Choice and context: testing a simple short-term choice rule

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Psychological studies of animal choice show that the immediate consequences of choice strongly influence preference. In contrast, evolutionary models emphasize the longer-term fitness consequences of choice. Building on recent work by Stephens & Anderson (2001, *Behavioral Ecology* **12**, 330–339), this study presents two experiments that address this conflict. Stephens & Anderson developed an alternative choice situation based on patch-leaving decisions and compared this to the binary choice, or self-control, situation typically used in psychological studies. They hypothesized that the same short-term choice rule could account for choice in both situations, maximizing long-term gains in the patch situation, but typically producing shortsighted results in the self-control case. Experiment 1 used captive blue jays, *Cyanocitta cristata*, to test this 'same rule' hypothesis. The results do not support this hypothesis, suggesting that if a single rule applies, it is probably a more complex rule. Stephens & Anderson also hypothesized that a rule based on the delay to the next meal could explain why the intertrial interval has little effect in binary choice studies, even though the analogous travel time strongly affects patch-leaving decisions. When an animal leaves a patch, it experiences a delay consisting of the travel time plus time spent searching in the patch until food is obtained. Experiment 2 tested the hypothesis that travel time and search time combine additively, behaving like a single delay. Using treatments that created the same combined delay via different combinations of travel and search time, we found no evidence of nonadditivity, suggesting that these two components may indeed be treated as a single delay.

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Animals often prefer small, quickly delivered food rewards, even when they could do better (sometimes much better) in the long run by waiting for larger, more delayed rewards (e.g. McDiarmid & Rilling 1965; Rachlin & Green 1972; Mazur 1987; Bateson & Kacelnik 1996; Stephens & Anderson 2001). This impulsivity is important in the analysis of food choice behaviour for two reasons. First, many behavioural ecologists interpret these results to mean that traditional 'long-term' models of the fitness value of food are wrong (Stephens & Krebs 1986; McNamara & Houston 1987; Bateson & Kacelnik 1996; Kacelnik & Bateson 1996). According to this argument, impulsivity occurs because animals discount the future, placing more value on food obtained immediately and less on delayed food benefits. Second, impulsivity may reflect the properties of underlying choice mechanisms or rules. These rules may exist because natural selection discounts long-term gains or because some constraint (e.g. neural, genetic, etc.) prevents the evolution of farsighted rules.

The majority of our information about animal impulsivity comes from binary choice studies (Ainslie

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1975; Green et al. 1981; Mazur 1984, 1986, 1987, 1989, 1991; Bateson & Kacelnik 1996). In a single trial from such a study, the subject waits for an experimentally determined intertrial interval (ITI), and then the apparatus offers a choice, such as between an alternative associated with a green light and another associated with a red light (Fig. 1). The subject has had experience with the lights and their consequences, which familiarize it with the small-immediate and large-delayed alternatives. Psychologists call these studies self-control experiments, because an animal choosing to wait for a larger but delayed reward is said to show self-control. The self-control preparation is a logically elegant way to ask an animal whether it is willing to wait, and under what conditions.

Two results arise from self-control studies (reviewed in Stephens & Anderson 2001). First, the effect of delay on preference is very strong. We can measure the effect of delay by fitting a discounting function that relates subjective value (as measured by the animal's preference) to delay. These fitted functions typically show that the first second of delay leads to a loss of 10–50% of the original value (Mazur 2000). Second, the intertrial interval has little or no effect on preference (Bateson & Kacelnik 1996; Goldshmidt et al. 1998; Gallistel & Gibbon 2000).

These results are surprising for two reasons. First, although it is logical that delay should decrease the value of an alternative via economic discounting, it is difficult to imagine discounting processes that can account for a 50% loss in a single second. Second, the intertrial interval is analogous to the travel or search time in studies of patch exploitation. In these studies, increases in travel time reliably cause animals to spend more time and extract more resources from each patch (Stephens & Krebs 1986). Why do not analogous increases in the ITI shift preference towards the larger, more delayed alternative? Gallistel & Gibbon (2000) have called this the 'subjective sunk time' effect, because animals behave as though the ITI is an irrelevant or 'sunk' cost.

These self-control results suggest that animal choice is shortsighted, depending only on the value of the food item (i.e. A_i) and the delay until it can be obtained (t_i). The simplest version of such a shortsighted rule is: choose option 1 if

$$\frac{A_1}{t_1} > \frac{A_2}{t_2}. \qquad (1)$$

We call this a delay-to-food rule, because an animal using it looks forward from the choice point (Fig. 1a) and asks which alternative will produce the higher short-term rate in the interval between the choice and food delivery. This rule agrees with self-control results because it predicts very strong discounting and no effect of the intertrial interval (τ) (Baum & Rachlin 1969; Mazur 1987; Bateson & Kacelnik 1996).

In some situations, however, an animal using this short-term rule will pay a significant long-term cost. Consider, for example, an animal that must choose between a small-immediate option, delivering 3 units of food after 1 min and a large-delayed option delivering 8 units of food after 4 min. The shortsighted rule (equation 1) favours the small-immediate option, because 3/1>8/4. Now suppose that the intertrial interval (τ) is 5 min. In this case, an animal consistently choosing the small-immediate option obtains 3/(5+1), or 0.5 units/min, while choosing the large-delayed option leads to 8/(5+4), or 0.89 units/min. Over the course of a few choices, an animal using the short-term rule pays a significant opportunity cost, obtaining 40% less food than an animal choosing the large-delayed option. With examples like this in mind, behavioural ecologists have argued that a long-term choice rule, such as: choose option 1 if

$$\frac{A_1}{\tau + t_1} > \frac{A_2}{\tau + t_2} \qquad (2)$$

would more accurately reflect the fitness consequences of food choice. This long-term rule predicts weaker delay discounting, and a shift towards the larger more delayed option when τ is large, which disagrees with the empirical findings of self-control studies.

Stephens & Anderson (2001) advanced a simple argument to reconcile the results of self-control experiments with the ideas of foraging theory. In an alternative choice situation that Stephens & Anderson called the patch
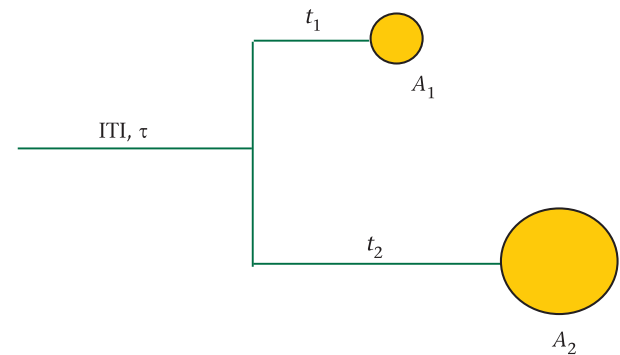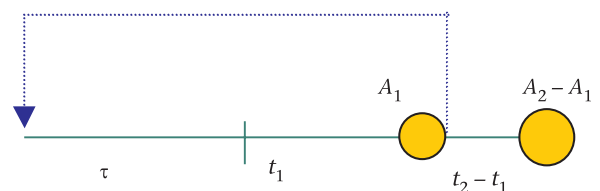
Figure 1. Trials in the self-control and patch contexts. (a) Self-control context: the subject waits for τ time units, and then the apparatus presents two stimuli. One stimulus is associated with a small-immediate option (amount A_1 delayed t_1), and the other is associated with a large-delayed option (amount A_2 delayed t_2). (b) Patch context: the subjects waits for τ time units, and then the apparatus presents a single stimulus. When this stimulus is accepted (a hop forward in our apparatus), a delay of t_1 seconds begins; when this delay expires the apparatus delivers amount A_1. At this point the subject may choose to 'leave' (i.e. start over), or to 'stay' (i.e. continue to wait) an additional $t_2 - t_1$ seconds to obtain amount $A_2 - A_1$. The self-control and patch contexts are comparable in the sense that the leave decision in the patch context and the 'small-immediate' choice in the self-control context both yield amount A_1 every $\tau + t_1$ seconds; similarly the stay decision in the patch context and the 'large-delayed' choice in the self-control context both yield amount A_2 every $\tau + t_2$ seconds.

