The adaptive value of preference for immediacy: when shortsighted rules have farsighted consequences

David W. Stephens and Dack Anderson
Ecology, Evolution and Behavior, University of Minnesota, St. Paul, MN 55108, USA

Results from the operant laboratory suggest that short-term benefits guide animal feeding decisions. These results appear to contradict evolutionarily-motivated models of foraging that emphasize long-term benefits. Because of this contradiction, some behavioral ecologists argue that natural selection must favor short-term benefits in some unknown way. This study addresses the contradiction by testing the feeding preferences of captive blue jays in two economically equivalent situations. The first situation follows the operant literature's ''self-control'' paradigm; jays make a binary choice between small-immediate and large-delayed options. The second situation is modeled on patch-use problems; the jays make a leave-stay decision in which ''leaving'' leads to small amount in a short time, and ''staying'' leads to larger amount in a longer time. In the self-control situations, the observed outcome agrees with short-term rate maximizing, as other investigators have reported. In the patch situation, the results agree more closely with long-term rate maximizing. The text explains how a rule of preference based on short-term rate comparisons can account for both situations. It is argued that natural selection may have favored short-term rules because they have long-term consequences in many natural foraging situations. *Key words:* blue jay, foraging, prey, self-control. *[Behav Ecol 12:330–339 (2001)]*

When a foraging blue jay detects a moth, it may attack or ignore it. If the jay successfully attacks, it obtains the moth after a delay involving pursuit and handling. If instead, it ignores the moth, it obtains its next meal at some later time. The jay's actions influence the timing and quantity of food. We can visualize this as a sequence of amounts arranged along a time-line (Figure 1), where G_i represents the size of the ith parcel of food gained, and t_i represents the interval between the i–1st and ith bit of food. The environment constrains the forager's options—the forager can't simply choose small t_i's and large G_i's. Foraging behavior interacts with the environment to determine a temporally structured stream of gains.

Since this is a ubiquitous problem, it seems reasonable to suppose that natural selection will have equipped animals with mechanisms that choose among time/amount sequences as shown in Figure 1 in some ''sensible'' way. This suggests two problems. First, how can we combine time and amount into an appropriate *currency* that correctly reflects the fitness consequences of different time/amount sequences? Second, what *decision rules* can foragers implement to select the currency-maximizing time/amount sequence from an environmentally determined set of possibilities? This article explores, via experiment and theory, the relationship between decision rules and currencies.

The next section reviews two contradictory points that form the background for our problem. First, evolutionary considerations suggest that foragers should choose among time/amount sequences in a farsighted way. Second, evidence from the operant laboratory contradicts this: subjects make shortsighted decisions; overemphasizing delay to the next food item, and under emphasizing the longer-term features of time/amount sequences. We review these issues in turn.

The logic of farsightedness

Foraging animals should evaluate the consequences of their actions over a long time horizon, because there are likely to be many prey attack decisions between each bout of reproductive activity (when the animal invests its resources in reproductive success). The traditional (Stephens and Krebs, 1986) long-term rate-maximizing currency reflects this logic:

$$\max \frac{\sum_{i=1}^{\infty} G_i}{\sum_{i=1}^{\infty} t_i} \tag{1}$$

However, the infinite time-horizon in (1) cannot be generally valid: food that becomes available after you've starved to death is not useful. Perhaps expression (1) is too farsighted. An alternative myopic currency (Bateson and Kacelnik, 1996; Baum and Rachlin, 1969) is:

$$\text{For each i,} \qquad \max \frac{G_i}{t_i} \tag{2}$$

That is, obtain the best rate on a one-decision-at-a-time basis. The shortsightedness of expression (2) becomes apparent when we consider a sequence of decisions. When a forager tries to extract the highest rate from each opportunity, it may be wasting time on a mediocre alternative that it would do better to pass by (see Stephens and Krebs, 1986: 16, for a numerical example).

Rate models and discounting

The long- and short-term models [(1) and (2)] are both extremes, one considers an infinite sequence of gains and the other considers only one. To construct intermediate-term models, we can introduce a discount rate that measures the proportional loss of value per s. If the discount rate is zero, then we have the long-term model because gains have the same value regardless of whether the forager obtains them
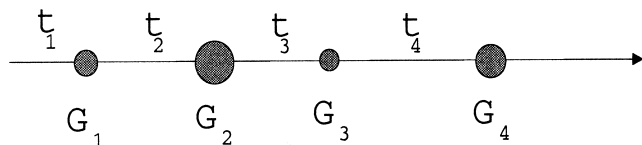
Figure 1
Diagram of a time/amount sequence. The t_i terms represent the intervals between resource encounters, and the G_i terms represent the magnitude of each resource.

Figure 2
A trial in a typical self-control experiment, where τ is the inter-trial interval, t_1 is the delay before the small amount G_1, t_2 is the delay before the large amount G_2, and ρ is a post-feeding delay.

early or late in a sequence. On the other hand, as the discount rate becomes large, we approach the short-term model.

We expect non-zero discounting for two reasons. First, there may be opportunity costs of delay (e.g., a forager loses the opportunity to use a delayed resource just as a human investor loses the opportunity to earn interest on a delayed payment). Second, delay implies a collection risk. That is, delay reduces the probability that the forager will collect a given benefit, because some intervening event—for example, an interruption by a predator or conspecific—might occur before the forager realizes the benefit.

While one certainly expects non-zero discount rates, it doesn't follow that the short-term model is more plausible than the long-term because discount rates are likely to be small. We expect small discount rates because we expect that the per-s rate of interruptions will normally be small, that is, fractions of an interruption event per s. Similarly, we expect that the amount of opportunity lost per s will also be small.

We will focus on the two rate models in this article, because they conveniently caricature the issues surrounding the time-scale of choice. Moreover, we argue that the long-term model makes the most evolutionary sense because: it gives a reasonable approximation of rate even when the time horizon is not infinite, it is farsighted enough to skip over bad options as explained above, and realistic discount rates are likely to be small.

Evidence of shortsightedness

Notwithstanding our argument that foragers should make far-sighted decisions, an impressive body of experimental evidence shows that animals often make myopic decisions. Most of this evidence comes from ''self-control'' experiments in the operant psychology lab. Figure 2 diagrams a single trial from a typical self-control experiment. The animal waits for time τ, and the apparatus presents a binary choice. The subject can choose either the small-immediate (wait t_1 s to obtain amount G_1), or the large-delayed (wait t_2 seconds to obtain amount G_2; $t_2 > t_1$ and $G_2 > G_1$) option. Typically, the subject has had prior experience that allows it to associate (for example) a red key with the small-immediate choice and a blue key with the large-delayed choice. In some experiments, there is a post-feeding delay (ρ in Figure 2) associated with one or both of the options. The investigator varies the amounts and delays, and records the proportion of choices made to each alternative. Psychologists say that a subject exhibits self-control if it waits for the larger delayed amount.

