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The effects of magnified effort demands on the response to resource variability

Ari P. Kirshenbaum
The University of Montana

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The effects of magnified effort demands on the response to resource variability

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Dissertation Defense, March 2001

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M.A. University of Montana, 1999

Presented in partial fulfillment of the requirements for a doctorate in philosophy

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3/30/2001

Date
The effects of magnified effort demands on the response to resource variability

Abstract

Reward magnitude and delay to reward were independently manipulated in two separate experiments examining the choice response to the presence of resource variability in rats. A dual-running wheel apparatus was used and the tangential force resistance required to displace both wheels was minimal (50g) for half the subjects, and extreme (120g) for the remaining subjects. Concurrent FI30-s and FI60-s schedules each delivered equivalent amounts of food reward per unit time (i.e. 5 and 10 pellets of food, respectively), and these conditions served as the baseline treatment for all subjects. Once stability of choice performance had occurred during the initial presentation of the baseline treatment, variability in reward magnitude was introduced on the long-delay schedule during phase B; FI60-s administering either 6 or 14 pellets per reinforcing event. The subjects re-experienced the baseline conditions, and initial choice performance was recovered. In phase C, the FI30-s schedule was then altered to deliver either 1 or 9 food pellets, and once stability in choice was achieved, the subjects were again presented with the baseline conditions, ultimately yielding a five phase ABACA design. Subjects in the minimal-response effort group behaved in a risk-indifferent manner while those subjects experiencing higher effort demands were universally risk-prone. A second manipulation was designed to mimic the procedure of the first, with the exception that the delay to reward was manipulated and magnitude was held constant. During phase B, the subjects experienced a mixed-delay interval (35 or 85-s) in place of the FI60-s schedule, and in phase C, a 5 or 55-s mixed interval replaced the FI30-s schedule. Variability in delay to reward produced risk-prone choice in the high-effort, but not the low-effort group. Furthermore, the degree of risk-prone behavior exhibited by the high-response effort groups was remarkably similar across the two different manipulations. Implications for the daily energy budget rule on risk-sensitive foraging are discussed in light of these findings.
I would like to express my deepest appreciation to the members of my committee for their guidance and constructive criticisms. I would especially like to thank Nabil Haddad and Allen Szalda-Petree for all the time and effort that they have spent with me while I was cultivating my philosophies and academic aspirations. They are truly two of the best teachers and finest human beings I have ever had the pleasure of working with and learning from, and I hope that I can continually make them proud by being a positive reflection of this program. Late night poker games spent with Allen and Nabil have been some of my most cherished memories, and most valuable educational experiences of graduate school, despite my inability to maintain a reasonable poker face. I would like to thank my wife, Molly Millwood, for her loving support and editorial contributions to this work. I would also like to express my appreciation for my dog, Nikita, because she is a constant reminder that although I may be an expert in animal behavior, I still have so much to learn. Finally and most importantly, I would like to thank my mother for encouraging my decision to pursue a career in psychology, and for etching her eternal respect and compassion for all animals in my mind and in my heart.
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Introduction

Natural resources may vary seasonally and daily. Therefore, it is reasonable to assume that foraging organisms possess the ability to alter their foraging strategies in order to match changing environmental constraints. The capacity to evaluate changes in resource availability, and to alter strategy accordingly, has an evolutionary utility because it may allow the forager to maximize caloric income under stochastic conditions. Since fitness will ultimately be determined by foraging efficiency, it is also imperative that organisms be sensitive to relative differences between concurrently available food sources.

Resources in nature are patchily distributed, and although some patches yield better overall payoffs than others, the immediate energetic value associated with a patch is a function of the rate of caloric gain within that patch. Rate of gain is relative to encounter rate, and encounter rate is inevitably variable. Thus, foraging strategy may be governed by the degree of variance in encounter rate. Understanding the organism’s response, or sensitivity, to resource variability is the primary focus of Risk-Sensitive Foraging (RSF) Theory.

Practically, a researcher investigating RSF will isolate variability by presenting the subject with a dilemma in which both options provide equivalent reward means, yet each option yields the reward at a different payoff schedule. Risk-sensitive foragers either avoid resource variability (risk averse), or prefer it (risk prone). It is important to note that the terminology of risk-sensitivity does not pertain to how susceptible the organism is to starvation. Rather, “risk averse” and “risk prone” describe the type of choice behavior demonstrated by the organism. Researchers have examined RSF in the context of variance in the quality of food (Tuttle, Wulfson, & Caraco, 1990), the quantity of food (Bateson &
RSF theory is comprised of a constellation of different models that make very different predictions about how foraging organisms respond to resource variability. Only a portion of these models claim that the relationship between energy expenditure and caloric gain influences choice, and there are several incarnations of the daily energy budget rule (Houston, 1991). The daily energy budget rule (DEB) states that when caloric gain exceeds the energy expended during foraging (a positive energy balance), the organism should be averse to risk and prefer a constant food source. If the organism expends more energy than it obtains while foraging (a negative energy balance), then it should prefer risk. When energy stores are low, it seems counterintuitive that an organism would deliberately increase its vulnerability to starvation by behaving in a risk-prone manner; however, a more variable alternative will occasionally lead to a more dense reinforcement schedule in the short run. Risk-prone behavior is advantageous when it occurs in short spurts because given a run of good luck, resources could potentially be acquired more efficiently. Alternatively, any prolonged tendency of an organism to behave in a risk-prone manner is myopic and optimistic; risk-prone foragers often sacrifice long-term gain to capitalize upon short-term consequences.

The DEB makes two basic assumptions: (1) there is a nonlinear relationship between fitness and caloric gain (Bateson & Kacelnik; 1998; Smallwood, 1996; Stephens & Krebs, 1986), and (2) foraging strategy is dependent upon the relationship between the organism’s
requirement for survival and the expected rate of caloric gain from a potential food source. A forager could have recently experienced a very profitable series of rewarding events and currently have a wealth of energy reserves, but behave in a risk-prone manner if confronting a situation where the rate of gain is minimal. Although the DEB rule is heuristic in that it describes the direction of a strategic shift, it does not necessarily provide a prediction of the degree of risk-sensitivity.

Overnight starvation is a rather insidious consequence of insufficient caloric income. For diurnal organisms operating with relatively small energy reserves, the approaching time horizon of nightfall is necessarily met with a surplus of caloric income. High metabolic rate might explain why the strongest support for the influence of the energy budget on choice has come from studies using small avian or mammalian species. Unfortunately, the majority of investigations involving larger mammals have provided contrary results. Experiments including rats on various concurrent time schedules have shown either risk aversion (Logan, 1965; Rider, 1983; Battalio, Kagel, & MacDonald, 1985; Kagel, MacDonald, Battalio, White, & Green, 1986; Hastarjo, Silerberg, & Hursh, 1990) or risk proneness (Logan, 1965; Pubols, 1962; Rider, 1983), independent of the energy state.