context, the forager makes a 'leave or stay' decision that is analogous to the choices animals make in natural patch exploitation (Fig. 1b). In this case, the animal waits for a programmed time (the ITI), then sees a single stimulus. It enters the patch (by hopping forward towards the stimulus in our preparation), waits for delay t_1, and receives amount A_1. Then it faces a choice: it can leave and start another ITI-wait-feed cycle, or it can continue waiting another $t_2 - t_1$ seconds in the 'patch' to obtain amount $A_2 - A_1$. This choice is equivalent to a self-control problem in that 'leaving' leads to amount A_1 every $\tau + t_1$ seconds, but staying leads to amount A_2 every $\tau + t_2$ seconds. Stephens & Anderson showed that foraging blue jays, *Cyanocitta cristata*, came much closer to maximizing their long-term intake rate in the patch situation, but were typically shortsighted in the self-control procedure. Stephens & Anderson observed that the delay-to-food rule (equation 1) could account for this behaviour, because the delay associated with leaving is $\tau + t_1$ after which the animal obtains A_1, but the delay associated

with staying is $t_2 - t_1$, after which the animal obtains $A_2 - A_1$. Thus, the delay-to-food rule becomes: leave if

$$\frac{A_1}{\tau + t_1} > \frac{A_2 - A_1}{t_2 - t_1}. \tag{3}$$

This rule is equivalent to the long-term rule, so that in the patch context, the shortsighted, delay-to-food rule functions as a good long-term rule. It is even better than the real long-term rule, because it leads to a cleaner discrimination (Stephens 2002). The intertrial interval is important when the short-term rule is applied in the patch context, because the intertrial interval is part of the delay associated with leaving.

A parsimonious account of these results is that the jays use the same short-term rule (e.g. equation 1), in both contexts, but this rule maximizes, or nearly maximizes, the long-term rate of gain in the patch context but not in the more widely studied self-control context. We might therefore speculate that animals use short-term rules because they perform well in many natural sequential decision-making situations, even if they perform poorly in less naturalistic binary choice experiments like self-control studies.
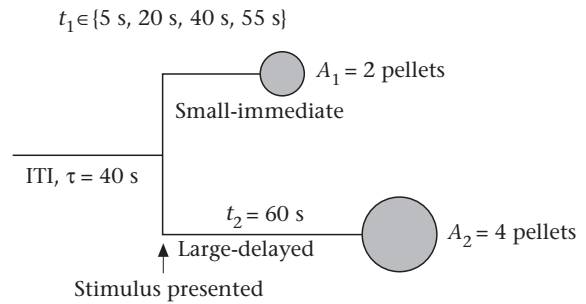
We conducted two experiments to explore these issues by asking the following questions. First, is the short-term rule proposed above used in both patch and self-control contexts, as Stephens & Anderson (2001) hypothesized? Experiment 1 tested this hypothesis by constructing patch and self-control choices that should give identical patterns of choice if the hypothesis is correct. Second, we wanted to know more about choice behaviour in the patch context, because it represents a promising experimental approach. Experiment 2 addressed this issue by asking whether the intertrial interval and first delay combine additively (to make a single large 'delay') in the patch context, as our models suggest.

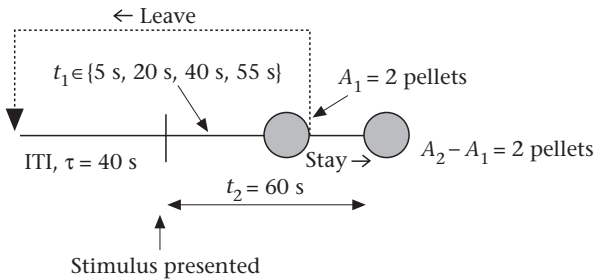## EXPERIMENT 1: THE SHORT-TERM RULE

Rationale

We studied three choice situations or contexts (Fig. 2). The first offered small-immediate versus large-delayed as a binary choice (Fig. 2a). We called this the Self-Control treatment. The second and third treatments were patch treatments, which should be equivalent to the Self-Control treatment under different hypotheses of choice. If animals use the long-term rate rule (i.e. equation 2), then the Patch-L treatment (Fig. 2b) should be equivalent to the Self-Control treatment, because here the leave choice leads to same long-term rate as the small-immediate choice in the Self-Control situation, and the stay choice leads to the same long-term intake rate as the large-delayed option. Our comparison of the Self-Control and Patch-L treatments replicates the study of Stephens & Anderson (2001). If, on the other hand, animals use a short-sighted choice rule (i.e. equation 1), which considers only the delay to and size of the next the food item (Stephens & Anderson 2001), then our Patch-S treatment (Fig. 2c) should be equivalent to the Self-
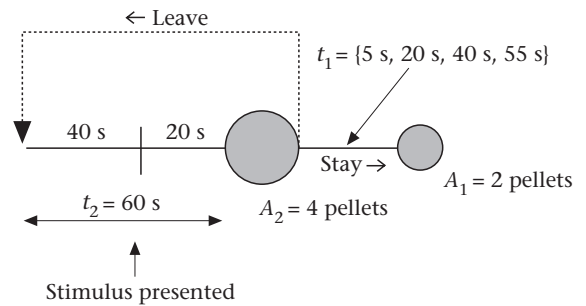

(a) Self-Control treatment

$t_1 \in \{5 \text{ s}, 20 \text{ s}, 40 \text{ s}, 55 \text{ s}\}$

$A_1 = 2$ pellets

Small-immediate

ITI, $\tau = 40$ s

$t_2 = 60$ s

$A_2 = 4$ pellets

Large-delayed

Stimulus presented

(b) Patch-L treatment

← Leave

$t_1 \in \{5 \text{ s}, 20 \text{ s}, 40 \text{ s}, 55 \text{ s}\}$

$A_1 = 2$ pellets

ITI, $\tau = 40$ s

Stay →

$A_2 - A_1 = 2$ pellets

$t_2 = 60$ s

Stimulus presented

(c) Patch-S treatment

← Leave

$t_1 = \{5 \text{ s}, 20 \text{ s}, 40 \text{ s}, 55 \text{ s}\}$

40 s | 20 s

Stay →

$A_1 = 2$ pellets

$t_2 = 60$ s

$A_2 = 4$ pellets

Stimulus presented

Figure 2. Treatments used in experiment 1. The figure shows (1) the three context treatments, (2) the delay-to-small (t_1) treatments and (3) the time and amount parameters that were fixed throughout the experiment (i.e. $t_2=60$ s, $\tau=40$ s, $A_1=2$ pellets, $A_2=4$ pellets). In the Patch-L treatment (b), the leave–stay decision has the same long-term consequences as the small-immediate versus large-delayed choice in the Self-Control treatment (a), because stay and small-immediate both lead to two pellets in $40+t_1$ seconds, while leave and large-delayed both lead to four pellets in 100 s. In the Patch-S (c) treatment the leave–stay decision has the same short-term consequences as the small-immediate versus large-delayed choice in the Self-Control treatment (a). That is, when an animal 'leaves' in the Patch-S treatment and when it chooses large-delayed in the Self-Control treatment, it obtains four pellets after a delay of 60 s. Similarly, when an animal 'stays' in the Patch-S treatment and when it chooses small-immediate in the Self-Control treatment, it obtains two pellets after a delay of t_1 seconds.

