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# Testing the Boundaries of “Paradoxical” Predictions: Pigeons Do Disregard Bad News

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Several studies have shown that, when offered a choice between an option followed by stimuli indicating whether or not reward is forthcoming and an option followed by noninformative stimuli, animals strongly prefer the former even when the latter is more profitable. Though this paradoxical preference appears to question the principles of optimal foraging theory, Vasconcelos, Monteiro, and Kacelnik (2015) proposed an optimality model that shows how such preference maximizes gains under certain conditions. In this paper, we tested the model's core assumption that a stimulus signaling the absence of food should not influence choice independently of its other properties, such as probability or duration. In 2 experiments, pigeons chose between 2 options: the “informative option” delivered food on 20% of the trials after a 10-s delay, signaled by a “good-news” stimulus, and delivered no food on the remaining 80% of the trials, signaled by a “bad-news” stimulus. The “noninformative option” delivered food after 10 s on 50% of the trials, regardless of the signal shown. In Experiment 1, the probability of the bad-news stimulus was manipulated from 0.80 to 1.00; in Experiment 2, the duration of the bad-news stimulus was increased every time pigeons preferred the informative option, reaching at least 200 s. Consistent with the model's predictions, pigeons clearly preferred the informative option even when the noninformative option delivered 9 (Experiment 1) and 35 (Experiment 2) times more food.

**Keywords:** suboptimal choice, optimal foraging, probability, delay, pigeons

Recent research has shown that, under certain circumstances, at least two species (pigeons, *Columba livia*, and European starlings, *Sturnus vulgaris*) behave suboptimally by “trading” food for information. For example, Stagner and Zentall (2010) gave pigeons a choice between two options (Figure 1). If pigeons chose the informative option, on 20% of the trials they saw a positive discriminative stimulus (a good-news stimulus) that was always

followed by food after 10 s; on the other 80% of the trials they saw a negative discriminative stimulus (a bad-news stimulus) that was presented for 10 s but always ended without food. If they chose the other option, the noninformative option, they saw one of two stimuli, and, after a 10-s delay, food was delivered on 50% of the trials regardless of the stimulus presented. Stagner and Zentall found that, even though the overall probability of food in the informative option was 2.5 times lower than in the noninformative option (20% vs. 50%, respectively), pigeons strongly preferred the informative option. Many other studies have reported analogous tradeoffs, including Kendall (1974); Mazur (1995, 1996); Spetch, Mondloch, Belke, and Dunn (1994); Stagner, Laude, and Zentall (2012); and Vasconcelos et al. (2015), to name just a few (for reviews see, McDevitt, Dunn, Spetch, & Ludvig, 2016; Zentall, 2014, 2016).

The failure to maximize food intake in this task has been framed as a violation of the foundational principles of optimal foraging theory (e.g., McDevitt et al., 2016; Zentall, 2016). Optimality modeling, the backbone of evolutionary approaches to behavioral sciences, is frequently questioned because both humans and other species sometimes fail to behave optimally (e.g., Gigerenzer & Selten, 2002). However, optimality models do not postulate that animals should choose optimally (or rationally) under all circumstances. The assumption is instead that current psychological mechanisms reflect those of ancestors that outperformed their conspecifics: if the present conditions reflect those prevalent in the past, these mechanisms ought to generate behavior that is adaptive

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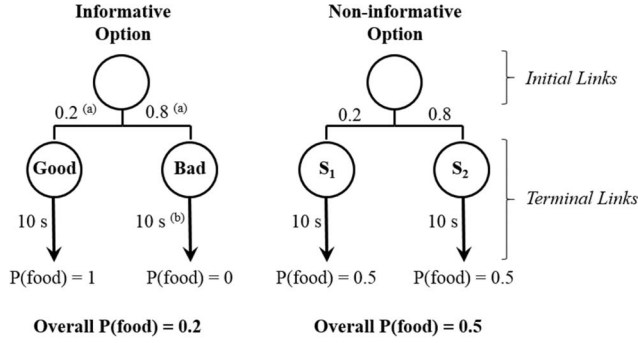


Figure 1. Scheme of outcomes for each option in Experiments 1 and 2. In Experiment 1, the probability (a) was manipulated across conditions. This probability was 0.80, 0.90, 0.95, 0.975 or 1.00. In Experiment 2, the delay (b) increased when pigeons preferred the informative option and decreased when they preferred the noninformative option. The probability of bad news was kept constant at 0.80.

on average. The failures to optimize are unquestionable, but we surmise that the derived attack on optimality is unwarranted, and reiterate the longstanding view that deviations from optimality predictions are fundamental raw materials for properly implemented programs of behavioral research. In the aforementioned experimental paradigm, providing animal subjects with information paradoxically induces suboptimal behavior. This is surprising because it might be expected that veridical information can only be good, as using it or not might be a matter of choice.