Theoretically, the energy budget of a species is not completely determined by current body mass, and this potentially could be one reason why some have failed to demonstrate changes in risk-sensitivity by manipulating resource levels alone. Another factor that may conceal the action of the DEB on risk-sensitivity in rats may be their relatively large energy reserves compared to the smaller mammals that have shown strategic shifts (Kagel et al., 1986). Therefore, it is plausible that the energy reserve serves as a buffer protecting the forager from becoming prone to risk.
Most studies with mammals have attempted to manipulate the energy balance from negative to positive by increasing either supplemental food (Lawes & Perrin, 1995; Zabludoff, Wecker & Caraco, 1988), reward amount obtained per reinforcing event (Barnard & Brown, 1985; Hastarjo et al., 1990; Leventhal, Morell, Morgan, & Perkins, 1959), or session length (Kagel et al., 1986; Hastarjo et al., 1990). One novel preparation used the round-eared elephant shrew (*Macroscelides proboscideus*) and manipulated ambient temperatures and ITI durations (Lawes & Perrin, 1995). Two investigations using grey jays (*Perisoreus canadensis*) manipulated ambient temperatures and increased ratio requirements (Ha, 1991; Ha, Lehner, & Farley, 1990). Although it seems likely that increasing ratio requirements would increase the cost associated with obtaining food, manipulating ratio schedules alone presents a possible confound because increasing the number of responses necessary to complete a trial also increases both the delay to reinforcement and session length (a.k.a. the time horizon). One method of dissecting the response-cost/time confound is to manipulate response-effort requirements, or the effort per response required to obtain food reward. While researchers studying foraging theory have done a thorough job of examining and manipulating delay to reward, magnitude of reward, and response-cost, response-effort has been relatively neglected.

Response-effort and reward-amount manipulations shifted risk-sensitive preferences in accordance with the predictions of the DEB rule (Kirshenbaum, Szalda-Petree, & Haddad, 2000). A dual-running wheel choice apparatus was utilized in which concurrent VI60-s and FI60-s schedules were presented to a group of twelve rats. Most studies employing rats have used minimal effort requirements (for exceptions, see Alling & Polling, 1995; Chelnois, Logue, Sheehy, & Mao, 1999; Collier, Hirsch, Levetsky, & Lesher, 1973; Keuhn, 1981).
Increasing response-effort demands successfully shifted preference towards the variable option. The amount of reward obtained during a single reinforcing event was then increased to compensate for increased response-effort requirements, and as a result, risk-averse tendencies developed (choice shifted toward the FI schedule). Overall, directional shifts toward risk-aversion were created by increasing reward amount within both high and low response-effort conditions; however, high-response effort fostered significant risk-sensitivity, while the low-effort condition did not.

The majority of studies demonstrating risk sensitivity have involved some type of energy-budget manipulation, but inconsistent results have led some researchers to look toward associative learning and psychophysics to provided an alternative explanation of RSF behavior. Kacelnik and his colleagues (Bateson & Kacelnik, 1995; Gibbon, Church, Fairhurst, & Kacelnik, 1988; Kacelnik & Bateson, 1996; Reborda & Kacelnik, 1991) have used an adaptation of Scalar Expectancy Theory (SET, Gibbon, 1977) to account for RSF. SET predicts that when a CS is presented to a subject, it creates a memory trace that decays hyperbolically with time until the presentation of the US. Following a reinforced trial, a value is attributed to the CS-US pair, and SET suggests that a CS-US pair separated by a variable interstimulus interval will be more highly valued than a CS-US pair separated by a fixed interstimulus interval. Therefore, SET predicts risk-proneness when delay is manipulated (for a more thorough explanation of the hyperbolic decay, see Bateson & Kacelnik, 1998).

The second important contribution of SET posits that the value remembered for a fixed time interval or amount is represented as a normal distribution with a mean centered around the experienced delay or amount, and a standard deviation relative to the mean. The representation of a variable amount or delay is fabricated from a sum of each normal
distribution based upon prior rewarding events. The shape of the summed distributions will be positively skewed because the represented distribution for a more immediate or a smaller reward has a condensed standard deviation (and thus a higher probability density in memory) than the memory for a more delayed or larger reward. Thus, it is the direction of the skew that is predictive of the direction of risk sensitivity: (1) Variability in delay should be preferred because the variable option is expected to yield shorter delays without compromising long-term gains, and (2) Variability in amount, on the other hand, should be avoided because the expected probability of the smaller amount reoccurring is much higher than the probability of a larger amount reoccurring. Therefore, SET predicts choice preference (either risk-prone or averse) as a result of whether delay or mean amount is experimentally manipulated (Bateson & Kacelnik, 1995, 1997, 1998; Kacelnik & Bateson, 1996).

Bateson and Kacelnik (1995) found evidence for SET using starlings (Sturnus vulgaris). The results showed that the subjects preferred variable delays when reinforcement amounts were equivalent, and variance in amount was avoided when the delays were the same. Furthermore, the researchers have demonstrated that starlings behave in a risk-prone manner when delay is manipulated, even when the rewards obtained are increased. Counter to the predictions of a DEB rule, no effect of energy budget on performance occurred (Kacelnik & Bateson, 1997).

The present experiment was designed to evaluate the assumptions of both the DEB rule and SET by manipulating reward magnitude and delay to reward independently. A dual-running wheel apparatus was utilized to examine the choice behavior of rats. The baseline phase for all experimental groups includes the presentation of concurrent FI30-s and FI60-s schedules, each providing 5 and 10 (respectively) units of reward per reinforcing event. The
reward magnitude manipulation consisted of introducing variability in amount on the long-delay schedule (FI60-s) during phase two and introducing variability on the short-delay (FI30-s) schedule in the fourth phase. All subjects re-experienced the baseline conditions after each introduction of variance, yielding a 5 phase ABACA design. In order to better assess whether the DEB rule is operating under these circumstances, half of the subjects experienced a greater level of force resistance in the running wheels throughout the entire duration of the study.

The delay to reward manipulation mimicked the same procedure as stated above, but introduced variability in delay (using a mixed-interval schedule) during phases two and four. Again, half the subjects in the second manipulation experienced magnified-effort requirements throughout all treatment conditions. Both manipulations were conducted simultaneously and are therefore analyzed and discussed simultaneously.

It was expected that baseline choice performance would differ significantly from random performance because delay discounting has been a supported and powerful phenomenon (Benson & Stephens, 1996; Fantino, 1987; 1969; Green, Fry & Myerson, 1994; Kagel, Green, & Caraco, 1986; Myerson & Green, 1995). When variability is introduced, sensitivity to risk was assessed by the direction of the shift away from baseline responding. The predictions of the DEB rule are completely based upon the differential response-effort requirements each group experiences. Because of the minimal caloric cost associated with obtaining food in the minimal-response effort conditions, these groups should express a lesser degree of risk-prone behavior than the magnified-response effort groups. Although SET predicts the subjects will behave in a risk-prone manner when delay is introduced, the reward magnitude manipulation should reveal constant risk aversion. According to the predictions
of SET, response-effort manipulations were not expected to result in significant differences between groups.

Methods

Subjects

Twenty-four naïve, male Sprague-Dawley rats (a laboratory strain of *Rattus Rattus*), approximately 90 days old at the beginning of the experiment were used. Upon arrival at the laboratory the rats were provided with ad-lib water and food for fourteen days. They were maintained at or above approximately 85% of their pre-deprivation individual body mass for the duration of the experiment. Water was continuously available in the home cages and in the experimental chambers. The subjects were provided with food supplements 1 hr following wheel-run training sessions. During the experimental sessions, the animals obtained 100% of their daily food income within the experimental chamber.

Apparatus

Two Wahman running wheels have been modified to allow computer monitoring of wheel movement. This was accomplished through a computer mouse attachment to the wheel axle via a system of reduction pulleys (Petree, Haddad, & Berger, 1992; Szalda-Petree, Karkowski, Brooks, & Haddad, 1994). Response effort was manipulated by applying pressure, via an adjusting tensioning bar, on a 7.62-cm aluminum disc approximately 1.3 cm thick attached to the wheel axle protruding from the non-movable side of the wheel (Haddad, Szalda-Petree, Karkowski, Foss, & Berger, 1994). Please refer to Kirshenbaum, Szalda-Petree, and Haddad (2000) for an illustration of the apparatus.