Control treatment. In the Patch-S treatment, the decision to leave leads to four pellets after a delay of 60 s, just as a large-delayed choice does in the Self-Control treatment; similarly a decision to stay leads to two pellets after a delay of t_1 seconds (we varied t_1 experimentally), just as the small-immediate choice does in the Self-Control treatment. A comparison of the Self-Control and Patch-S treatments tests the hypothesis of Stephens & Anderson,
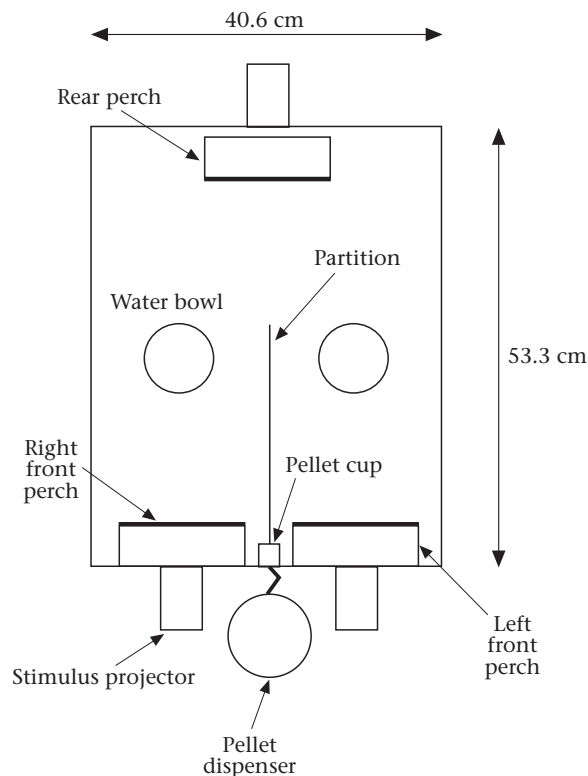
40.6 cm

Rear perch

Partition

Water bowl

53.3 cm

Right front perch

Pellet cup

Stimulus projector

Left front perch

Pellet dispenser

Figure 3. Top view of the apparatus.

because if animals use the same short-term choice rule, which depends only the delay to and size of the next food item, then we should see identical behaviour in the Self-Control and Patch-S treatments.

Methods

Subjects

The subjects were six adult blue jays of mixed experimental histories and unknown sex (band numbers b1, b84, b106, b122, b130 and b140). When not in the experiment, we maintained these individuals in our blue jay colony in individual cages under a constant 13:11 h light:dark cycle.

Treatments

The experiment followed a three-by-four factorial, within-subjects (or repeated measures) design. Each subject experienced the three context treatments (i.e. Self-Control, Patch-L and Patch-S), and four levels of delay-to-small (or DTS, i.e. $t_1 \, \varepsilon \, \{5 \text{ s}, 20 \text{ s}, 40 \text{ s}, 55 \text{ s}\}$). The other parameters did not change (large amount: $A_2=$ four 20-mg food pellets; small amount: $A_1=$two 20-mg food pellets; ITI, relevant only in the Self-Control and Patch-L treatments: $\tau=40$ s; delay-to-large: $t_2=60$ s).

Apparatus

The experimental apparatus was a conventional rectangular operant box (Fig. 3). Each box was equipped with three perches, three corresponding stimulus lights and an automated food pellet dispenser. A microswitch attached

to each perch could detect whether a bird was present. The stimulus lights were equipped with white, blue, yellow, green and red bulbs.

Within-trial procedures

Figure 4 presents a diagram of the patch and self-control procedures. The following paragraphs provide brief descriptions of these two procedures.

Self-Control. (1) The rear light (always white) switched on, indicating the beginning of the trial. A hop on the rear perch initiated the intertrial interval, and an additional white lamp was switched on in the rear stimulus projector to indicate the ITI. (2) After the ITI expired and if the subject was on the rear perch, the apparatus switched on the two front lights, offering the subject a choice. The subject had to be on the rear perch when the choice was offered so that we knew that it was equidistant from both alternatives. (3) The subject hopped forward to one of the two front perches to signify its choice, the apparatus switched off the light on the unchosen side, and a white light was switched on on the chosen side. This white light made the coloured light appear washed out and indicated the onset of the delay to food. (For example, if green and red lights were offered, the subject might hop forward to the green, the red would be extinguished and the green would show green and white.) (4) Food was dispensed according to the experimental schedule after the programmed delay expired. As in step 2, the subject had to be on the chosen front perch before food would be delivered. After food was delivered, the process began again at step 1.

Patch. We first describe a trial in which the animal stayed to collect both food deliveries, and then explain how a choice (leaving) was made. The steps in such a patch trial were as follows. (1) The rear light was illuminated, indicating a new trial. A hop on the rear perch started the intertrial interval and the rear light was washed out. (2) When the ITI expired, one of the two front lights was illuminated, indicating a 'patch encounter'. (3) A hop on the perch associated with the illuminated cue light washed out the cue light and initiated the delay to the first food delivery; a hop on the other front perch did nothing. (4) When the programmed delay to the first food delivery expired, the pellet feeder dispensed the programmed amount, and a new cue colour displayed for 1 s. (5) If the bird remained on the food perch for 1 s, this new cue colour was washed out and the delay to the second food delivery began; the final allotment of food was dispensed after this second delay expired, and the process began again at step 1.