Vasconcelos and colleagues (2015) recognized the quandary and set out to analyze the paradigm from an optimal foraging perspective informed by relevant knowledge from learning theory. In particular, Vasconcelos and colleagues proposed that in their natural environment animals do not pay the cost of waiting when cues signaling the absence of food are available; instead, they use this information to search for other foraging opportunities. This strategy will, however, backfire in any laboratory task that forces the animal to wait in the presence of a signal for the absence of food (i.e., when the information cannot be properly used). Because animals may apply the same strategy within and without the

laboratory—ignore the bad-news stimulus—the cost of waiting in the presence of the bad-news stimulus is ignored and is not associated with the chosen option. Under such circumstances, the behavior of the animals will indeed be suboptimal, because they are using a mechanism which evolved and it is advantageous in their natural environment (domain of selection) but is detrimental in the task depicted in Figure 1 (domain of testing). If the data are consistent with this hypothesis, suboptimal choice in this task does not contradict optimal foraging theory as it is due to a mismatch between the domain of selection and the domain of testing (e.g., Houston, McNamara, & Steer, 2007; Stevens & Stephens, 2010).

Assuming that the rate of food intake is an appropriate proxy for the long-term fitness consequences of foraging activities, natural selection ought to have pruned behavior to maximize this currency (Stephens & Krebs, 1986). Consider, then, an animal that maximizes such currency. While foraging, the animal starts by *searching* for a food item, for  $s$  seconds. When an item is found, the animal stops searching and starts *pursuing* the item, for  $t$  seconds. After  $t$ , the animal may catch the item (with probability  $p$ ) and start consuming it (a *handling* time,  $h$ ) or it may lose the item, thus ending the foraging cycle and starting a new one by searching again. If all the delays are included in the rate computation, the rate of return ( $R$ ) that the animal gets if it chooses exclusively one food source or prey type (assuming energy content equal to unity) is

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

where  $R_i$  is the rate of return in energy/time from option  $i$ . For simplicity and to keep the analogy with the task shown in Figure 1, Vasconcelos et al. (2015) assumed that (a)  $p$  corresponds to the probability of reinforcement, (b)  $s$  corresponds to the intertrial interval (ITI), (c)  $t$  is the delay associated to each terminal link, (d)  $h$  is the time to consume the reward, and (e)  $t$  and  $h$  are equal across options. Because  $R_i$  monotonically increases with  $p_i$ , Equation 1 predicts that animals should always prefer the option yielding the higher probability of reinforcement. Figure 2a shows how preference should change as both  $p_{\text{Info}}$  and  $p_{\text{Noninfo}}$  vary. The white circle corresponds to the typical probabilities used ( $p_{\text{Info}} = .2$  and  $p_{\text{Noninfo}} = .5$ ; e.g., Stagner et al., 2012; Stagner & Zentall, 2010; Zentall & Stagner, 2011) and the black circles correspond to other

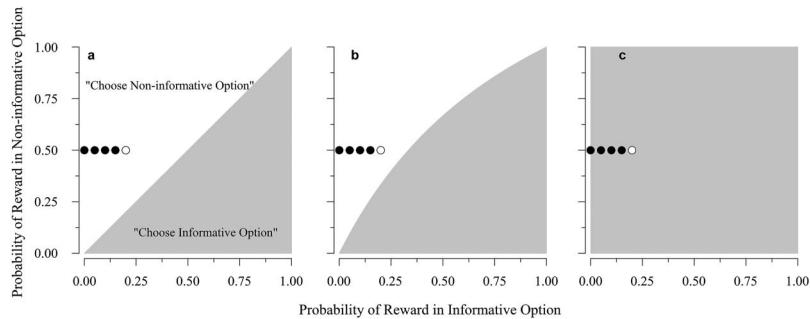


Figure 2. Contour plot of the preferences predicted by the Vasconcelos et al.'s (2015) model in the entire parameter space of  $p_{\text{Info}} \times p_{\text{Noninfo}}$ . The shaded and white areas indicate a predicted preference for the Informative and noninformative options, respectively. In all panels,  $t = 10$  s, and the black and white circles represent conditions where  $p_{\text{Noninfo}} = .5$  and  $p_{\text{Info}}$  varied in steps of .05, from .00 to .20. (a) Predictions using rate functions including all delays, (b) predictions using rate functions without delays leading to no reward, and (c) predictions using rate functions without delays leading to no reward and without ITIs.

probability combinations tested by Vasconcelos and collaborators. The predicted and obtained preferences are at odds: the rate functions predict preference for the noninformative option in all conditions, but animals systematically prefer the informative option, except when  $p_{\text{Info}} = 0$ .

