

# The discounting-by-interruptions hypothesis: model and experiment

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Experimental animals often prefer small but immediate rewards even when larger-delayed rewards provide a higher rate of intake. This impulsivity has important implications for models of foraging and cooperation. Behavioral ecologists have hypothesized that animals discount delayed rewards because delay imposes a collection risk. According to this long-standing hypothesis, delay reduces value because an interruption that occurs while an animal is waiting may prevent it from collecting the delayed reward. Although there have been many experimental demonstrations of animal preferences for immediacy, none have included any interruptions. This paper develops a simple model of discounting by interruptions and then tests this model experimentally. The model considers the effects of interruption rate and duration on choice behavior. The experiment tests the effects of interruptions on the choice behavior of captive blue jays (*Cyanocitta cristata*) using a factorial design that manipulates the rate and duration of interruptions. The results do not support the discounting-by-interruptions hypothesis. This represents one of several lines of evidence suggesting that investigators should seek alternative explanations of the animal impulsivity. *Key words:* choice, decision making, discounting, foraging, impulsivity. [*Behav Ecol* 19:154–162 (2008)]

Animals make impulsive choices. That is, when we offer an animal a choice between one option that yields a small amount of food quickly and another that delivers a larger amount after a longer delay, the animal often prefers the smaller-sooner option even when the larger-later option produces a higher overall rate of intake (McDiarmid and Rilling 1965; Rachlin and Green 1972; Ainslie 1974; Mazur 1987; Bateson and Kacelnik 1996; Stephens and Anderson 2001). This phenomenon is important for several reasons. First, it contradicts models of foraging behavior based on rate maximization, and so it raises questions about how we might construct improved models of foraging behavior (Stephens and Krebs 1986; Bateson and Kacelnik 1996). Second, it is important in social behavior, where interacting animals must forego immediate gains to foster a relationship that will only pay off in the long term (e.g., Stephens et al. 1995, 2002). Finally, it is relevant to problems in human mental health. For example, more impulsive individuals are more susceptible to addiction (see, e.g., Bickel and Marsch 2001; Heyman and Dunn 2002), and impulsivity is a key symptom of attention-deficit hyperactivity disorder (King et al. 2003).

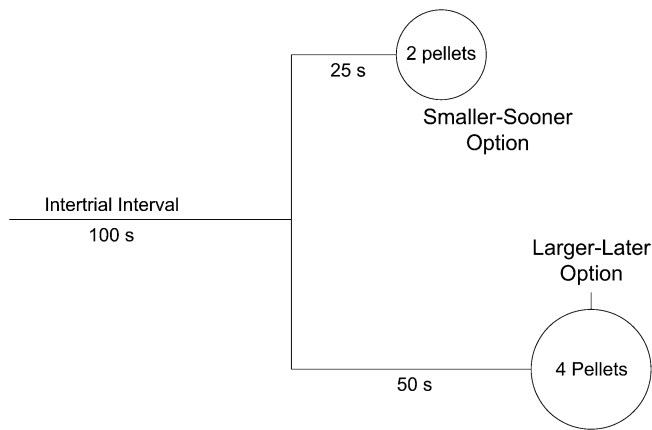
Students of nonhuman impulsivity have emphasized “discounting” as the basic explanation of animal preferences for immediate benefits (Kagel et al. 1986; Stephens and Krebs 1986; McNamara and Houston 1987; Sozou 1998; Sozou and Seymour 2003). According to the discounting interpretation, nonhuman animals prefer immediate food rewards because the passage of time reduces, or discounts, the value of delayed food rewards. This agrees with ideas from economics and finance where we would all agree that a sensible human investor should prefer \$100 today to \$100 delivered next year. Delay can discount the value of benefits for 2 reasons. First, delay can impose an opportunity cost: \$100 invested today will

be worth more than \$100 after a year has passed. Second, delay can impose a collection risk: \$100 today is a sure thing, but many things can happen during a year to prevent the investor from collecting his delayed \$100.

The literature of nonhuman discounting has focused almost exclusively on the “collection risk” explanation of discounting (Kagel et al. 1986; McNamara and Houston 1987; Benson and Stephens 1996; Sozou 1998). Specifically, theoreticians have argued that delay reduces the value of benefits because something may interrupt an animal while it waits for a delayed payoff, ultimately preventing it from collecting the delayed reward. This “discounting-by-interruptions” account of impulsive choice behavior has dominated thinking about the causes of animal impulsivity. Although many experimental studies have demonstrated animal impulsivity, none of these studies actually included interruptions. Given the prominence of the discounting-by-interruptions account of impulsivity, it is important to ask directly whether interruptions influence animal preferences for delayed food rewards, as one would predict. We present an experimental test of the effects of interruptions on choice behavior. As far as we are aware, this is the first experiment to test the effect of interruptions on impulsivity.

To lay the groundwork for our experiment, we developed a new model of discounting by interruptions. This was necessary because no existing models consider the effect of interruption duration. We have argued elsewhere (Stephens 2002) that implausibly frequent interruptions would be required to explain observed animal impulsivity, so our model explored the hypothesis that long interruptions might amplify the effect of interruptions on impulsivity even if they occur at a low rate. The model and experiment both focus on the binary choice situation shown in Figure 1. Experiments of this type offer subjects a choice between a smaller-sooner option (leading to a small amount of food after a short delay) and a larger-later option (offering a larger amount of food after a longer delay). Operationally, we say that an animal behaves impulsively if it chooses the smaller-sooner option when the larger-later option provides food at a higher rate.

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**Figure 1**  
Diagram of the self-control preparation used in this study. After waiting for a fixed time (the intertrial interval), the subject faces a choice between a larger-later option and smaller-sooner option.

**THE MODEL**

The model’s goal is to predict the proportional choice of the smaller-sooner versus larger-later options in a simple binary choice situation as shown in Figure 1. Psychologists sometimes call this experimental situation the “self-control paradigm.” We imagine that interruptions occur randomly. To generate collection risk, we assume that an animal loses any food item that it may be waiting for when an interruption occurs, and this means that the animal must wait until its next choice opportunity to obtain food. The model proceeds in 2 steps. Step 1 derives a model of the value associated with smaller-sooner and larger-later options and how these values depend on interruption rate and duration. Step 2 presents a model that compares the values derived in step 1 to predict the relative frequency of choice.