Leaving. The subject could leave the patch at any time, and it signified this by a hop on the rear perch at any time after a patch visit had been initiated. The rear cue light was illuminated throughout a patch visit. When leaving occurred, the subject typically returned to the rear perch within a few seconds of the first food delivery.
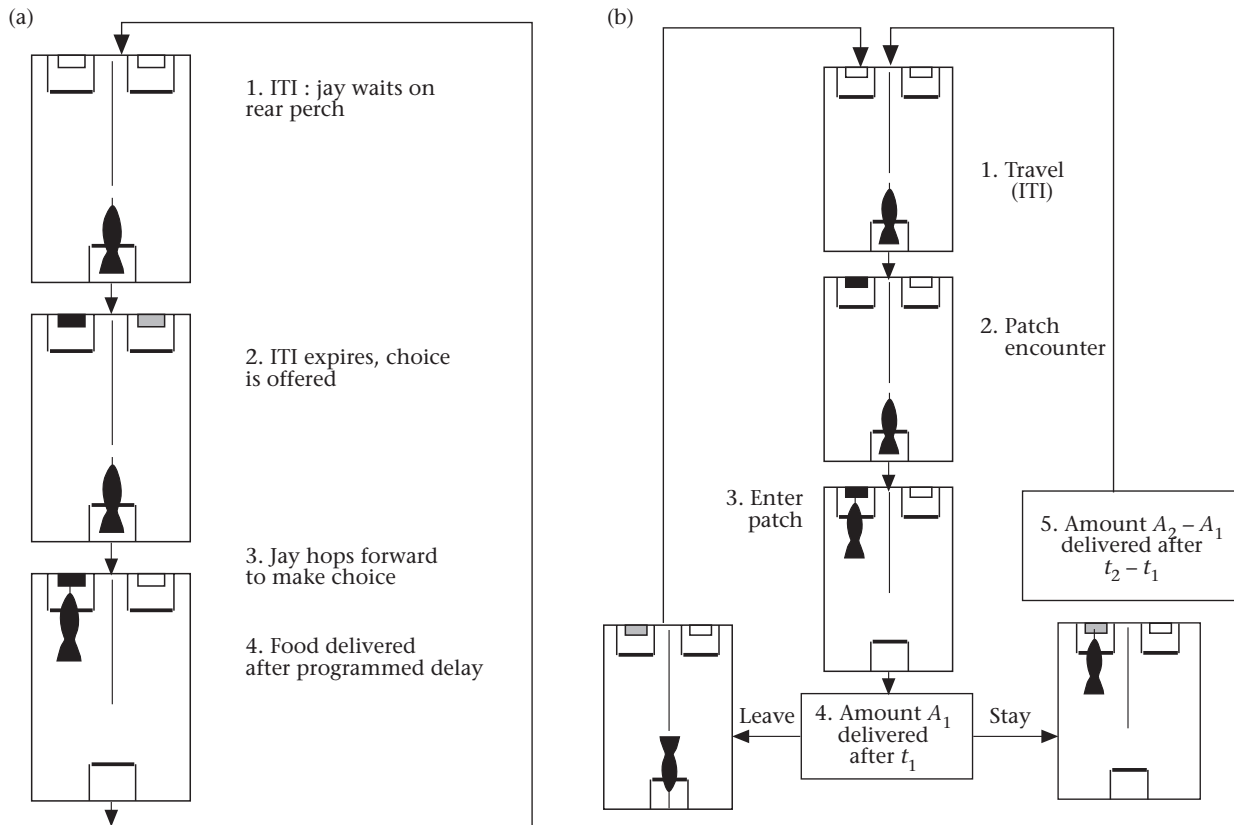
Figure 4. Cartoons representing the (a) Self-Control and (b) Patch procedures.

Forced or no-choice trials

Forty per cent of the trials were forced or no-choice trials. In the Self-Control treatments, for example, 40% of the trials offered only one choice. The computer controlling the experiment chose randomly between forced and free trials, with the restriction that the subject must have experienced four forced trials during each block of 10 trials. The properties of each forced trial (e.g. large-delayed on the left, large-delayed on right, small-immediate on left, small-immediate on right) were also determined randomly. Similarly, there were two basic types of forced trial available in the patch treatments: 'stay' trials, in which the leave option was not available until the second group of pellets had been delivered, and 'leave' trials, in which the second pellet delivery was not available. Both types could occur on the right or left side of the apparatus, giving a total of four forced trial types.

Closed economy

The experiment was conducted as a modified closed economy. The subjects spent 23 h per day in the apparatus and normally obtained all their food from it. The experiment began at 0700 hours every day and ended at 1600 hours. There was a pause from 1100 to 1200 hours each day; during this interval, the subjects were weighed and returned to their home cages, so that the apparatus could be cleaned and checked. An advantage of the closed economy is that we did not deprive the birds of food to maintain high levels of motivation; they simply had to

respond to obtain food. To avoid situations where a bird obtained too little food (possibly leading to starvation) or too much food (possibly leading to a lack of motivation in future trials), we adopted the following minimum and maximum rules. The minimum rule was that we supplemented a bird's food to 7 g per day if it had obtained less than 7 g at the end of the daily session (at 1600 hours). The maximum rule was that the daily session was terminated any time after 1400 hours if the bird had obtained 10 g of food.

Training

We trained all subjects using conventional shaping techniques. The jays were first trained to a task that we call 'light following', in which the subject waited on the rear perch until one of the front lights was switched on, then hopped forward to the corresponding perch. Once the subject was trained, we gradually increased the delay between arrival on the front perch and food delivery.

Treatment order and treatment transitions

Each subject experienced all 12 combinations of context and delay-to-small (i.e. (Self-Control, Patch-L, Patch-S) by ($t_1 \in$ {5 s, 20 s, 40 s, 55 s})) treatments. The order of treatments was randomized with the following restrictions. We first randomized the order of context treatments, then randomized the order of delay-to-small treatments within contexts. Thus, each individual experienced all delay-to-small treatments within a
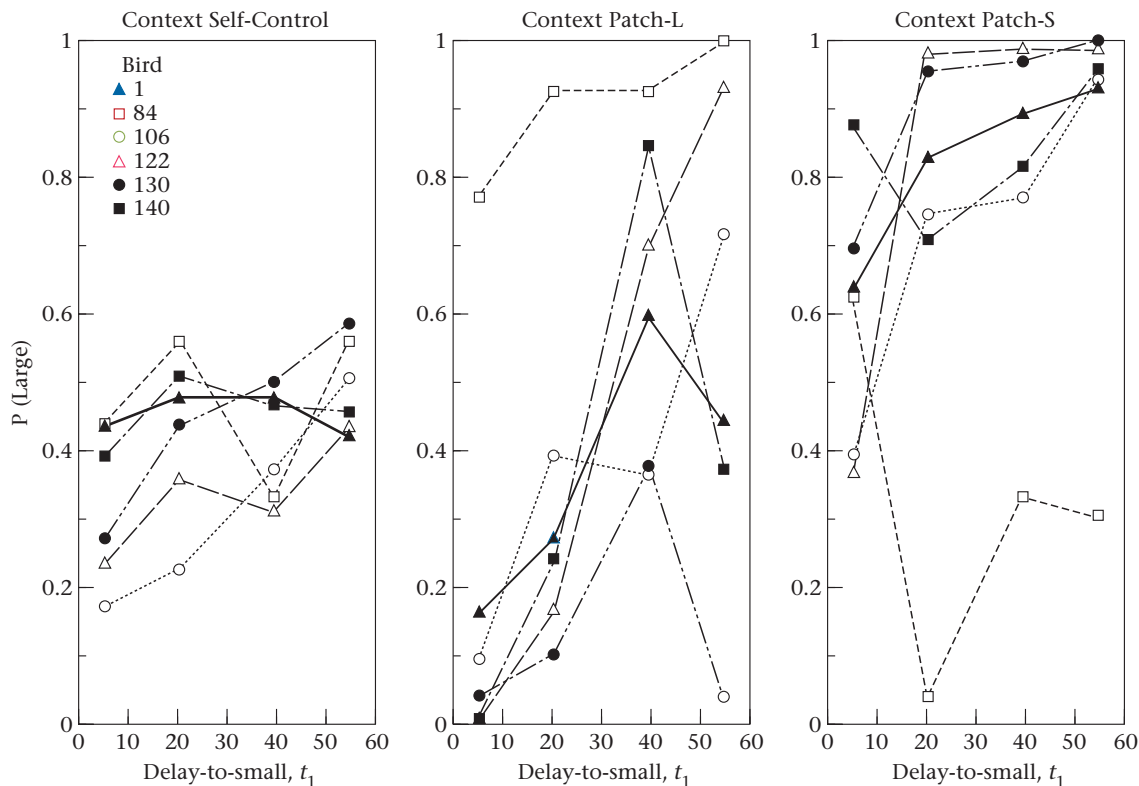
Figure 5. Results of experiment 1 for each bird shown as separate panels for each context treatment.

context treatment before moving on to the next context. To minimize the effects of transitions from one context treatment to the next, each individual experienced a baseline treatment for 4 days before beginning the actual 'data-collecting' treatments. During these baseline treatments, the temporal parameters were set to $\tau = 60$ s, $t_1 = 30$ s and $t_2 = 75$ s. Following this baseline treatment, each individual experienced each of the four delay-to-small treatments for 3 days before changing to a new context.