A Lexan choice box (23 cm X 23 cm X 23 cm) was placed between the two wheels and linked to each wheel via a 12 cm-long tunnel 8 cm in diameter. Reinforcers were
delivered to the food cup located along the forward wall of the choice box, equidistant from both running wheel entrances (see figure 1). Small 2.5 mV white lamps (1 cm in diameter X 2 cm long) were located directly above the entrances to each tunnel. Each pair of wheels and their accompanying choice box was housed in a large (0.6 m X 0.6 m X 1.2 m) sound-attenuated cabinet with a blower to provide ventilation and masking noise. A clear plastic water bottle was located on the ceiling of the choice box with its curved licket protruding into the choice box just above the food cup.

Procedure

All subjects first received magazine training in which each subject was confined to the Lexan choice box where pellets were delivered on a VT 25-s schedule for five 15-min sessions. Wheel-run training was conducted using a FR schedule that was gradually increased from 5 to 300 cm. Both wheels were made available at this time. Following eight 30-min sessions of double-wheel run training, a few of the subjects were exhibiting a side-bias. Therefore, a single 30-min bias relief session was used in which only one of the two running wheels was available for those subjects expressing a bias.

To control for a possible position bias, all the schedules throughout the study were pseudo-randomly assigned to the running wheels such that no running wheel was associated with a given schedule for more than two consecutive sessions. A 2.5 mV white lamp signaled either the short-delay (30-s) interval schedule or the long-delay (60-s) interval schedule for all the experimental groups. Use of the signal lights was counterbalanced, resulting in the lamp signaling the short-delay schedule for half the subjects in each group and the long-delay schedule for the remaining subjects. The signal lamp remained on for the entire session.

An experimental trial was initiated when any running (1 cm or greater) was detected.
on either schedule/wheel and movement of the wheel initiated the interval schedule. The alternate schedule/wheel was then made unavailable by engaging a braking system, until reinforcement was obtained from the selected wheel. The distance requirement (ratio length required to complete the interval schedules) for reinforcement under both schedules was 60 cm (1/2 rotation of the wheel). Once a schedule/trial was completed, the wheel/schedule was then braked while the food reward was delivered in the choice box. The braking of the wheel was intended to serve as a secondary signal that food had become available. The food delivery system delivered a 45 mg Noyes food pellet at a rate of approximately one pellet per second. Following food delivery, both wheel/schedules were again made available. In the event that only one food pellet was delivered, both wheels/schedules were locked in place for 5-s.

Each experimental session lasted for 36 trials; 6 of these were forced-choice trials. The forced-choice procedure included three pairs of trials inter-dispersed within session (trials 1,2; 13,14; and 25,26). During a forced-choice trial, one wheel was braked from the beginning of the trial, thus leaving the other operable. The succeeding trial then forced the subject into the opposite wheel/schedule. The forced-choice trials were eliminated from the data during analysis.

Throughout the duration of the investigation, choice was determined by the number of responses emitted on two concurrent interval schedules. The twenty-four subjects were separated between the two manipulations, with twelve subjects in each. Within each manipulation, the subjects were again divided into two groups of six; one low-response effort group and one high-response effort group. For the low-response effort groups, 50 g of tangential force resistance was required to displace the running wheel throughout the experiment. The high-response effort groups experienced 120 g resistance, but they were
presented with the exact same treatments in the same order as their low-response effort counterparts. Whether it be reward magnitude or delay to reward that was manipulated, variability was introduced during the third and fourth phases (i.e. phases B and C; see Table 1). Each phase continued until stable choices were obtained. Stability was defined as no significantly upward or downward trend in choices across three consecutive sessions.

Table 1. For the reward magnitude manipulation, the number of food pellets delivered per experimental phase is listed beneath the appropriate interval schedules. Since reinforcer magnitude was held constant in the second manipulation, the interval schedule is listed beneath the appropriate reinforcer amount. The average number of 30-s interval choices (out of a total possible 30 choices) for each phase are also listed below. Standard errors are specified within the parentheses.

**Reward magnitude manipulation**

<table>
<thead>
<tr>
<th>Phase</th>
<th>FI30-s</th>
<th>FI60-s</th>
<th>Low effort: 50g</th>
<th>High effort: 120g</th>
</tr>
</thead>
<tbody>
<tr>
<td>A-I</td>
<td>5</td>
<td>10</td>
<td>18.61 (.34)</td>
<td>18.28 (1.07)</td>
</tr>
<tr>
<td>B</td>
<td>5</td>
<td>6 or 14</td>
<td>17.22 (.45)</td>
<td>12.67 (.64)*</td>
</tr>
<tr>
<td>A-II</td>
<td>5</td>
<td>10</td>
<td>18.00 (.38)</td>
<td>19.22 (.86)</td>
</tr>
<tr>
<td>C</td>
<td>1 or 9</td>
<td>10</td>
<td>18.61 (.53)</td>
<td>22.89 (1.08)*</td>
</tr>
<tr>
<td>A-III</td>
<td>5</td>
<td>10</td>
<td>18.61 (.43)</td>
<td>17.94 (.70)</td>
</tr>
</tbody>
</table>

**Delay to reward manipulation**

<table>
<thead>
<tr>
<th>Phase</th>
<th>5 pellets</th>
<th>10 pellets</th>
<th>Low effort: 50g</th>
<th>High effort: 120g</th>
</tr>
</thead>
<tbody>
<tr>
<td>A-I</td>
<td>FI30-s</td>
<td>FI60-s</td>
<td>18.61 (.4)</td>
<td>18.95 (.82)</td>
</tr>
<tr>
<td>B</td>
<td>FI30-s</td>
<td>MI{35 or 85-s}</td>
<td>17.11 (.7)</td>
<td>12.83 (.93)*</td>
</tr>
<tr>
<td>A-II</td>
<td>FI30-s</td>
<td>FI60-s</td>
<td>18.22 (.46)</td>
<td>18.83 (.41)</td>
</tr>
<tr>
<td>C</td>
<td>MI{5 or 55-s}</td>
<td>FI60-s</td>
<td>17.95 (.59)</td>
<td>22.61 (1.35)*</td>
</tr>
<tr>
<td>A-III</td>
<td>FI30-s</td>
<td>FI60-s</td>
<td>18.61 (.45)</td>
<td>17.78 (.75)</td>
</tr>
</tbody>
</table>

**Note.** n = 6 for each group, * indicates risk-prone choice.
Results

For each phase, the number of choices on the short-delay (i.e. the FI-30-s schedule, and the MI30-s schedule for groups experiencing variability in delay during phase C only) interval option were averaged across the last three sessions yielding a mean choice for each subject at each phase. A repeated measures ANOVA performed on mean choices obtained from each group across the three baseline conditions (phases A-I, A-II, and A-III) revealed no significant differences in choice performance for any group, all Fs (2, 10) < 0.912, all ps > .05. Therefore, the choice data obtained from each baseline presentation has been collapsed. A 2 (response-effort) X 2 (manipulation) X 3 (phase) mixed design ANOVA was performed comparing the number of short-delayed interval choice responses. The ANOVA revealed a significant response-effort main effect, $F (2, 40) = 54.165$, $p < .05$, and a significant response-effort X phase interaction, $F (2, 40) = 34.384$, $p < .05$. Post hoc analysis, using Tukey's HSD, revealed that all pairwise comparisons were significantly different for both high effort groups (all ps < .05), but no differences were obtained for pairwise comparisons for the low-response effort groups. For both manipulations, the high-response effort groups favored variability when it was introduced during phases B and C. Alternatively, the low-response effort groups failed to alter choice performance in the presence of variability. The average number of short-delay choices per experimental phase and per experimental group is listed above in Table 1. Figure 1 illustrates short-delay choices per group across all experimental phases.