**Step 1. How interruption affects value**

We need an expression for the overall value or benefit associated with larger-later and smaller-sooner options when interruptions occur. Although there are several possible measures of “value,” we will use intake rate because it has a long history in the area and because one of our variables (interruption duration) affects rate but not some other possible measures of value.

To begin, we ignore the fact that the animal faces a choice and imagine a situation in which an animal has only one option. That is, it waits for an intertrial interval of  $\tau$ , then waits for a delay to  $t$ , and finally receives an amount  $A$ . We assume that an interruption can occur at any time and that the occurrence of interruptions follows a Poisson process with rate  $h$ . This means that the probability that an interruption will not occur in a given time  $t$  is  $e^{-ht}$ . Now, the rate is just the average amount gained per trial divided by the average time spent per trial. We can calculate the average amount fairly easily.

*Expected amount per trial*

To calculate this, we recognize 2 types of trials: interrupted trials and uninterrupted trials. An uninterrupted trial occurs only if no interruption occurs in time  $\tau + t$ , and we know this happens with probability  $e^{-h(\tau+t)}$ . The complementary probability of an interrupted trial is  $1 - e^{-h(\tau+t)}$ . Now our decision-making subject gets amount  $A$  from an uninterrupted trial and zero from an interrupted trial, so the average amount gained is

$$Ae^{-h(\tau+t)} + 0 \cdot (1 - e^{-h(\tau+t)}) = Ae^{-h(\tau+t)}.$$

*Expected time per trial*

Finding the expected trial duration is a bit trickier. If nothing interrupts the trial, it lasts  $\tau + t$  seconds. But if an interruption occurs, the trial lasts some unknown but shorter time, say  $T_i$  (for “interrupted” time). So the expected duration of a trial would be

$$(\tau + t)e^{-h(\tau+t)} + (1 - e^{-h(\tau+t)})(T_i + d) \tag{1}$$

where  $d$  is the duration of an interruption (one of our experiment’s treatment variables). This expression would solve the problem, except that we do not know the value of  $T_i$ . The variable  $T_i$  is the expected duration of a trial given that an interruption occurs. The Appendix shows that

$$T_i = \frac{1}{h} - \frac{e^{-h(\tau+t)}}{1 - e^{-h(\tau+t)}}(\tau + t). \tag{2}$$

Substituting this back into the equation for the expected trial duration (Equation 1), we find that the expected trial duration is

$$\left(d + \frac{1}{h}\right)(1 - e^{-h(\tau+t)}). \tag{3}$$

So the rate of intake is just the expected amount over the expected duration or

$$\frac{Ae^{-h(\tau+t)}}{\left(d + \frac{1}{h}\right)(1 - e^{-h(\tau+t)})}. \tag{4}$$

We call this expression, “the interrupted rate.” Notice that this becomes the conventional expression for intake rate

$$\frac{A}{\tau + t},$$

when  $h$  goes to zero.

Now, if we return to a choice situation. We have rate

$$r_1 = \frac{A_1 e^{-h(\tau+t_1)}}{\left(d + \frac{1}{h}\right)(1 - e^{-h(\tau+t_1)})} \tag{5}$$

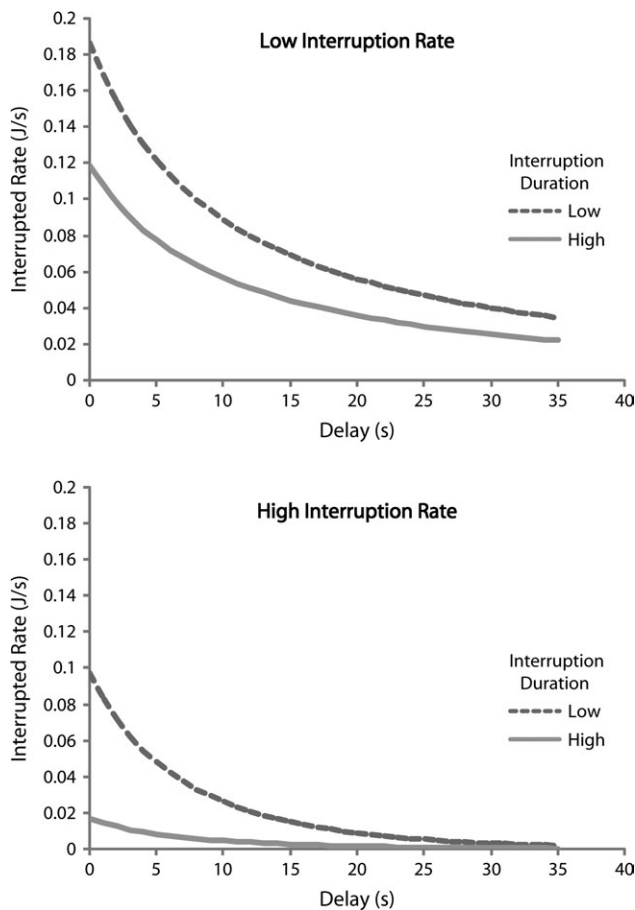
for option 1, which provides amount  $A_1$  after delay  $t_1$ , and

$$r_2 = \frac{A_2 e^{-h(\tau+t_2)}}{\left(d + \frac{1}{h}\right)(1 - e^{-h(\tau+t_2)})} \tag{6}$$

for option 2, which provides amount  $A_2$  after delay  $t_2$ . In broad outline, this model produces “hyperbolic” discounting (Ainslie 1974; Mazur 1987) because it is derived from a rate model and it predicts the phenomenon of preference reversal. As expected, increasing the interruption rate or the interruption duration decreases the value of a delayed reward (Figure 2). More interestingly, the model predicts an interaction between interruption rate and duration. Specifically, interruption duration has a larger effect when interruption rates are high. Obviously, this must be true in the extreme case where the interruption rate is zero (i.e., no interruptions occur) because changing the interruption duration when no interruptions occur cannot affect value.

