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# Do Pigeons (*Columba livia*) Use Information About the Absence of Food Appropriately? A Further Look Into Suboptimal Choice

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In the natural environment, when an animal encounters a stimulus that signals the absence of food—a ‘bad-news’ stimulus—it will most likely redirect its search to another patch or prey. Because the animal does not pay the opportunity cost of waiting in the presence of a bad-news stimulus, the properties of the stimulus (e.g., its duration and probability) may have little impact in the evolution of the decision processes deployed in these circumstances. Hence, in the laboratory, when animals are forced to experience a bad-news stimulus they seem to *ignore* its duration, even though they pay the cost of waiting. Under certain circumstances, this insensitivity to the opportunity cost can lead to suboptimal preferences, such as a preference for an option yielding a low rather than a high rate of reinforcement. In 2 experiments, we tested Vasconcelos, Monteiro, and Kacelnik’s (2015) assumption that, if given the opportunity, animals will escape the bad-news stimulus. To predict when an escape response should occur, we incorporated ideas from the prey choice model into Vasconcelos et al. (2015) model and made 2 novel predictions. Namely, both longer intertrial intervals and longer durations of signals predicting food or no food should lead to higher proportions of escape responses. The results of 2 experiments with pigeons supported these predictions.

**Keywords:** bad news, escape response, pigeons, prey choice model, suboptimal choice

The outcome of any foraging cycle is by nature uncertain. Many factors contribute to this uncertainty, some related to the environment, others related to the behavioral abilities of foragers. A particular behavior does not always lead to the same outcome, and environmental cues seldom correlate perfectly with the presence or absence of food in their vicinity.

In uncertain environments, reliable information about important events should be highly valued. For example, information that reduces uncertainty about the presence of food in natural foraging environments or about food delivery in laboratory preparations is undoubtedly important and should therefore be properly weighed. Surprisingly, however, under certain labora-

tory preparations animals will forego food to secure information (e.g., Fortes, Vasconcelos, & Machado, 2016; Kendall, 1974; Mazur, 1995, 1996; Spetch, Mondloch, Belke, & Dunn, 1994; Stagner, Laude, & Zentall, 2012; Stagner & Zentall, 2010; Smith, Bailey, Chow, Beckmann, & Zentall, 2016; Smith & Zentall, 2016; Vasconcelos, Monteiro, & Kacelnik, 2015; Zentall & Stagner, 2011; for reviews, see McDevitt, Dunn, Spetch, & Ludvig, 2016; Zentall, 2014, 2016).

For example, Stagner and Zentall (2010) showed that pigeons (*Columba livia*) prefer an Informative Option that signals immediately whether food will occur or not, but yields less food on average, over a Noninformative Option that does not signal whether food will follow, but yields more food on average. Figure 1 shows their experimental task. After pigeons chose one of two options, a stimulus appeared for 10 s. When they chose the Informative Option, on 20% of the trials, a stimulus was presented that always ended with food (the  $S^+$  or “good-news” stimulus); on the remaining 80% of these trials, a stimulus was presented that never ended with food (the  $S^-$  or “bad-news” stimulus). If they chose the Noninformative Option, one of two stimuli was presented and both ended with food 50% of the time (the  $S_1$  and  $S_2$ , or  $S^{+/-}$  stimuli). Although the overall probability of food was higher in the Noninformative Option than in the Informative Option (.50 vs. .20), pigeons reliably chose the latter. In this task pigeons behaved suboptimally in the sense that they preferred the leaner option.

According to Vasconcelos and colleagues (2015), the decision mechanism animals deploy in this task evolved to optimize behavior in natural foraging tasks: If a cue signaling the absence of food ( $S^-$ ) is detected, the animal should redirect its foraging efforts by moving away and searching at other locations or for other prey

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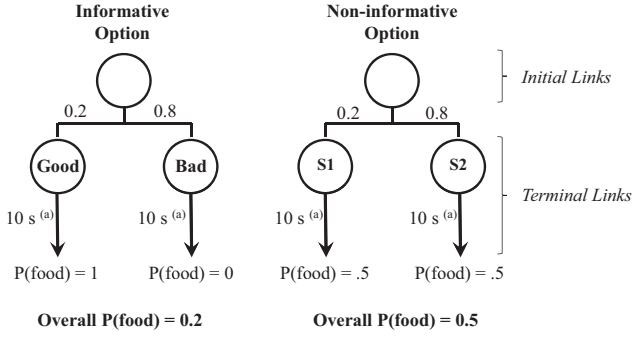


Figure 1. Schematic of outcomes for each option in the first condition of Experiments 1 and 2. In the 20-s Terminal Links Phase of Experiment 2 the terminal links (a) increased to 20 s.

items, for example (Stephens, Brown, & Ydenberg, 2007; Stephens & Krebs, 1986). Because the animal moves away, it disengages from the bad-news stimulus ( $S^-$ ), thus avoiding any opportunity costs. Hence, the properties of the  $S^-$  stimulus (such as its duration and probability of occurrence) may be inconsequential and bear no effect on decision making in natural settings. However, in typical laboratory settings, animals are forced to remain in the presence of the bad-news stimulus and cannot efficiently use the information it conveys. Although animals cannot escape from the bad-news stimulus, they disengage from the task and disregard the stimulus as they do in natural foraging tasks. Disregarding the bad-news stimulus—an adequate strategy in the natural environment because it avoids opportunity costs—may lead to suboptimal behavior in the laboratory when the animal is forced to pay the cost of waiting for no food. This mismatch between the domain of selection (the natural environment) and the domain of testing (the laboratory), may underlie some instances of apparently paradoxical behaviors (Houston, McNamara, & Steer, 2007; Kacelnik, 2003; Stephens & Anderson, 2001; Stephens & Dunlap, 2009; Stephens, Kerr, & Fernández-Juricic, 2004; Stephens & McLinn, 2003; Stevens & Stephens, 2010). Based on these ideas and on optimal foraging theory (Stephens & Krebs, 1986), Vasconcelos et al. (2015) developed the Reinforcement Rate Model (RRM) to account for results observed in tasks similar to that depicted in Figure 1.

### The Reinforcement Rate Model

According to optimal foraging theory, the long-term fitness consequences of foraging are usually well captured by the rate of food and therefore natural selection ought to have favored animals behaving as if maximizing this currency (Stephens & Krebs, 1986). Consider the following scenario: A predator encounters prey  $i$  and starts pursuing it; with probability  $p_i$ , the predator catches the prey and consumes it, and with probability  $1 - p_i$ , the prey escapes and the predator starts a new foraging cycle. Assuming prey types of equal energy content (1 unit), the rate of intake with prey  $i$  ( $R_i$ ) is given by:

$$R_i = \frac{p_i}{s + p_i \times (t + h) + (1 - p_i) \times t} \quad (1)$$

where  $s$  is the average search time,  $p_i$  is the probability of capturing

prey  $i$ ,  $t$  the pursuing time, and  $h$  the handling (and consuming) time.

