data. Risk sensitivity predicted that subjects would be risk-averse in the positive budget condition, and switch to a more risk-prone strategy in the negative condition. All subjects demonstrated the opposite pattern of results; subjects were consistently risk-prone in the positive budget condition, and shifted to growing risk-aversion (or risk-indifference) as budget became negative. Although these findings contradict risk sensitivity, the data are consistent with traditional optimal foraging theory (Hanson and Green 1989). As search costs increased, with

increasing initial links, subjects adopted a more generalist approach to choice, reflected in their decrease in preference for the VR toward indifference. The manipulation of initial-link values with equal mean outcomes provided an unambiguous test only of delay-reduction theory, which was indeed supported.

EXPERIMENT 2B: SEARCH COST WITH UNEQUAL OUTCOMES

In Experiment 2B, subjects were offered a choice between two alternatives that differed in both mean value and variance. Given the robust nature of preference for variable schedules of reinforcement, subjects should demonstrate strong preferences for a variable schedule with a greater mean response requirement over smaller, but fixed, schedule, even when the rate of reinforcement favors the constant alternative (Fantino 1967). But as resources become scarce, subjects might better defend against an energetic deficit by choosing the smaller fixed schedule over the variable schedule. Again, DRT predicts that preference should decline toward indifference as initial-link length is increased.

However, a rate maximization view predicts a greater shift in risk taking: as budget becomes increasingly negative (associated with a reduction in rate of food intake and body weight), subjects should actively prefer the fixed schedule correlated with the higher rate of reinforcement. Thus, when offered a choice between a VR 40 versus an FR 20 schedule, pigeons might exhibit a complete preference reversal, opting for the FR 20 under conditions with longer initial-link response requirements. Models in behavioral ecology do not make explicit predictions here, given that traditional optimal foraging theories do not predict preference for the VR 40 associated with the poorer profitability ratio.

Method

Subjects

Four different White Carneaux pigeons (*Columba livia*) served as subjects (W1, W2, W3, W4).

Apparatus and Procedure

Both the set of experimental chambers and the general procedure were identical to those employed in previous experiments.

Positive Budget

Initial-link schedule values were relatively short, at concurrent VR 60; the outcome comparison was between VR 40 and FR 20.

Negative Budget

The negative budget condition was identical to the positive budget condition save that initial-link response requirements were now increased four-fold, from concurrent VR 60 to concurrent VR 240.

Reversals

The positive and negative budget conditions were replicated, but the location of the VR 40 and FR 20 terminal-link alternatives was switched.

Results and Discussion

Mean time allocation and choice proportions are displayed in Figure 6 as a function of budget condition. Mean choice proportion in the positive budget condition reflected a strong preference for the VR 40 relative to the FR 20, with a mean of .97. There was little variability across subjects, with two subjects (W1 and W4) showing exclusive preference for the VR 40 schedule. In the negative budget condition, preference for the VR 40 over the FR 20 dropped significantly ($F(1,3) = 10.60$, $p = 0.05$)

and clearly reversed (i.e., substantially below .50) for one subject (W1). However, there was a large degree of variability across subjects in the negative budget condition (choice ranged from .74 to .06 preference for the VR 40). Subjects' choice proportions reversed in the positive reversal condition, although mean choice was lower in the reversal condition (.83) compared to the initial positive budget condition (.97). Choice proportions again declined significantly in the negative reversal condition ($F(1,3) = 11.15$, $p = 0.04$). Preference reversals favoring the FR 20 were clearly indicated in data from three of the four subjects, with subject W3 at indifference.

Body weights differed between conditions with a mean difference of 15% between the positive and negative budget condition and 13% between the reversal conditions. Three of the four subjects (excluding subject W2) dropped below 80% in the first negative budget condition; all subjects dropped below 80% in the negative reversal condition. There was a significant positive correlation between preference for the variable schedule and percent body weight [$r = .83$, $t(14) = 5.57$, $p < .0005$]. These findings suggest that as body weights dropped, preference for the VR 40 dropped.