Data analysis

The experiment used a conventional repeated measures (or within-subjects) design. To assess the subject's preferences, we calculated the proportion of 'large' alternatives chosen (P(Large); Fig. 2) in the last one-third of the free trials (within a given context and delay-to-small treatment combination) as our dependent measure. We considered the effects of context and delay-to-small using repeated measures analysis of variance (ANOVA) and nonparametric techniques.

Results

Overview of the data

As predicted, P(Large) increased with the delay-to-small in all three contexts (Fig. 5). This increase, however, seemed to have different properties in each context. For most birds, delay-to-small had a stronger effect on

preference in the Patch-L treatment than in the Self-Control treatment. The relation between delay-to-small and P(Large) was very shallow in Self-Control. Finally, for most birds, P(Large) was generally higher in the Patch-S treatment.

We must qualify these generalizations with the phrase 'for most birds', because bird 84 showed a pattern of choice behaviour that stood out from the rest. Specifically, bird 84 showed higher levels of P(Large) in the Patch-L treatment, and lower levels in the Patch-S treatment. This created several problems in our statistical analysis. First, the behaviour of bird 84 meant that the between-subjects variability was much greater in the Patch treatments than in the Self-Control treatment, which violates a key assumption of parametric analysis. Second, bird 84's behaviour was so different that it suggested some procedural or inherent qualitative difference that we could not detect, so we may be justified in treating bird 84 as an outlier. As a partial solution to these problems, our analysis used both parametric analysis of variance that excluded bird 84 and supporting nonparametric analysis that included bird 84.

Two techniques are justified here because nonparametric analysis offers only a limited set of statistical models (i.e. there are nonparametric tests for one-way repeated measures designs, e.g. Friedman's test, but not for two-way designs as employed here). In contrast, parametric ANOVA offers a rich set of models and follow-up analyses.

Table 1. Analysis of variance table for experiment 1, arcsine-transformed P(Large)

Source of variation	SS	df	MS	F	P
Context	4.199	2	2.099	31.756	0.000157*
Error: bird*context	0.529	8	0.066	—	—
DTS	1.711	3	0.570	16.42	0.000151*
Error: bird*DTS	0.417	12	0.035	—	—
Context*DTS	0.477	6	0.079	2.475	0.0524
Error: bird*context*DTS	0.770	24	0.032	—	—

DTS: Delay-to-small.

ANOVA results

A repeated measures analysis of arcsine transformed P(Large), excluding bird 84, showed a nearly significant context by delay-to-small interaction and highly significant main effects of both context and delay-to-small (DTS; Table 1, Fig. 6). Planned comparison tests showed significant differences between the Patch-S treatment and the two other context treatments (Self-Control versus Patch-S, $F_{1,4}=113.34$, $P=0.0004$; Patch-S versus Patch-L, $F_{1,4}=34.45$, $P=0.004$), but no difference between the Self-Control and Patch-L treatments ($F_{1,4}=1.35$, $P=0.309$). A nonparametric comparison, including data from bird 84, corroborated a significant difference between the Self-Control and Patch-S treatments (Wilcoxon matched-pairs test of context averages: $T=1.0$, $N=6$, $P<0.05$).

Discussion

Although there were some discrepancies (e.g. the individual variation evidenced by subject 84, and the nonsignificant interaction), the Self-Control and Patch-S contexts differed. This result led us to reject the hypothesis of Stephens & Anderson (2001) that subjects use the simple short-term rule (equation 1) in both self-control and patch contexts. This conclusion suggests that we should consider either a more complex rule or the possibility that different rules are used in the two contexts. Our results showed no difference between Self-Control and Patch-L treatments, which may be considered a failure to replicate the results of Stephens & Anderson (2001), who studied these treatments in a larger experiment. However, Stephens & Anderson did not find a main effect of context, but instead found a pattern of significant interactions involving choice context. Our data are qualitatively consistent with this result (Fig. 5). The delay-to-small had a stronger effect on preference in the Patch-L treatment (a context*DTS interaction), which, although nonsignificant in the present study, was significant in Stephens & Anderson's (2001) more powerful study of this effect.

EXPERIMENT 2: TESTING THE ADDITIVITY OF ITI AND DELAY

Rationale

Following Bateson & Kacelnik (1996), Stephens & Anderson (2001) argued that the intertrial interval, or travel time, can be important in the patch context even when animals use a shortsighted choice rule, because the travel time/intertrial interval is part of the delay to food when the subject chooses to 'leave'. This idea is important, despite the results of experiment 1, because it may explain how travel time can be important in studies of patch exploitation (Cowie 1977; Kacelnik 1984; Stephens & Krebs 1986), although the analogous intertrial interval is unimportant in self-control style experiments.

However, the delay that an animal experiences when it 'leaves' in the experimental patch context is different from the delay that it experiences after it makes a choice in a self-control procedure. Specifically, the delay following a 'leave' has two pieces, an interval spent waiting for the next patch (waiting on the rear perch in our procedure), and an interval waiting for the first food delivery 'within the patch' (waiting on the front perch in our procedure). One simple explanation for the differences observed between Patch-S and Self-Control treatments in experiment 1 is that the two-piece delay experienced in the Patch-S treatment is not equivalent to the one-piece delay-to-large in the Self-Control treatment.

Experiment 2 tested whether the two components of delay combine additively as the models of Stephens & Anderson suggest. In experiment 2, we constructed a range of patch situations (Fig. 7). Here, the sum of the ITI and the delay to the first food delivery was constant (in symbols: $\tau+t_1=T(Leave)$), even though in some treatments this was composed of a short ITI and long delay, and in others it consisted of a long ITI and short delay.
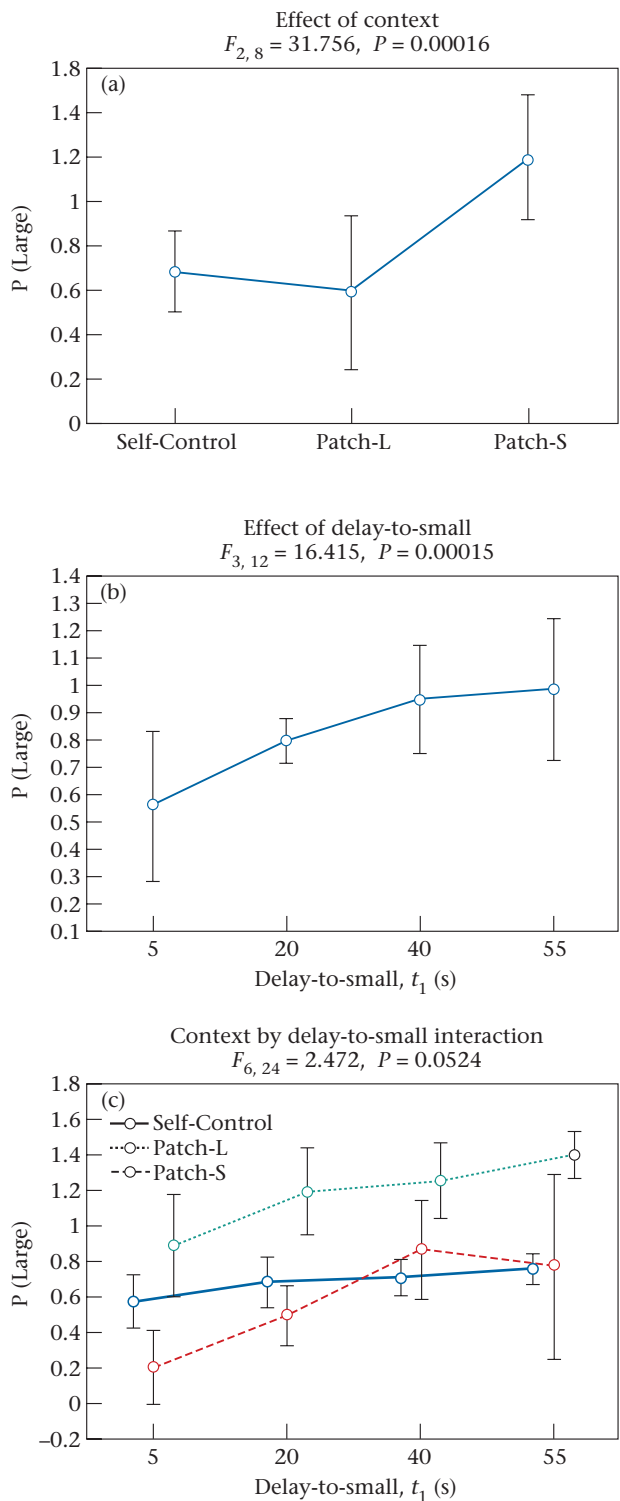
Methods