In the experimental situation depicted in Figure 1,  $s$  is the intertrial interval (ITI),  $p_i$  is the probability of reward in a given option,  $t$  is the duration of the terminal-link stimuli, and  $h$  is the reinforcement duration. To include the foregoing ecological analysis according to which animals ought to disregard the bad-news stimulus, the time spent in its presence should drop from Equation 1. Also, the ITI duration ( $s$  in Equation 1) should be inconsequential vis-à-vis choice because (a) it occurs *after* the reward and *before* the choice, not *between* choice and reward as the searching time  $s$  (see Bateson & Kacelnik, 1996; Logue, Smith, & Rachlin, 1985; Mazur, 1989; Spetch, Belke, Barnett, Dunn, & Pierce, 1990; Spetch et al., 1994; Stephens & Anderson, 2001), and (b) it is common to all outcomes (for a detailed explanation, see Vasconcelos et al., 2015). With these modifications, the reward rate equations for the Informative and Noninformative options are given by Equations 2 and 3, respectively:

$$R_{Info} = \frac{P_{Info}}{p_{Info} \times (t + h)} = \frac{1}{t + h} \quad (2)$$

$$\begin{aligned} R_{Non-info} &= \frac{P_{Non-info}}{p_{Non-info} \times (t + h) + (1 - p_{Non-info}) \times t} \\ &= \frac{P_{Non-info}}{t + p_{Non-info} \times h} \\ &= \frac{1}{\frac{t}{0.5} + h} \end{aligned} \quad (3)$$

where  $p_{Info}$  and  $p_{Noninfo}$  are the overall probabilities of reward in the Informative and Noninformative options, respectively. With these rate functions,  $R_{Info}$  is always greater than  $R_{Noninfo}$ , thus predicting a preference for the Informative Option. Also, because  $1 - p_{info}$  is not included in  $R_{info}$ , animals should still prefer the Informative Option regardless of the duration of the bad-news stimulus and the overall probability of reward in the Informative Option (except if it is zero). These predictions have been recently confirmed by Fortes and collaborators (2016).

Yet, one of the core assumptions of the RRM remains untested, namely, that under the same conditions encountered in the wild, when animals see a stimulus predicting the absence of food, they use that information and move away to search for another patch or prey. What would happen, then, if in the present task animals had the option of escaping from the bad-news stimulus? Because escaping was not included as a possible strategy in the original version of the RRM and yet it is needed to predict the circumstances under which animals should accept or reject a prey item, we modified the RRM to incorporate the core ideas of the prey choice model (Charnov, 1976).

### The Prey Model and the RRM

Stated simply, the prey model (Charnov, 1976) predicts that animals should accept or reject an item depending on which of these actions yields a higher long-term reward rate. Note, however, the difference between this long-term maximization and the long-term maximization described for the RRM. For the latter, the reinforcement rate of *each option* (Informative and Noninformative) is calculated separately and the prediction is

that animals should prefer the one yielding the highest rate. With the prey model, the options of interest are no longer the Informative and Noninformative but Accept versus Reject—a prey item in the natural habitat, a terminal-link stimulus in the laboratory. Thus we focus our attention on the average rate of food intake (with the Informative and Noninformative options, together) under two scenarios: (a) when animals always accept the bad-news stimulus and all the other stimuli, a generalist strategy, and (b) when animals always reject the bad-news stimulus but accept all other stimuli, a specialist strategy. These two strategies are defined by the animal's choices during the four terminal links—whether it accepts all of them, or rejects the bad-news one; for the initial link choice (Informative vs. Noninformative options), we continue to assume a systematic preference for the Informative Option.

The model predicts that the action yielding the highest rate should be always implemented because intermediate proportions of rejection never maximize food intake (see proof in Charnov, 1976; Stephens & Krebs, 1986). The whole strategy set includes more action alternatives (e.g., accept the  $S^+$  and one of the  $S^{+/-}$ , and reject the other stimuli), but we consider only these two cases as they encompass the aforementioned untested assumption of the RRM.

In the original instantiation of the RRM, it was assumed that animals disregard both the bad-news stimulus and the ITI duration, but because we are now interested in the choice between accepting versus rejecting a terminal-link stimulus, animals should pay attention to the consequences of each possible course of action. If the animal decides to reject or accept a terminal link immediately at its onset, with the decision latency negligible relative to terminal link duration, then a) rejecting should be affected by ITI duration but not by the terminal link duration, whereas b) accepting should be affected by terminal link duration but not the ITI duration. In other words, only the immediate consequence of the decision is taken into account. It follows that adopting the generalist strategy of accepting all options yields the long-term rate ( $R_{accept}$ ) given by Equation 4,

$$R_{accept} = \frac{p_{reward}}{t + p_{reward} \times h} = \frac{1}{\frac{t}{p_{reward}} + h} \quad (4)$$

where  $p_{reward}$  is the overall probability of reward given by the weighted average of probabilities in the Informative and Noninformative options, and the remaining parameters retain their previous meaning.

When animals adopt the specialist strategy of rejecting the bad-news stimulus but not the others, the durations taken into account depend on which stimulus is presented—if the bad-news, only the ITI duration ( $s$ ) is taken into account; if the other stimuli, only the terminal-link duration ( $t$ ) is taken into account. Thus, the long-term rate ( $R_{reject}$ ) for this strategy is given by

$$R_{reject} = \frac{p_{reward}}{p_{bad-news} \times s + (1 - p_{bad-news}) \times t + p_{reward} \times h} \quad (5)$$

From Equations 4 and 5 we predict that animals should escape from the bad-news stimulus when

$$\frac{R_{reject} > R_{accept}}{\frac{p_{reward}}{p_{bad-news} \times s + (1 - p_{bad-news}) \times t + p_{reward} \times h} > \frac{1}{\frac{t}{p_{reward}} + h}}$$

which simplifies to

$$s < t \quad (6)$$

In other words, animals should escape the bad-news stimulus if the ITI duration is shorter than the terminal-link durations. Neither the probability of reinforcement ( $p_{reward}$ ) nor the reward duration ( $h$ ) should influence the decision to escape.

Figure 2 shows the reward rate both for accepting ( $R_{accept}$  from Equation 4, white dots) and escaping ( $R_{reject}$  from Equation 5, black dots) the bad-news stimulus. The left panel shows the rates as a function of the ITI duration, with the terminal-link durations constant at 10 s (i.e., Equations 4 and 5 with  $s$  varying and  $t = 10$  s); the right panel shows the rates as a function of the

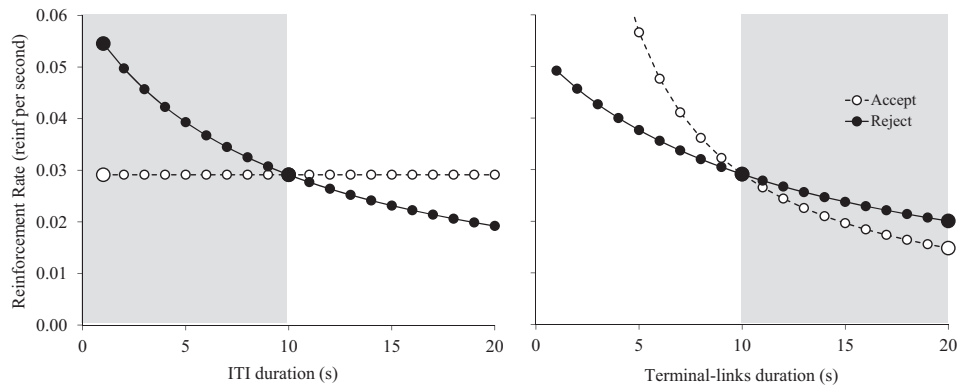


Figure 2. Reward rate functions when accepting (white dots) and rejecting (black dots) the bad-news stimulus, as a function of ITI duration (left panel) and terminal-link duration (right panel). Rejecting the bad-news is the best action within the shaded region. The larger dots identify the values tested in the present experiments. Parameter  $h$  was set at 1 s.

terminal-link duration, with the ITI duration constant at 10 s (i.e., Equations 4 and 5 with  $t$  varying and  $s = 10$  s).

When animals always accept the bad-news stimulus (and all other terminal-link stimuli), only the terminal-link durations are taken into account. Thus, because  $R_{accept}$  is independent of the ITI duration (cf. Equation 4) the left panel of Figure 2 shows  $R_{accept}$  as a horizontal line. Conversely, when animals reject the bad-news stimulus,  $R_{reject}$  is strongly affected by the ITI duration, varying inversely with it (cf. Equation 5) which translates into the decreasing hyperbola shown in the left panel of Figure 2. Hence, as derived in Equation 6, when the ITI is less than 10 s (the terminal-link duration), animals should reject the bad-news stimulus ( $R_{reject} > R_{accept}$ ; shaded area) and accept it otherwise.