Delay-reduction theory predicted a decline in preference for the VR 40 schedule as initial-link values increased, consistent with the basic pattern of the current data. However, DRT predicted a decline to, but not past, the indifference point (or indifference range around .50). Four of the eight cases clearly violate this prediction (subject W1 in the negative budget condition, and subjects W1, W2 and W4 in the negative reversal condition), supporting the rate-maximization view posited by behavioral economics: as rate of reinforcement decreased with increasing initial-link length, subjects should have demonstrated reliable preferences favoring the FR 20 schedule over the VR 40 schedule,

since the FR 20 was associated with a higher rate of reinforcement (as evidenced by the shorter time it took subjects to complete the FR 20). Subjects were more likely to demonstrate preference reversals in the reversal conditions: either partial side bias or experience with the manipulation may account for this effect. Possible carry-over bias was evident in choice proportions from subjects W3 and W4, as they failed to demonstrate a clean return to baseline performance in the positive reversal condition. The moderate side biases, though, are insufficient to account for the extent of the reversals observed. It is possible that having previously gone through the deprivation state, subjects were more sensitive to the budget manipulation. However, subjects took longer on average to complete the reversal conditions; a heightened sensitivity to the change in budget should have corresponded with a relatively faster time to stability. Only subject W1 demonstrated clear preference reversals under both the negative and negative reversal conditions. However one accounts for the reversals, it is clear that all subjects showed an increasing preference for the fixed schedule associated with the higher rate of reinforcement as budget decreased, supporting a rate-maximization view, since subjects should favor the alternative associated with a higher rate of energetic intake more as resource scarcity increases.

EXPERIMENT 3A: HANDLING COSTS: EQUAL OUTCOMES

The final two studies manipulated budget by changing the terminal-link schedule values across conditions. Within behavioral ecology, the terminal links of a concurrent chain might be analogous to the cost of handling a prey item. Within behavioral economics, the terminal links would best be conceptualized as the cost or price of a particular good. As terminal-link values increase, both food intake and body weights should decline (as long

as session length is held constant). All experiments took baseline measures of preference under conditions that employed relatively short terminal links; terminal-link values were then increased five-fold to decrease energetic intake. The ratio between the terminal-link values was always maintained across conditions.

Delay-reduction theory makes explicit predictions concerning increases in terminal-link values: as terminal links increase, choice proportion for the preferred alternative should increase (Fantino, Preston and Dunn 1993). Economic theories of utility maximization would suggest that, regardless of initial preferences, as budget worsens, subjects should increasingly favor alternatives that provide the best means of optimizing expected food intake. With mean outcomes equal in Experiment 3A, this view is silent on the effects of a leaner budget on choice. In Experiment 3B, however, with unequal mean outcomes, the richer outcome should become increasingly preferred as budget worsens. According to risk sensitivity, preference should increase for the schedule with the higher variance as budget decreases. Thus, preference for a VR X over an FR X should increase with increases in X (in Experiment 3A), a prediction consistent with that of DRT.

Method

Subjects

Four different White Carneaux pigeons (Columba livia) served as subjects (T1, T2, T3, T4).

Apparatus and Procedure

The experimental chambers employed and the general procedure used in this experiment were identical to those employed in all prior studies. Pretraining was again instituted with these new subjects.

Positive Budget

Initial-link schedule values were concurrent VR 60 for all subjects. The terminal-link values began at VR 20 and FR 20.

Negative Budget

The terminal-link schedule values were increased five-fold, to VR 100 versus FR 100, reducing the opportunity to earn food sufficiently to drop body weights in all subjects.

Results and Discussion

Time allocation and choice proportions are presented in Figure 7 as a function of budget condition and represent data averaged across subjects. Time allocations and choice proportions above .50 represent preference for the VR 20 schedule, and correspond to risk-prone preferences. Performance indicated a moderate initial preference for the VR 20 schedule, corresponding to moderate risk-prone behavior. Preference for the VR 20 relative to the FR 20 increased from .59 preference for the variable schedule to .89 preference for the VR 20 across the first two conditions, and increased from .67 to .89 preference for the VR 20 in the reversal conditions. If choice proportions are averaged across the two positive budget conditions and the two negative budget conditions, there was a mean increase in risk-prone behavior from .63 to .89. Variability across subjects was greater in the positive budget conditions than in the negative budget conditions. The increase in preference for the VR schedule across budget

manipulations was statistically significant ($F(1,7) = 32.3$, $p < 0.0006$) when comparing the aggregate data (averaged across subjects and reversal conditions). This finding is consistent even when comparing the two budget manipulations independently.

Subjects' body weights declined from a mean of 89% in the positive budget condition to 79 % in the negative budget condition, and from 86% in the positive reversal condition to 78% in the negative reversal condition. The correlation between body weight and risk preference was significant at [$r = -.68$, $t(.025, 14 \text{ df}) = -3.47$, $p < .005$]. Thus, as body weights decreased with increases in mean terminal-link value, preference for the variable schedule was likely to increase. Absolute food intake dropped sharply from the positive to negative budget condition for all birds, indicating that birds were earning significantly fewer reinforcers in the negative budget condition than in the positive budget condition. Both delay-reduction theory and risk sensitivity predicted an increase in preference for the VR schedule as terminal-link values increased, consistent with the current data.