Consider now an animal sculpted by natural selection to use information and therefore search for alternatives when sure of no impending reward. Such an animal would ignore the time spent in the presence of the bad-news stimulus. From Equation 1,  $R_{\text{Info}}$  becomes

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

where  $p_{\text{Info}}$  refers to the probability of reward in the informative option (i.e., the probability of good news). Because the probability of bad news ( $1 - p_{\text{Info}}$ ) is absent in Equation 2, it does not influence  $R_{\text{Info}}$ , and therefore should not affect preference. On the contrary, because in the noninformative option food delivery is not reliably signaled, the animal actively waits. Thus, the rate of intake in the noninformative option,  $R_{\text{Noninfo}}$  remains

$$R_{\text{Noninfo}} = \frac{p_{\text{Noninfo}}}{s + p_{\text{Noninfo}} \times (t + h) + (1 - p_{\text{Noninfo}}) \times t} = \frac{1}{\frac{s + t}{p_{\text{Noninfo}}} + h} \quad (3)$$

Figure 2b shows the same information as Figure 2a, now using Equations 2 and 3. Notably, the new functions predict again that animals should prefer the noninformative option. The derivations of Equations 2 and 3 include the ITI (or the time spent searching in the natural environment,  $s$ ). However, there is an important difference between the ITI in the laboratory and the searching time in the natural environment: whereas  $s$  in the natural environment occurs *after* the animal decides to start searching (and is thus included in the rate computations of all options), the ITI in laboratory preparations occurs *before* the animal starts the trial and after its outcome. In such cases, learning theory has shown that the ITI may not be attributed to a specific option and is thus unlikely to influence preference (e.g., Logue, Smith, & Rachlin, 1985; Mazur, 1989; Spetch et al., 1994; Stephens & Anderson, 2001). Figure 2c shows that when the ITI is dropped from the rate functions ( $s = 0$  in Equations 2 and 3) the model predicts a preference for the informative option, except when  $p_{\text{Info}} = 0$  or  $p_{\text{Noninfo}} = 1$ . In other words, when the probability of reinforcement in the noninformative option is constant, manipulations of the probability of the bad- and good-news stimuli in the informative option should not affect preference, unless the bad-news stimulus is always presented. Another counterintuitive prediction derived from Equation 2 is that the time spent in the presence of the bad-news stimulus should also be irrelevant: by eliminating the bad-new trials from Equation 2, the time  $t$  spent in the presence of the bad-news stimulus is eliminated.

In summary, if Vasconcelos et al.'s (2015) optimality analysis is correct, then animals were shaped by natural selection to behave as if ignoring the bad-news stimulus, independently of its *probability* and *duration*. These predictions may seem paradoxical if the reinforcement rates include all within-trial delays, but if the bad-

news stimulus is not taken into account, its associated probability and duration become inconsequential and the paradox vanishes. We tested these predictions, as well as their boundary conditions, in two experiments.

## Experiment 1: Probability of Bad News

In this experiment, we increased the probability of bad news in the informative option from .80 to 1.00 (and therefore decreased the probability of good news from .20 to 0.00). The probability of food following each nondiscriminative stimulus in the noninformative option remained at .5. Our goal was twofold: (a) confirm Vasconcelos et al.'s (2015) findings that the probability of bad news bears little to no weight on choice, but using a counter-balanced design. In the original findings, the probability of bad news was manipulated in an ascending order which does not exclude the hypothesis that resistance to change may have played an important role, and (b) track the change in preference for the informative option with a more fine-grained distribution of parameters. In Vasconcelos et al.'s study, preference decreased abruptly from indifference to virtually zero when the probability of bad news increased from .95 to 1.00. We aimed at sampling the underlying preference function with more parameter values. The model predicts a preference for the informative option except when  $p_{\text{Info}} = 0$ .