During phase B, choice performance for the high-response effort groups significantly shifted away from baseline in the direction of the variable alternative. Although this adjustment in choice could be considered to be indicative of a shift toward random...
performance, high-effort choice in this phase significantly deviates from chance performance ($t$'s (11) > 4.157, ps < .05).

Figure 1. Short-delay (30-s) interval choice performance across experimental phases.
Pre and post-session body mass was documented throughout the length of the study (see Figure 2). Given that the subjects received 100% of their total daily food income within the experimental chamber, the high-response effort group was expected to demonstrate a lesser pre and post-session body mass than the low-response effort groups (see Table 2). Pre and post-session body mass was averaged over the final three sessions of each phase for each subject. The total averaged pre session body mass of the low-response effort groups was compared to the averaged pre-session body mass of the high-response effort groups, and although differences did exist, they were not significant ($t(22) = .626, p > .05$). Furthermore, the same analysis was conducted comparing the post-session body mass between the low and high-response effort groups, but again the differences failed to reach significance ($t(22) = .790, p > .05$).

Figure 2. Average pre and post-session body mass, in grams, throughout the duration of the experiment. The dashed line represents the average 85% body mass of all subjects, the blue lines represent the averaged body mass of the high-response-effort groups, and the red, the averaged body mass of the low-response-effort groups.
Table 2. Total averaged pre and post-session body mass percentages. Response latencies and distance traveled per trial are also listed below.

<table>
<thead>
<tr>
<th>Group</th>
<th>Pre-session</th>
<th>Post-session</th>
<th>Response latency</th>
<th>Distance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Avg. low-response effort groups</td>
<td>81.96%</td>
<td>89.58%</td>
<td>3.53-s</td>
<td>548.46 cm</td>
</tr>
<tr>
<td>Avg. high-response effort groups</td>
<td>80.26%</td>
<td>88.26%</td>
<td>4.03-s</td>
<td>505.32 cm</td>
</tr>
</tbody>
</table>

Using data obtained from the final session of each phase, each subject’s average latency to complete a response was analyzed. A 2 (response-effort) X 5 (phase) ANOVA was performed, and no phase main effect was revealed, $F(4, 88) = 1.099$, $p > .05$, nor was there a response-effort X phase interaction, $F(4, 88) = 1.623$, $p > .05$. Thus, increased response effort failed to produce a significantly longer response latency (see Table 2).

The pattern of choices across the session was analyzed for those subjects exhibiting risk-prone behavior. The final session from phases B and C was divided into thirds in order to assess approximately when, during the session, risk-prone behavior became dominant, and 2 (phase) X 3 (block) ANOVAs were performed using the number of risk-prone choices per block. No significant differences were discovered for either high-response effort group, $F$s (2,20) > 3.182, $p$s > .06. Thus, the subjects distributed their risk-prone choices evenly throughout the final sessions of phases B and C (see Figure 3).

The increased response-effort requirement was also expected to create a reduction in overall running distance per trial, but differences across phases were not expected to exist. Again, averaging the final three sessions of each phase and examining the distance run per trial on the short-delay interval, the baseline treatments were compared using a repeated measure ANOVA. Significant differences were discovered across baseline treatments, $F(2,46) = 11.243$, $p < .05$. A 2 (response effort) X 2 (schedule manipulation) X 5 (phase) ANOVA
was performed revealing a main effect of phase, $F(4, 80) = 31.258, p < .05$, and a significant phase X response-effort interaction, $F(4, 80) = 5.883, p < .05$). No phase X experiment interaction was discovered, $F(4, 80) = 1.358, p > .05$, nor was there a significant phase X response effort X schedule manipulation interaction, $F(4, 80) = 1.542, p > .05$, see figure 4. Therefore, no conclusions can be made from the distance per trial data.

Figure 3. Average number of risk-prone choice emitted (with standard error bars) during the final session of phases B and C.
Discussion

Each group responded in a similar fashion to the absence of variability during the baseline treatments. Baseline responding was characterized by a slight short-delay (FI30-s interval) preference, and choice performance did not shift across the three recurrent presentations of the baseline conditions. The choice behavior exhibited during the baseline conditions is especially interesting because the long-delay (FI60-s) schedule would have provided the maximum caloric gain in the long run; however, this myopic behavioral tendency is not surprising. Given that each schedule terminated in the delivery of the same number of food pellets per unit time, it seems reasonable to assume that the value of the reward associated with the longer delay is discounted as a function of the duration of the longer delay. It is possible that the subjects were intentionally minimizing the amount of time they were spending inside the experimental chambers by choosing the interval of the shorter...
duration, but this hypothesis is extremely unlikely given that the subjects were obtaining all of their caloric income during the experimental sessions.

When variability in reward magnitude was introduced during phase B, the high-response effort group responded in a risk-prone fashion, shifting choice performance away from baseline in the direction of the variable FI60-s interval. When variability in reward magnitude was associated with the FI30-s schedule during phase C, the high-response effort group again shifted their performance toward the variable alternative. The low-response effort group failed to alter choice performance to a significant degree whenever reward magnitude was made variable. The relative insensitivity to resource variability displayed by the low-effort group under these circumstances is not representative of a lack of discrimination; if it were, the data would reflect random performance (or choice equally distributed across both schedules) when they clearly do not. The relative risk-indifference of the low-response effort group is perplexing, but not unexplainable.

When the delay to reward was manipulated, a similar pattern is evidenced by the two response-effort groups. Again, the high-response effort group behaved in a clear risk-prone fashion, shifting their performance toward the mixed-interval in phases B and C. Also consistent with the findings from the magnitude manipulation, the low-response effort group responded to variability in delay to reward in a risk-indifferent manner.

The results display a significant difference between response-effort groups, with the high-response effort groups each favoring variability to the same degree. Interestingly, the differences between low and high response-effort groups became evident only when variability was introduced. The occurrence of risk-prone behavior under these circumstances strongly supports the predictions of the DEB rule. Moreover, these results suggest that the increased
cost associated with high-response effort successfully impacts the relationship between caloric gain and energy expenditure, thereby increasing the likelihood that risk-prone behavior will prevail. The disparities in foraging strategy between high and low-effort groups cannot be readily attributed to any factor other than response-effort; differences in body mass and response latencies between effort groups were not significantly different. Extreme-response effort conditions produce risk-sensitivity more reliably than minimal-response effort conditions, and these results are entirely consonant with those reported by Kirshenbaum, Szalda-Petree, and Haddad (2000).

SET predicts that variability in reward amount ought to be avoided. Thus, the reward magnitude manipulation failed to generate any results congruent with SET. The results from the reward delay manipulation are not entirely contrary to the predictions of SET; however, SET fails to provide an explanation for why the disparity between response-effort groups exists when the delays inherent to each schedule are not significantly different. Furthermore, SET predicts that risk-prone behavior ought to be stronger when variability in delay is associated with the short-delay interval than when it is associated with the long-delay interval. Clearly the data do not support such a hypothesis.