EXPERIMENT 3B: HANDLING COSTS: UNEQUAL OUTCOME

In Experiment 3B, subjects were offered a choice between two alternatives that differed in both mean value and variance. Pigeons may prefer a variable schedule with a greater mean response requirement over a smaller, but fixed, schedule, even when the rate of reinforcement favors the constant alternative. But as resources become scarce, subjects may better compensate for an energetic deficit by choosing the smaller fixed schedule over the variable schedule. Applying the same logic as in Experiment 3A, DRT predicts that preference should increase for the VR schedule as terminal-link schedule values increase. A rate maximization view predicts the opposite result: as budget becomes

increasingly negative (associated with a reduction in rate of food intake and body weight), subjects can defend their compromised food intake better by choosing the fixed schedule correlated with the higher rate of reinforcement.

Method

Subjects

Four different White Carneaux pigeons (Columba livia) served as subjects (G1, G2, G3, G4).

Apparatus and Procedure

The experimental chambers employed and the general procedure used in this experiment were identical to those employed in all prior studies. Pretraining was again instituted for these new subjects.

Positive Budget

Initial-link values were arranged as concurrent VR 60 schedules. Terminal-link schedule values were relatively short; subjects were offered a choice between a VR 40 and FR 20 schedule.

Negative Budget

The terminal-link response requirements were now increased five-fold, from a choice between a VR 40 versus FR 20 to a choice between a VR 200 versus FR 100.

Results and Discussion

Variability in initial and subsequent performance required separation of subject G2's data (Figure 8 top graph) from the data averaged across subjects G1, G3 and G4.

The full gambit of risk behavior was observed in the positive budget condition, from mild risk aversion (subject G1) to risk neutrality (subject G2) and moderate to strong risk-

prone behavior (subjects G4 and G3, respectively). Budget manipulation also produced idiosyncratic behavior: as terminal links increased, subjects G1 and G3 demonstrated an increase in preference for the [now] FR 100 schedule over the VR 200 schedule; in contrast, subjects G2 and G4 demonstrated increased preference for the [now] VR 200 over the FR 100 schedule. Most subjects showed a similar pattern of behavior in the reversal conditions; however, only subject G2 exhibited preference for the VR 200 over the FR 100 in the negative budget reversal condition. Subject G4 demonstrated a robust preference for the FR 100 alternative in the negative budget reversal condition (thus, his preference measures were included in the bottom graph for both negative budget conditions). Three of the eight comparisons possible demonstrated increased preference for the VR 2X schedule when resource availability decreased, while the remaining five comparisons exhibited a preference reversal pattern that favored the FR X schedule. Only subject G2 demonstrated replicable preferences for the variable schedule in the negative budget conditions, despite a substantial drop in food intake under conditions in which the VR 200 was favored over the FR 100 outcome.

Body weights differed by 10% between the positive and negative budget condition and by 11% between the reversal conditions, indicating that the terminal-link manipulation had the expected effect on body reserves. Only one subject (G2) dropped below 80% in the first negative budget condition; all subjects save G4 dropped below 80% in the negative reversal condition. The correlation between percent body weight and choice proportion was not statistically significant [$r = .11$, $t(.025, 10 \text{ df}) = .41$, ns] due to the variable pattern of data across subjects.

The data from this experiment provide partial support for both delay-reduction theory and a rate-maximization approach: DRT correctly predicted an increase in preference for the variable schedule as terminal links increased, in three of eight cases; a rate-maximization approach correctly predicted a preference reversal that favored the smaller fixed schedule in the remaining five cases. It appears that different subjects were differentially sensitive to aspects of the outcome schedules (resource level, favoring the shorter FR according to a rate-maximization view; conditioned reinforcer strength, favoring the longer VR according to delay-reduction theory).

GENERAL CONCLUSION

Complex behavior, such as foraging, is not a simple function of a single dimension or attribute of the environment. Many characteristics of the foraging context, such as cost of accepting a prey item over an alternative, quality of reinforcement available, the time course for the foraging cycle, and alternative behaviors that compete with foraging but are equally necessary for survival and overall fitness (predator avoidance, territorial defense, mating) all may contribute to a foraging organism's decision criterion when faced with a prey-selection task (Stephens and Krebs 1986). One such attribute proposed to affect behavior is sensitivity to stochasticity, with changes in environmental resources moderating that sensitivity. Behavioral ecologists have cogently argued that foragers' sensitivity to prey items associated with risk is constrained by budgetary considerations, as described by risk sensitivity (Caraco 1980; Stephens 1981).