Whereas the ITI duration affects only  $R_{reject}$ , the terminal-link duration influences both  $R_{reject}$  and  $R_{accept}$ : When animals reject the bad-news stimulus, they nonetheless take into account the terminal-link duration of the other, accepted terminal stimuli; when they accept the bad-news stimulus (and all other stimuli), they take into account all terminal-link durations. As the duration of the terminal links increases, both reward rates decrease (Figure 2, right panel). However, because all terminal-link durations are included in  $R_{accept}$ , but  $R_{reject}$  excludes the bad-news stimulus duration, the former function is steeper. Again consistent with Equation 6, when the terminal-link duration is longer than 10 s (the duration of the ITI), animals should reject the bad-news stimulus ( $R_{reject} > R_{accept}$ ; shaded area) and accept it otherwise.

### The Present Experiments

The main goal of the present experiments was to test the foregoing prediction of the RRM that animals should escape in the presence of the bad-news stimulus. To that end, we exposed pigeons to the standard task but, during the terminal links, we gave them a choice between continuing in the situation (accepting) and escaping from the situation (rejecting). To that end, we resorted to a modified version of a sequential-encounters procedure (e.g., Abarca & Fantino, 1982; Abarca, Fantino, & Ito, 1985; Fantino & Preston, 1988; Freidin, Aw, & Kacelnik, 2009; Hanson & Green, 1989a, 1989b; Lea, 1979; Mazur, 2007, 2008).

A second goal was to test whether escaping was affected by the ITI and the terminal-link durations as predicted by the prey model modification of the RRM. Even though optimality can only be achieved by either always or never escaping, several experiments have shown that the probability of escaping is usually intermediate (Abarca & Fantino, 1982; Abarca, Fantino, & Ito, 1985; Fantino & Preston, 1988; Freidin et al., 2009; Hanson & Green, 1989a, 1989b; Lea, 1979; Mazur, 2007, 2008). Matters would be simpler if decision makers showed exclusive preferences (as predicted by rigorous maximization of outcomes), but frequently they do not, perhaps because exclusive allocation has costs in unstable environments as it strips the decision maker from information about alternatives never chosen. This empirical finding led to the claim that preference between options is, at least approximately, proportional to the subjective ratio of rewards. Accordingly, we predicted that the probability of escaping depended on the relative gain from escaping versus accepting the bad-news stimulus. For example, shortening the ITI duration should lead to more escape responses compared with increasing the terminal-link duration (compare the distance between the black and white dots in Figure 2). In Exper-

iment 1, we manipulated the ITI duration and in Experiment 2 we manipulated the terminal-link durations.

Finally, the study of escape behavior may also help to clarify semantics. Several researchers have suggested that the bad-news stimulus is *ignored* or *not taken into account* (e.g., Fortes et al., 2016; Mazur, 1991, 1995, 1996; McDevitt et al., 2016; Pisklak, McDevitt, Dunn, & Spetch, 2015; Spetch et al., 1994; Stagner et al., 2012; Vasconcelos et al., 2015; Zentall, 2016; Zentall, Laude, Stagner, & Smith, 2015). Exploring the conditions under which animals escape the bad-news stimulus may allow us to better understand what is meant by *ignored* or *not taken into account*. On the one hand, if ignoring the bad-news stimulus means that the animal is subjectively in a situation where the bad-news stimulus is never presented, then it should *never* escape. On the other hand, ignoring the bad-news stimulus may mean that, even though the animal is aware of its presence, it simply disengages from the task and does not associate the presentation of this stimulus with the choice of the Informative Option (i.e., a problem of credit attribution). In this case, the animal should (under certain circumstances) escape the bad-news stimulus because by doing so the delay to the next possible reward decreases. The prediction of the RRM that animals should escape the bad-news stimulus presupposes the latter.

### Experiment 1 – The Effect of the ITI Duration on Escape Behavior

#### Method

**Subjects.** Eight pigeons (*Columba livia*) with previous experience in timing procedures participated. The birds were housed individually in a room with controlled temperature (around 21°C), and with a 11h:13h dark/light cycle (lights on at 8 a.m.). In their home cages, animals had water and grit always available. The birds started the experiment when they were at 80% of their free-feeding weights. The pigeons were cared for in accordance with the animal care guidelines of the National Veterinary Agency and the University of Minho.

**Apparatus.** Four operant chambers for pigeons were used. All chambers were enclosed in an opaque box equipped with a fan that circulated air and masked outside noises. Three of the chambers were manufactured by Med Associates, and were 28.5 cm high, 24 cm long, and 30 cm wide. The front panel had three horizontally aligned keys, each 2.5 cm in diameter, 6 cm apart, center-to-center. The bottom edge of the keys was 21 cm from the floor. Below the keys there was a 6-cm-wide  $\times$  5-cm-high feeder opening, centrally aligned and 4 cm above the floor. When the feeder was raised, a 1.1-W light illuminated the food. On the panel opposite to the front panel, a 2.8-W houselight, 23 cm above the floor, illuminated the whole box. The fourth chamber was custom-built and it was equal to the other boxes except for the following measures: it was 31 cm high, 33 cm long, and 33 cm wide; the keys were 9 cm apart, center-to-center; the feeder opening was 6 cm wide  $\times$  4.5 cm high, 6.5 cm above the floor, and the houselight was 27.5 cm above the floor.

A personal computer with a custom-made Visual Basic, 2010 program controlled the events and recorded data via Whisker software (Cardinal & Aitken, 2010).

#### Procedure.

**Pretraining.** Pigeons received one session in which they had to peck each of the stimuli used in this task: red, green, yellow,



blue, and white on the left and right keys, and white and a vertical white bar on a black background on the center key. Each session had 48 trials, 4 trials per stimulus. Each trial began with a response key illuminated with one of the stimuli; a single peck at that key turned its light off and ended the trial with a 3-s reinforcer. The trials were separated by a 10-s ITI with only the houselight on. The houselight turned off when the trial started. The peck requirement increased to 10 during the second and third pretraining sessions.

**Escaping from terminal links.** Each session comprised 120 trials divided into four 30-trial blocks. Within each block, there were 20 forced-choice (10 per option) and 10 free-choice trials, randomly intermixed. On a forced-choice trial only one option was presented. At the beginning of a forced-choice trial, a white hue on the center key flashed (250 ms on, 250 ms off). A peck at this key turned it off and turned on one of the side keys with a white hue (initial links, Figure 1). For half of the birds the Informative Option was always on the left and the Noninformative Option was always on the right; for the remaining birds the opposite was true. A peck on the white side key initiated the 10-s terminal link. If the Informative Option was presented, on 20% of the trials the good-news stimulus was turned on (e.g., red), and after 10 s food was delivered; on the remaining 80% of the trials the bad-news stimulus was turned on (e.g., green), and 10 s after the trial ended without food. If the Noninformative Option was presented instead, on 20% of the trials one stimulus was turned on (e.g., yellow) and on the other 80% of the trials a different stimulus (e.g., blue) was turned on. In both cases, the stimulus stayed on for 10 s and was followed by food on half of the trials. After all trials, a 10-s ITI with the houselight on followed. The terminal-link colors associated with each option were counterbalanced across pigeons, with the constraint that red and green were always associated with one option and yellow and blue were always associated with the other option.

The free-choice trials were exactly the same as the forced-choice trials, except that during the initial link the two side keys were illuminated; one peck at one of the side keys turned the other key off. Afterward, the trial proceeded as described for forced-choice trials.

Importantly, once a terminal-link stimulus was presented, the animals could escape from it. Specifically, on all trials, a vertical white bar (on a dark background) turned on at the center key (escape key) simultaneously with the terminal-link stimulus. If the pigeon pecked the escape key once, the trial ended immediately without food, the 10-s ITI followed, and then a new trial started. This phase lasted 10 sessions.