Perhaps the most interesting discovery was that the high-response effort groups treated variability in the same fashion; variability in reward magnitude led to precisely the same extent of risk-prone behavior that was exhibited by the subjects confronting variability in delay to reward. Given these results, one might conclude that the degree of variability associated with each schedule was the most important factor governing the degree of risk-prone choice. However, the breadth of variability was not manipulated by the present design. Hamm and Shettleworth (1987) manipulated reward magnitude and discovered increasing risk
aversion when the variance of the risky option was increased. This study is potentially
confounded because along with increasing magnitude variability of the risky option, the
researchers also created a mixed-interval schedule. A number of empirical investigations have
demonstrated augmenting risk aversion as variability increases (e.g. Hastjarjo et al., 1990;
Staddon & Innis, 1966). Alternatively, some have shown that an increase in the variability of
the risky option is associated with increasing risk-prone behavior (Zabludoff et al., 1988).
Barnard, Brown, Houston, & McNamara (1985) found that shrews were risk-prone when
variance was low and means were high, but risk-indifferent when the mean and variance were
both high. Several investigations have demonstrated a tradeoff between reward mean and
variance (Battalio et al. 1985; Caraco & Lima, 1985; Caraco, Martindale, & Whittam, 1980;
and Stephens & Paton, 1986). Overall, past investigations have demonstrated that the degree
of variability is a mediating factor governing the extent of risk sensitivity, but it is debatable
whether the results of the present study can be taken to support this conclusion. Suggestions
for future research include comparing the effects of reward and delay when both are equally
variant versus when they are not.

Extremely small variance in the risky option produces indifference (Caraco, 1981),
notwithstanding that it is difficult to separate indifference from a lack of discrimination on
most occasions. Risk-sensitivity requires that the forager be able to discriminate between the
schedules; the more likely an organism is to discriminate between two options, the more likely
it is that the organism will be sensitive to risk (Caraco, 1983). However, discrimination cannot
be influencing the extent of sensitivity to risk unto itself. If this were true, the low and high-
effort groups would have performed similarly, and/or the choice performance exhibited by the
low-effort groups would have deteriorated during the presentations of variability. It is
hypothesized that the energetic stress experienced by the high-effort groups does not promote
discrimination per se, but rather forces the subjects to alter foraging strategy to meet
magnified environmental demands.

The number of free-choice trials within a session may also be limiting the degree of
risk-prone behavior. If this were the case, then there should be a significant increase in the
number of risk-prone choices from the beginning to the end of the session. The analysis of
within-session choice responding does not demonstrate any pattern of choice; the subjects
were consistently sampling from the non-preferred schedule throughout the duration of the
session and distributing their risk-prone choices evenly. Sampling behavior may be limiting
the degree of risk-sensitivity, but it is not clear how sampling behavior can be removed from
the forager's behavioral repertoire. Caraco (1981) has suggested that sampling behavior is
beneficial to the organism because it allows the forager to make moment-by-moment
assessments in order to determine the relative values of the options available.

Both options available to the rats, whether variable or not, provided the same amount
of food per unit time. When variability was introduced, the variable option was programmed
to deliver food with an arithmetic mean equivalent to the non-variable option. Thus, the
likelihood that the variable option would allow the subject to molar maximize was equivalent
to the probability that the variable option would return less caloric gain than the constant
option. Under these circumstances, risk-prone behavior could result in short-term caloric
maximization given a run of good luck, but not long term maximization. Figure 2 illustrates
that while there were infinitesimal fluctuations in post-session body mass, no monotonic
increase or decrease in body mass was evident during phases B and C. The tools used to
assess caloric gain in this experiment did not give the resolution necessary to assess the
momentary utility of risk-prone behavior. It is difficult to assess the fitness value that risk-prone behavior serves in any experiment, but this does not necessarily imply a weakness of the DEB rule. The DEB rule does not suggest that the direction of risk-sensitivity is determined by the ability of the forager to detect the utility of a foraging option, only that the forager is able to detect resource variability.

It can be suggested that magnified response-effort requirements negated the buffering capability of the forager's energy reserve, thus unveiling risk-prone behavior in rats. The potential of a food source to provide adequate energetic gain is compromised by magnified effort demands, thereby making it necessary for an organism to shift foraging strategy when resources become variable. Past research manipulating response effort and reward amount suggests that these factors lie on the same continuum in terms of risk sensitivity (Kirshenbaum et al., 2000); however, it is not clear whether these components are geometrically interchangeable. Future research should target the relationship between caloric income and response-effort in the absence of resource variability. The daily energy budget rule, although parsimonious and heuristic in design, served as the best predictor of the direction of risk-sensitivity in this experiment.
References


Full Literature Review

If foraging strategy is dependent upon the economic relationship between energy expenditure and caloric gain, then it is feasible that the forager may alter its strategy as energetic demand increases and the rate of gain abates. The ability to alter foraging strategy in order to match changing environmental constraints has an evolutionary utility because it allows the organism to maximize fitness under varying degrees resource availability. On the other hand, it is also plausible that foraging engages a single cognitive process that is inflexible. If this is the case, then the choice for one food source over another is completely determined by the perceptual presentation of the foraging alternatives.

In general, molar maximization models of choice behavior suggest that the forager should prefer a food source that provides the maximum amount of food per unit time. Optimal foraging theory (Hanson, 1987; Krebs, 1978, Pyke, 1984) assumes that organisms will employ foraging strategies that minimize energy expenditure and maximize caloric intake in order to exploit the long-term rate of caloric gain. If the ratio between caloric intake and energy expenditure equals one, then the organism has reached an ecological bliss point. Nature, very much like the laboratory, fails to provide the means necessary to meet bliss. Hanson (1987) has provided six basic assumptions of optimal foraging theory:

1. Searching for and handling prey are mutually exclusive activities.
2. Individual prey are encountered randomly and sequentially.
3. Prey types are clearly discriminable and instantly recognizable.
4. Prey are categorized according to energy gain (E) and handling cost (h).
5. The value of a prey type to the forager is determined by energy gain per unit of handling cost, i.e. E/h.
6. The forager has an accurate knowledge of environmental parameters, i.e., E, h, search costs, encounter rates, etc.
In order to forage optimally, the organism must have accurate information on the availability of food resources where availability is determined by the delay to rewarding event, reward amount (usually density), and the degree of variability in delay and amount. *Risk-sensitive foraging theory* specifically targets the organism’s response to resource variability. Practically, a researcher investigating risk-sensitive foraging (RSF) will isolate variability by presenting the subject with a dilemma in which both options provide equivalent reward means, yet each option yields the reward at a different payoff schedule. Risk-sensitive foragers either avoid resource variability (*risk averse*), or prefer it (*risk prone*). It is important to note that the terminology of risk-sensitivity does not pertain to how susceptible the organism is to starvation; “risk averse” and “risk prone” describe the type of choice behavior demonstrated by the organism.

Optimal foraging theory predicts for risk-indifference or risk-aversion when two appetitive options yield equivalent reward amounts per unit time; however, there are many instances of risk-prone behavior in the literature (Bateson & Kacelnik, 1998). The tendency to behave in a risk-prone manner is myopic and is therefore contradictory to the long-term rate of gain assumption of optimal foraging theory. Researchers have examined RSF in the context of variance in the quality of food (Tuttle, Wulfson, & Caraco, 1990), the quantity of food (Bateson & Kacelnik, 1995; Barnard & Brown, 1985; Caraco, 1981, 1983; Carter & Dill, 1990; Hamm & Shettleworth, 1987, Hastajaro, Silerberg, & Hursh, 1990; Wunderle, Castro, & Fetcher, 1987), and the delay to the next rewarding event (Bateson & Kacelnik, 1995; 1997).

Risk-sensitive foraging theory is comprised of a constellation of different models that make very different predictions about how foraging organisms respond to variability. In
general, researchers investigating risk can be segregated into one of two models: functional or mechanical models. Coincidentally, the models are also discipline specific with behavior ecologists using a functional approach and psychologists favoring a mechanistic approach.