Yet risk sensitivity may not be determined solely by internal and external resources. Social dominance, the threat of competition, and the social context (individual or flock foraging patterns) all affect the degree of sensitivity to changes in

budget (Barnard, Brown and Gray-Wallis 1983; Barnard and Brown 1985b; McNamara and Houston 1992). In fact, McNamara and Houston (1992) have provided several modifications to simple risk sensitivity to accommodate some of these additional constraints. However, this research has also provided evidence of yet another constraint, or secondary source of behavioral control--sensitivity to changes in conditioned reinforcer value as described by delay-reduction theory (the only viewpoint of those considered that accounts for the results of Experiment 2A).

Recall that in Experiment 3B, two subjects (G2 and G4) demonstrated a strong preference for a VR 200 schedule over an FR 100 schedule, even though this preference reduced rate of reinforcement threefold. When subjects chose the VR schedule more often, they were likely to earn an average of 10-15 fewer reinforcers than other subjects. Consider the performance of G4 in the first negative budget condition (where he demonstrated a strong preference for the VR 200) and in the negative reversal condition (where he demonstrated a preference reversal, favoring the FR 100 schedule). This subject earned an average of 14 more reinforcers by favoring the smaller fixed schedule over the variable schedule, an increase that constituted approximately 25% of its daily energy intake. This suggests that choice responding that favored the VR 200 schedule had a strong negative impact on food intake. Organisms sensitive to resource scarcity alone should have chosen the FR schedule at near exclusivity to better compensate for loss of consumption, as predicted by an economic theory of rate maximization. Yet in 3 of the 8 cases, subjects increased preference for the variable alternative, even though it was associated with the considerably poorer profitability ratio.

These seemingly counterintuitive findings that violate assumptions of energy optimization are accurately predicted by DRT. Such results are not unique. Williams and Fantino (1994) pitted conditioned reinforcer value against profitability ratios in an attempt to describe the primary determinant of choice behavior in a foraging analogue. The predictions of rate maximization were upheld only when consistent with delay-reduction theory. Under conditions where the two approaches made divergent predictions, choice behavior unequivocally favored DRT over a rate-maximization view of optimal foraging theory. Williams and Fantino concluded that, "...choice tracks cues that signal a greater reduction in delay to reinforcement and not simple prey density ratios," although they noted that conditioned reinforcement and prey density ratios are likely to be highly correlated in the natural environment. Thus, sensitivity to changes in reductions in delay to reinforcement provides a useful principle which may also govern foraging-related choices (Fantino 1987).

Nor can delay-reduction theory provide a complete account of the data. In the above example, DRT accurately predicted only 3 out of 8 cases. The remaining 5 cases were better described by a rate-maximization approach assuming sensitivity to resource availability. Experiment 1, (where session length was manipulated) also provided evidence that delay-reduction's account of choice is incomplete. In Experiment 1B, subjects were presented a choice between VR 40 versus FR 20 terminal-link schedules. Session length was subsequently shortened from two hours to one-half hour. Although DRT predicted no change in behavior, since, as a relativistic model it does not take into account absolute time horizons, choice proportions changed for all subjects, and 3 of 4 subjects showed strong preference reversals that favored the smaller FR schedule when

budget was adversely affected. Thus, an account of choice, specifically preference for variability, based solely on principles derived from conditioned reinforcement models like delay-reduction theory, proves incomplete.

The data presented in this research offer support for multiple accounts of risk-sensitive changes in behavior (Table 1). Experiments that allowed divergent predictions of risk sensitivity to be tested provided partial evidence that behavior is sensitive to factors such as resource scarcity. In addition, understanding changes in conditioned reinforcer value, as described by delay-reduction theory, seems critical to describing behavior that appears suboptimal with respect to simple rate-maximization accounts of behavior. Choice models in psychology must begin to address the role of motivation in a more empirical fashion if they are to capture the full determinants of behavior (Snyderman 1983). Theoretical modeling, favored by behavioral ecologists, must also take into consideration the different mechanisms by which resource deficits may arise in the environment. A major finding in the present experiments is that all energetic deficits do not produce the same effects on risk behavior: increased search costs reduced risk-prone behavior, while increased handling costs increased risk taking. The opposing effects of these two changes in cost (search and handling costs) are predicted by DRT, which requires increasing preference as equal handling costs increase but decreasing preference as equal search costs increase. But as noted throughout, DRT cannot account for other aspects of the present results. A very different picture had emerged in Williams and Fantino (1994) in which all eleven relevant comparisons favored DRT over the rate-maximization view. That study did not manipulate economic context, however. It is clear that different approaches will be differentially effective in accounting for choice