It is useful to consider the long-term rate model's predictions for the self-control situation (Figure 2). The rate associated with choosing alternative 1 for many trials is:

$$\frac{G_1}{\tau + t_1 + p},$$

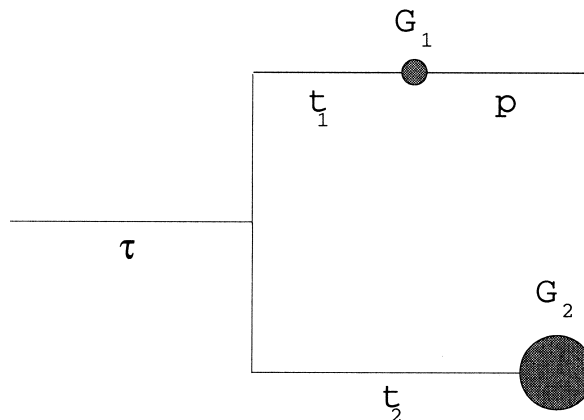while the rate associated with alternative 2 is:

$$\frac{G_2}{\tau + t_2}.$$

So the long-term rate model predicts that animals should prefer alternative 1 when:

$$\frac{G_1}{\tau + t_1 + p} > \frac{G_2}{\tau + t_2}$$

In the long-term model all the temporal elements contribute to the rate and ought to be ''considered'' in determining preference. However, the experimental evidence shows that animals do not treat these three temporal elements equally.

The delay to food
Investigators universally agree that the time between when a choice is made and food is delivered (t_1 and t_2 in Figure 2) is a key determinant of animal preferences. There are several pioneering studies in this area, including those of Rachlin and Green (1972) and Ainslie (1974). In these studies and others, direct manipulation of delay affects preference in a powerful and consistent way. For example, McDiarmid and Rilling (1965) showed that pigeons preferred a schedule with a 6 s delay to initial food delivery to an option with a 24 s delay to food, even though the 24 s option delivered twice as much food over a 2 min period.

Post-feeding delay
Several studies have shown that post-feeding delays (p in Figure 2) have virtually no effect on preference (e.g., Green et al., 1981; Logue et al., 1985; Mazur and Logue, 1978; Snyderman, 1987). This challenges our view that animal choices should be farsighted, because the delay to food (t_1) and the post-feeding delay (p) should be equivalent from a ''long-term'' perspective.

Inter-trial interval
Most investigators feel that the inter-trial interval (ITI), like the post-feeding delay, has little effect on preference. Mazur (1989) manipulated the ITI and found virtually no effect on preference. Bateson and Kacelnik (1996) performed a preference experiment, and compared their data to several rate-based models. They found that a model excluding the ITI, (i.e., maximize G_i/t_i) gave the best fit.

The strength of animal preferences for immediacy also disagrees with farsighted models. For example, hyperbolic models of discounting, derived from the self-control data (Ainslie, 1975; Mazur, 1984, 1986, 1987; Mazur et al., 1985), suggest that the first s of delay can cut value in half. While several discounting processes probably reduce the value of delayed

benefits, it is hard to imagine plausible processes that could justify such severe discounting.

Summary: the contradiction
Evolutionary models disagree with self-control results. They disagree qualitatively, for example, over the role of the intertrial interval, which is important in the long-term calculations of evolutionary models, but relatively unimportant in self-control experiments. They also disagree quantitatively over the strength of preference for immediacy. While evolutionary models can accommodate small discounting effects, self-control experiments show that brief delays can have large effects.

How should we interpret this disagreement?
When a model disagrees with data, we must accept the data and reject the model. Following this principle, many behavioral ecologists (e.g., Bateson and Kacelnik, 1996; Stephens, 1996) have taken self-control results to mean that our traditional "long-term" currencies must be wrong, concluding that natural selection must have emphasized short-term consequences in some way that we do not understand. The problem here is that it is difficult to construct a reasonable economic model that predicts the strong preferences for immediacy that self-control studies show. For example, a model offered by Green and Myerson (1996) assumes that the rate of interruptions increases smoothly and systematically after a forager encounters a stimulus predicting a delayed food reward. While this correctly predicts some features of the self-control data, the only justification for this assumption is that it fits the data. There are no interruptions, decreasing or otherwise, in typical self-control studies.

Is there some other way to resolve the conflict? The simplest alternative is that self-control data are not an accurate guide to the economic forces that have shaped choice. Specifically, although the overall pattern of preference for immediacy is impressive and highly repeatable within the self-control paradigm, does it necessarily mean that animals always make myopic choices? Could the decision-making mechanism that seems so frustratingly myopic in self-control situations lead to more understandable farsighted consequences in other situations?

Self-control and patch-use

We were attracted to this second possibility by an empirical conflict between the self-control and patch-exploitation literatures. To understand this conflict, the reader must first understand the parallel between the patch-exploitation and self-control. The elementary theory of patch exploitation (the marginal-value theorem, see Charnov, 1976; Stephens and Krebs, 1986) considers the effect of patch residence time on the long-term rate of food intake. Figure 3A shows a graphical analysis of this problem. This well-known plot shows how travel time affects the rate-maximizing patch residence time. This model predicts that foragers should spend more time in patches extracting more resources when travel times are longer.