Functional Models

Jensen's inequality

Stephens (1981) demonstrated that the relationship between energy gain and fitness is non-linear. It was this first basic conclusion that kindled interest in how an organism would respond to variability. The fundamental assumption of RSF theory begins with the function $y = f(x)$, where $y$ represents fitness and $x$ the amount of food obtained from a foraging option. This function can be applied to any foraging situation so that the units of fitness ($y$) can be determined given any income of sustenance ($x$). One of the methodological requirements of RSF research is that one of two food source alternatives must be variable, therefore the function stated above must be modified to account for such variability.

The fitness value of a foraging option can be derived by averaging the income of a variable option ($E\{x\}$) prior to the application of the function, written as $E\{y\} = f(E\{x\})$. The average value of a foraging option can also be evaluated following the assessment of the function of $x$, so that $E\{y\} = E\{f(x)\}$. If the function of $x$ was perfectly linear, there would be no argument whether the averaging of values occurs prior to or after the assessment of the function because each formula would lead to the same outcome, or $f(E\{x\}) = E(f\{x\})$. In this instance the utility of a foraging option, or the fitness obtained from a unit of $x$, increases in a uniform manner as income obtained increases.

Jensen's inequality specifically states that $f(E\{x\})$ may not equal $E(f\{x\})$, therefore the relationship between fitness and income is nonlinear. If the utility function between income
and fitness is negatively accelerating, then obtaining \( f(E(x)) \) will yield a higher value than \( E(f(x)) \). Furthermore, if the fitness utility of a food source decreases with increasing income (as depicted by the negatively accelerated curve, figure 1), then a variable or risky food source would provide no benefit to the forager and risk-aversion would occur, \( E(f(x)) < f(E(x)) \). The opposite is true if the utility function is positively accelerating (Bateson & Kacelnik, 1998; Smallwood, 1996; Stephens & Krebs, 1986).

**Figure 1.**

Fitness is plotted on the y-axis and income on the x-axis. If \( y = f(x) \) is negatively accelerating, then the utility of a food source decreases as income increases. In such a situation, the constant food source (\( \alpha \)) provides a higher return on average than the variable option (\( \beta \)). A foraging strategy that exploits a variable reward is profitable only when the fitness utility is positively accelerating.

**Energy budget models**

Jensen’s inequality has provided the foundation for models of RSF that focus on the functional relationship between caloric gain and Darwinian fitness. Functional models suggest that approaching starvation may induce alterations in foraging strategy. Optimal foraging theory fails to account for risk-proneness because it assumes that the forager will maximize the long-term rate of gain; risk-sensitive foragers often sacrifice long-term gain to capitalize upon short-term consequences.
Overnight starvation is a rather insidious consequence of insufficient caloric income. For diurnal organisms operating with relatively small energy reserves, the approaching time horizon of nightfall is necessarily met with a surplus of caloric income. In order to meet caloric demands that have not been met, RSF theory suggests that these organisms will alter their strategy in order to maximize the probability of survival.

There are several incarnations of the daily energy budget rule (Houston, 1991). The daily energy budget rule (DEB) states that when caloric gain exceeds the energy expended during foraging (a positive energy balance), the organism should be averse to risk and prefer a constant food source. If the organism expends more energy than it obtains while foraging (a negative energy balance), then it should prefer to take a gamble and choose a variable option over a constant one. When energy stores are low, it seems counterintuitive that an organism would deliberately increase its vulnerability to starvation by behaving in a risk-prone manner; however, a more variable alternative will occasionally lead to a more dense reinforcement schedule in the short run. Theoretically, a run of good luck could solve the crisis of a negative energy balance quickly and replenish energy reserves.

Stephens’s (1981) model of the energy budget accounts for more than just immediate caloric gain and energy expenditure. Choice is determined by a delicate balance between initial energy reserves ($x$), time available for foraging ($T$), mean rate of income ($\mu$), and the organism’s caloric requirement for survival ($R$). Using these terms, the energy budget is positive if

$$x + \mu T > R,$$

and negative if

$$x + \mu T < R.$$

Researchers have argued that foraging animals may formulate a set of expectations regarding future returns that are based upon past experience. The z-score model (Stephens
& Charnov, 1982; Stephens & Paton, 1986) posits that the forager forms a cost-benefit expectation of an available food source in order to minimize energetic shortfall. The z-score model can be mathematically illustrated as:

\[ z = \frac{R - \mu}{\sigma} \]

where \( z \) is the indifference constant, \( \mu \) is the mean food reward, \( \sigma \) is the standard deviation of food reward and \( R \) is the amount of food that the forager requires for survival (Stephens & Paton, 1986). This model suggests that a forager will sacrifice mean amount in order to avoid variance, but mean and variance are "imperfect substitutes." Caraco and Lima (1985) have added that mean is substituted for variance at a decreasing rate so that in order to maintain risk-indifference, increasing variance needs to be met with an abating increase in reward. Thus, there is a curvilinear relationship between variance and mean that is negatively accelerating.

Stephens and Paton (1986) placed six wild-caught Rufus hummingbirds (Selaphorous rufus) in a free choice preparation in which one option yielded a high mean amount with a high variance, whereas the other yielded a low mean amount with a low variance. Risk-prone tendencies were observed in the low-line treatment, and preferences shifted to the more constant alternative (the low-variance condition) when reward amount was increased in the high-line treatment. Stephens and Paton presented these results as support for the z-score model.

Two classic investigations support a general DEB rule by demonstrating increasing risk-prone choice behavior as a result of depleting energy reserves. In two experiments with dark-eyed juncos (Junco heymalis), Caraco (1981) found that the constant reward was
preferred when food intake exceeded energy expenditure and the variable reward was preferred when the subject's energy budget was negative. Barnard and Brown (1985) tested risk sensitivity in common shrews (*Sorex araneus*) using concurrent feeding sites, one fixed amount and one variable. The transition from risk-aversion to risk-proneness occurred when the shrews were fed an amount that was below their physiological requirement.

The DEB makes two basic assumptions: (1) there is a nonlinear relationship between fitness and caloric gain (Bateson & Kacelnik; 1998; Smallwood, 1996; Stephens & Krebs, 1986), and (2) foraging strategy is dependent upon the relationship between the organism's requirement for survival and the *expected rate of caloric gain from a potential food source*. A forager could have recently experienced a very profitable series of rewarding events and currently have a wealth of energy reserves, but behave in a risk-prone manner if confronting a situation where the rate of gain is minimal. Although the DEB rule is heuristic in that it eloquently describes the direction of a strategic shift, it does not provide a prediction of the degree of risk-sensitivity. The rule has only occasionally been experimentally validated (Barnard & Brown, 1985; Caraco, Martindal, & Whittam, 1980, Caraco, 1981; 1983; Stephens & Paton, 1986).

The strongest support for the influence of the energy budget on choice has come from studies using small avian or mammalian species, but the majority of investigations involving larger mammals have provided contrary results. Experiments including rats on various concurrent time schedules have shown either risk aversion (Logan, 1965; Rider, 1983; Battalio, Kagel, & MacDonald, 1985; Kagel, MacDonald, Battalio, White, & Green, 1986; Hastarjo, Silerberg, & Hursh, 1990) or risk proneness (Logan, 1965; Pubols, 1962; Rider, 1983), independent of the energy state. Zabludoff, Wecker, and Caraco (1988) found
evidence of risk sensitivity when body mass was manipulated below 85% ad-lib mass, but as Kacelnik and Bateson (1996) have argued, the data obtained were confounded by an increase in the variability of the risky option as body mass decreased. Theoretically, the energy budget of a species is not completely determined by current body mass, and this potentially could be one reason why some have failed to demonstrate changes in risk-sensitivity by manipulating resource levels alone. Another factor that may conceal the action of the DEB on risk-sensitivity in rats may be their relatively large energy reserves compared to the smaller mammals that have shown strategic shifts (Kagel, MacDonald, Battalio, White, & Green, 1986).