depending upon the variables being manipulated. The present results, taken as a whole, demonstrate that changes in risk sensitivity depend upon both the manner in which budget is manipulated and the choice alternatives presented. Only an integrative approach to risk can reconcile observed differences across budget manipulations and across individual subjects.

It must be acknowledged that none of the theories was specifically devised to address choice behavior in a concurrent-chains procedure utilizing ratio schedules in the initial and terminal components. Thus, it has been necessary to adopt a flexible interpretation of each approach to fit the needs and constraints of the paradigm employed. Ratio schedules were used because they capture the work-intensive nature of active foraging better than strict time-based schedules; the energetic cost of searching for and handling a prey item may be manipulated more precisely with ratio schedules. Although no single theoretical account was compatible with all of the data, nonetheless, data from each of the seven experiments were consistent with at least one of the three accounts considered (Table 1). Changes in risk preferences under manipulation of local contingencies such as schedule requirements were well accounted for by a delay reduction analysis. In addition, changes in global variables like deprivation that were not accompanied by explicit changes in schedule values produced changes in risk behavior consistent with explanations that incorporate sensitivity to resource availability. These studies have found evidence that pigeons' foraging is sensitive to alterations in budget, particularly when sensitivity to budget manipulations produces a dramatic impact on food intake, findings consistent with the behavioral ecology literature. The results suggest that although none of the three approaches assessed in this paper provides a complete account

of choice behavior as a function of economic context, each incorporates principles that play a major role in determining such choices.

The present experiments show that our manipulations produced reliable changes in body weight and that these changes generally correlated with changes in preference for the more variable of the two outcomes. Thus, the results support the view that economic context can affect risky choice when such decisions have a substantial impact on reinforcement.

Review Copy

REFERENCES

- Abarca, N. & Fantino, E. (1982). Choice and foraging. Journal of the Experimental Analysis of Behavior, 38, 117-123.
- Barnard, C. J., & Brown, C. A. J. (1985a). Risk-sensitive foraging in common shrews (*Sorex araneus* L.). Behavioral Ecology and Sociobiology, 16, 161-164.
- Barnard, C. J., & Brown, C. A. J. (1985b). Competition affects risk-sensitivity in foraging shrews. Behavioral Ecology and Sociobiology, 16, 379-382.
- Barnard, C. J., Brown, C. A. J. & Gray-Wallis, J. (1983). Time and energy budgets and competition in the common shrew. Behavioral Ecology and Sociobiology, 13, 13-18.
- Bateson, M., & Kacelnik, A. (1995). Preferences for fixed and variable food sources: Variability in amount and delay. Journal of the Experimental Analysis of Behavior, 63, 313-329.
- Battalio, R. C., Kagel, J. H., & MacDonald, D. N. (1985). Animals' choices over uncertain outcomes: Some initial experimental results. American Economic Review, 75, 599-613.
- Baum, W. M., & Rachlin, H. C. (1969). Choice as time allocation. Journal of the Experimental Analysis of Behavior, 12, 861-874.
- Caraco, T. (1980). On foraging time allocation in a stochastic environment. Ecology, 61, 119-128.
- Caraco, T. (1981). Energy budgets, risk, and foraging preferences in dark-eyed juncos (*Junco hyemalis*). Behavioural Ecology and Sociobiology, 8, 527-531.