When a forager exploits a food patch it makes a decision that is analogous to a self-control experiment, because it must decide whether to spend a short time in the patch obtaining a small amount, or spend a longer time obtaining more. To emphasize this similarity, we can plot a self-control experiment's small-immediate and large-delayed options in a time/gain space that parallels the classic marginal-value theorem plot, (Figure 3B; Stephens et al., 1986). Moreover, we see that travel time, which is analogous to the ITI, should have an effect on preference: as the travel time (ITI) increases animals should shift their preference from the small-immediate to the
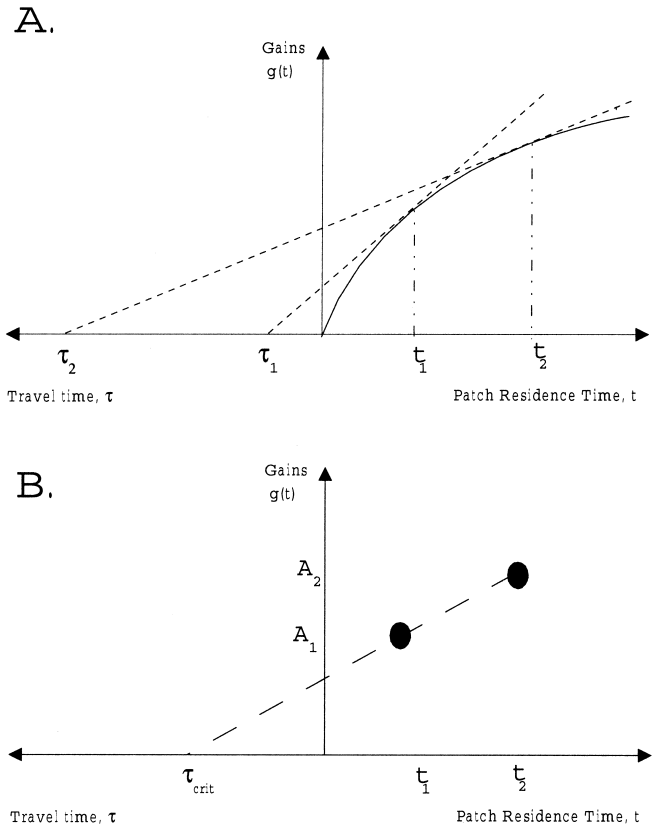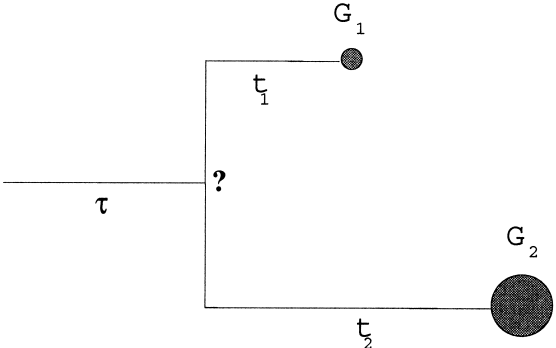

Figure 3
Graphical solution of the marginal-value theorem. (A) The solid curve on the right gives the relationship between patch residence time and gains, $g(t)$. The travel time (τ) is plotted on the left side of the abscissa, increasing from right to left. The slope of a line drawn from (τ, 0) on the left to any point on the gain curve [t, $g(t)$] is the rate of gain associated with patch residence time t. One can see that this slope will be maximized, if we choose a t such that this slope is just tangent to the gain curve. For a short travel time τ_1 the corresponding "best" residence time t_1 will also be short. If the travel time is longer (e.g., τ_2), then the optimal residence will be also be longer (t_2). (B) Self-control experiments offer a "two point gain function," because the subject can choose a small amount A_1 in a short time t_1, or a large amount A_2 in a longer time t_2. The logic of the marginal value theorem suggests that there exists a critical travel time τ_{crit}: if the experimental travel time is smaller than τ_{crit}, the subject should prefer small-immediate; if the travel times is greater than τ_{crit}, the subjects should prefer large-delayed.

large-delayed option. Theoretically, this restates our claim that farsighted foragers should be sensitive to the ITI. Empirically, however, it raises a new question: why do patch experiments consistently show animals spending longer to extract more when travel times are long (Stephens and Krebs, 1986), when self-control experiments show little effect of the analogous ITI?

Experimental rationale
This empirical disagreement stimulated our study. We realized that while patch exploitation and self-control problems are similar economically, they differ in many ways. For example, in a self-control experiment, the animal makes a binary choice—left or right, red or green—but in patch exploitation, the animal chooses whether to continue or to leave and pursue the option of a future patch. Figure 4 shows economically identical patch and self-control problems that we used in our experiment. In the self-control problem the forager simply chooses either option 1 or 2. In the patch problem the forager

Self-control paradigm
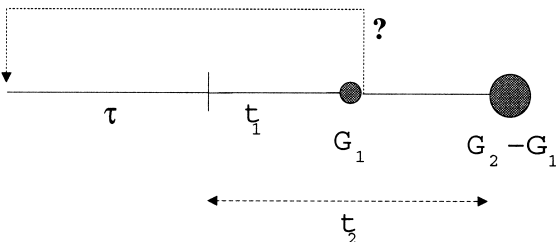

Patch-use paradigm

Figure 4
Two ''equivalent'' decision contexts. In the self-control paradigm the subject makes a binary choice between small-immediate and large-delayed. In the patch paradigm, the forager's choice has equivalent consequences, but the forager decides whether to stay in the patch and collect $G_2 - G_1$ additional units of food or to leave immediately after obtaining the small amount G_1.

waits (travels) for time τ and then encounters a single stimulus (a patch), it then waits t_1 s to obtain G_1. Now, it faces a choice, it can ''leave'' the patch, starting an new cycle of travel and patch encounter, or it can continue for further time $t_2 - t_1$ to obtain an additional $G_2 - G_1$. If the forager takes the ''leave'' option it gains G_1 in total time $\tau + t_1$. If it takes the ''stay'' option, it obtains G_2 in $\tau + t_2$. These, of course, are the same time and amount consequences (or equivalently, the same two-point gain function, Figure 3B) as in the self-control problem.

By constructing economically equivalent patch and self-control situations, our experiment considers the economic significance of self-control results. If, as some have supposed, short-term consequences shaped the mechanisms of choice in a general way, then we should observe the same patterns of choice in patch and self-control situations. If, instead, we find

that patch and self-control results disagree, this will suggest that self-control results are not a reliable guide to the economic forces that have shaped animal preferences.

METHODS

Overview
Our experiment tests foragers in ''equivalent'' patch and self-control contexts as shown in Fig. 4. Since empirical evidence shows an effect of ITI in patch studies, but not in self-control studies, we tested each context at three different ITI's (30 s, 60 s, and 90 s). Table 1 shows our experimental design. Within each combination of context (patch or self-control) and ITI we assessed preferences via factorial tests of delay-to-large (DTL = t_2) and delay-to-small (DTS = t_1) as shown in Table 1. The notation P(L) in Table 1 indicates that we used proportional choice of large (P(Large)) as our measure of preference. We used four 20-mg food pellets for the large amount ($G_2 = 4$) and two food pellets for the small amount ($G_1 = 2$).

Procedural details
The subjects were six adult blue jays (*Cyanocitta cristata*) of unknown sex and mixed experimental histories. Figure 5 shows a top view of the apparatus. The apparatus has two operational stimulus lights and three perches equipped with microswitches. Birds exhibited their preferences by selecting which perch to hop on at a given time. We ran the experiment as a modified closed economy; the jays spent 23 h per day in the apparatus and obtained all of their food there. The experimentally programmed contingencies were in force from 0700 to 1600 CST daily, with a 1-h break from 1100 to 1200. During the break, we removed each bird from the apparatus, weighed it, and cleaned the apparatus. A white noise generator provided masking noise. A clock turned the house lights on at 0600 and off at 1800 daily.