**Step 2. Relative frequency of choice**

The next problem is to move from the 2 measures of value ( $r_1$  and  $r_2$ ) to a statement about how the difference between



**Figure 2**  
Plots showing how delay changes the interrupted rate for several different conditions. The top panel shows a low-interruption rate ( $h = 0.01$ ) case, and the bottom panel shows a higher interruption rate ( $h = 0.1$ ). Both panels show a plot for a high ( $d = 60$  s) and low ( $d = 2$  s) interruption duration. The rates calculated here assume an intertrial interval ( $\tau$ ) of 10 s and delay ( $t$ ) of 25 s and an amount ( $A$ ) of 25.

$r_1$  and  $r_2$  influences choice probability. In a naive model of choice, we might expect that the decision maker should choose option 1 if  $r_1 > r_2$  and option 2 otherwise, but we know that this sort of exclusive choice is unrealistic. To construct a probabilistic model of choice, we use a mathematical framework similar to that used by Gibbon in his scalar expectancy theory (Gibbon 1977).

In this model, we assume that the decision maker has internal representations of the values of the 2 options but that these representations are noisy. Specifically, we model these internal representations as 2 normal distributions with means  $r_1$  and  $r_2$ , respectively, and variances  $\sigma_1^2$  and  $\sigma_2^2$ . When the animal makes a choice, it draws a realization from each of the 2 distributions, say  $x_1$  from the option 1 distribution and  $x_2$  from the option 2 distribution and it selects option 2 if  $x_1 > x_2$ . So, the probability of choosing option 1 is  $P(x_1 > x_2)$  or equivalently  $P(x_1 - x_2 > 0)$ . The distribution of the difference of 2 normally distributed random variables is (again) normally distributed with mean  $r_1 - r_2$  and variance  $\sigma^2 = \sigma_1^2 + \sigma_2^2$ . So, the predicted probability of choice is

$$P(\text{option1}) = P(X_1 - X_2 > 0) = 1 - \Phi\left(\frac{r_1 - r_2}{\sigma^2}\right), \quad (7)$$

where  $\Phi$  is the cumulative density function of a standard normal distribution. To complete the calculation, we simply

substitute our equations for  $r_1$  and  $r_2$  (Equations 5 and 6) into the right-hand side of this expression. Notice that although most parameters in this model are easily measurable or experimentally manipulated (e.g., the amounts, delays, and interruption rates), the variance is an unknown property of the decision-making animal and must be estimated from choice behavior. It therefore represents a fitted parameter in our model. In principle, we can estimate the unknown value of  $\sigma^2$  from any observed choice probability where we also know the value of  $r_1$  and  $r_2$  because this gives an equation with only one unknown ( $\sigma^2$ ).

Figure 3 shows the relationship between delay to the smaller-sooner option and the probability of choosing the smaller-sooner option that our model predicts for a range of conditions. Each panel shows 2 levels of variance, and the 4 panels show different combinations of interruption rate and interruption duration. The variance parameter ( $\sigma^2$ ) measures the accuracy with which the subject can choose the option with the highest interrupted rate. When the variance ( $\sigma^2$ ) is low, the subject can choose more accurately, and we see a well-defined sigmoid transition between choosing the smaller-sooner and choosing the larger-later as delay increases. When the variance ( $\sigma^2$ ) is high, the subject chooses less accurately, and we see a less sigmoid, more linear pattern. As expected when interruption rates ( $h$ ) are high, subjects should prefer the smaller-sooner option at higher delays. Notice that the 50:50 point is higher in the 2 “high interruption rate” panels on the right. Finally, the interruption duration has little effect on predicted behavior when the interruption rate is low (the 2 panels on the right), but when the interruption rate is higher, increasing duration has the effect of “flattening” the relationship between delay and choice because high interruption durations reduce the absolute value of the difference in interrupted rates.

Our model compares the difference between the 2 alternatives, even though some students of psychophysics prefer ratio (rather than difference) comparisons (Gescheider 1985). We prefer the difference approach here because it is easier to incorporate stochasticity in a difference model. A ratio comparison might produce a better fit. We comment, however, that psychophysicists (e.g., Gibbon 1977) do use this “difference-of-normals” approach in certain situations.