The methods of experiment 2 follow experiment 1 except as detailed here.

Subjects

Subjects were six adult blue jays with mixed experimental histories and unknown sex (band numbers b4, b80, b84, b106, b122 and b130). This was the same group as in experiment 1, except that birds 4 and 80 replaced birds 1 and 140.
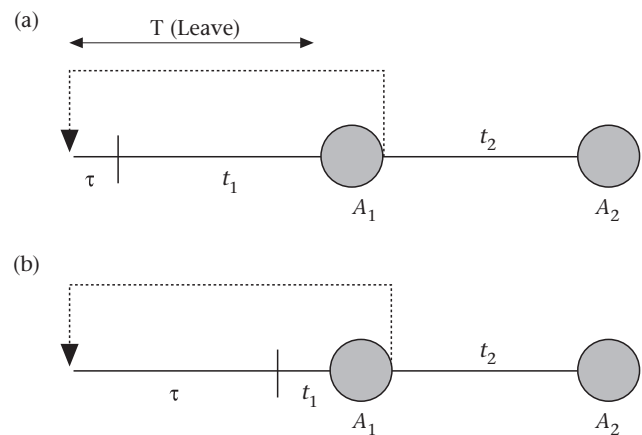
Treatments

We used a two-by-three factorial design with two levels of the delay associated with leaving, T(Leave)=20 s and

Effect of context
$F_{2, 8} = 31.756, \ P = 0.00016$

(a)

Effect of delay-to-small
$F_{3, 12} = 16.415, \ P = 0.00015$

(b)

Context by delay-to-small interaction
$F_{6, 24} = 2.472, \ P = 0.0524$

(c)
- —○— Self-Control
- ···○··· Patch-L
- -○- Patch-S

Figure 6. Graphical summaries of the effects studied in experiment 1. (a) Main effect of context, (b) main effect of delay-to-small, (c) interaction of context and delay-to-small.

T(Leave)=80 s, which we call the 'leave delay', and three levels of P(ITI), $\tau/(\tau+t_1)$ or $\tau/(T(Leave))$, equal to 0.2, 0.5, 0.8, which is the proportion of the leave delay allocated to the ITI (Table 2).

(a)

T (Leave)

(b)

Figure 7. Two hypothetical treatments in experiment 2. The sum of τ (ITI) plus t_1 (delay) is held constant, but in some cases (a) there is a short ITI and long delay, and in other cases (b) there is a long ITI and short delay.

Table 2. Treatment parameters for experiment 2

T(Leave) (s)	P(ITI)	τ (s)	t_1 (s)	t_2 (s)	A_1	A_2
20	0.2	4	16	40	2 pellets	2 pellets
20	0.5	10	10	40	2 pellets	2 pellets
20	0.8	16	4	40	2 pellets	2 pellets
80	0.2	16	64	40	2 pellets	2 pellets
80	0.5	40	40	40	2 pellets	2 pellets
80	0.8	64	16	40	2 pellets	2 pellets

T(Leave)=Leave delay; P(ITI)=proportion of leave delay allocated to the intertrial interval; τ=intertrial interval; $t_{1,2}$=delay until the food item could be obtained; $A_{1,2}$=value of food item.

Treatment order

The experiment followed a repeated measures (i.e. within-subjects) design such that all subjects experienced all treatments. A randomly selected Latin square determined the order of treatments. For example, if b140 experienced $k=80$, P(ITI)=0.5 first, then no other subject was allowed to experience this treatment first, and so forth. Latin square randomization is possible only when the number of subjects matches the number of treatments. Birds experienced a baseline treatment with $\tau=t_1=25$ s for 3 days before the real treatment began. A treatment lasted for 5 days. The pattern was 3 days of baseline followed by 5 days of experimental treatment, and each subject repeated this pattern until it had completed all six treatments.
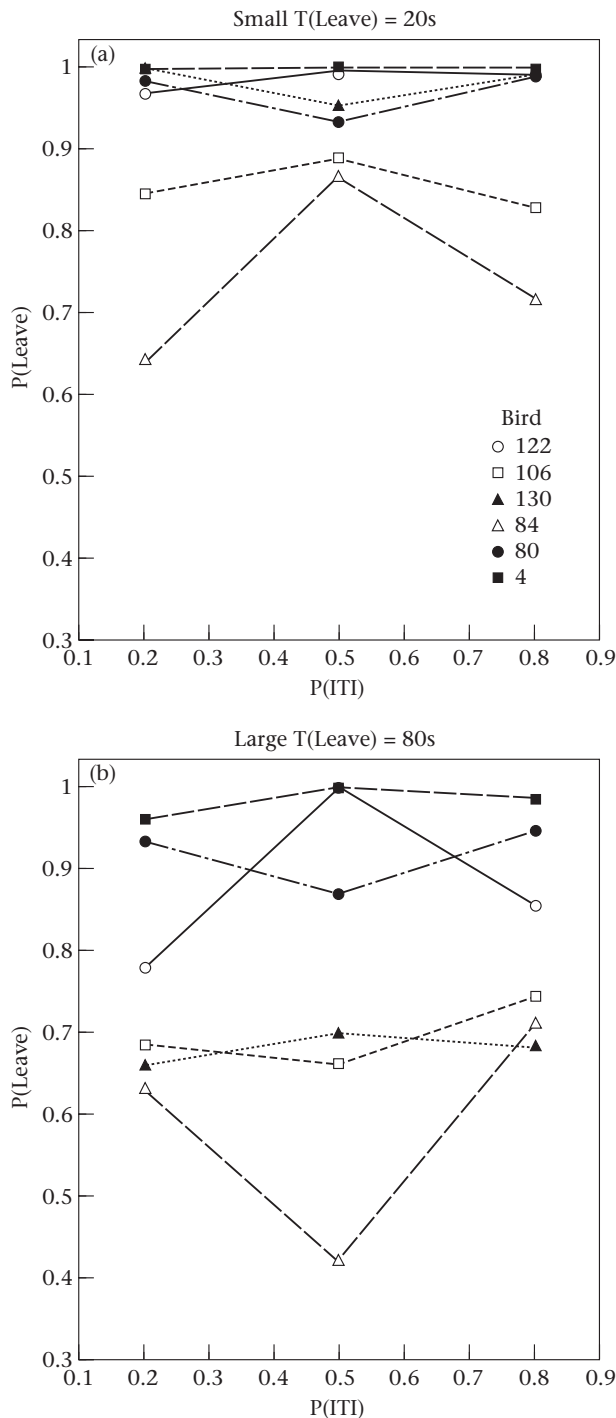
Statistical analysis

We calculated the frequency of 'leave' choices in the last one-third of the free trials within each treatment, denoted by P(Leave), and used this as the dependent variable in our analyses.