**Forced-escape trials.** Because escape responses decreased systematically and unexpectedly across the previous phase, we introduced forced-escape trials to ensure constant exposure to the contingencies associated with pecking the escape key. This phase was equal to the previous one, but on 40 new trials the pigeons were forced to peck the escape key. That is, on these trials, after the initial-link peck, the side key was turned off and only the vertical bar on the center key was presented (the escape key). A peck at this key turned it off and initiated the 10-s ITI. At the end of the ITI, a new trial began. There were 20 forced-escape trials after an initial link on the left and 20 after an initial link on the right. These trials were equally distributed across the four blocks of 30 trials, totaling 160 trials. This phase lasted for 15 sessions.

**1-s ITI.** In this phase everything remained the same, except that all ITIs were 1-s long. This phase lasted for 10 sessions.

**Escaping from initial links.** According to Vasconcelos et al. (2015), animals should not escape during the initial links because these stimuli provide no information about impending food. This phase was the same as the previous one, with the following exceptions: (a) animals could escape during the initial links, and (b) 40 new trials were added to force the animals to peck the escape key during the initial link. On all forced- and free-choice trials, when the side(s) key(s) was/were turned on white, the vertical white bar was also presented at the center, escape key. To avoid escape responses caused by bursts of responses at the flashing, attention key, a self-initiated fixed-interval schedule was in effect in the escape key. The first peck at this key initiated a 1-s interval. After the interval elapsed, if the center key was pecked again the trial was cancelled immediately, and a 1-s ITI followed. If one of the side keys was pecked, the terminal link started as usual. On the additional 40, forced trials, after the peck at the center key that initiated the trial, only the center vertical bar was presented, with the same schedule described above. Each 50-trial block had 20 trials in which the animals were forced to escape (10 in the initial link and 10 in the terminal link), and 30 trials in which the animals could escape (10 forced-choice trials with each option and 10 free-choice trials). The sessions comprised four blocks, for a total of 200 trials. This phase lasted for 10 sessions.

**Design summary.** Table 1 shows a summary schematic of the experiment. Given that all phases included forced and free-choice trials, we show only whether the escape key was available and whether there were forced-escape trials for each experimental phase.

## Results and Discussion

Unless stated otherwise, the mean values were collected from the last three sessions of each condition. In all statistical analyses, a significance level of 0.05 was adopted.

**Preference.** Figure 3 shows the mean proportion of choices of the Informative Option ( $\pm$  SEM) over sessions. All animals showed an initial tendency to choose the optimal, Noninformative Option, a result commonly reported in the literature (e.g., Laude, Stagner, & Zentall, 2014; Zentall & Stagner, 2011). Then, all birds developed a strong preference for the Informative Option, which was significantly above chance by the fifth session,  $t(7) = 3.66$ ,  $p < .01$ ,  $d = 1.29$ , 95% CI for Cohen's  $d = [0.13, 2.46]$ . Preference for the Informative Option remained almost exclusive throughout the following phases.

Table 1  
Design of Experiment 1

Experimental phase	Escape key		Forced escape trials
	Initial links	Terminal links	
Escaping from terminal links	No	Yes	No
Forced-escape trials	No	Yes	Yes
1-s ITI	No	Yes	Yes
Escaping from initial links	Yes	Yes	Yes

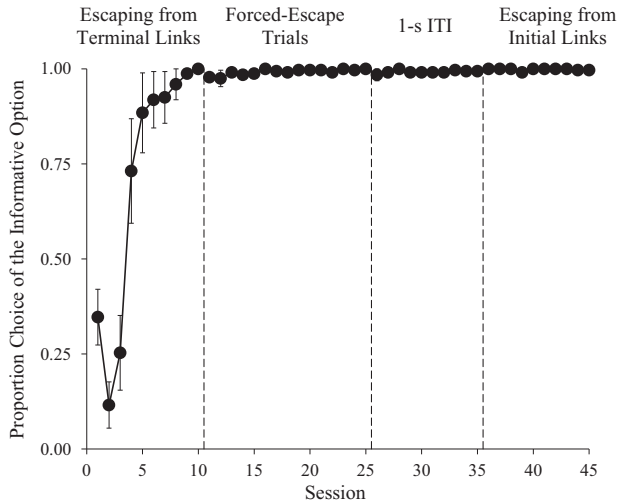


Figure 3. Mean proportion of choices of the Informative Option across sessions in Experiment 1. The error bars are the standard error of the mean.

**Escape responses.** Figure 4 shows the mean proportion of escape responses ( $\pm$  SEM) for each of the terminal-link stimuli. In the first session, birds escaped from all terminal stimuli:  $M_{\text{bad news}} = .62$  ( $SEM = .09$ ),  $M_{\text{good news}} = .28$  ( $SEM = .11$ ),  $M_{S1} = .43$  ( $SEM = .12$ ), and  $M_{S2} = .48$  ( $SEM = .11$ ). In subsequent sessions, escaping occurred almost exclusively in the presence of the bad-news stimulus.

During the Escaping from Terminal Links Phase, escaping the bad-news stimulus decreased over sessions, with an average of 5% of escapes in the tenth session. When forced-escape trials were introduced in the Forced-Escape Trials Phase, the proportion of escapes increased and stabilized around .26 ( $SEM = .003$ ). In this phase, the perceived reinforcement rate was the same whether or

not animals escaped from the bad-news stimulus, so we expected the proportion of escaping to be around 50% (cf. left panel of Figure 2). However, the observed proportion was below indifference,  $t(7) = 3.24$ ,  $p = .01$ ,  $d = 1.15$ , 95% CI = [0.00, 2.29], thus revealing a bias against escaping. This bias may have been caused by the asymmetry of the response requirements: Whereas escaping required a peck at the center key, accepting the option did not require any specific response and was thus the “default” choice. This is consistent with previous findings in which the default was escaping (Lea, 1979): If pigeons did not peck any key for approximately 4 s, the option was rejected, but if they pecked the key the option was accepted. In a condition where 50% of escaping was expected, the pigeons showed a bias toward escaping. In the same vein, when Mazur (2007) required one peck both to reject and to accept the option, there was no bias: escape responses were close to 50%.

Finally, during the last two phases with a 1-s ITI—and therefore a significantly higher overall reward rate for rejecting than for accepting the bad-news stimulus (cf. left panel of Figure 2)—escaping increased considerably and stabilized around .80. The increase in the proportion of escape responses from the Forced-Escape Trials Phase to the 1-s ITI Phase was statistically significant,  $t(7) = 8.90$ ,  $p < .001$ ,  $d = 3.15$ , 95% CI = [1.52, 4.77]. Averaged across the last three sessions, pigeons escaped from bad news on the majority (>50%) of the trials both in the 1-s ITI Phase,  $t(7) = 8.11$ ,  $p < .001$ ,  $d = 2.87$ , 95% CI = [1.32, 4.41] and in the Escaping from Initial Links Phase,  $t(7) = 5.23$ ,  $p = .001$ ,  $d = 1.85$ , 95% CI = [0.57, 3.13].

In the last phase, animals could escape both during the initial and the terminal links. As predicted, they seldom escaped during the initial link: Only three of eight birds pecked the escape key during the initial links, always during forced-choice trials with the Noninformative Option, but on fewer than 2.5% of these trials.