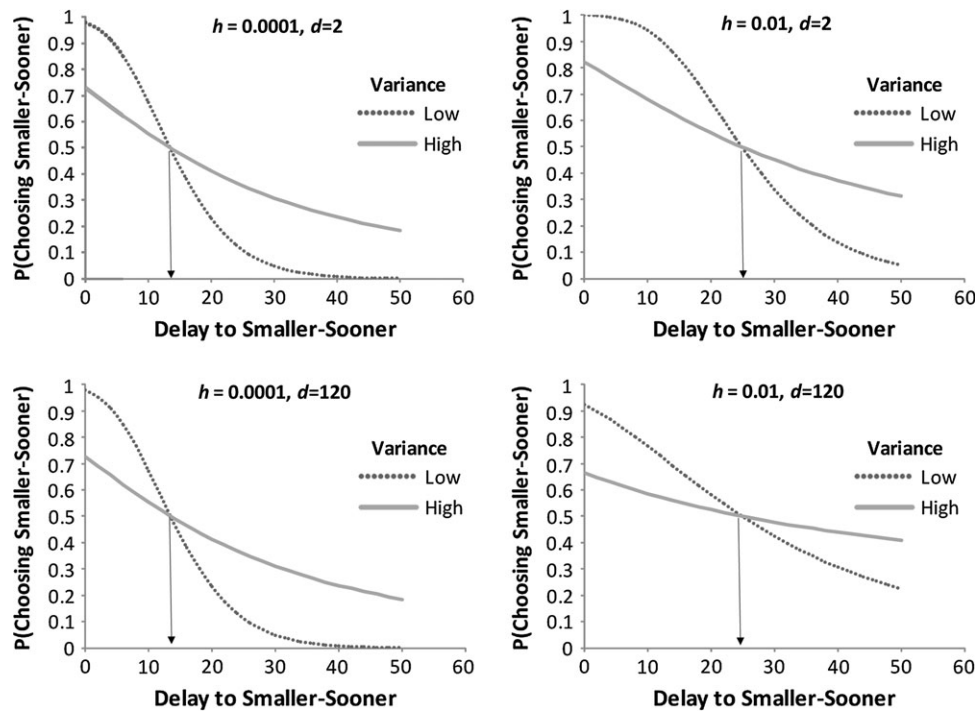
## EXPERIMENT

We designed an experiment to test the effects of interruption rate and interruption duration on impulsive choice. Following our model, we manipulated interruption rate and duration in a factorial design. To obtain some information about choice in the absence of interruptions, we also tested our subjects in 2 treatments without interruptions. We created interruptions by simply introducing “time-out” events that occurred at random times while the animal was making a sequence of choices, so that an interruption could occur at any time during a trial, either before or after the animal made its choice. When an interruption occurred, the animal lost whatever it was waiting for and had to “start over” (i.e., start a new trial) after the interruption ended. Notice that an interruption “interrupts” the foraging process (i.e., the sequence of trials), even though it ends the current trial. Natural interruptions might be caused by predators, conspecifics, or some sort of nonbiological event (e.g., weather), but the economically salient feature of interruptions is that they prevent a forager from collecting delayed benefits.

## Methods

### Apparatus

Figure 4 shows the apparatus used in this experiment. Each box was equipped with 2 front perch levers—one on the left



**Figure 3**

The predicted effects of interruption rate and duration on impulsivity. Each panel shows the relationship between the probability of choosing the smaller-sooner option and the delay associated with the smaller-sooner for our experimental parameters, for a situation in which the smaller-sooner option offers amount 2, the larger-later option offers amount 3 after a delay of 50 s, and the time between presentations ( $\tau$ ) is 60 s. In addition, each panel shows 2 plots, one for high choice variance (low discriminability of value) and a low choice variance (high discriminability of value). Finally, each panel shows the delay at which subjects should be indifferent (i.e., 50:50 choice) between the smaller-sooner and larger-later option. The first column shows 2 cases with a low interruption rate ( $h = 0.0001$ ). In this case, the interruption duration has virtually no effect. The second column shows 2 with a higher interruption ( $h = 0.01$ ), whereas interruption duration still has little effect on the indifference point it tends to “flatten” the predicted relationship between delay and choice probability as described in the text.

and one on the right, a rear perch lever, and a food cup. We positioned a stimulus light above each perch, and a magazine light above the food cup indicated food delivery. A houselight in the box’s ceiling provided illumination. We attached each box to a computer using commercially available interfacing equipment (Med Associates Inc, St. Albans, VT). We used programs written in the MED-PC IV language to control the contingencies that birds experienced in the apparatus.

*Subjects and training*

Twelve blue jays (*Cyanocitta cristata*) of unknown gender and mixed experimental history served as subjects (band numbers 5, 11, 13, 20, 24, 51, 76, 78, 81, 92, 93, and 208). We trained subjects using conventional shaping techniques. In preparation for this experiment, we trained each jay to perform a task called *light following*. In the light following task, the subject waits on the back perch and hops forward to obtain food at the one of the front perches when the computer switches on the associated stimulus light. We considered a bird ready for the experiment when it had mastered this task.

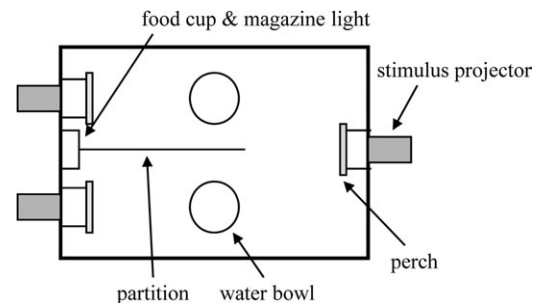
*Closed economy*

We maintained our subjects in a modified closed economy. That is, subjects spent 23 h/day in the apparatus and obtained all their food from the apparatus. The exception to this rule was that we supplemented a subject’s daily ration of food (at 1700 h) if it obtained less than 8 g of food during the experimental day. Following our animal care protocol, we adjusted this “feed-up” amount in increments of 0.5 g. We adjusted it

upward if a bird failed to maintain a healthy body weight, and we adjusted in downward if a bird gained weight or was not motivated to feed. After the experiment started, we adjusted feed-up amounts only rarely. Houselights provided illumination from 0700 to 1900 h, and birds performed trials from 0800 to 1200 h and 1300 to 1700 h.

*Trials*

Figure 1 shows the general structure of an experimental trial. Experimental trials followed the self-control paradigm, which is widely used in studies of impulsivity. In this procedure, the subject waited for fixed time (called the intertrial interval). When the intertrial interval expired, the apparatus offered



**Figure 4**  
An overhead view of the apparatus used in this experiment. The apparatus was 41 cm wide, 53 cm long, and 46 cm high.

a choice between a smaller-sooner option and a larger-later option. After an intertrial interval of 100 s, the subject could choose between a smaller-sooner option that produced 2 food pellets after a delay of 25 s and a larger-later option that produced 4 food pellets after a delay of 50 s. Notice that choosing the smaller-sooner option is an impulsive error in this situation because the smaller-sooner option yields an overall intake rate of  $2/125 = 0.016$  pellets/s, whereas the larger-later option yields an overall intake rate of  $4/150 = 0.027$  pellets/s. To ensure that subjects had experience with both alternatives, we interspersed forced trials (in which the apparatus offers only one option) among the free choice trials. To achieve this, we organized trials in blocks of 32. The first 8 trials in a block were forced trials, and the final 24 trials were free trials. During the sequence of 8 forced trials within each block, the computer randomly determined which option would be offered (smaller-sooner or larger-later) and on which side of the apparatus. During free trials, the computer randomly determined whether the smaller-sooner option appears on the right or left side of the apparatus.

To signal the start of new trial, the computer began flashing the light associated with rear perch. When the subject occupied the rear perch, the light stopped flashing and the intertrial interval began. When the intertrial interval expired, the 2 stimulus lights associated with the front perches began flashing and the experimental computer randomly chose whether the smaller-sooner option was shown on the right or left. The bird chose between the 2 alternatives by hopping forward to its adjacent perch. Once the bird was on its front perch, the computer switched off the unchosen light, the light on the "chosen side" stopped flashing and began burning steadily, and the delay associated with chosen option began. After this delay expired, the pellet feeder dispensed the appropriate amount of food. We randomly selected the pairs of colors associated with the 2 options for the following list: blue-yellow, green-red, red-yellow, and red-blue. After selecting a color pair for each bird, we assigned the stimulus color associated with the smaller-sooner options randomly for each bird, but these assignments remained the same throughout the experiment for each bird.