Results and Discussion

There was considerable individual variation in P(Leave) for each subject and treatment, and a relatively clear-cut

Figure 8. Results of experiment 2. These plots show separate lines for each subject, and provide a breakdown of the results for each treatment. (a) a case where leaving leads to food after a delay of 20 s; (b) a case where leaving leads to food after a delay of 80 s.

effect of the 'leave-delay' treatment, but there was no obvious effect of the P(ITI) variable (Fig. 8). An analysis of variance supported these conclusions, showing a significant main effect of T(Leave), but no other significant effects (Table 3). To evaluate whether this experiment was powerful enough to detect a biologically meaningful effect of the P(ITI) variable, we used the PASS software

system (Hintze 2001) to calculate the power of our analysis for a range of hypothesized effect sizes from 25 to 125% of the observed T(Leave) effect (where the ANOVA effect is measured as a standard deviation). As expected, the power of our analysis depended on the size of the hypothesized effect (range 13–99%). For an hypothesized P(ITI) effect of about the same size as the observed T(Leave) effect, the power of our analysis was 98%. In summary, the results offer no evidence against the assumption that the ITI and delay to first food delivery combine additively to act as single long 'delay' in the patch context, although if biologically significant effects were small, we may not have detected them.

GENERAL DISCUSSION

Key Results

The results of experiment 1 do not support the hypothesis that a single rule, based on the delay to and amount of the next food reward, accounts for choice in both the patch and self-control contexts. We conclude that either subjects use different rules in the two choice situations, or they use a single more complex rule. A striking feature of experiment 1 is the comparative flatness of the subjects' response to changes in the delay-to-small in the self-control context (Fig. 5), which suggests that subjects were more sensitive to temporal differences in patch situations. In contrast, experiment 2 lends support to the hypothesis that travel time and delay to the first food delivery combine additively, behaving in effect like a single large delay 'in the patch context'. This evidence may explain how the travel time can be important in patch situations (as many studies of foraging have reported), although the analogous intertrial interval has little effect in binary choice situations like self-control (e.g. Goldshmidt et al. 1998).

Related Studies

Despite the large literature of choice (Fantino & Abarca 1985; Stephens & Krebs 1986; Gibbon et al. 1988; Mazur 1991), there are no parallel studies to the present study, because this is only the second one to study choice in the patch context and the first to test rules of choice in patch and self-control situations. However, many studies have advanced and tested rules of choice, typically as applied to binary choice situations. Several studies (Baum & Rachlin 1969; Bateson & Kacelnik 1996; Stephens & Anderson 2001) have advocated a rule based on the ratio of amount over delay, as studied here. For example, Bateson & Kacelnik (1996) concluded that this short-term rule gave the best fit to their data. However, the hyperbolic choice rule (or hyperbolic discounting) predicts choice more accurately in many choice situations (Ainslie 1975; Mazur 1987). The hyperbolic model asserts that animals choose the option with the larger

$$\frac{A_i}{1+kt_i}$$

where k is a fitted parameter that measures the intensity of discounting. Although we recognize the empirical

Table 3. Analysis of variance of arcsine-transformed P(Leave)

Source of variation	SS	df	MS	F	P
T(Leave)	0.377	1	0.377	13.06	0.015*
Error: bird*T(Leave)	0.144	5	0.029		
P(ITI)	0.013	2	0.007	0.558	0.589
Error: bird*P(ITI)	0.119	10	0.012		
T(Leave)*P(ITI)	0.005	2	0.002	0.145	0.866
Error: bird*T(Leave)*P(ITI)	0.159	10	0.016		

P(Leave)=Frequency of leave choices. All other variables defined in Table 2.

advantages of the hyperbolic model, we have focused on the short-term model here for several reasons. First, the two models often make similar predictions. The key difference occurs when delays (t_i) are small (when $t_i=0$, the term A_i/t_i approaches infinity, obscuring information about differences in the amount of food reward). Second, Stephens & Anderson (2001) suggested that the short-term rate rule may have special relevance to the patch situation, because an animal applying this rule would maximize its long-term rate of intake in the patch context, but not in the self-control context. The results of experiment 1, however, exclude any model based only on the delay to, and size of, the next food reward, because the Self-Control and Patch-S treatments were arranged so that the leave versus stay alternatives of Patch-S and the small-immediate versus large-delayed alternatives of Self-Control led to the same amounts of food after the same delays. So, for example, experiment 1 excludes the basic version of the hyperbolic model that considers only the delay to, and amount of, the first food item associated with a choice.

Implications

The idea that the delay to the first food delivery is an important determinant of choice is a venerable one (McDiarmid & Rilling 1965; Green et al. 1981). Many studies have shown, for example, that delays imposed after food delivery have little if any effect on choice (Mazur & Logue 1978; Green et al. 1981; Logue et al. 1985; Snyderman 1987). Indeed, some workers (e.g. Moore 1982) claimed that additional food deliveries (i.e. beyond the first delivery associated with a choice) had little effect on choice. Other studies have demonstrated long-term effects on choice (Mazur 1986; Brunner & Gibbon 1995).

If we assume that a single rule applies in both patch and self-control contexts, rejecting the less parsimonious idea that different rules apply in the two situations, then our results imply that this single rule must be one in which something other than the delay to the next food item is important. There are two related possibilities. First, a subject's general level of hunger probably varied between the Self-Control and Patch-S treatments, because subjects could obtain food at a faster rate in Patch-S (a feeding cycle takes an additional 40 s for ITI in the Self-Control treatment). Thus, subjects were probably, on

average, hungrier in the Self-Control treatment. There is evidence that hunger influences choice in self-control situations (Snyderman 1983), and hungrier animals are more likely to choose the small-immediate option, which agrees with the Patch-S versus Self-Control difference observed here. Therefore, one possibility is that the jays used the same hunger-sensitive rule in both situations. This hunger-sensitive rule could be a minor modification of the short-term rule that we have rejected. For example, it could be a rule of the form: take option 1 if

$$\frac{A_1}{t_1} > c \frac{A_2}{t_2},$$

where c is a 'bias' parameter that decreases with hunger (therefore favouring the small-immediate option number 1). In contrast, the logic of our experiment assumes that c does not depend on hunger.

The second possibility is that choice depends on the consequences of choice beyond the first food delivery. Although the delay to the first food delivery is widely considered a key determinant of choice, there is evidence that events beyond this first food delivery can be important. For example, Mazur (1994) showed that delivering food within the ITI shifts preference towards the small-immediate choice in self-control experiments (see Stephens et al. 1986 for a similar study using honeybees). This result shows that there is at least some sensitivity to events beyond the current trial. Several authors (Mazur 1986; Brunner & Gibbon 1995; Brunner 1999) have studied self-control situations in which an alternative can lead to several food deliveries. These are sometimes called parallel discounting studies, and they show surprising sensitivity to events after the first food delivery. Brunner & Gibbon (1995), for example, showed consistent effects of the delay between the first and second food deliveries, and argued that a simple additive combination of hyperbolic-discounted values gave the best fit to their data (see also Mazur 1994). Parallel discounting applies to our patch context, because the 'stay' decision leads to two deliveries before the next opportunity to make a choice (Fig. 2; the additional amount associated with staying and the first delivery associated with the next patch encounter). Although the logic of parallel discounting applies, it seems unlikely that this, on its own, can account for the differences observed in experiment 1. This parallel discounting logic led us to expect an increase in preference

for the stay option, but we observed the opposite: our subjects were, on average, less likely to choose the stay option in the Patch-S treatment than the equivalent small-immediate option in Self-Control.