## Method

**Subjects.** Six pigeons (*Columba livia*), maintained at about 80% of their free-feeding weights participated in the experiment. All had limited experience unrelated to the present contingencies. They were housed individually in a temperature-controlled colony room (about 21 °C) on a 13 hr:11 hr light/dark cycle (lights on at 8 a.m.). Grit and water were always available in the home cage.

**Apparatus.** Three Med Associates operant boxes for pigeons were used. The boxes were 28.5 cm high, 24 cm long, and 30 cm wide. Each box was enclosed in a sound-attenuating chamber, equipped with a ventilation fan that also masked outside noises. The response panel had three centrally-aligned keys, 6 cm apart, center-to-center. The keys were circular with 2.5 cm in diameter, and the lowest edge was 21 cm above the floor grid. Below the response keys, centrally aligned and 4 cm above the floor grid there was a grain hopper opening (6 cm wide  $\times$  5 cm high). When activated, the food hopper was illuminated with a 1.1-W light. In the wall opposite to the response panel, centrally located and 23 cm above the floor there was a houselight (2.8 W) that illuminated the whole box. A personal computer controlled the events and recorded data via Whisker software (Cardinal & Aitken, 2010).

### Procedure.

**Pretraining.** All birds were trained to peck all stimuli used in the task: red, green, yellow, blue, and white on the left and right keys, and white on the center key. Each session consisted of 44 trials, 4 trials with each stimulus. On each trial, one randomly selected stimulus turned on and after one peck food was available for 3 s. A 10-s ITI with the houselight on separated the trials. In the second pretraining session, the peck requirement was increased to 10.

**Training.** Each session comprised 120 trials, divided into four blocks of 30 trials. Each 30-trial block included 20 forced-

choice trials (10 with each option) and 10 free-choice trials, randomly interspersed. At the beginning of a free-choice trial, the white center key started flashing (250 ms on, 250 ms off). One peck at this key turned it off and illuminated the side keys (both white hues, see Figure 1), starting the initial links. For each bird the informative and the noninformative options were always presented on the same side, but side allocation was counterbalanced across pigeons. If the pigeon pecked the informative option key, the noninformative option key turned off, and the bad-news stimulus (e.g., green) was turned on with probability  $p$ . Ten seconds after, the terminal-link stimulus was turned off and a 10-s ITI with the houselight on followed. Pecks during the terminal links were recorded but had no programmed consequence. On the remaining  $1 - p$  proportion of trials, the good-news stimulus (e.g., red) was turned on for 10 s, food was delivered immediately after, and the illuminated ITI followed.

If the pigeon instead pecked the noninformative option key, the informative option key was turned off, and on 20% of the trials one terminal stimulus (e.g., yellow) was turned on; on the remaining 80% of the trials the other terminal stimulus (e.g., blue) was turned on. In both noninformative terminal links, the key remained lit for 10 s, food was delivered on a randomly selected half on the trials, and the 10-s ITI followed. The terminal-link hues were counterbalanced across pigeons, with the restriction that red and green were always associated with one option and yellow and blue were always associated with the other option. The reinforcer duration varied from bird to bird (between 2.5 and 6 s) in order to avoid feeding outside the experimental chamber.

The forced-choice trials were structurally similar to free-choice trials, except that after a peck to the flashing center key only one of the side keys, the informative or the noninformative option, was turned on. Both on forced- and free-choice trials, if a peck to the center key (to start the trial) or to the side keys (initial-link phase) did not occur within 15 s since the key illumination, the trial ended, a 2-min timeout followed with all lights off, and the trial was repeated. After about 10 sessions, the timeouts occurred rarely (on less than 1% of the trials).

The probability of bad news,  $p$ , varied from 0.80 to 1.00 according to Table 1. The first three conditions experienced by each bird lasted for 20 sessions, and the last two conditions lasted for 30 sessions. In each condition, the mean proportion of choices during the last three sessions was used as the measure of preference. A significance level of 0.05 was used in all analyses.