#### *Interruptions*

When an interruption occurred, the computer switched off the houselight, all stimuli went dark, and the computer ignored any responses the subject made during the interruption. In addition, an interruption cancelled any delivery that the subject may have been waiting for. The computer initiated a new trial at the end of the programmed interruption. So, an interruption ended the current trial, but the jay returned to foraging (with a new trial) when the interruption ended. Interruptions occurred according to a Poisson process (as in our model), so that time from the end of one interruption to the beginning of the next was an exponentially distributed random variable. Notice that this means that an interruption could occur at any time during the trial.

#### *Treatments and treatment order*

The experiment followed a within-subjects design in which each subject experienced all 8 treatments: 2 treatments without interruptions and 6 treatments created by a factorial combination of 2 levels of interruption rate and 3 levels of interruption duration. We ran the first "no interruption" treatments before the factorial treatments, and we ran the second no interruption treatment after the factorial treatments. In the factorial treatments, we used 2 levels of interruption rate and 3 levels of interruption duration. In the low-interruption rate treatment, subjects experienced 0.0012 interruptions/s, which is roughly one interruption every

13 min (roughly 6 trials). In the high-rate treatment, subjects experienced 0.0024 (approximately one every 6.5 min) interruptions per second or roughly one interruption every 7 min (roughly 3 trials). The 3 levels of interruption duration were 2, 60, and 120 s. We randomly selected the order of these 6 treatments for each individual. We tested each bird in each treatment for 900 free trials.

#### **Data reduction**

A computer recorded data for each trial and treatment. To look for patterns of acquisition, we divided the 900 free trials within each treatment into 3 blocks of 300. In analyses where we need a single measure of performance for each treatment, we use the final 300 trials within each treatment. For example, our basic measure of impulsivity is the relative frequency with which a subject chose the smaller-sooner option, denoted by  $P(\text{smaller-sooner})$  in the final 300 free trials of a treatment. Greater  $P(\text{smaller-sooner})$  values indicate higher levels of impulsivity.

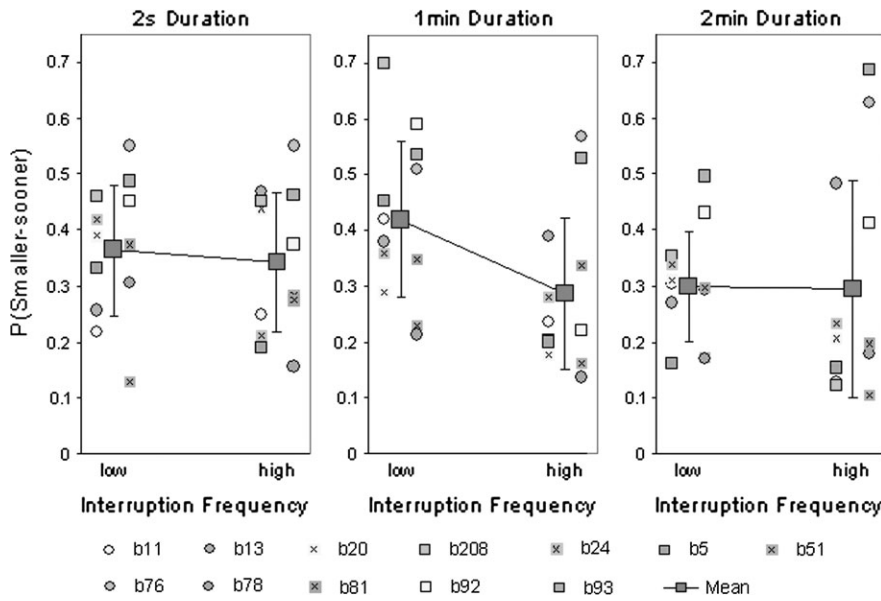
#### **Results**

##### *Overview*

Figure 5 summarizes the results of the interrupted treatments by bird, interruption frequency, and interruption duration. As the figure shows, the individual birds vary considerably. It is clear, however, that the figure does not support the idea that impulsiveness [measured as preference for the small-immediate option,  $P(\text{smaller-sooner})$ ] increases with interruption frequency. In addition, the figure suggests that the treatments with a 1-min interruption duration differ from the others.

##### *Analysis of variance results*

As a first step in our analysis, we performed a 1-way repeated-measures analysis of variance (ANOVA) that considered all 8 treatments of the experiment. This analysis considers the before and after no interruptions treatments in the same analysis as the 6 treatments in the factorial design (3 levels of interruption duration and 2 levels of interruption frequency). Although it may seem natural to include no interruptions as a third level of interruption frequency, we could not do this because changes in interruption duration have no meaning when there are no interruptions. This 1-way analysis, therefore, provides a way to analyze all the data within a single framework. This analysis shows clear evidence of a treatment effect ( $F_{7,77} = 3.49, P = 0.0026$ ). Inspection of the data suggests that 2 treatments, "no interruptions before" and "low interruption rate, 60-s interruption duration" seem to produce higher levels of impulsivity than the other treatments. We used Fisher's least significant difference technique to test for differences between these 2 treatments and all others. This analysis showed that the 'no interruptions before' treatment differed significantly from all treatments except 2 (low interruption rate, 2-s interruption duration, and low interruption rate, 60-s interruption duration). In addition, the low interruption rate, 60-s interruption duration treatment also differed significantly from all treatments but 2 (low interruption rate, 2-s interruption duration, and high interruption rate, 2-s interruption duration). Our analysis showed no other pairwise comparisons to be significantly different, so one of these 2 treatments is involved in all the significant differences detected in our post hoc analysis. Notably these 2 treatments also produced the highest levels of impulsivity (measured as proportional choice of the smaller-sooner option). Superficially, at least, this would seem to contradict the hypothesis that interruptions increase impulsiveness because we observed



**Figure 5**  
An overview of our results. The plots show the relative frequency with which each individual chose the smaller-sooner option [denoted by  $P(\text{smaller-sooner})$ ] for each treatment.

significantly higher levels of impulsivity in 2 cases with relatively low interruption rates.