Table 1 shows the temporal parameters for each treatment. The experiment followed a within-subjects design with each jay experiencing all combinations of the treatment variables. A process of nested randomizations determined the order of treatments. Each bird completed a full set of treatments in one decision context (patch or self-control) before changing to the other; we assigned three birds to ''self-control first'' and three to ''patch first.'' Before beginning a new context, the birds experienced 7 days of baseline treatments with the temporal parameters (delays and ITI) set to the averages of the experimental parameters; this was an attempt to minimize the effects of learning a new choice paradigm in the transition from self-control to patch or vice-versa. We randomized the order of ITI treatments within each decision context. Similarly, we randomized the order of each delay-to-large treatment within each decision context/ITI cell, and we randomized the order of delay-to-small treatments within each delay-to-large block.

Table 1
Overview of experimental design

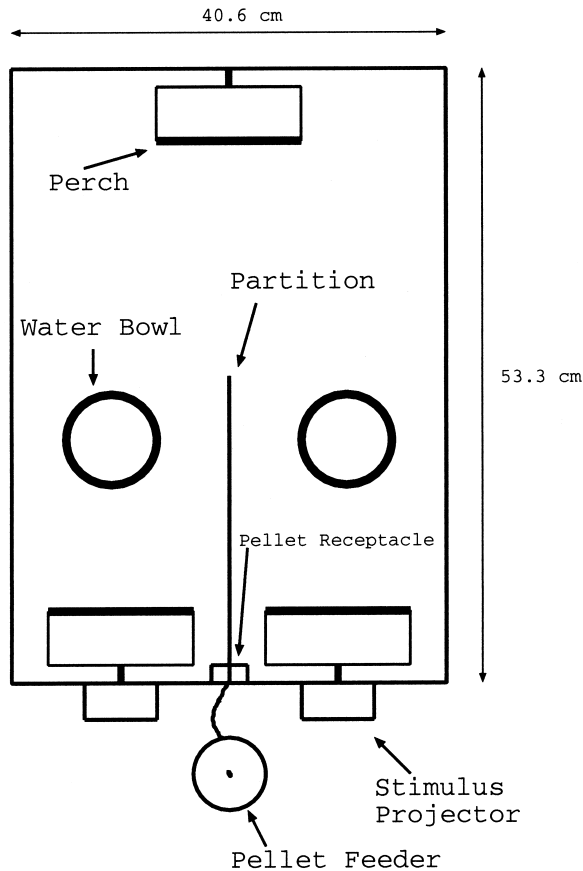|		30 s ITI		60 s ITI		90 s ITI	
		DTL		DTL		DTL	
		60 s	90 s	60 s	90 s	60 s	90 s
Self-Control DTS	5 s	P (L)	P (L)	P (L)	P (L)	P (L)	P (L)
	50 s	P (L)	P (L)	P (L)	P (L)	P (L)	P (L)
Patch DTS	5 s	P (L)	P (L)	P (L)	P (L)	P (L)	P (L)
	50 s	P (L)	P (L)	P (L)	P (L)	P (L)	P (L)

Figure 5
Top view of experimental apparatus.

We assigned a pair of stimulus colors to each bird for each context. We assigned blue-yellow to patch, and red-green to self-control for three of the birds, and vice-versa for the remaining three. The meaning of a color (e.g., red associated with small-immediate), was assigned randomly but was consistent throughout a context treatment.

Training
We trained subjects using shaping (sometimes called the method of successive approximations). We considered an individual trained when it reliably performed a task we called light-following. In the light-following task, the bird sits on the rear perch, until the computer switches on one of the two front stimulus lights; then the bird hops forward and collects a few food pellets when it lands on the front perch adjacent to the illuminated light.

Within trial details
The following paragraphs explain how we implemented the self-control and patch contexts.
   Self-control. During the ITI, no stimuli were present and birds typically waited on the rear perch. After the ITI expired, the computer switched on a pair of stimulus lights near the front perches if the bird was waiting on the rear perch. The bird then chose a side by hopping forward. When the bird made its choice, the computer switched off the unchosen light, and "washed out" the color of the chosen stimulus light (by turning on two clear bulbs in the stimulus projector; this signaled the "waiting" period). The computer dispensed the pellets after the programmed delay elapsed if the bird was on the food perch. A hop on the rear perch started the next ITI.

Patch. The ITI phase was identical to self-control. After the ITI expired, the computer presented the stimulus color associated with the small amount on a randomly chosen side of the apparatus, (again, the bird must have been on the rear perch for this presentation to occur). When the bird hopped forward, the "small color" was washed out, and the programmed delay began. When the programmed small delay expired, the computer dispensed two pellets and the color associated with the large was displayed for 1 s and then washed out; the programmed delay to large $(t_2 - t_1)$ began when the first two pellets were dispensed. If the bird was on the front perch when the programmed delay expired, then the remaining two pellets were dispensed. At any time after the initial hop forward, a hop on the rear perch canceled the trial and started a new ITI; that is, the bird was free to "leave the patch" at any time.
   Further details. We organized sequences of trials into blocks of 32. Each block began with eight forced-choice trials (in which subjects were forced to take either the large or small option) and 24 free-choice trials from which we collected preference data. The purpose of the forced-choice trials was to insure that subjects had some experience with each option. The most basic element of our design was a simple preference test for a fixed context, ITI, delay-to-large and delay-to-small. In each preference test, we recorded the number of times the subject obtained the larger four pellet amount. Each preference test lasted for 3 days. We used relative frequency of choice in the last third of the free trials as our estimate of preference, (typically, there were between 100 and 120 trials in this "last third"). We call this measurement "P(Large)."
   We would have preferred to use a stability criterion to terminate each preference test, but the large number of tests required (24 for each individual) made this impractical. The possible problem with our fixed duration tests is that both preference (which we want to measure) and rates of preference acquisition (which we don't want to measure) can affect the outcome. However, the general agreement between our results and well documented self-control procedure (see results and discussion) leads us to think that we have reasonable measures of preference.
   Latencies and the control of timing. We did not have absolute control over the timing of events in this experiment, because jays seldom respond immediately when the apparatus offers a choice. This means that realized intervals are always longer than programmed intervals. This could be a special problem here, because we tried to create equivalent self-control and patch situations. If, for example, latencies to respond were consistently longer in the patch situation, then this would undermine the logic of our experiment. To consider this possibility, we calculated the difference between programmed trial durations and realized trial durations for every free choice trial. We summarized this data by calculating mean differences for each subject in each condition, and then performed a repeated-measures analysis of variance (like that shown in Table 2) using this mean differences as the dependent measure. This ANOVA showed no significant (5% level) effects (e.g., effect of context, $F_{1,5} = 0.35$, $P \approx 0.58$).