- Caraco, T. (1982). Aspects of risk aversion in foraging white-crowned sparrows. Animal Behaviour, 30, 719-727.
- Caraco, T. & Lima, S. L. (1987). Survival, energy budgets and foraging risk. In M. L. Commons, A. Kacelnik & S. Shettleworth (Eds.), Quantitative analyses of behavior, Vol. VI: Foraging, (pp. 1-22). Hilldale, NJ: Lawrence Erlbaum Associates.
- Caraco, T., Martindale, S. & Wittam, T. S. (1980). An empirical demonstration of risk sensitive foraging preferences. Animal Behavior, 28, 820-830.
- Case, D. A. & Fantino, E. (1981). The delay-reduction hypothesis of conditioned reinforcement and punishment: Observing behavior. Journal of the Experimental Analysis of Behavior, 35, 93-108.
- Case, D. A., Nichols, P., and Fantino, E. (1995). Pigeons' preference for variable-interval water reinforcement under widely varied water budgets. Journal of the Experimental Analysis of Behavior, 64, 299-311.
- Duncan, B. & Fantino, E. (1970). The psychological distance to reward. Journal of the Experimental Analysis of Behavior, 14, 73-86.
- Fantino, E. (1967). Preference for mixed versus fixed-ratio schedules. Journal of the Experimental Analysis of Behavior, 10, 35-43.
- Fantino, E. (1969a). Choice and rate of reinforcement. Journal of the Experimental Analysis of Behavior, 12, 723-730.
- Fantino, E. (1969b). Conditioned reinforcement, choice, and the psychological distance to reward. In D. P. Hendry (Ed.), Conditioned Reinforcement, (pp. 163-191). Homewood, IL: Dorsey Press.

- Fantino, E. (1977). Conditioned reinforcement: Choice and information. In W. K. Honig, & J. E. R. Staddon (Eds.), Handbook of operant behavior, (pp. 313-339). Englewood Cliffs, NJ: Prentice-Hall.
- Fantino, E. (1987). Operant conditioning simulations of foraging and the delay-reduction hypothesis. In A. C. Kamil, J. R. Krebs & H. R. Pulliam (Eds.), Foraging Behavior, (pp. 193-214). Englewood Cliffs, NJ: Prentice-Hall.
- Fantino, E. (1988). Conditioned reinforcement and reproductive success. Behavioral and Brain Sciences, 11, 135.
- Fantino, E. & Abarca, N. (1985). Choice, optimal foraging and the delay-reduction hypothesis. Behavioral and Brain Sciences, 8, 315-362.
- Fantino, E. & Case, D. A. (1983). Human observing: Maintained by stimuli correlated with reinforcement but not extinction. Journal of the Experimental Analysis of Behavior, 40, 193-210.
- Fantino, E. & Logan, C. A. (1979). The experimental analysis of behavior: A biological approach. San Francisco: Freeman Press.
- Fantino, E. & Preston, R. A. (1988). Choice and foraging: The effects of accessibility on acceptability. Journal of the Experimental Analysis of Behavior, 50, 395-403.
- Fantino, E., Preston, R. A., & Dunn, R. (1993). Delay-reduction: Current status. Journal of the Experimental Analysis of Behavior, 60, 159-169.
- Fleshler, M., & Hoffman, H. S. (1962). A progression for generating variable-interval schedules. Journal of the Experimental Analysis of Behavior, 5, 529-530.
- Grace, R.C. (1994). A contextual model of concurrent-chains choice. Journal of the Experimental Analysis of Behavior, 61, 113-129.

- Hanson, J. & Green, L. (1989). Foraging decisions: Prey choice by pigeons. Animal Behaviour, 37, 429-443.
- Hastjarjo, T. & Silberberg, A. (1992). Effects of reinforcer delays on choice as a function of income level. Journal of the Experimental Analysis of Behavior, 57, 389-399.
- Hastjarjo, T., Silberberg, A., & Hursh, S. R. (1990). Risky choice as a function of amount and variance in food supply. Journal of the Experimental Analysis of Behavior, 53, 155-161.
- Herrnstein, R. J. (1964). Aperiodicity as a factor in choice. Journal of the Experimental Analysis of Behavior, 7, 179-182.
- Herrnstein, R. J. (1970). On the law of effect. Journal of the experimental Analysis of Behavior, 13, 243-266.
- Houston, A. I. (1991). Risk-sensitive foraging theory and operant psychology. Journal of the Experimental Analysis of Behavior, 56, 585-589.
- Houston, A. I., & McNamara, J. M. (1985). The choice of two prey types that minimizes the probability of starvation. Behavioral Ecology and Sociobiology, 17, 135-141.
- Hursh, S. R. (1978). The economics of daily consumption controlling food- and water-reinforced responding. Journal of the Experimental Analysis of Behavior, 29, 475-491.
- Hursh, S. R. (1980). Economic concepts for the analysis of behavior. Journal of the Experimental Analysis of Behavior, 34, 219-238.
- Ito M. & Asaki, K. (1982). Choice behavior in rats in a concurrent-chains schedule: Amount and delay of reinforcement. Journal of the Experimental Analysis of Behavior, 37, 383-392.