A second analysis tested the interaction between interruption duration and interruption rate using factorial ANOVA. As explained above, this analysis excludes the before and after no interruption treatments. This analysis reveals a significant interaction between frequency and duration ( $F_{2,22} = 3.83, P = 0.037$ ). This interaction shows the elevated impulsivity of the low interruption rate, 60-s duration treatment in a slightly different context. Analyzed in this way, the observed pattern suggests that although interruption rate had little effect in the 2- and 120-s duration treatments, impulsivity declined with interruption rate in the 60-s treatment (see Figure 6). In addition, this analysis found a significant main effect of interruption duration ( $F_{2,22} = 3.97, P = 0.033$ ) but no main effect of interruption rate ( $F_{1,11} = 2.47, P = 0.14$ ).

*Predictions versus observations*

Using the model developed above, we calculated how interruption rate and duration should affect proportional choice of the smaller-sooner option. These calculations required that we estimate one parameter from the data. We used the mean probability of choice from the 2 no interruptions treatments to estimate the required parameter (see Appendix for details). Using this parameter, we then made predictions for the 6 interruption frequency/interruption duration treatments. Figure 7 plots these predicted values versus observed values (averaged for all subjects). As the figure shows, the observed pattern of choice differs markedly from the predictions. Our model predicts that impulsivity (measured as proportional choice of the smaller-sooner alternative) should increase with interruption rate and with the interruption duration. However, the data show a tendency for a decrease in impulsivity with increasing interruption rate, and we find the lowest values of “impulsivity” in the highest duration treatment.

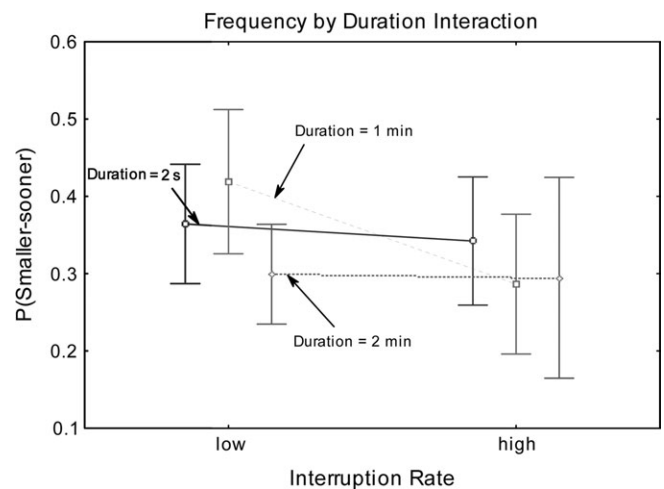
**Discussion**

*Significance*

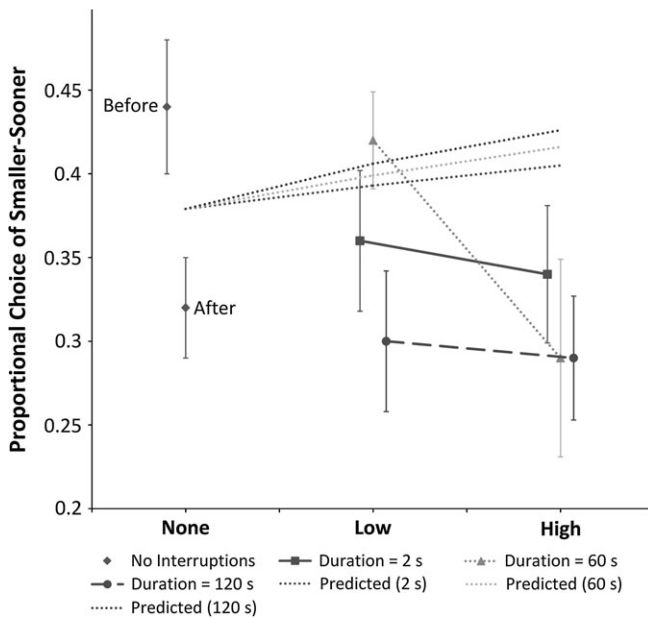
We present a simple model of discounting by interruptions that makes experimentally testable predictions about the effects of interruptions on preference. In agreement with the

widely accepted discounting-by-interruptions hypothesis, our model predicts that animals should be more impulsive when interruptions occur at higher rates and when they last longer. This paper presents the first experimental analysis of the effects of interruptions on animal impulsivity. This is important because the discounting-by-interruptions hypothesis has dominated thinking about the adaptive value of animal impulsivity. Our data does not support this discounting-by-interruptions explanation of animal impulsivity. The failure of interruptions to influence impulsivity as predicted should lead us to consider alternative explanations.

Students of impulsivity have suggested 2 alternatives to the discounting-by-interruptions hypothesis. The first possibility is discounting by lost opportunity. For human investors, discounting by lost opportunity occurs because the investor can use money obtained today to produce a return, whereas she cannot invest delayed income until later. Students of animal behavior have tended to dismiss this idea because it is not



**Figure 6**  
The significant interaction between frequency and duration observed in our experiment ( $F_{2,22} = 3.83, P = 0.037$ ). The error bars show 95% confidence limits.



**Figure 7** Comparison of predicted and observed values. The solid lines show the observed relative frequency with which our subjects chose the smaller-sooner option, averaged across all 12 subjects for each treatment; the error bars extend one standard error from the observed mean. The dotted lines show the predicted probability of choice derived from the model presented in the Appendix. Note that we estimated the variance parameter ( $\sigma^2$ ) for our model from the mean of the 2 no interruptions treatments so that the predictions for the 3 conditions emerge from this point.

clear how we can formulate a “return on investment” for nonhuman animals. Perhaps, we should reconsider whether the discounting-by-lost-opportunity hypothesis may be relevant to animal behavior. Second, our research group has advocated the “ecological rationality” hypothesis (Stephens and Anderson 2001; Stephens 2002; Stephens et al. 2004), which holds that natural selection has favored impulsive decision rules because they produce high long-term gains in naturally occurring choice situations. The ecological rationality hypothesis argues that observed impulsivity is an artifact of the binary, mutually exclusive choice situation used in many operant studies. The ecological rationality hypothesis can, in principle, explain impulsivity without interruptions (or any discounting process). We feel that evidence against the discounting-by-interruption hypothesis indirectly supports the alternative ecological rationality hypothesis. The occurrence of some discounting, however, seems both logical and inevitable, but we question whether naturally occurring discounting (via interruptions or lost opportunity) is sufficient to explain observed impulsivity.