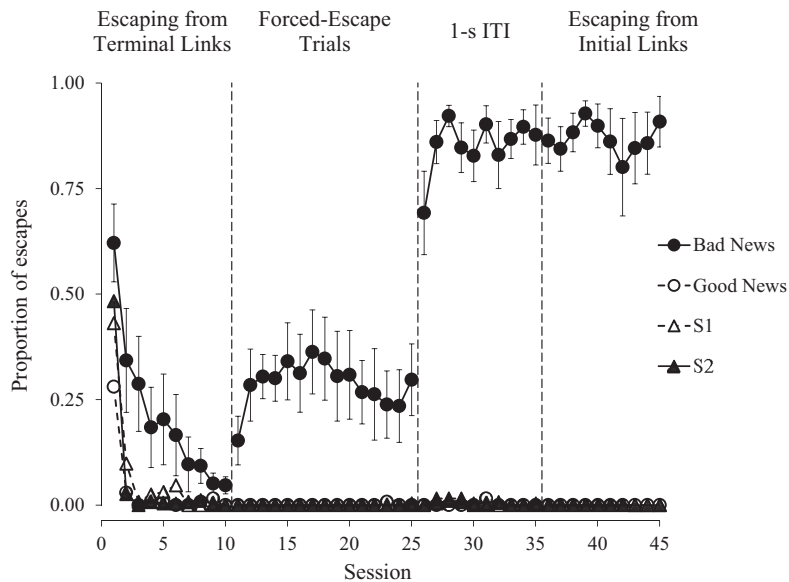


Figure 4. Mean proportion of escape responses for each terminal-link stimulus in Experiment 1. The error bars are the standard error of the mean.

In summary, the predictions of the modified version of the RRM were confirmed. First, the pigeons escaped only from the bad-news stimulus, not from the other terminal-link stimuli. Second, the pigeons escaped more when the overall reward rate was higher for escaping than for accepting. And third, the pigeons almost never escaped during the initial links.

## Experiment 2 – The Effect of the Terminal-Link Duration on Escape Behavior

In Experiment 1, even though pigeons used the escape key on the Forced-Escape Trials Phase, they seemed to have a bias against escaping, which could have been the result of the different requirements for escaping and accepting the stimulus. Another factor that may have contributed to this bias was avoidance of the escape key due to its proximity to the bad-news stimulus. Unsystematic observations revealed that when the bad-news stimulus was presented, the pigeons turned their back to it, and consequently also to the escape key. Thus, in Experiment 2 we placed the escape key away from the bad-news stimulus to test whether pigeons would escape more often. This procedural modification also made the test of the RRM more sensitive because it allowed the pigeon's natural behavior in the presence of a discrete  $S^-$  (i.e., moving away from it) to co-occur with the operant behavior of pecking the escape key. To test the second prediction of RRM, we manipulated the duration of the terminal links, while keeping the ITI constant. If the model is correct, the pigeons should escape more as the terminal-link duration increased.

## Method

**Subjects.** Four pigeons (*Columba livia*) participated. All birds had experience with timing and choice experiments. None of the birds had experience with a long operant box. The animals were kept in the same conditions as in Experiment 1.

**Apparatus.** One custom-built, long operant box was used (see Figure 5). The box was placed in a shelf covered by wood panels on all sides except in the front, where it was covered by a blackout roller blind. Behind the box, two speakers, one on each side, were connected to a mini laptop that produced continuous white noise during the session.

The box had three intelligence panels, one on the left side, one on the right side, and one centered in the back wall. Each panel was equipped with three horizontally aligned keys, each 2.5-cm in diameter. The keys were 8 cm apart, center-to-center, and 24 cm above the floor (measured from their lowest edge). A feeder opening (5-cm high  $\times$  6-cm long) was centrally located on each panel, 9 cm above the floor. When activated, the food hopper was illuminated with a 1.1-W light. Above the keys, centrally located and 1.5 cm below the ceiling, a 2.8-W houselight illuminated the box. We used only the right key of the left panel, the center key of the central panel and the left key of the right panel, henceforth referred to as the left, center, and right keys, respectively.

The box floor consisted of three movable panels of equal size. Each panel rested on a pivot that was centrally located underneath the panel. Depending on the pigeon's location, the panel could tilt to the right or to the left, in each case activating a switch. We numbered the switches from 1 (the left side of the leftmost floor panel) to 6 (the right side of the rightmost floor panel).

A personal computer with a custom Visual Basic, 2010 program controlled the events and recorded data via Whisker software (Cardinal & Aitken, 2010).

**Procedure.** Because the standard task had not been implemented in a long operant box, we first replicated it and only afterward introduced the escape key.

**Pretraining.** None of the birds had experience with a long operant box, so they were first trained to eat from each feeder. Next, each bird received two sessions with 44 trials in which one peck at the left or right key illuminated with red, green, yellow, blue, or white light, or at the center key illuminated with white light, was reinforced with 3-s of access to food. The reinforcer was delivered by the feeder located in the same panel as the pecked key. The three houselights were always on except during reinforcement, and a 10-s ITI separated the trials. The peck requirement was then increased to 10 during 2 additional sessions.

**Training.** The procedure was the same as in the Escaping from Terminal Links Phase of Experiment 1 (see Figure 1), except that (a) there was no escape key available, (b) a long operant chamber was used, and (c) the stimuli were presented on different panels: the flashing attention key on the center key of the center panel and the Informative and Noninformative Options on opposite panels, counterbalanced across birds.

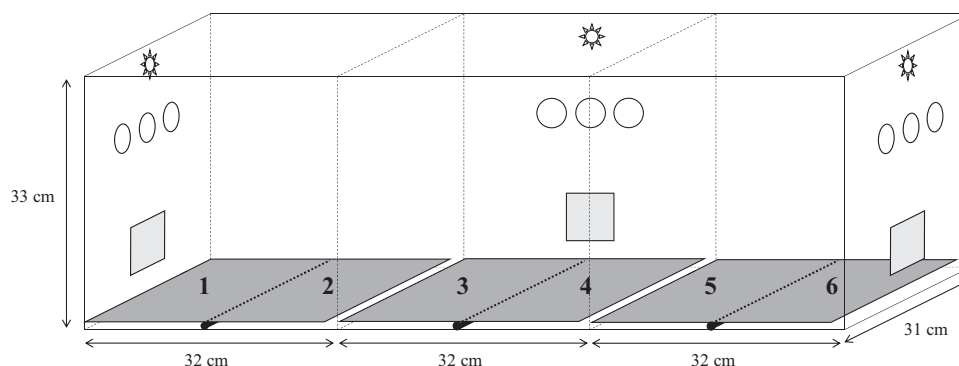


Figure 5. Diagram of the long operant chamber used in Experiment 2 (courtesy of Álvaro Viúdez). The switches on the floor are numbered from 1 to 6.



**Reversal.** In this phase, the location of the Informative and Noninformative options was reversed. This phase ensured that the results observed in the previous phase reflected a preference for one of the options and not a preference for one of the side keys. In all other respects the sessions remained the same as in the previous phase. This phase also lasted for 10 sessions.

**Escaping from 10-s terminal links.** In this phase, birds could escape the terminal links on all trials. After pecking the white hue in one of the side panels (initial link), the same key displayed the terminal-link stimulus and the white center key (the escape key) was turned on. If the pigeon moved to the central panel and pecked the escape key during the terminal link, all keylights were turned off and a 10-s ITI followed.

Forty trials in which the animals were forced to peck the escape key were also added. On a forced-escape trial, after one of the side keys was turned on white (initial link), one peck at that key turned it off and the escape key turned on at the central panel. The trial only proceeded when the pigeon pecked the escape key, which was followed by the ITI. Although the white center key was used both to start and escape the trial, its two functions were distinctly signaled: The keylight was flashing to start, but continuously on to escape the trial. The sessions were divided into four 40-trial blocks (10 free-choice trials, 10 forced-choice trials with each option and 5 forced-escape trials with each option), totaling 160 trials. This phase lasted for 10 sessions.

**Escaping from 20-s terminal links.** Next, the terminal-link duration was increased from 10 to 20 s. Sessions comprised two 40-trial blocks and were run for 20 days. The data of each two sessions were collapsed in order to make them comparable to the previous phase. The remaining details remained as in the previous phase.