RESULTS

Self-control experiments show strong preferences for immediacy that have lead behavioral ecologists to question their ideas about the fitness value of food gains. Our experiment explores the generality of these results by asking whether blue jays choose short-term consequences in equivalent patch and self-control situations.

Table 2
Partial ANOVA Table

Source of Variation	df	Sum of Squares	Mean Square	F	p (F)
Delay to Large (DTL)	1	1.102	1.102	69.655	.0004
Residuals (Bird × DTL)	5	0.0791	0.0158		
Delay to Small (DTS)	1	10.622	10.622	115.33	.0001
Residuals (Bird × DTS)	5	0.460	0.092		
Context × ITI	2	0.423	0.211	8.025	.008
Residuals (Bird × Context × ITI)	10	0.263	0.026		
Context × DTS	1	1.511	1.511	51.274	.0008
Residuals (Bird × Context × DTS)	5	0.147	0.029		
Context × ITI × DTS	2	0.795	0.398	28.867	7×10^{-5}
Residuals (Bird × Context × ITI × DTS)	10	0.138	0.014		
All Other SVs	101	5.341			

Overview
Figure 6 shows an overview of our results. The figure shows different patterns of choice in the self-control and patch contexts. To describe these differences, we consider the 50 and 5 s levels of delay-to-small separately. When the delay-to-small was 50 s (the right half of Figure 6), the ITI had no effect on preference, but the jays were more likely to choose the large outcome in the patch context (mean P(Large) for patch: 76%, mean for self-control 48%). When the delay-to-small was 5 s (the left half of Figure 6) the results were more complex. As expected, preference for large was greatly reduced (mean P(Large) for patch: 16%, mean for self-control 21%), but the most striking feature of these data is an interaction between context and ITI. In patch, preference for large increased with ITI, while in self-control preference for large decreased with ITI.

Table 2 presents a partial analysis of variance table that supports this interpretation. The dependent measures in this ANOVA are arcsin transformed versions of the P(Large) data (Figure 6). The analysis follows Myers and Well's (1995) recommendations for within-subjects (repeated measures) ANOVA. Table 2 only shows sources of variation with significant effects; all other terms were not significant. The pattern of significant effects shown in Table 2 supports the following interpretation. There is simple additive effect of delay to large (DTL); larger delays shift preference away from the large option, as one expects. Delay to small (DTS) interacts in a complex way with inter-trial interval (ITI) and context as Figure 6 for delays-to-small of 5 s there is an ITI/Context interaction with preference for large increasing with ITI in the patch context, but decreasing with ITI in the self-control context. For delays-to-small of 50 s, however, there is no effect of ITI but a strong additive effect of context.

ITI effects
The interaction of ITI and context (when delay-to-small was 5 s) is a striking result, but the trends shown in the grouped data (Figure 6) are subtle. So, a critical reader may wonder whether this result holds within subjects. Although preference does vary from one individual to the next, Figure 7 shows that the effect of ITI is remarkably consistent. In self-control the birds had stronger preferences for large when the ITI was small (with one exception; Bird 70, Delay to large = 60 s). In patch the birds had a stronger preference for large when the ITI was large (without exception).

Broadly speaking, long-term theory predicts increasing preference for large with increasing ITI. In considering the patch data, one is bound to wonder why we see the predicted pattern when the delay-to-small is 5 s, but not when the delay-to-small is 50 s. Long-term theory does not predict that pref-

erence for large will always increase with ITI, because proportional choice cannot exceed 100%. This means that there must be broad conditions where the ITI has no effect. The patch data agree with this idea, the ITI effect is most striking when overall preference for large is low, but difficult to detect when preference for large is high. We know of no rationale for the decreasing preference for large that we observed in some self-control conditions. It is difficult to assess the novelty of this result, because direct manipulation of ITI is relatively rare in self-control studies.

DISCUSSION

We tested situations where a leave-stay choice had the same consequences as a binary, self-control–style choice. The data show different outcomes in these different choice contexts. Specifically, blue jays switched to large-delayed outcomes more readily in the patch situation. In addition, preference for large increased with ITI as predicted by long-term theory in the patch situation, but not in the self-control situation.

Behavioral ecologists have accepted self-control data as evidence against the long-term rate currency of elementary foraging theory. Our results challenge this view, because they show that animals do not exhibit the same preferences in an economically equivalent situation. Which situation provides the most accurate picture of the forces that have shaped animal feeding preferences? In what follows, we develop a hypothesis that resolves the conflict between self-control experiments and long-term models. Our development proceeds in two steps. First, we compare our patch and self-control treatments to the long and short-term models, outlined in the introduction. Second, we show how the same decision rule can, in theory, lead to long-term rate maximizing in the patch situation, and the characteristically myopic choice of self-control.

The rate models
To begin, we compare our results to the farsighted long-term rate model (Equation 1) and the myopic short-term rate model (Equation 2), because these models represent different ways to value temporal arrangements of benefits.

Long-term model
The currency of long-term rate maximization predicts preference for the large (four pellet) alternative when:

$$\frac{4}{\tau + DTL} > \frac{2}{\tau + DTS}$$

where τ is the ITI and DTL and DTS represent the delays to large and small, respectively. This calculation assumes that
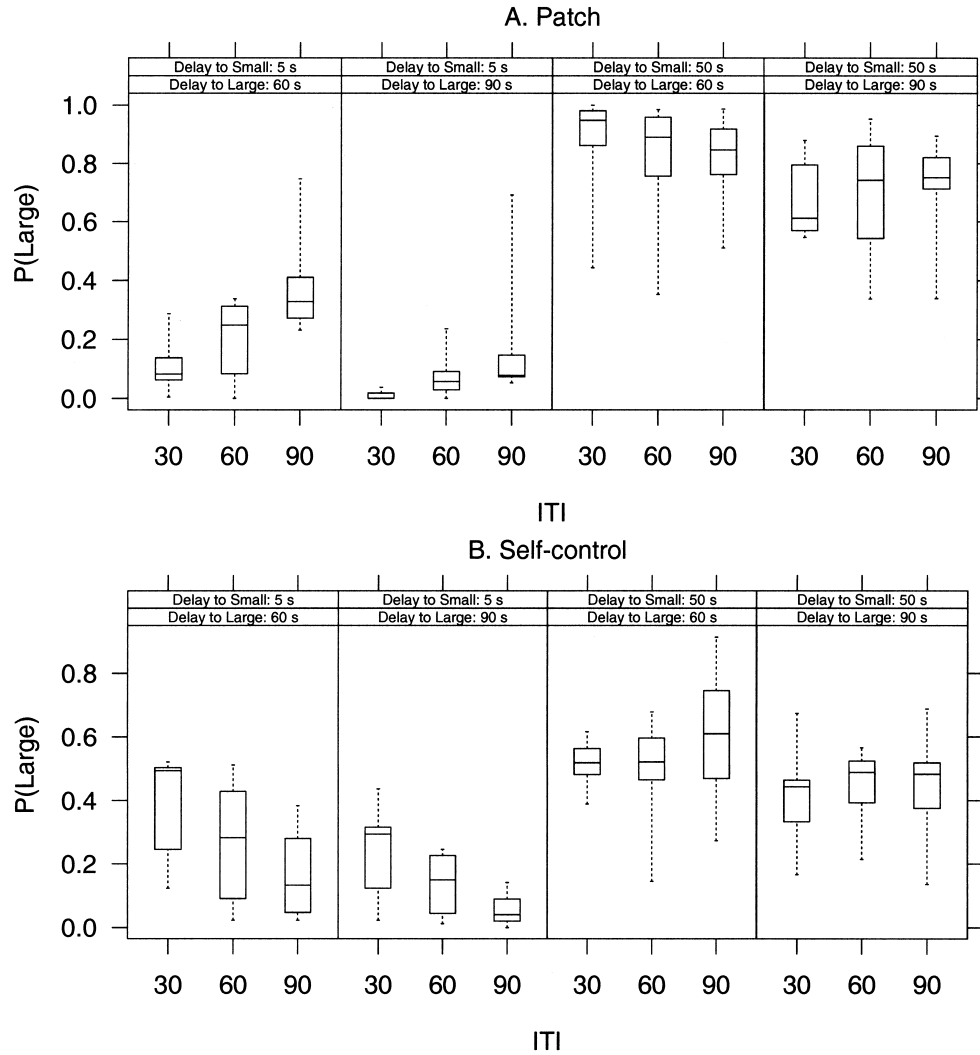
A. Patch

B. Self-control

Figure 6
The proportion of free choice trials in which jays obtained the larger (four pellet amount) broken down by context (self-control or patch), ITI, Delay-to-large and delay to small. Box and whisker plots summarize distribution of results for the six individuals tested. The whiskers show the minimum and maximum. The top of box shows the 0.75 quantile and the bottom shows the 0.25 quantile. The line through the box shows the median.

four pellets are twice as valuable as two pellets. In reality, the relationship between amount and value will be non-linear. We assume a linear relationship here, so that we may focus on the temporal elements of the problem.

Now, consider the difference

$$\Delta LTR = \frac{4}{\tau + DTL} - \frac{2}{\tau + DTS}. \tag{3}$$

When ΔLTR is negative, the small option yields a higher long term rate of gain; when it is positive, the large option gives the higher rate. A naive version of the long-term rate model predicts 0% choice of large when ΔLTR is negative, and 100% choice of large when ΔLTR is positive. This step function prediction is unrealistic, however, because many sources of variability affect animal behavior. Instead, one expects a sigmoid dose-response curve. Figure 8 plots ΔLTR versus P(Large) for the patch and self-control contexts. The figure shows a well defined sigmoid relationship in the patch context, and a more amorphous increasing relationship in the self-control context. Figure 8 also shows the least-squares fits for probits-style dose-response curves (which assume that the response threshold

follows a normal distribution, see Finney, 1962; Stephens, 1985, for a discussion of the probits technique). The patch data gives a better fit to this standard dose-response model in two ways. First, the patch data give a higher R^2 value (0.61 for patch and 0.19 for self-control). Second, the calculated indifference threshold is much closer to the predicted value of zero in the patch data (0.0052 for patch, 0.021 for self-control). We conclude, therefore, that the outcome in the patch context agrees, at least crudely, with the long-term rate model, while the self-control treatment does not.

Short-term model
Next, we consider the short-term rate model suggested by Bateson and Kacelnik (1996, and supported by much of the self-control literature). This model predicts preference for large when:

$$\frac{4}{DTL} > \frac{2}{DTS}$$

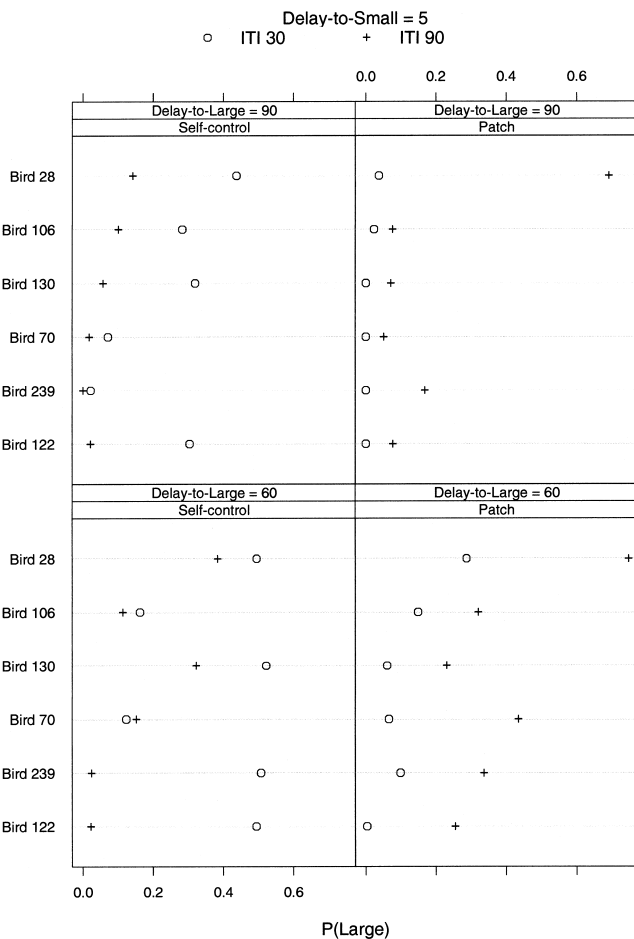Following the analysis above, we create a dose variable:

Figure 7
A comparison of measured p(Large) values at two levels of ITI for each subject in each condition when the delay-to-small is 5 s.

$$\Delta \text{STR} = \frac{4}{\text{DTL}} - \frac{2}{\text{DTS}}.$$

Table 3 shows ΔSTR calculations for our experiment. The table shows two clusters of ΔSTR. When the delay to small is 5 s, ΔSTR is about $-\frac{1}{3}$ predicting a relatively strong preference for the small, two pellet, option. However, when the delay to small is 50 s ΔSTR values are near zero, predicting indifference or a weak preference for large. These predictions agree with the results of our self-control treatments, where we observed preference for small when DTS = 5, and approximate indifference when DTS = 50. In contrast, jays in the patch treatment show a clear preference for the large alternative in the DTS = 50 condition.