#### Results in context

The discounting-by-interruptions hypothesis has a long history in behavioral ecology. The early papers that introduced the problem of impulsive choice to behavioral ecologists (Kagel et al. 1986; Stephens and Krebs 1986; McNamara and Houston 1987) typically emphasized this hypothesis. A paper by McNamara and Houston (1987) articulated a fairly complete theory of how interruptions could promote a preference for immediacy. Although several other papers developed the hypothesis (e.g., Benson and Stephens 1996; Green and Myerson 1996; Stephens 2002), a relatively recent paper by Sozou (1998) represents the most sophisticated development

of the discounting-by-interruptions hypothesis. Although behavioral ecologists have been concerned with how selection can favor impulsive choice, animal psychologists have continued to describe the properties of this behavior. Many results from animal psychology support the so-called hyperbolic discounting model (Ainslie 1974; Mazur 1987). According to this model, animals behave as if the perceived value of delayed food follows the expression:

$$\frac{A}{1 + kt}$$

where  $t$  is the delay from choice point until the animal obtains amount  $A$  and  $k$  is a fitted parameter. Notice that in the phrase “hyperbolic model of discounting,” psychologists are using the word discounting in a different sense than it is used in the phrase “discounting by interruptions.” In discounting by interruptions, we mean that interruptions reduce the value of delayed food rewards; but in the hyperbolic model of discounting, psychologists mean that animals behave as if the value of delayed food decays according to a hyperbolic equation. In practice, hyperbolic discounting refers to a mathematical description of observed impulsivity, whereas discounting by interruptions refers to an explanatory hypothesis about the economic cause of impulsivity. Even if we reject explanatory discounting models, descriptive models like the hyperbolic discounting model can be valid and useful.

#### Clarifications

As the first study to assess the effect of interruptions on animal impulsivity directly, our study raises several questions. For example, we created interruptions by imposing periodic blackouts. From an economic perspective, all that matters is that interruptions prevent the subject from collecting a food item that it is waiting for; however, one may wonder whether another type of interruption may be more effective. We can imagine 3 more naturalistic ways to create interruptions. First, one could simulate prey escape, following the hypothesis that foragers attacking mobile prey face a collection risk if they wait too long because mobile prey can escape. Second, one could simulate social interruptions in which simulated or real group mates steal food. Finally, one could simulate predatory attacks that interrupt foraging. Each of these provides interesting possibilities for further study.

Another issue is how one should calculate the predicted effects of interruptions on impulsivity. We used a modified rate model, but we acknowledge that some alternative formulation may capture the effects of interruptions more accurately. However, our observations differ so radically from our expectations that we think the details of how we calculated predicted values may be relatively unimportant.

#### Limitations and further questions

Although the discounting-by-interruptions hypothesis focuses on the adaptive value of impulsivity, our experiment clearly does not address the evolutionary history of impulsive behavior. Instead, following the traditions of experimental behavioral ecology, our experiment asks whether the observed properties of impulsive behavior are consistent with the hypothesis that interruptions have shaped impulsive choice. A proponent of the discounting-by-interruptions hypothesis might argue, however, that although interruptions have shaped the properties of impulsive behavior during the course of evolution, impulsivity is not sensitive to short-term changes in interruption rate. According to this “hardwired” hypothesis, our experiment’s expectation that animals should adjust their behavior in response to experienced interruptions is unreasonable. Although we acknowledge that impulsivity

may be hardwired, we offer 3 arguments against this view. First, we did find effects of interruptions on impulsivity, but these were not consistent with discounting-by-interruptions hypothesis. Second, existing demonstrations of animal impulsivity use novel situations in which the subject must use its experience to adjust its behavior, so a proponent of this argument must argue that animals can adjust their responses to delay (e.g.) but not its response to the level of interruptions. Finally, the hardwired hypothesis leads us to ask why animal discounting would be insensitive to experience. This could occur because natural interruption rates do not change or because they change so unpredictably that flexible impulsivity does not pay (Stephens 1991). Both extremes seem implausible to us. Interruption rates probably change in many situations (changes in group size that affect interruption by conspecifics, changes in predation risk that follow seasonal or diurnal patterns), and many of these patterns probably persist long enough to make adjustments worthwhile. A point in favor of the hardwired hypothesis, however, is that it may be difficult to detect changes in the rate of infrequent events, and this may limit the value of responses to changes in interruption rates.

Finally, a critic might argue that our treatments were not extreme enough to create a response. Our model agrees with this critique to some extent because it predicts a relatively small effect of interruption rate. If, however, only extreme interruption rates can influence preference behavior, then one must question the relevance of interruptions to animal impulsivity. Of course, we agree that further studies with more extreme treatments would be informative, but we feel that the departures from predictions observed in our study provide important evidence against the discounting-by-interruptions hypothesis. As Stephens has argued elsewhere (Stephens 2002), interruption rates in nature are probably relatively low (probably much less than 0.01/s) on average. This does not preclude the possibility that interruption rates could be quite high in some situations. For example, in social groups, competing conspecifics may create very high interruption rates. A problem here is that we know very little about naturally occurring interruptions.

*Summary*

Animal impulsivity represents a basic problem in animal choice behavior. The long-standing discounting-by-interruptions hypothesis holds that impulsive choice occurs because the risk of interruptions reduces the value of delayed benefits. This paper presents the first experimental evidence showing how interruptions affect preferences. Our results do not support the discounting-by-interruptions hypothesis. Instead our results suggest that investigators should develop alternative explanations of impulsivity, such as the ecological rationality hypothesis (Stephens et al. 2004).