## Results and Discussion

Unless stated otherwise, for all analyses the mean values refer to the last three sessions of each condition. A significance level of 0.05 was used in all analyses.

**Preference.** Figure 6 shows the mean proportion of choices of the Informative Option ( $\pm$  SEM) across sessions. During the Training Phase, all birds acquired a strong preference for the Informative Option ( $M = .98$ ,  $SEM = .03$ ) that was significantly above chance,  $t(3) = 19.00$ ,  $p < .01$ ,  $d = 9.50$ , 95% CI = [3.09, 15.91]. In the first session of the Reversal Phase, all animals preferred the previously preferred side, now assigned to the Noninformative Option,  $M = .06$ ,  $SEM = .05$ . After a few sessions, all birds reversed preference, choosing the Informative Option significantly above chance ( $M = .99$ ,  $SEM = .01$ ),  $t(3) = 62.07$ ,  $p < .01$ ,  $d = 31.04$ , 95% CI = [10.70, 51.38]. This preference remained stable and high (>93%) in all subsequent phases.

**Escape responses.** Although birds never escaped from the good-news stimulus or from the terminal links of the Noninformative Option, they did escape from the bad-news stimulus. Figure 7 shows the proportion of escape responses when the bad-news stimulus was presented. As in Experiment 1, when the escape key was first introduced—Escaping from 10-s Terminal Links Phase—the pigeons pecked at it, but escaping decreased across sessions. The proportion of escape responses during this phase stabilized around .10 ( $SEM = .06$ ) and remained below 50%,  $t(3) = 7.24$ ,  $p < .01$ ,  $d = 3.62$ , 95% CI = [0.76, 6.47].

In this experiment, the distance between the escape and the bad-news keys dramatically increased, but comparing phases with the same parameters (Forced-Escape Trials in Experiment 1 and Escaping from 10-s Terminal Links in Experiment 2), the mean

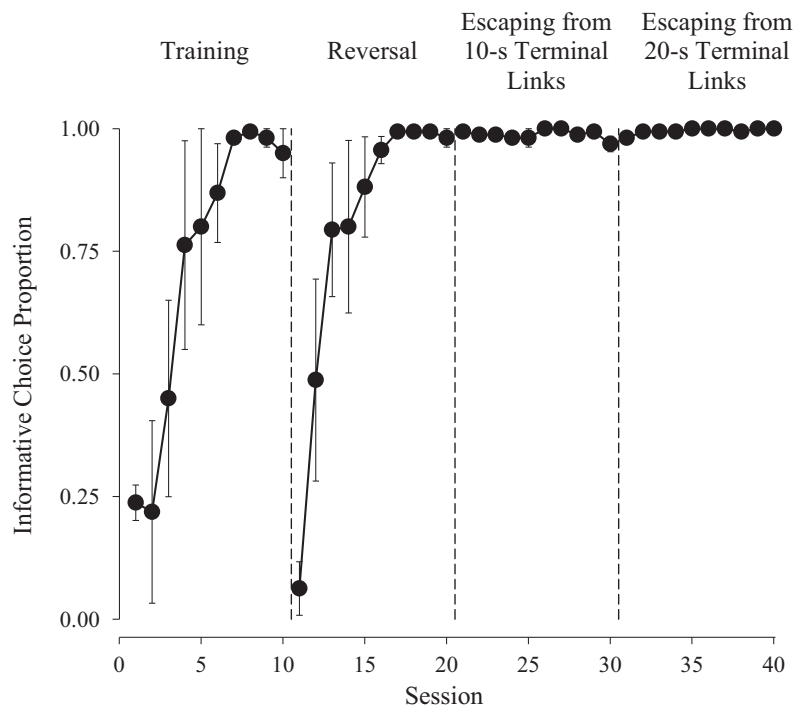


Figure 6. Mean proportion of choices of the Informative Option across sessions in Experiment 2. The error bars are the standard error of the mean.

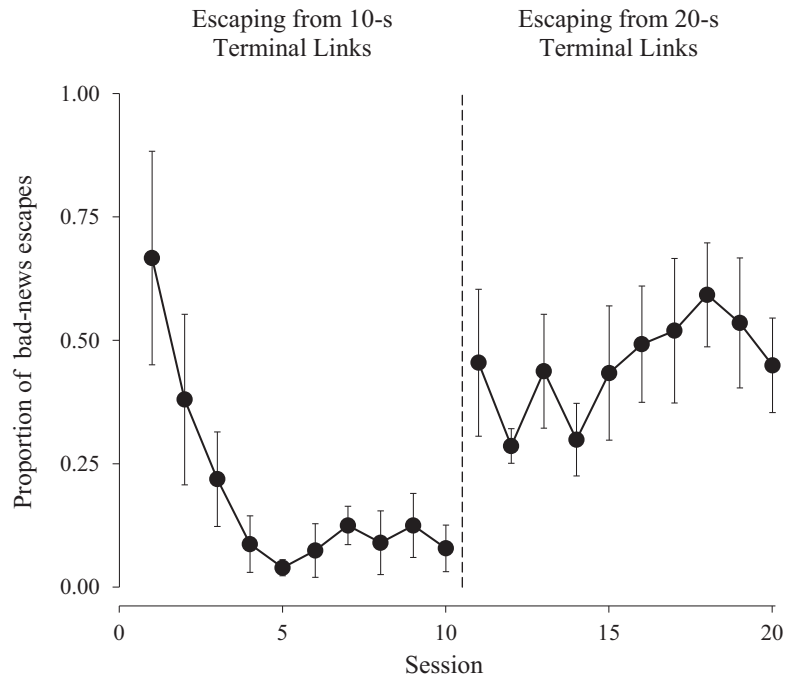


Figure 7. Mean proportion of escape responses during the bad-news terminal link. The error bars are the standard error of the mean.

proportion of escape responses decreased from .26 in Experiment 1 to .10 in Experiment 2, suggesting that the proportion of escapes in Experiment 1 cannot be fully explained by the relative position of the escape key. These results suggest that the bias against escaping was most likely due to the different peck requirements for accepting and rejecting the bad-news stimulus (i.e., no peck vs. peck, respectively).

When the terminal-link duration increased from 10 to 20 s and the reward rate for rejecting the bad-news stimulus was higher than for accepting it, the proportion of escape responses increased to .53 ( $SEM = .11$ ), a value not significantly different from 50%,  $t(3) = 0.24$ ,  $p = .83$ ,  $d = 0.12$ , 95% CI =  $[-1.48, 1.72]$ . This increase in escape responses from the 10-s to the 20-s Terminal Links Phase was statistically significant,  $t(3) = 5.31$ ,  $p = .01$ ,  $d = 2.65$ , 95% CI =  $[0.29, 5.01]$ , a result consistent with the predictions of the RRM (cf. right panel of Figure 2).

**Movement.** The floor switches recorded the birds' movements during the terminal links. Figure 8 shows the average position of the birds when they had no means of escaping (Training and Reversal phases) or did not escape the terminal link (Escaping from the 10-s and 20-s Terminal Links phases). To facilitate interpretation, the data are presented as if all birds had the Informative Option on the left (box location = 1) and the Noninformative Option on the right (box location = 6).