- Kacelnik, A. & Bateson, M. (1996). Risky theories: The effects of variance on foraging decisions. American Zoologist, 36, 402-434.
- Kagel, J. H., Green, L., & Caraco, T. (1986). When foragers discount the future: Constraint or adaptation? Animal Behaviour, 34, 271-283.
- Kagel, J. H., MacDonald, D. N., Battalio, R. C., White, S., & Green, L. (1986). Risk aversion in rats (*Rattus norvegicus*) under varying levels of resource availability. Journal of Comparative Psychology, 100, 95-100.
- Krebs, J. R. (1978). Optimal foraging: Decision rules for predators. In J. R. Krebs & N. B. Davies (Eds.), Behavioural ecology: An evolutionary approach, (pp. 23-63). Blackwell Scientific Publication: Oxford.
- LaFiette, M. H. & Fantino, E. (1989). Responding on concurrent-chains schedules in open and closed economics. Journal of the Experimental Analysis of Behavior, 51, 329-342.
- MacArthur, R. A., & Pianka, E. R. (1966). On optimal use of a patchy environment. American Naturalist, 100, 603-609.
- McNamara, J. M., & Houston, A. I. (1986). The common currency for behavioral decisions. American Naturalist, 127, 358-378.
- McNamara, J. M., & Houston, A. I. (1992). Risk-sensitive foraging: A review of the theory. Bulletin of Mathematical Biology, 54, 355-378.
- McSweeney, F. K. (1992). Rate of reinforcement and session duration as determinants of within-session patterns of responding. Animal Learning and Behavior, 20, 160-169.

- McSweeney, F. K., Roll, J. M., & Cannon, C. B. (1994). The generality of within-session patterns of responding: Rate of reinforcement and session length. Animal Learning and Behavior, 22, 252-266.
- Navarick, D. J. & Fantino, E. (1976). Self-control and general models of choice. Journal of Experimental Psychology: Animal Behavior Processes, 2, 75-87.
- Oaten, A. (1977). Optimal foraging in patches: A case for stochasticity. Theoretical Population Biology, 12, 263-285.
- Plowright, C. M. S., & Shettleworth, S. J. (1991). Time horizon and choice by pigeons in a prey-selection task. Animal Learning and Behavior, 19, 103-112.
- Pyke, G. H., Pulliam, H. R., & Charnov, E. L. (1977). Optimal foraging: A selective review of theory and tests. Quarterly Review of Biology, 52, 137-154.
- Rachlin, H. & Green, L. (1972). Commitment, choice and self-control. Journal of the Experimental Analysis of Behavior, 17, 15-22.
- Real, L. A., & Caraco, T. (1986). Risk and foraging in stochastic environments. Annual Review of Ecology and Systematics, 17, 371-390.
- Schrader, S. M., & Green, L. (1990). The economics of leisure in psychological studies of choice. In L. Green & J. H. Kagel (Eds.), Advances in Behavioral Economics, (pp. 226-252). New Jersey: Ablex Publishing Corp.
- Silberberg, A., Bauman, R. & Hursh, S. (1993). Stock optimizing: Maximizing reinforcers per session on a variable-interval schedule. Journal of the Experimental Analysis of Behavior, 59, 389-399.
- Snyderman, M. (1983). Optimal prey selection: The effects of food deprivation. Behaviour Analysis Letters, 3, 359-369.

Spetch, M. L., & Dunn, R. (1987). Choice between reliable and unreliable outcomes:

Mixed percentage-reinforcement in concurrent-chains. Journal of the Experimental Analysis of Behavior, 47, 57-72.

Stephens, D. W. (1981). The logic of risk-sensitive foraging preferences. Animal Behaviour, 29, 628-629.

Stephens, D. W. & Charnov, E. L. (1982). Optimal foraging: Some simple stochastic models. Behavioral Ecology and Sociobiology, 10, 251-263.

Stephens, D. W., & Krebs, J. R. (1986). Foraging Theory. Princeton, New Jersey: Princeton University Press.

Squires, N. & Fantino, E. (1971). A model of choice in simple concurrent and concurrent-chains schedules. Journal of the Experimental Analysis of Behavior, 15, 27-38.

Williams, W. A. and Fantino, E. (1994). Delay-reduction and optimal foraging: Variable-ratio search in a foraging analogue. Journal of the Experimental Analysis of Behavior, 61, 465-477.

Zabludoff, S. D., Wecker, J., & Caraco, T. (1988). Foraging choice in laboratory rats: Constant vs. variable delay. Behavioural Processes, 16, 95-110.