**APPENDIX: MODEL AND PREDICTED VALUES**

This appendix gives the derivation for the expected duration of an interrupted trial (denoted by  $T_i$ ), and it explains how we calculated the model's single fitted parameter ( $\sigma^2$ ) and used this value to calculate predicted levels of impulsivity.

*Expected duration of an interrupted trial*

The variable  $T_i$  is the expected duration of a trial given that an interruption occurs. Let  $X$  be the random variable that represents the duration of an interrupted trial. So that  $T_i$  is the expected value of  $X$ —in symbols  $T_i = E(X)$ —and the random variable  $X$  is drawn from an exponential distribution truncated between 0 and  $t + \tau$ , say  $f(x)$ . In symbols, this is

**Table A1**

**Predicted choice of smaller-sooner option [ $P(\text{small})$ ]**

Interruption frequency	Interruption duration (s)		
	2	60	120
Low	0.393	0.399	0.406
High	0.405	0.416	0.426

$$f(x) = \begin{cases} \frac{he^{-hx}}{1-e^{-h(t+\tau)}}, & 0 < x < t + \tau, \\ 0, & \text{otherwise.} \end{cases}$$

Using this distribution, we can calculate the expected value of  $T_i$  directly

$$T_i = E(X) = \int_0^{t+\tau} xf(x)dx = \int_0^{t+\tau} x \frac{he^{-hx}}{1-e^{-h(t+\tau)}} dx.$$

After performing the integration and simplifying slightly we find

$$T_i = \frac{1}{h} - \frac{e^{-h(t+\tau)}}{1-e^{-h(t+\tau)}}(\tau + t) \tag{A2}$$

which is the value we seek.

*Estimation of the unknown variance and explicit predictions*

We used the measured frequency of choice in our no interruption treatments (which we conducted before and after the main factorial experiment that varied interruption rate and interruption duration). We observed an average choice of the smaller-sooner option in these no interruption treatments of 0.379599, this gives the equation:

$$1 - 0.379599 = 1 - \Phi\left(\frac{\eta_1 - \eta_2}{\sigma^2}\right)\Big|_{h=0, d=0} \tag{A3}$$

Note that we interpret “option 1” to be the larger-later option, so we need the complement of 0.379599 to apply equation (1.8); note also that we evaluate the right-hand side (as indicated) with an interruption rate of zero. We used a numerical root finding routine to find  $\sigma^2$  estimating a value of 0.03479. Using this value, it is straightforward to calculate quantitative predictions from expression (1.7). Table A1 shows the predicted values.

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**REFERENCES**

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

- Bateson M, Kacelnik A. 1996. Rate currencies and the foraging starling: the fallacy of the averages revisited. *Behav Ecol.* 7:341–352.
- Benson K, Stephens DW. 1996. Interruptions, tradeoffs and temporal discounting. *Am Zool.* 36:506–517.
- Bickel WK, Marsch LA. 2001. Toward a behavioral economic understanding of drug dependence: delay discounting processes. *Addiction.* 96:73–86.
- Gescheider GA. 1985. *Psychophysics: method, theory, and application.* 2nd ed. Hillsdale (NJ): Lawrence Erlbaum Associates.
- Gibbon J. 1977. Scalar expectancy theory and Weber's law in animal timing. *Psychol Rev.* 84:279–325.
- Green L, Myerson J. 1996. Exponential versus hyperbolic discounting of delayed outcomes: risk and waiting time. *Am Zool.* 36:496–505.
- Heyman GM, Dunn B. 2002. Decision biases and persistent illicit drug use: an experimental study of distributed choice and addiction. *Drug Alcohol Depend.* 67:193–203.
- Kagel JH, Green L, Caraco T. 1986. When foragers discount the future: constraint or adaptation? *Anim Behav.* 34:271–283.
- King JA, Tenney J, Rossi V, Colamussi L, Burdick S. 2003. Neural substrates underlying impulsivity. *Annals NY Acad Sci.* 1008:160–169.
- Mazur JE. 1987. An adjusting procedure for studying delayed reinforcement. In: Commons ML, Mazur JE, Nevin JA, Rachlin H, editors. *Quantitative analyses of behavior: the effect of delay and of intervening events on reinforcement value.* Hillsdale (NJ): Lawrence Erlbaum Associates. p. 55–73.
- McDiarmid CF, Rilling ME. 1965. Reinforcement delay and reinforcement rate as determinants of schedule preference. *Psychon Sci.* 2:195–196.
- McNamara JM, Houston AI. 1987. A general framework for understanding the effects of variability and interruptions on foraging behaviour. *Acta Biotheor.* 36:3–22.
- Rachlin H, Green L. 1972. Commitment, choice and self-control. *J Exp Anal Behav.* 17:15–22.
- Sozou PD. 1998. On hyperbolic discounting and uncertain hazard rates. *Proc R Soc Lond B.* 265:2015–2020.
- Sozou PD, Seymour RM. 2003. Augmented discounting: interaction between ageing and time-preference behaviour. *Proc R Soc Lond B Biol Sci.* 270:1047–1053.
- Stephens DW. 1991. Change, regularity and value in the evolution of animal learning. *Behav Ecol.* 2:77–89.
- Stephens DW. 2002. Discrimination, discounting and impulsivity: a role for an informational constraint. *Philos Trans R Soc.* 357: 1527–1537.
- Stephens DW, Anderson D. 2001. The adaptive value of preference for immediacy: when shortsighted rules have farsighted consequences. *Behav Ecol.* 12:330–339.
- Stephens DW, Kerr B, Fernandez-Juricic E. 2004. Impulsiveness without discounting: the ecological rationality hypothesis. *Proc R Soc Lond B.* 271:2459–2465.
- Stephens DW, Krebs JR. 1986. *Foraging theory.* Princeton (NJ): Princeton University Press.
- Stephens DW, McLinn CM, Stevens JR. 2002. Discounting and reciprocity in an Iterated Prisoner's Dilemma. *Science.* 298:2216–2218.
- Stephens DW, Nishimura K, Toyer KB. 1995. Error and discounting in the Iterated Prisoner's Dilemma. *J Theor Biol.* 176:457–469.