The top left panel of Figure 8 shows that during the Training Phase pigeons stayed near the chosen key except when the bad-news stimulus was presented. In this case, pigeons moved to the center of the box and waited until the next trial. When the position of the keys was reversed, the animals adopted the same strategy, staying near the good-news, S1, and S2 stimuli, and moving away from the bad-news stimulus (Figure 8, top right and bottom pan-

els). When the terminal links were 20-s long (Figure 8, bottom right panel), the motion pattern in the presence of the bad-news stimulus was slightly different, with most pigeons moving toward the side of the Noninformative Option (locations 1 and 2) and then back to the center of the box (locations 3 and 4). The inset in the lower right panel illustrates this pattern during two bad-news trials for one pigeon. Because the time at which pigeons arrived at, and departed from, the Noninformative Option side varied from trial to trial, the average function seen in Figure 8 is smoother than the actual movement during a single trial. Comparing the last two phases (bottom panels), the proportion of trials in which animals moved to the opposite, Noninformative Option side increased significantly in the Escaping from 20-s Terminal Links Phase,  $t(3) = 6.71$ ,  $p < .01$ ,  $d = 3.36$ , 95% CI =  $[0.64, 6.07]$ , with changes ranging from a 0.29- to a 15.73-fold difference between phases.

Moving farther away from the negative stimulus could be the result of either greater aversiveness of the bad-news stimulus when it was presented for 20 s, or simply the result of having more time to move. When the pigeons escaped the bad-news stimulus, their motion pattern (not shown) was similar to that in Figure 8, except that when they arrived at the center of the box they pecked the escape key right away thus reducing the trial duration.

These results confirm previous unsystematic observations in standard operant chambers: The animals move away from the bad-news stimulus (see also Dinsmoor, Mueller, Martin, & Bowe, 1982; Rand, 1977). When the escape key was available, the pigeons did not always peck at it, but on most trials they continued to move away from the bad-news stimulus. In particular, they moved to the center of the box or the side opposite the bad-news key, on 93% ( $SEM = 3\%$ ) of the trials when the terminal links

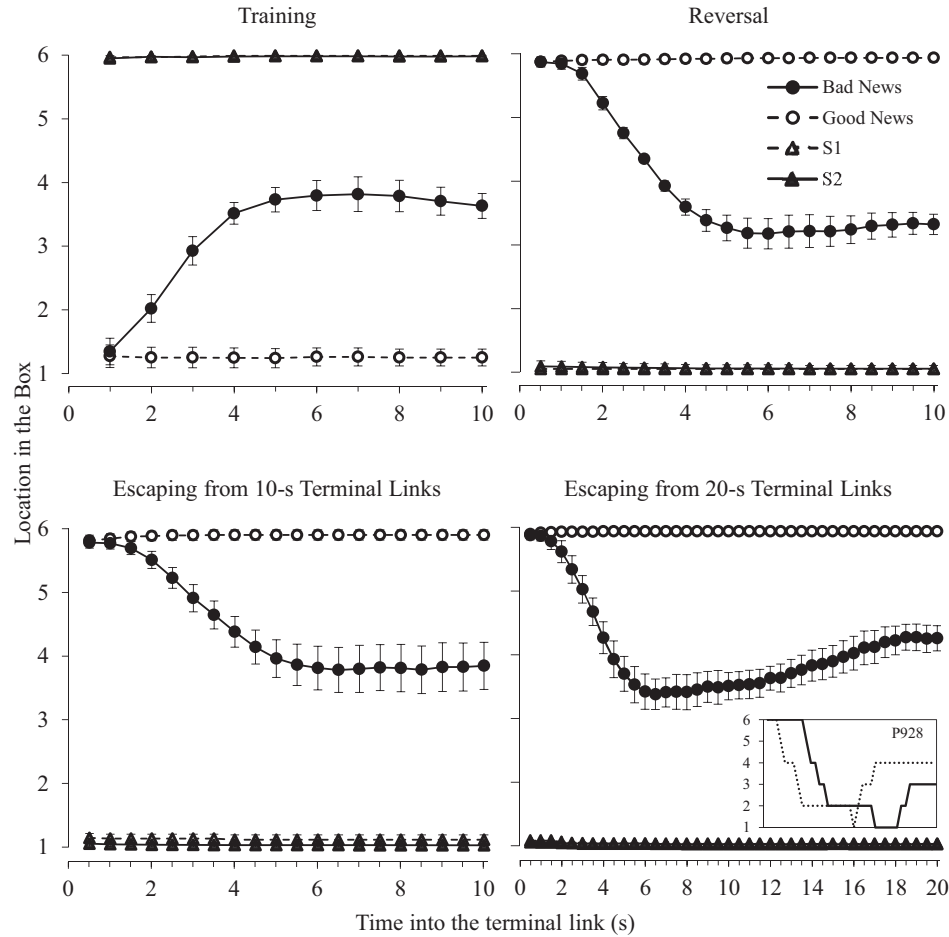


Figure 8. Mean location in the long operant box during each terminal-link stimulus. Each panel shows the results of a phase of Experiment 2. The error bars are the standard error of the mean. The inset (bottom right panel) shows two bad-news trials for pigeon P928. During the Training Phase, time into the terminal link was divided in 1-s bins, and in subsequent phases 0.5-s bins were used.

were 10-s long, and on 98% ( $SEM = 1\%$ ) when they were 20-s long.

Why did pigeons move toward the escape key on most trials, but only on some trials pecked at it? Perhaps moving away from the bad-news stimulus and pecking the escape key are not controlled by the same variables. That is, perhaps pigeons move away from the negative stimulus because in the natural environment the probability of encountering food increases if they move away from a patch without food. Moving away from the bad-news stimulus may be an unconditional response to that stimulus, and for that reason it occurs on almost all trials. On the other hand, pecking the escape key may be controlled by the consequences of pecking, more specifically, by the change in the reward rate caused by pecking. This may be the reason why pecking occurred only when it was advantageous to do so.

### General Discussion

When animals are given a choice between 20% signaled reinforcement and 50% unsignaled reinforcement, they consistently choose the option that yields less reinforcement but immediately

informs whether food will be delivered or not (e.g., Fortes et al., 2016; Stagner & Zentall, 2010; Zentall & Stagner, 2011; Stagner et al., 2012; see Zentall, 2016 and McDevitt et al., 2016 for reviews). The most consistent account to explain these findings is that animals take into account the stimuli that are associated with food—both in the Informative and Noninformative options—but ignore the stimulus that is never followed by food—the bad-news stimulus in the Informative Option. This in turn leads to a higher perceived reward rate in the Informative Option.

Vasconcelos and colleagues (2015) asserted that the suboptimal choice in this task stems “from testing the animals in a situation where information is useless, while the birds’ psychological processes are adapted to a world in which information alters the subsequent behavior” (p. 9). Thus, in the present experiments we made information useful, by allowing birds to escape from the stimulus shown, and we expected them to use that information appropriately. To make specific predictions, we adapted the core ideas of Charnov’s prey model (Charnov, 1976). We predicted the following: (a) animals should only escape from the bad-news stimulus; (b) escaping should increase as the reward rate for

escaping relative to accepting increases, such as when the ITI duration was decreased (Experiment 1) or the terminal-link duration was increased (Experiment 2), and; (c) the probability of escaping should be associated with the degree of improvement in the reward rate when rejecting versus accepting the bad-news stimulus.

Experiments 1 and 2 confirmed the first prediction: The pigeons escaped only from the bad-news stimulus. Moreover, consistent with other studies with the successive-encounters procedure, escaping was not all-or-none, but assumed intermediate values (Abarca & Fantino, 1982; Abarca, Fantino, & Ito, 1985; Fantino & Preston, 1988; Freidin et al., 2009; Hanson & Green, 1989a, 1989b; Lea, 1979; Mazur, 2007, 2008).

The prediction that escaping should increase as the reward rate for escaping relative to accepting increases was also borne out. Experiment 1 showed that decreasing the ITI duration from 10 to 1 s significantly increased the proportion of escape responses from the bad-news stimulus, and Experiment 2 showed that increasing the terminal-link duration from 10 to 20 s had the same effect.