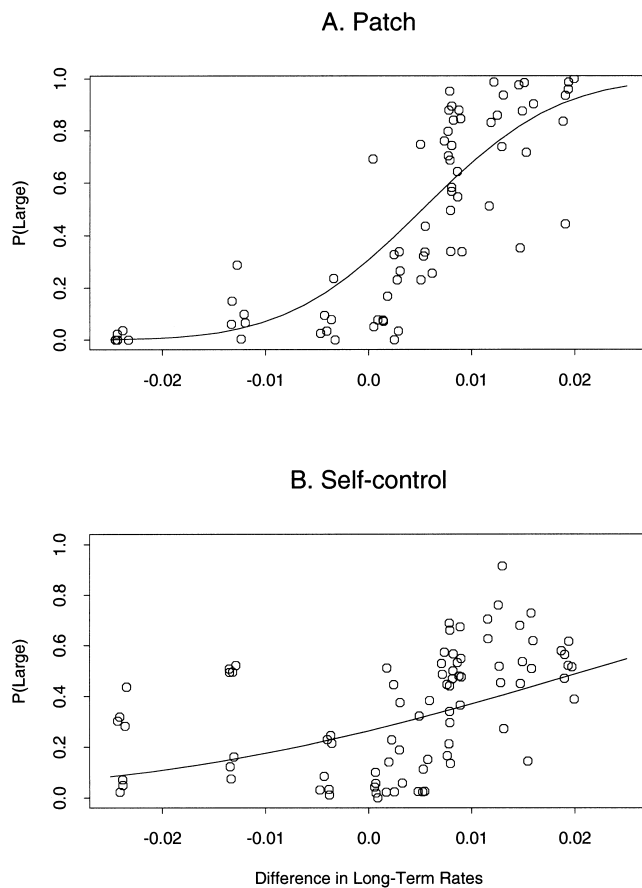Our self-control treatment agrees with the results of other

Figure 8
A plot of ΔLTR (as defined in Equation 3) versus p(Large) the proportion of free trial in which the subjects obtained the larger four pellet amount. The figure plots the results of both the patch (A) and self-control (B) treatments. The experiment created 12 levels of ΔLTR: a small amount of random variation was added to the ΔLTR values used in this plot so that points would not be plotted on top of each other. The solid curves show least-squares fits of probits-style dose-response relationships; $R^2 = .61$ for patch, and $R^2 = .19$ for self-control.

binary choice studies (e.g., Bateson and Kacelnik, 1996; Mazur, 1987; Mazur et al., 1985) that support short-term rate models. In a different, economically equivalent, choice situation modeled on patch exploitation, we find that the outcome agrees more closely with the long-term rate currency.

The "same rule/different outcomes" hypothesis
While the outcomes differ in the patch and self-control contexts, it does not necessarily follow that the jays use different choice rules in the different contexts. The jays might use a

Table 3
Calculation of ΔSTR

DTS	DTL	ΔSTR	Prediction	Median p (Large)	
				Self-Control	Patch
5	90	−0.3556	Prefer small	.07	.04
5	60	−0.3333	Prefer small	.19	.24
50	90	0.0444	Indifference/weak preference for large	.48	.72
50	60	0.0667	Indifference/weak preference for large	.54	.89

rule that compares short-term rates in both cases; such that these short-term rate comparisons achieve long-term rate maximization in the patch context, but not in self-control.

To see why our economic result does not imply a farsighted rule or even a different rule, consider the general form of the short-term rule:

$$\text{Choose ``2'' if} \quad \frac{G_2}{t_2} > \frac{G_1}{t_1} \quad (4)$$

When applied in the self-control context this rule (like the self-control data) disagrees with long-term maximization, ignoring the ITI and any post-feeding delay.

Consider, however, how one might apply this rule to the patch context (cf. Figure 4): after obtaining the small amount G_1 the subject must choose between "starting over" which leads to G_1 after a delay of $\tau + t_1$, and "continuing" which leads to $G_2 - G_1$ after a delay of $t_2 - t_1$. The short-term rule (4), therefore, predicts:

$$\text{Choose ``2'' if} \quad \frac{G_2 - G_1}{t_2 - t_1} > \frac{G_1}{\tau + t_1}$$

or equivalently, when:

$$\Delta\text{STR} = \frac{G_2 - G_1}{t_2 - t_1} - \frac{G_1}{\tau + t_1} > 0 \quad (5)$$

where ΔSTR is the difference in short-term rates. Applying a short-term rule in the patch context predicts sensitivity to the ITI-like term τ (because it is part of a key delay). Some algebra reveals a more startling result:

$$\underbrace{\frac{t_2 - t_1}{\tau + t_2}\left[\frac{G_2 - G_1}{t_2 - t_1} - \frac{G_1}{\tau + t_1}\right]}_{\Delta\text{STR}} = \underbrace{\frac{G_2}{\tau + t_2} - \frac{G_1}{\tau + t_1}}_{\Delta\text{LTR}} \quad (6)$$

where the term in square brackets is the difference in short-term rates (ΔSTR), and the right-hand side is the difference in long-term rates (ΔLTR). In our patch context, then, the short-term rule *always* agrees with, and even amplifies (because $(t_2 - t_1)/(\tau + t_2) < 1$), the difference in long-term rates; even though the same rule leads to notoriously short-sighted behavior in the self-control context. The simplest account of our results, therefore, is that jays use the same short-term rule in both situations, and this short-term rule approximates long-term maximizing in the patch situations, but not in the self-control situation.

Adaptive short-term rules

This suggests the following hypothesis. Natural selection has favored a mechanism based on short-term rate comparisons because these rules approximate long-term rate maximization in many natural decision contexts. Prey choice situations involving binary, mutually exclusive choice (as in self-control studies) are probably rare in nature, so animals may not be equipped to behave appropriately in these situations. While self-control studies give an accurate view of the rules of choice; we must consider the natural contexts of choice behavior, if we are to understand the adaptive value of these rules. The idea that "local rules" can achieve global consequences is not new. Among others Staddon (1983) emphasized a link between local rules and global consequences. Bateson and Kacelnik (1996) used similar reasoning to explain why there is an "ITI/travel time" effect in patch studies and not in self-control experiments.