## Results and Discussion

Figure 3 shows the average preference for the informative option ( $\pm 1$  SEM) as a function of the probability of the bad-news stimulus. When the probability of bad news was 0.80, we replicated previous results, with pigeons strongly preferring the sub-optimal, informative option ( $M = .99$ ,  $SEM = 0.01$ ). As the probability of bad news increased, preference for the informative option decreased significantly as revealed by a repeated-measures analysis of variance (ANOVA),  $F(4, 20) = 24.76$ ,  $p < .001$ ,  $\eta_G^2 = 0.75$ . Overall, preference was significantly above chance when  $p = .80$ ,  $.90$ , and  $.95$  (one-sample  $t$  tests:  $t(5) = 89.00$ ,  $p < .001$ ,  $d = 36.33$ , 95% CI for  $d$  [18.85, 53.82];  $t(5) = 8.26$ ,  $p < .001$ ,  $d = 3.37$ , 95% CI [1.33, 5.41];  $t(5) = 2.71$ ,  $p = .04$ ,  $d = 1.11$ , 95% CI [-0.24, 2.45], respectively), and was significantly below chance when  $p = 1.00$ ,  $t(5) = -58.00$ ,  $p < .001$ ,  $d = 23.68$ , 95% CI [12.24, 35.11]. When  $p = .975$ , animals were, on average, indifferent between the options,  $t(5) = 0.26$ ,  $p = .81$ ,  $d = 0.11$ , 95% CI [-1.13, 1.35]. For this condition, we conducted a Bayesian  $t$ -test (Rouder, Speckman, Sun, Morey, & Iverson, 2009) using JASP software (Love et al., 2015) to determine the likelihood of the null hypothesis over the alternative. The analysis yielded a Bayes factor of 2.61 in favor of the null hypothesis.

Although Figure 3 shows that the higher the probability of bad news, the less animals preferred the informative option, this continuously decreasing function was highly influenced by the results of one animal, P236 (first data column in Table 1). When  $p = .90$ , five birds chose suboptimally at least 99% of the time, whereas for P236 preference was 67.5%. Similarly, when  $p = .95$ , the same five birds chose suboptimally at least 86% of the time, but preference for P236 was already at 22.5%. Thus, increasing the probability of bad news from 0.80 to 0.95 had only a small effect on preference, except for P236. It is worth noting that pigeon P236 was the bird that experienced the greatest increase in the probability of bad news: from 0.80 in the first condition to 0.975 in the second condition. Possibly, after experiencing this hefty change, this bird would have needed more sessions than the others to recover preference for the informative option in subsequent conditions.

When the probability of bad news was 0.975, a maximum of two rewards per session were delivered in the informative option: one on forced-choice trials and possibly one more on a free-choice trial. Despite this fact, pigeons' preference was quite variable: three preferred the informative option significantly above chance (P604, P229 and P751; binomial test  $p < .001$ ), two preferred the

Table 1  
Individual Preferences for the Informative Option in Experiment 1 for Each Probability Condition

| Condition  | Pigeon  |          |          |          |          |          | Mean |
|------------|---------|----------|----------|----------|----------|----------|------|
|            | P236    | P604     | P229     | P389     | P230     | P751     |      |
| $p = .80$  | .97 (1) | 1.00 (3) | 1.00 (4) | 1.00 (2) | 1.00 (2) | 1.00 (1) | .99  |
| $p = .90$  | .68 (3) | 1.00 (1) | 1.00 (2) | 1.00 (4) | .99 (4)  | .99 (3)  | .94  |
| $p = .95$  | .23 (4) | 1.00 (2) | .99 (1)  | .99 (3)  | .96 (1)  | .86 (2)  | .84  |
| $p = .975$ | .11 (2) | 1.00 (4) | .69 (3)  | .06 (1)  | .50 (3)  | .89 (4)  | .54  |
| $p = 1.00$ | .00 (5) | .00 (5)  | .01 (5)  | .01 (5)  | .05 (5)  | .01 (5)  | .02  |

Note. Numbers in parenthesis show the order of each condition for each bird.



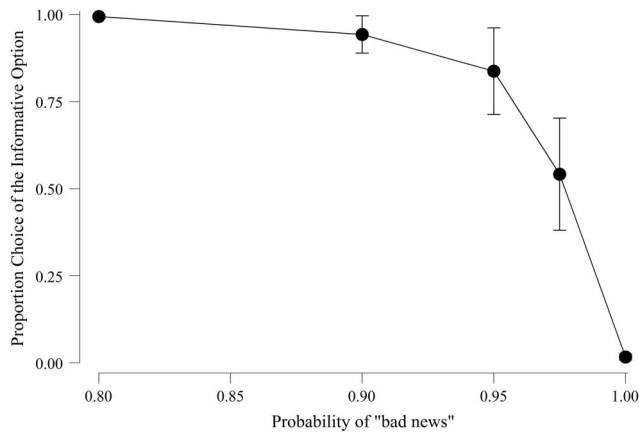


Figure 3. Mean proportion of choices for the informative option in the last three sessions of each condition in Experiment 1. The error bars are the standard error of the mean.

noninformative option (P236 and P389; binomial  $p < .001$ ) and P230 was indifferent between the two options (binomial  $p = .54$ ). A closer look at the data revealed important order effects (individual data are presented in Figure 4 and Table 1). When the condition with  $p = .975$  was either the first or the second condition (as for P389 and P236), preference for the informative option was clearly below chance. Moreover, the later in training  $p = .975$  was in effect, the higher was the preference for the informative option.