FOOTNOTE

This research was funded by NSF Grant IBN 9870900 and NIMH Grant MH57127.

Reprints may be obtained from Edmund Fantino, Department of Psychology, University of California at San Diego, La Jolla, California, 92093-0109.

Review Copy

Table 1.

Support provided for the three general theoretical approaches distinguished in this study (delay reduction from psychology; risk sensitivity from behavioral ecology; rate maximization from behavioral economics).

Study	Delay Reduction	Risk Sensitivity	Rate Maximization
Experiment 1A: Session Duration: Equal Mean Outcomes	np	strong	np
Experiment 1B: Session Duration: Unequal Mean Outcomes	np	np	strong
Experiment 1C: Session Duration: Ratio <u>vs.</u> Interval Outcomes	np	np	strong
Experiment 2A: Choice Phase Duration: Equal Mean Outcomes	strong	negative	np
Experiment 2B: Choice Phase Duration: Unequal Mean Outcomes	mixed	np	mixed
Experiment 3A: Handling Phase Duration: Equal Mean Outcomes	strong	strong	np
Experiment 3B: Handling Phase Duration: Unequal Mean Outcomes	mixed	np	mixed

“np” stands for “no clear prediction made.”

FIGURE CAPTIONS

Figure 1. A concurrent-chains diagram. (a) The sequence of events when responses on the left key are reinforced. (b) The analogous sequence of events when responses to the right alternative are reinforced. Equal initial-link schedules, signaled by identical white key lights, arrange access to mutually exclusive terminal links. Responses in the presence of the terminal links, correlated with distinct colored key lights, are reinforced with several seconds' access to grain. Unlike the more typical concurrent-chains procedure, ratio schedules were employed in the initial and terminal links.

Figure 2. Choice proportion (dark bars) and time allocation (hatched bars) for the VR 20 alternative in Experiment 1A averaged across subjects. Session length was decreased from two hours in the positive budget to one-half hour in the negative budget condition. These conditions were replicated using longer initial-link schedule values (concurrent VR 120) to decrease initial preferences, and are represented by Pos. Long and Neg. Long conditions. The last Pos. Long condition was a replication of the positive budget condition with VR 120 initial links. Subjects reliably increased risk-prone preferences as budget declined, consistent with ecology's risk sensitivity.

Figure 3. Choice proportion (dark bars) and time allocation (hatched bars) for the VR 40 (versus FR 20) alternative in Experiment 1B. (a) Subject S1 (top graph) increased preference for the VR 40 schedule in the negative budget condition, which may be explained by delay-reduction theory. (b) Preference measures averaged across subjects S2, S3 and S4 (bottom graph) demonstrated increased risk aversion favoring

the FR 20 alternative as budget worsened, consistent with predictions from a rate-maximizing approach.

Figure 4. Mean choice proportion and time allocation for the VR 50 (versus VI 20 s) alternative in Experiment 1C. As session length, and thus budget, decreased, subjects demonstrated increased preferences for the VR 50 schedule, consistent with a rate-maximization approach.

Figure 5. Mean choice proportion and time allocation for the VR 20 (versus FR 20) alternative in Experiment 2A. Initial-link schedules were increased four-fold from VR 60 to VR 240 in the negative budget condition. Choice behavior declined toward indifference, providing best support for delay-reduction theory.

Figure 6. Average choice proportion and time allocation for the VR 40 (versus FR 20) alternative in Experiment 2B. Initial-link length was increased four-fold in the negative budget condition, from VR 60 to VR 240. The increased preference for the smaller FR 20 reflects partial support for both delay reduction and a rate-maximization approach.

Figure 7. Mean choice proportion and time allocation for the VR X (versus FR X) alternative in Experiment 3A. Terminal-link length (X) was increased five-fold, from 20 to 100, in the negative budget condition. Increased preference for the variable-ratio schedule provides strong support for both risk sensitivity and delay reduction.

Figure 8. Choice proportion and time allocation for the VR 2X (versus FR X) alternative in Experiment 3B. The value of X was increased from 20 to 100 in the negative budget condition. (a) Results from subject G2 indicate an increased preference for the VR 200 schedule over the FR 100 alternative under both negative

budget conditions, consistent with predictions from delay reduction. (b) Aggregate data from subjects G1, G3 and G4 reflect strong preference reversals favoring the constant schedule in the negative budget conditions. Subject G4, however, demonstrated an increased preference for the variable schedule in the first negative budget condition, but a preference reversal in the negative budget reversal condition. Their data provide overall strong support for a rate-maximization approach.