Most studies with mammals have attempted to manipulate the energy balance from negative to positive by increasing either supplemental food (Lawes & Perrin, 1995; Zabludoff et al., 1988), reward amount obtained per reinforcing event (Barnard & Brown, 1985; Hastarjo et al., 1990; Leventhal, Morell, Morgan, & Perkins, 1959), or session length (Kagel et al., 1986; Hastarjo et al., 1990). One novel preparation used the round-eared elephant shrew (*Macroscelides proboscideus*) and manipulated ambient temperatures and ITI durations (Lawes & Perrin, 1995). Two investigations using grey jays (*Perisoreus canadensis*) manipulated ambient temperatures and increased ratio requirements (Ha, 1991; Ha, Lehner, & Farley, 1990). Although it seems plausible that increasing ratio requirements would increase the cost associated with obtaining food, manipulating ratio schedules alone presents a possible confound because increasing the number of responses necessary to complete a trial also increases both the delay to reinforcement and session length (a.k.a. the time horizon). One method of dissecting the response-cost/time confound is to manipulate response-effort requirements.
Response-effort and reward-amount manipulations shifted risk-sensitive preferences in accordance with the predictions of the DEB rule (Kirshenbaum, Szalda-Petree, & Haddad, under review). A dual-running wheel choice apparatus was utilized in which concurrent VI and FI schedules were presented. Most studies employing rats have been conducted using minimal effort requirements (for exceptions, see Chelnois, Logue, Sheehy, & Mao, 1999; Collier, Hirsch, Levetsky, & Lesher, 1973; Keehn, 1981). Increasing the response-effort required to obtain a single reinforcing event successfully shifted preference towards the variable option. The amount of reward obtained during a single reinforcing event was then increased to compensate for increased response-effort requirements, and as a result, risk-averse tendencies developed (choice shifted to the fixed interval schedule). A directional shift toward risk-aversion was created by increasing reward amount within both high and low response-effort conditions; however, high-response effort fostered significant risk-aversion while the low-effort condition did not. It is hypothesized that shifts in choice were most evident during high-effort conditions because the increased cost associated with foraging forced the subjects to alter their strategy in order to meet augmented environmental demands.

In a second examination of response-effort effects, reward amount was the variable component and congruent with the previous study, increased response effort revealed a risk-prone tendency. The experiment was conducted using twelve rats, six in each group. The subjects were presented with two simultaneously available FI60-s schedules, one schedule provided 5 food pellets and the other provided either 1 or 9. The groups experienced two experimental phases in opposite order from one another; there was one low-response effort (20g) and one high-response effort (120g) condition for each group.
Figure 2. The response effort/reward amount interaction.

![Figure 2: The response effort/reward amount interaction.](image)

Table 1. Variable option choice percentages and standard error for each group.

<table>
<thead>
<tr>
<th>Phase</th>
<th>Group 1</th>
<th>Group 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>One</td>
<td>62% (120g) 1.02</td>
<td>50% (20g) 0.69</td>
</tr>
<tr>
<td>Two</td>
<td>52% (20g) 0.31</td>
<td>61% (120g) 0.77</td>
</tr>
</tbody>
</table>

Note: The last four days of each phase were averaged in order to provide a percentage for each phase. n = 6 for each group.

Increasing response-effort also increased the standard error for each group. Paired t-tests were performed comparing the two conditions, t(5) = 4.089 (p < 0.05) for group 1, t(5) = 3.035 (p < 0.05) for group 2. Comparisons between the two groups revealed no significant differences, p > 0.05. The data suggest two possibilities: (1) increased response-effort requirements force the subjects to engage in a risk-prone behavioral pattern in order to meet increased energetic demands, and (2) failure to demonstrate risk-sensitivity using rats as subjects may be due to the minimal energetic requirements of most experimental preparations.
Mechanical Models

Delay, variance, and effort discounting

While ecological models of choice attempt to ascertain what function RSF behavior serves, psychological models are concerned with the environmental factors that determine choice. Operant research on choice has focused primarily on reinforcement magnitude and the delay to reinforcement when two options yield unequal means.

The traditional self-control preparation is a good test for economic models such as the matching law (Baum, 1974; Herrnstein, 1961). The matching law assumes that choice is determined by the relative reinforcement densities presented on two options. The matching law predicts for self-control because despite the longer delays to reinforcement, the self-control option administers more reward per unit time. In most situations, subjects prefer to minimize delays rather than maximize caloric intake. Baum’s (1974; 1979) modification of the matching law introduces a bias coefficient \( a \) to account for undermatching:

\[
\frac{B_1}{B_1 + B_2} = \frac{r_1}{r_1 + r_2} \left( \frac{a}{a + 1} \right)
\]

Undermatching is most likely to occur when the experimental procedure utilizes a changeover delay. The bias coefficient allows the matching law to account for risk sensitivity because it can quantitatively assess the impact of variance on choice, but it does not provide a theoretical contribution as to why a forager should prefer or avoid risk.

The delay-reduction hypothesis (Fantino, 1987; 1969) is an extension of the matching law that predicts for exclusive preference as a function of delay-discounting. Most investigations of self-control have been conducted using Lea’s (1979) chaining procedure in which the foraging subject is required to respond to both initial and terminal link operants.
The delay-reduction hypothesis depicts choice as the result of both terminal and initial link delays, but only terminal link delays are modeled below for the sake of simplicity. The average delay-to-reinforcement for both options is represented in the equation as $T$. If $T$ is greater than both the average delays to reinforcement for both options ($t_s$ and $t_i$: self control and impulsivity, respectively), then:

$$\frac{R_S}{R_S + R_I} = \frac{r_S(T - t_S)}{r_S(T - t_S) + r_I(T - t_I)}$$

where $R_S$ and $R_I$ represent responding to the self-control and impulsive options, and $r_t$ and $r_S$ are representative of reinforcement rates. The equation above results in partial choice to account for reinforcement-response matching. In addition, DRH accounts for exclusive preference with the following equations.

If $t_I < T < t_S$, then DRH predicts exclusive impulsivity:

$$\frac{R_I}{R_I + R_S} = 1$$

If $t_I > T > t_S$, then DRH predicts for self-control:

$$\frac{R_I}{R_I + R_S} = 0$$

And if the delay reduction is calculated for both $R_S$ and $R_I$, then:

$$R_S = T - t_S \quad \text{and} \quad R_I = T - t_I$$

If the calculated delay reduction is negative, then responding on that alternative will result in longer delays-to-reinforcement than responding using the entire system (i.e. both options), the equations above come from Fantino (1987). The delay-reduction hypothesis...
adds to the mechanical definition of risk sensitivity because of its basic assumption that delay acts to discount the value of a reward. The discounting of future rewards may be an adaptive response because there is an inherent risk associated with long delays; long delays present a risk of possible interruption or what can also be called an uncertainty of obtaining the delayed reward. The discounting of future rewards is dependent upon several factors: (1) the delayed reward is preferred when individuals have had prior experience with delayed reward (Mazur & Logue, 1978), (2) the delayed reward becomes more desirable as the forager's energetic condition improves (Snyderman, 1983), (3) as the delay between choice and food administration increases so will the preference for the delayed, larger reward (Green, Fisher, Perlow, & Sherman, 1981; Kagel, Green, & Caraco, 1986; Rachlin & Green, 1972), and (4) as the effort required to obtain the reward is increased, the preference for the immediate reward decreases (Chelonis, Logue, Sheehy, & Mao, 1999).