Because the first condition ended after 20 sessions, regardless of the probability in effect, the pigeon that started with  $p = .975$ , P389, had less contact with the good-news stimulus in this condition compared to other conditions. For that reason, one could argue that preference for the informative option did not develop because the discrimination between the good- and bad-news stimuli was not well established. One way to measure discrimination between two stimuli is by calculating the discrimination ratio, that is, the responses made in the presence of the positive stimulus (i.e., the good news), divided by the sum of responses to the positive and negative stimuli (i.e., the good- and bad-news stimuli). A perfect discrimination would yield a ratio of 1, meaning that the bird only pecked the positive stimulus. The average discrimination ratio during the last three sessions of Condition  $p = .975$ , from Order 1 to 4 was 0.81, 1.00, 0.91 and 0.88, respectively, suggesting a good discrimination regardless of order for all pigeons. Thus, the increase in preference for the suboptimal alternative as the Condition  $p = .975$  occurred later in training may indicate a resistance to change due to the experimental history. Notably, the order effects found in Condition  $p = .975$  confirm our concerns regarding their conceivable effect in Vasconcelos et al.'s (2015) results.

In summary, the results show that pigeons preferred the informative option even when the noninformative option provided much more food (50% vs. 5% of reinforced trials). These findings are even more extreme than those reported by Vasconcelos et al. (2015), as their starlings were already indifferent when  $p = .95$ . Currently, it is unclear whether this difference is reliable and, in the affirmative, whether it is due to different experimental histories, procedural details (e.g., ascending vs. counterbalanced  $p$ ) or even to species differences. Assuming, for the sake of the argument, (a) that all within-trial delays are included in the computa-

tions of rate, (b) a handling time of 3 s for both options, and (d) that the ITI is not considered then, according to Equation 1, the preferred, informative option yielded about 0.296 reinforcements per minute, whereas the noninformative option yielded 2.609, an almost ninefold difference favoring the latter. However, if the time waiting in the presence of bad news is excluded, the situation is reversed with the informative and noninformative options yielding approximately 4.615 and 2.609 reinforcements per minute, respectively; under this scenario, the informative option is 1.77 richer than the noninformative option.

Although less extreme, other researchers have reported findings similar to ours. For example, Zentall, Laude, Stagner, and Smith (2015) showed that preference was equally suboptimal when the probability of good news was 25% or 50% while the other alternative provided unsignaled food 75% of the time. In this case, the rate of intake in the noninformative option was *only* 2.63 larger when all within-trial delays are included. In a somewhat related procedure, Mazur (1996) gave pigeons a choice between two options, one certain and the other probabilistic. The former delivered a certain,  $x$ -s delayed reinforcer, whereas the latter led immediately to the ITI with probability  $p$  and offered a signaled, 20-s delayed reinforcer with probability  $1 - p$ . Using an adjusting-delay procedure, Mazur found that animals were indifferent between the options when  $x = 20$  s, for all tested  $p$ . Mazur did not test a probability of bad news higher than 0.80, and Vasconcelos et al. (2015) tested with 0.95 and 1.00. We tested an intermediate value, 0.975, and obtained mixed results. It remains possible that with more sessions of training the preference for the informative option would be stronger, even with a very low probability of reinforcement.

Although our average data revealed a modulation of preference for the informative option as a function of the probability of bad news, this was mostly due to the results of one animal (P236) and to the order effects observed in condition  $p = .975$ . If we exclude P236, preference for the informative option in conditions  $p = .80$ ,  $p = .90$ , and  $p = .95$  would be 100%, 99.6%, and 96.0%, respectively, thus revealing a slight decrease in preference as  $p$