The model predicted higher rates of escaping from the bad-news stimulus when the ITI was shorter than the terminal link than when they had the same duration (in Experiment 1, more when  $s = 1$  and  $t = 10$  than when  $s = t = 10$ ; in Experiment 2, more when  $s = 10$  and  $t = 20$  than when  $s = t = 10$ ). But one could argue, perhaps with greater parsimony, that the pigeons escaped more when  $s < t$  than when  $s = t$  for two different reasons. In Experiment 1, the reduction in the delay to food was more noticeable when  $s = 1$  than when  $s = 10$  because in the former condition the intervals were all relatively short. In Experiment 2, escaping was more likely when  $t = 20$  than when  $t = 10$  simply because a longer terminal link affords more opportunities to escape. Both arguments invoke obvious facts—escaping from the bad-news stimulus always reduces the average delay to food, and a longer terminal link always affords more opportunities to escape—but whether these facts explain the increased rate of escaping when  $s < t$  remains to

be checked in studies designed explicitly to disentangle them from the model's account. In the meantime, we identify two problems with these alternative accounts. First, if pigeons were indeed sensitive to the delay reduction in Experiment 1, then why did they not reverse preference from the Informative to the Non-Informative option and thereby reduce even more the delay to food? Should the same sensitivity to delay reduction not lead to optimal choice? Second, if pigeons escaped more in Experiment 2 simply because they had more time to escape, the number of escape responses within the first 10 s of the terminal link should be the same in the two conditions. The data of four pigeons were inconclusive—three pigeons showed an increase in the number of escapes (changes ranged from a 0.29- to a 38.68-fold difference) and one a decrease (a 2.38-fold difference). Future experiments need to clarify these two issues. Would animals escape from the bad-news stimulus if the only consequence of escaping was the termination of the stimulus (no reduction in delay to food)? In other words, are bad news aversive such that simply removing them (negatively) reinforces pecking an escape key? Laude et al.'s (2014) findings that bad-news are no longer aversive once animals learn the task suggest otherwise.

Finally, to analyze the prediction that the probability of escaping should correlate positively with the degree of improvement in reward rate when rejecting versus accepting the bad-news stimulus, Figure 9 shows the observed proportion of bad-news escape responses in each phase (black dots) and the relative increase in the reward rate when escaping the bad-news stimulus (white dots). The latter was given by  $(R_{\text{reject}} - R_{\text{accept}})/(R_{\text{accept}})$ .

As Figure 9 shows, animals escaped more frequently from the bad-news stimulus when it was more profitable (Pearson's correlation between the proportion of escape responses and the relative gain of escaping,  $r = .98$ ,  $p = .022$ ). However, the predictions of the modified RRM model should be taken only as approximations to what the animal is expected to do. First, we did not take into account the latencies to peck the keys, even though these latencies

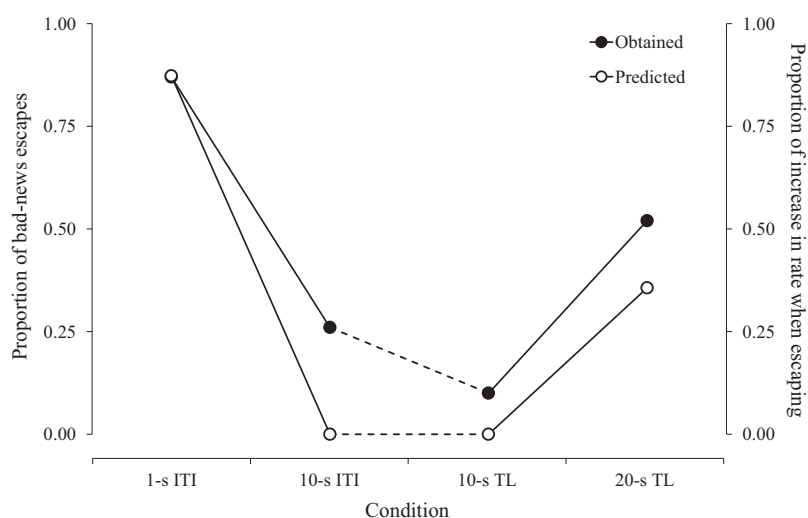


Figure 9. Mean proportion of observed escape responses (left y axis) in each condition (black dots) and predicted increase in the reinforcement rate when escaping (right y axis) according to the Reinforcement Rate Model (white dots). The filled symbols should be read on the left y axis and the open symbols should be read on the right y axis.

change the delays to reward. Second, we assumed that all intervals—terminal links signaled by different stimuli and the ITI—have similar effects on the perceived reward rate, although there is evidence that questions the assumption (e.g., Fortes, Vasconcelos, & Machado, 2015). Third, even though the prey model from which the RRM was adapted predicts an all-or-none pattern of escape responses, we and others have consistently found intermediate values of escaping (the possible reasons for this are discussed elsewhere, e.g., Lea, 1979; Mazur, 2008; Shettleworth, 1988). Based on these findings, we predicted that the proportion of escape responses from the bad-news stimulus would match the relative increase in the reward rate when escaping relative to accepting, but alternative measures and decision rules remain to be tested.

The issue of latencies is particularly relevant from an optimality perspective because they are paradoxical—any self-imposed delay imposes opportunity costs and therefore decreases net return. Our modeling did not include latencies because at the moment it is uncertain whether the animal is sensitive to their effects on reinforcement rates and how that sensitivity varies with the terminal-link stimulus. For instance, perhaps latencies associated with the bad-news stimulus are ignored just as the actual stimulus duration seems to be (see Fortes et al., 2016). Yet, for the sake of argument let us assume that all latencies influence the rate of return. Assuming further that animals have a similar moving pattern when they do and do not escape a trial, then they would have taken around 4 s to escape the trial (see in Figure 8 when they arrive to the center of the box). This escape latency, partly constrained by the apparatus, should objectively be added to  $s$  in the denominator of Equation 5, thus decreasing  $R_{reject}$ . The predictions of such a model are qualitatively similar to those depicted in Figure 9, except that animals should not escape when the terminal-link duration equals the ITI, because now the ITI ( $s$ ) includes the objectively programmed delay and the latency to escape (thus in fact exceeding the terminal-link duration). Our data suggest that latencies should be excluded from the computations of rate, but the issue justifies further studies.

The fact that animals escaped from the bad-news stimulus indicates that this stimulus was not ignored in the sense that animals did not behave as if the stimulus was not present: Escaping from the stimulus requires its identification as a signal for the absence of food. Moreover, the animals showed an almost exclusive preference for the Informative Option in all conditions, suggesting that this stimulus may not have been attributed to this option, even though the choice of this option was followed by the bad-news stimulus 80% of the time. Hence, when the pigeons escaped from the bad-news stimulus on approximately 26% of the trials (cf. Figure 4, Escaping from Terminal Links Phase in Experiment 1), they also showed an exclusive preference for the Informative Option (see Figure 3). If the escape key increased engagement with the task by increasing attention to the bad-news stimulus, thus strengthening the association between this stimulus and the Informative Option, then on the 74% of the trials in which the pigeons did not escape the bad-news stimulus should have affected the value of the Informative Option. Nonetheless, preference for this option instead of decreasing remained high. Altogether, the strong preference for the Informative Option and the escape responses from the bad-news stimulus indicate that this stimulus was *ignored* or *not taken into account* in the sense that the animal did not associate the bad news with the Informative Option.

This in turn explains the staggering lack of effect of increasing the bad-news stimulus duration to 200 s on the value of the Informative Option reported by Fortes et al. (2016). As previous explanations for suboptimal choice in this task do not specify what is meant by *not taking into account* the bad-news stimulus, the results and implications of the present experiments are particularly relevant to understand the choice mechanism involved in this task.

To conclude, in the present experiments we changed a previously studied task to make it more similar to a natural foraging task. We made information about the absence of food useful, and the animals' responses were in line with the core assumptions and predictions of the RRM. The experiments also showed that animals do pay attention to the bad-news stimulus, for they reliably move away from it and, in some conditions, act to eliminate it from the situation but, surprisingly, this stimulus is not associated with the Informative Option.

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