Mazur has proposed that the discounting function of a delayed reward is relevant to the specific species. Mazur's (1989) *delay discounting with exponent equation* is a modified matching function, but it includes a species-specific discounting variable (x):

\[ V_i = \frac{A_i}{1 + D_i x} \]

The value (V) of a delayed reward is determined by the relationship between amount (A) and delay (D). One has been added to the denominator to prevent exclusive choice when the difference between an immediate and a delayed reward is nominal.

Scientists examine self control in non-human species using food as the contingent reward in an attempt to understand the underlying mechanisms involved in decision making.
Green, Fry and Myerson (1994) have demonstrated that with humans, like their laboratory counterparts, the value of a reward decreases as delay to reward increases. The relationship between reward value and delay can be illustrated as a decelerating hyperbolic function (see also Myerson & Green, 1995). Interestingly, Green, Fry and Myerson discovered that the hyperbolic function was slightly different between age groups; the hyperbola became increasingly shallow as age increased. It remains unclear if the depth of the hyperbolic scallop is actually a reflective of some developmental shift in cognition, or whether these results are representative of a cohort effect.

Variance and effort discounting act very similarly to models of delay discounting presented in the psychological literature. Both variance and effort discounting suggest that the value of a particular return is relative to reward access. As variance or response-effort increase, the value of a particular commodity decreases. Increased response-effort has a direct impact on caloric return, therefore options that are more costly have a lesser value (Keehn, 1981) and variance introduces a degree of uncertainty in resource acquisition (Real, 1980). According to Real’s variance discounting model, when two option yield equivalent reward means, variance ought to be avoided under any circumstance. Thus, risk-aversion is a constant. The variance discounted model suggests that mean and reward are perfect substitutes for one another, a stark contrast to the z-score model presented in the earlier section.

**Scalar expectancy theory**

Some researchers (Bateson & Kacelnik, 1995; Kacelnik & Bateson, 1996; Reborda & Kacelnik, 1991) have used an adaptation of scalar expectancy theory (SET, Gibbon, 1977) to account for RSF. The foundation of SET rests on an eccentric account of Pavlovian
conditioning. When a CS is presented to a subject, it creates a memory trace that decays with time until the presentation of the US. Following a reinforced trial, a value is attributed to the CS-US pair and research suggests that the memory trace of the CS decays in a hyperbolic manner (Gibbon, 1977). The hyperbolic decay is crucial because it suggests that when mean delays are equivalent, a CS followed by a variable delay to the onset of the US (a variable CS-US delay pair) will be more highly valued than a fixed CS-US delay pair. SET predicts for risk-proneness when delay is manipulated because choice is determined by the value of the CS-US pair.

The second important contribution of SET posits that the value remembered for a fixed time interval or amount is represented as a normal distribution with a mean centered around the experienced delay or amount and a standard deviation relative to the mean. The representation of a variable amount or delay is fabricated from a sum of each normal distribution based upon the experienced reward instances. The shape of the summed distributions will be positively skewed because the represented distribution for the smaller or more immediate reward has a condensed standard deviation (and thus a higher probability density in memory) than the memory for a larger or more delayed reward. Thus, it is the direction of the skew that is predictive of the direction of risk sensitivity: (1) Variability in delay should be preferred because the variable option is expected to yield shorter delays without compromising long-term gains, and (2) Variability in amount, on the other hand, should be avoided because the expected probability of the smaller amount reoccurring is much higher than the probability of a more valuable amount reoccurring. Therefore, SET predicts choice preference (either risk-prone or averse) as a result of whether delay or mean amount

Figure 3. Theoretical memory distributions proposed by SET. Probability density in memory is reflected on the y-axis.

Bateson and Kacelnik (1995) found evidence for SET using starlings (*Sturnus vulgaris*). The results showed that the subjects preferred variable delays when reinforcement amounts were equivalent, and variance in amount was avoided when the delays were the same. Furthermore, the researchers have demonstrated that starlings behave in a risk-prone manner when delay is manipulated, even when the rewards obtained are increased. Counter to the predictions of a DEB rule, no effect of energy budget on performance occurred (Kacelnik & Bateson, 1997).

Proponents of SET recognize that there are problems with the model. For instance, SET suggests that foragers should be risk-indifferent when the geometric mean of the variable option (the square root of the product of the variable option samples) equals the fixed option, the rational for this prediction comes from Weber's Law. Bateson and Kacelnik (1996) and Mazur (1984, 1986, as cited in Bateson & Kacelnik, 1998) have empirically demonstrated
that indifference occurs at the harmonic mean when delay is manipulated. In addition to this, SET predicts that the direction of risk sensitivity is independent of energy states and is therefore in conflict with any investigation that has documented a strategic shift when energy budgets are manipulated. Finally, Bateson and Kacelnik (1998) acknowledge that when amount and delay co-vary, SET fails to make any prediction of risk-sensitive foraging.

In an empirical attempt to validate the predictions of SET and variance discounting, rats were presented with two concurrent fixed-interval schedules within the dual running-wheel apparatus. During the first phase, all the subjects displayed a choice preference for the short-delayed schedule (FI 30-s, four units of reward per reinforcing event) over the long-delayed schedule (FI 60-s, eight units of reward). There were 36 trials per session, 30 of which were free choice trials. Given that this was a trial-limited procedure, even though reward per unit time was equivalent between the two options, choice for the long-delayed option would yield a more substantial income. Congruent with delay discounting, the FI 30-s schedule was chosen at an average of 59%. Following three consecutive days of stable choice performance, the second phase of the experiment began. The twelve subjects were divided in half so that one group experienced a variable food amount when the 30-s schedule was chosen (1 or 7 pellets) and the other group experienced a variable food amount after the completion of the 60-s schedule (either 5 or 11 food pellets). Variability in amount was preferred in both groups during the second treatment (see below).
The red lines represent the short-delay choices when variability was presented on the 30-s schedule. The blue lines represent the short-delay choices when variability was presented on the 60-s schedule. The graph depicts the final three sessions of each phase, n = 6 for both groups.

The last three sessions of each phase were used for data analysis. The introduction of variability had a significant effect on choice performance (t(5) = 6.047 and t(5) = 3.47, p's < .05, groups 1 and 2, respectively). There was a significant difference between the groups in phase two (t(5) = 4.086, p < .05) but not in phase one (t(5) = .235, p = .824). The average running distances per trial were examined (average running distance was divided by the average number of choice trials for that schedule) and distances significantly increased on both schedules when variability was introduced for group 1, t(5) = 4.8 and t(5) = 3.5, p's < .05 (FI30-s and FI60-s schedule, respectively), but not for group 2. Overall, the manipulations of the independent variable do not result in systematic alterations in running distances.

The predictions of variance discounting and SET were not supported. The results are possibly confounded because the subjects were 5-months old and had prior experience with
several different concurrent schedules. Although I do not believe that these results are reflective of the addressed confound, they are anomalous. There is, however, one possible theoretical explanation. The experiment was conducted using 60g of tangential force resistance and the subjects were receiving 100% of their daily income within the experimental chambers. It is plausible that the subjects were operating on a negative energy balance when variance was introduced, and this would explain the consistent risk prone behavior exhibited by both groups. Of course, the only way to verify whether the energy budget is applicable to this situation would have been to manipulate either response-effort requirements or the amount of reward received per reinforcing event. These results are possibly quite valuable, but obviously a replication needs to be performed.
References for Full Literature Review


Effects of Delay and of Intervening Events on Reinforcement Value (pp. 55-77). Hillsdale, New Jersey: Lawrence Erlbaum Associates.


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