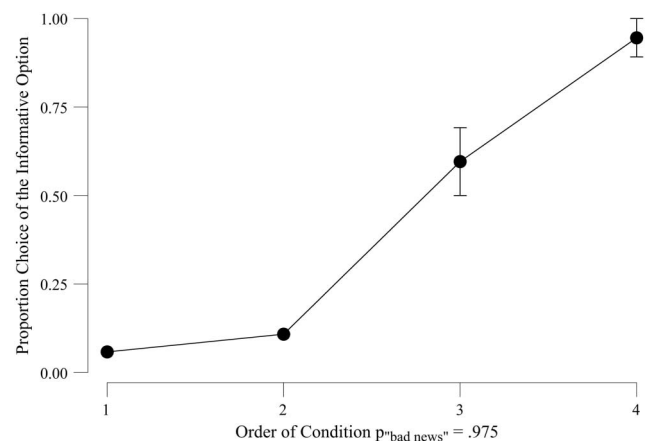


Figure 4. Mean proportion of choices of the informative option in the last three sessions of Condition  $p = .975$  as a function of order of presentation (cf., Table 1). For Orders 1 and 2, data refers to only one bird and for Orders 3 and 4 data refers to two birds. The error bars are the standard error of the mean.

increases. Then, when  $p = .975$ , preference would be 63% but the order effects obtained in this condition make this preference difficult to interpret. Finally, as predicted, when  $p = 1.0$ , preference decreased to 2%. Altogether, these results are generally consistent with the predictions of Vasconcelos et al.'s (2015) model, in that only when  $p = 1$  did animals consistently prefer the optimal, noninformative option. They also suggest that the reinforcement history and the transition between probabilities may be important factors to take into account.

## Experiment 2: Duration of Bad News

In this experiment, we manipulated the duration of the bad-news stimulus (hereafter the bad-news delay). Recall that one of the predictions of Vasconcelos et al.'s (2015) model is that the duration of this stimulus ought to be irrelevant vis-à-vis preference. This is a highly counterintuitive hypothesis and a stronger test of the model. To test whether the prediction holds and study its boundary conditions, we used a titration procedure: when pigeons preferred the informative option, we increased the bad-news delay; when they preferred the noninformative option we decreased the bad-news delay.

## Method

**Subjects.** Eight pigeons (*Columba livia*) participated in this experiment. All birds were maintained as described in Experiment 1. Previous to this experiment, all birds participated in a choice experiment in which they acquired an exclusive preference for one of the side keys. To guarantee that pigeons would not show a preference for the informative option due to a preexisting side bias, the informative option was assigned to the nonpreferred side in the previous experiment for all birds. If anything, this assignment would favor a bias *against* the informative option.

**Apparatus.** The three operant boxes from Experiment 1 and a custom-built box were used. The latter box was similar to the former with the following exceptions: (a) it was 31 cm high, 33 cm long, and 33 cm wide; (b) the three keys were 9 cm apart, center-to-center; (c) the grain hopper opening was 6 cm long  $\times$  4.5 cm high and 6.5 cm above the floor grid; and (d) the houselight was located 27.5 cm above the floor.

**Procedure.** The general procedure was the same as in Experiment 1, with the following exceptions: (a) the probability of the bad-news stimulus was kept constant at .80, (b) there was no limit on the time to peck the center and side keys (i.e., there were no timeouts), and (c) the experiment had two conditions: first, an adjusting-delay procedure was implemented for the bad-news delay and then the bad-news delay was fixed as described below.

**Pretraining.** The pretraining was the same as in Experiment 1.

**Adjusting-delay condition.** Each session was divided into blocks of 30 trials. Within each block, the first 20 trials were forced-choice trials (10 with the noninformative option and 10 with the informative option, interspersed) and the last 10 trials were free-choice trials. After each 30-trial block, the bad-news delay could increase, decrease, or stay the same depending on the pigeon's choices in the previous block. If the pigeon chose the informative option on two trials or less, the delay decreased by 5 s; if it chose the informative option on eight trials or more, the delay increased by 5 s; otherwise, the delay remained the same.

In the first block of the first session the bad-news delay was set at 10 s. In the following sessions, the bad-news delay on the first block of trials was computed for each bird based on its choices in the last block of the previous session. The lower limit for the bad-news duration was 0 s. In that case, if the pigeon chose the informative option, the good-news stimulus appeared for 10 s on 20% of the trials and on the remaining 80% of the trials the choice peck was immediately followed by the ITI. Although we did not plan to include an upper limit for the bad-news delay, as the experiment proceeded it became necessary to do so. Therefore, the maximum delay that could be set at the beginning of a session was 200 s even though it could surpass 200 s within a session. This condition was run until the bad-news delay was considered stable or reached 200 s, whichever came first.