This hypothesis raises several questions. First, the claim that foragers use the same rule in patch and self-control contexts can be tested directly. For example, an investigator might arrange situations where a decision "to leave" implies the same delay and amount as the "large" alternative in a parallel self-control treatment, while the decision to stay has the same time/amount consequences as the "small" alternative. Second, our patch condition represents a narrow slice of "natural" foraging problems. There are many other situations to explore; for example, patches with more than two food items; or diet choice problems where a forager must choose whether to attack or ignore sequentially presented food items.

Why short-term rules?

We argue that long-term rate rules, and short-term rate rules accomplish the same thing in patch use (and possibly other) situations. That is, they are equivalent adaptive peaks. Why, then, should animals use short-term rules instead of long-term? There are three possibilities. (1) It may be completely haphazard. The two rules are equivalent and one arose instead of the other via simple randomness. (2) Alternatively, it may reflect a feature of the neural and sensory mechanisms of choice. The neural machinery may be better suited to short-term rules, because common neural motifs such as opponent-processing may adapt more readily to a comparison of local rates. (3) Finally, short-term rules may have some advantage that we do not yet appreciate. There may, for example, be a psychophysical advantage as Equation 6 suggests, because short-term comparisons can make long-term differences more detectable. In addition, short-term rules might be advantageous because they reflect the small effects of discounting (collection risk, and lost opportunity risk). These possibilities are not, of course, mutually exclusive.

CONCLUSION

There have been two lines of evidence against the long-term rate currency of foraging theory: the strong preferences for immediacy seen in self-control studies, and data demonstrating so-called risk-sensitive preferences. Studies of risk-sensitivity show that animals prefer variable delays (see Kacelnik and Bateson, 1996, for review) even though infinite time-horizon rate models predict indifference to variability. We have argued that the self-control literature's evidence of short-term rules is not necessarily evidence of a short-term currency, because short-term rules can have long-term consequences in, at least some, natural decision contexts. We are not, however, trying to rehabilitate the long-term rate currency of classical foraging theory, because the risk-sensitivity data argues against it, and because there are a priori reasons to reject its infinite time-horizon. What alternative do we offer? We hypothesize that a long, but not infinite, term rate currency incorporating plausible levels of discounting will account for observed patterns of preference. A currency, however, is not enough. We must also understand how this currency has shaped the rules of choice in specific natural foraging situations. This suggests research focused on how currency and context have combined to shape decision rules.

REFERENCES

Ainslie, G, 1974. Impulse control in pigeons. J Exp Anal Behav 21: 485–489.

Ainslie, G, 1975. Specious reward: a behavioral theory of impulsiveness and impulse control. Psychol Bull 82:463–496.

Bateson M, Kacelnik A, 1996. Rate currencies and the foraging starling: the fallacy of the averages revisited. Behav Ecol 7:341–352.

Bateson M, Whitehead SC, 1996. The energetic cost of alternative rate currencies in the foraging starling. Ecology 77:1303–1307.

Baum W, Rachlin H, 1969. Choice as time allocation. J Exp Anal Behav 12:861–874.

Benson K, Stephens DW, 1996. Interruptions, tradeoffs and temporal discounting. Am Zool 36:506–517.

Charnov EL, 1976. Optimal foraging: the marginal value theorem. Theor Popul Biol 9:129–136.

Cleveland WS, 1993. Visualizing data. Summit, New Jersey: Hobart Press.

Finney DJ, 1962. Probit analysis. New York: Cambridge University Press.

Green L Jr, Fisher EB, Perlow S, Sherman L, 1981. Preference reversal and self-control: choice as a function of reward amount and delay. Behav Anal Lett 1:244–256.

Green L, Myerson J, 1996. Exponential versus hyperbolic discounting of delayed outcomes: risk and waiting time. Am Zool 36:496–505.

Kacelnik A, Bateson M, 1996. Risky theories—the effects of variance on foraging decisions. Am Zool 36:402–434.

Logue AW, Smith ME, Rachlin H, 1985. Sensitivity of pigeons to prereinforcer and postreinforcer delay. Anim Learning Behav 13:181–186.

Mazur JE, 1984. Tests of an equivalence rule for fixed and variable reinforcer delays. J Exp Psychol: Anim Behav Proc 10:426–436.

Mazur JE, 1986. Choice between single and multiple delayed reinforcers. J Exp Anal Behav 46:67–77.

Mazur JE, 1987. An adjusting procedure for studying delayed reinforcement. In: Quantitative analyses of behavior: the effect of delay and of intervening events on reinforcement value (Commons ML, Mazur JE, Nevin JA, Rachlin H, eds.). Hillsdale, New Jersey: Lawrence Erlbaum Associates; 55–73.

Mazur JE, 1989. Theories of probabilistic reinforcement. J Exp Anal Behav 51:87–99.

Mazur JE, Logue AW, 1978. Choice in a ''self-control'' paradigm: effects of a fading procedure. J Exp Anal Behav 30:11–17.

Mazur JE, Snyderman M, Coe D, 1985. Influences of delay and rate of reinforcement on discrete-trial choice. J Exp Psych: Anim Behav Proc 11:565–575.

McDiarmid CF, Rilling ME, 1965. Reinforcement delay and reinforcement rate as determinants of schedule preference. Psychonomic Sci 2:195–196.

Myers JL, Well AD, 1995. Research design and statistical analysis. Hillsdale, New Jersey: Lawrence Erlbaum and Associates.

Rachlin H, Green L, 1972. Commitment, choice and self-control. J Exp Anal Behav 17:15–22.

Snyderman M, 1987. Prey selection and self-control. In: Quantitative analyses of behavior: the effect of delay and of intervening events on reinforcement value. (Commons ML, Mazur JE, Nevin JA, Rachlin H, eds.). Hillsdale, New Jersey: Lawrence Erlbaum Associates.

Staddon JER, 1983. Adaptive behavior and learning. New York: Cambridge University Press.

Stephens DW, 1985. How important are partial preferences? Anim Behav 33:667–669.

Stephens DW, 1996. On the relationship between the feedback control of digestion and the temporal pattern of food intake. Biol Bull 191:85–91.

Stephens DW, Krebs JR, 1986. Foraging theory. Monographs in behavior and ecology. Princeton, New Jersey: Princeton University Press.

Stephens DW, Lynch JF, Sorensen AE, Gordon C, 1986. Preference and profitability: theory and experiment. Am Nat 27:533–553.

Stephens DW, Nishimura K, Toyer KB, 1995. Error and discounting in the iterated prisoner's dilemma. J Theor Biol 76:457–469.