Limitations and Future Research

This study leaves many questions unanswered. For example, we wanted to test hunger and motivational effects in both patch and self-control contexts, as discussed above. More broadly, we do not know whether our results are peculiar to our closed-economy procedures or to blue jays, or are more general. To assess the generality of our results, we need more studies, ideally in other laboratories, that challenge our results by testing different species in different situations. For example, one extension of our results would be a patch versus self-control comparison in which 'stay' is equivalent to the large-delayed choice, instead of 'leave' as in our experiment 1.

Our results also suggest several experiments to assess longer-term effects in both patch and self-control contexts. One possibility follows Mazur's (1994) experiment in which additional food provided during the ITI enriches the 'environment' and should shift preference towards small-immediate options ('high profitability' items; Stephens & Krebs 1986). Would this enrichment affect patch and self-control treatments in the same way? Any observed differences may be important clues to the rules of choice. A second possibility is a direct comparison to parallel or multi-item discounting studies that compare the 'stay' option in a patch context to a self-control option that offers two food deliveries.

Conclusions

Choice is a fundamental issue in animal behaviour, but a complete understanding of how the timing and amount of benefits influence choice is elusive. Most empirical results come from logically elegant binary choice experiments such as the self-control framework. However, our results show that it can be difficult to generalize from this binary choice framework to a more naturalistic sequential choice framework based on patch-leaving. Although this raises many intriguing and specific questions, as outlined above, it also makes a broader point about the importance of considering and developing alternative paradigms of choice, especially sequential choice, that can contribute to a general theory of animal choice behaviour.

Acknowledgments

References

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

Bateson, M. & Kacelnik, A. 1996. Rate currencies and the foraging starling: the fallacy of the averages revisited. *Behavioral Ecology*, **7**, 341–352.

Baum, W. & Rachlin, H. 1969. Choice as time allocation. *Journal of the Experimental Analysis of Behavior*, **12**, 861–874.

Brunner, D. 1999. Preference for sequences of rewards: further tests of a parallel discounting model. *Behavioural Processes*, **45**, 87–99.

Brunner, D. & Gibbon, J. 1995. Value of food aggregates: parallel versus serial discounting. *Animal Behaviour*, **50**, 1627–1634.

Cowie, R. J. 1977. Optimal foraging in great tits (*Parus major*). *Nature*, **268**, 137–139.

Fantino, E. & Abarca, N. 1985. Choice, optimal foraging, and the delay reduction hypothesis. *Behavioral and Brain Sciences*, **8**, 315–362.

Gallistel, C. R. & Gibbon, J. 2000. Time, rate and conditioning. *Psychological Review*, **107**, 289–344.

Gibbon, J., Church, R. M., Fairhust, S. & Kacelnik, A. 1988. Scalar expectancy theory and choice between delayed rewards. *Psychological Review*, **95**, 102–114.

Goldshmidt, J. N., Lattal, K. M. & Fantino, E. 1998. Context effect on choice. *Journal of the Experimental Analysis of Behavior*, **70**, 301–320.

Green, L., Fisher, E. B. Jr, Perlow, S. & Sherman, L. 1981. Preference reversal and self-control: choice as a function of reward amount and delay. *Behavior Analysis Letters*, **1**, 244–256.

Hintze, J. 2001. *NCSS and PASS*. Kaysville, Utah: Number Cruncher Statistical Systems.

Kacelnik, A. 1984. Central place foraging in starlings (*Sturnus vulgaris*). 1. Patch residence time. *Journal of Animal Ecology*, **53**, 283–300.

Kacelnik, A. & Bateson, M. 1996. Risky theories: the effects of variance on foraging decisions. *American Zoologist*, **36**, 402–434.

Logue, A. W., Smith, M. E. & Rachlin, H. 1985. Sensitivity of pigeons to prereinforcer and postreinforcer delay. *Animal Learning and Behavior*, **13**, 181–186.

McDiarmid, C. F. & Rilling, M. E. 1965. Reinforcement delay and reinforcement rate as determinants of schedule preference. *Psychonomic Science*, **2**, 195–196.

McNamara, J. M. & Houston, A. I. 1987. A general framework for understanding the effects of variability and interruptions on foraging behaviour. *Acta Biotheoretica*, **36**, 3–22.

Mazur, J. E. 1984. Tests of an equivalence rule for fixed and variable reinforcer delays. *Journal of Experimental Psychology: Animal Behavior Processes*, **10**, 426–436.

Mazur, J. E. 1986. Choice between single and multiple delayed reinforcers. *Journal of the Experimental Analysis of Behavior*, **46**, 67–77.

Mazur, J. E. 1987. An adjusting procedure for studying delayed reinforcement. In: *Quantitative Analyses of Behavior: the Effect of Delay and of Intervening Events on Reinforcement Value* (Ed. by M. L. Commons, J. E. Mazur, J. A. Nevin & H. Rachlin), pp. 55–73. Hillsdale, New Jersey: L. Erlbaum.

Mazur, J. E. 1989. Theories of probabilistic reinforcement. *Journal of the Experimental Analysis of Behavior*, **51**, 87–99.

Mazur, J. 1991. Choice. In: *Experimental Analysis of Behavior, Parts 1 & 2. Techniques in the Behavioral and Neural Sciences. Vol. 6* (Ed. by I. H. Iversen & K. A. Lattal), pp. 219–250. Amsterdam: Elsevier.

Mazur, J. E. 1994. Effects of intertrial reinforcers on self-control choice. *Journal of the Experimental Analysis of Behavior*, **61,** 83–96.

Mazur, J. E. 2000. Tradeoffs among delay, rate and amount of reinforcement. *Behavioural Processes*, **49,** 1–10.

Mazur, J. E. & Logue, A. W. 1978. Choice in a 'self-control' paradigm: effects of a fading procedure. *Journal of the Experimental Analysis of Behavior*, **30,** 11–17.

Moore, J. 1982. Choice and multiple reinforcers. *Journal of the Experimental Analysis of Behavior*, **37,** 115–122.

Rachlin, H. & Green, L. 1972. Commitment, choice and self-control. *Journal of the Experimental Analysis of Behavior*, **17,** 15–22.

Snyderman, M. 1983. Optimal prey selection: the effects of food deprivation. *Behaviour Analysis Letters*, **3,** 359–369.

Snyderman, M. 1987. Prey selection and self-control. In: *Quantitative Analyses of Behavior: the Effect of Delay and of Intervening Events on Reinforcement Value* (Ed. by M. L. Commons, J. E. Mazur, J. A. Nevin & H. Rachlin), pp. 283–308. Hillsdale, New Jersey: L. Erlbaum.

Stephens, D. W. 2002. Discrimination, discounting and impulsivity: a role for an informational constraint. *Philosophical Transactions of the Royal Society of London, Series B*, **357,** 1527–1537.

Stephens, D. W. & Anderson, D. 2001. The adaptive value of preference for immediacy: when shortsighted rules have far-sighted consequences. *Behavioral Ecology*, **12,** 330–339.

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

Stephens, D. W., Lynch, J. F., Sorensen, A. E. & Gordon, C. 1986. Preference and profitability: theory and experiment. *American Naturalist*, **127,** 533–553.