Because increasing the bad-news delay made the sessions longer, we decreased the number of 30-trial blocks per session as the delay increased. If the delay at the beginning of a session was equal to or shorter than 120 s, the session comprised five blocks (150 trials); if the delay was between 120 s and 180 s inclusive, the session comprised four blocks (120 trials); and if the delay was longer than 180 s, the session comprised three blocks (90 trials).

**Fixed-delay condition.** To evaluate whether preference for the informative option could be caused by the adjustment of the bad-news delay, we ended the experiment with three sessions in which the bad-news delay was kept constant at the value reached in the adjusting-delay condition or at 200 s when it surpassed this value. Each session comprised three 30-trial blocks.

## Results and Discussion

**Adjusting-delay condition.** All birds started the experiment by preferring the optimal, noninformative option, most likely because this option was assigned to the preferred key in their previous experiment. As a consequence of choosing the noninformative option, during the first session, the bad-news delay decreased to 0 s. Of interest was whether this bias for the noninformative option would attenuate and pigeons would start choosing the informative option. After several sessions, pigeons did start to choose the informative option eight or more times in each block of free-choice trials, thus increasing the bad-news delay (Figure 5).

All birds continued to systematically prefer the informative option and the bad-news delay increased to at least 200 s in one session. Due to an experimenter error, pigeon P876 ended the adjusting-delay condition when it reached 195 s. For the other birds, the maximum bad-news delay was 200 s for birds P463, PG13, P948, and PG35; 205 s for P665 and P748; and 210 s for P022. The fact that the birds reached the maximum delay suggests that the duration of the bad-news stimulus did not influence the value of the informative option (Figure 6, left panel).

During the first session, the bad-news duration decreased to 0 s. Therefore, when the informative option was chosen, the pigeons experienced the good-news stimulus on 20% of the trials and the immediate onset of the ITI on the remaining 80% of the trials. There are possibly two reasons (not necessarily mutually exclusive) for animals to start preferring the informative option. First, animals may have stopped paying attention to the ITI because, as for the bad-news stimulus, it ended without reinforcement; consequently, the informative option was perceived as always delivering food. Second, animals may have continued to pay attention and

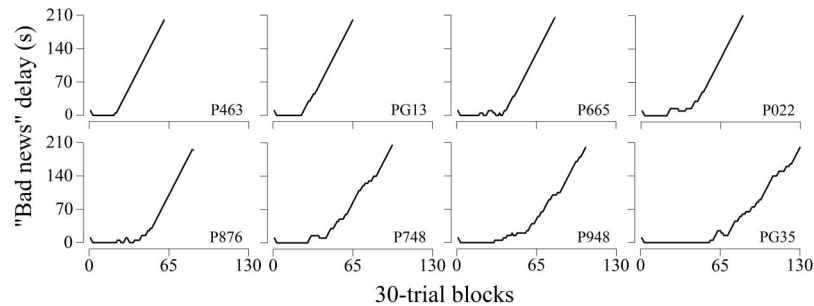


Figure 5. Bad-news duration (in seconds) in each 30-trial block during the adjusting-delay condition.

actively wait in the presence of the noninformative stimuli, paying the cost of not receiving food on half of the trials. Interestingly, on the first few occasions the bad-news stimulus was presented, the pigeons pecked at it as much as they pecked at the good-news stimulus (discrimination ratio close to 0.5). With additional exposure to the bad-news stimulus, the pigeons ceased pecking at it and the discrimination ratio increased to 1.0. This means that, for a suboptimal preference to develop, it is not necessary to have a specific stimulus associated with the absence of food in the informative option, as preference can at least start emerging when the bad news is the ITI.

**Fixed-delay condition.** The right panel of Figure 6 shows preference for the informative option during the fixed-delay condition.

In the last block of the adjusting-delay condition all birds were choosing the informative option at least 80% of time (left panel of Figure 6). When the bad-news delay was fixed at 200 s, one bird showed a substantial decrease in preference (PG35; see individual data in the Appendix). The reasons for the decrease are unclear, given that the delay (and all the other parameters) remained the same as in the last block of the previous session. This was, however, the bird with higher variability in performance in both conditions, suggesting caution in the interpretation of this decrease.

Even though preference for the informative option during the first block decreased for some birds, by the last block (last data point in Figure 6) all of them were choosing the informative option

reliably above chance ( $M = .95$ ,  $SEM = 0.04$ ,  $t(7) = 11.91$ ,  $p < .01$ ,  $d = 4.21$ , 95% CI [2.24, 6.18]). In fact, preference during the last three blocks of the fixed-delay condition and the last three blocks of the adjusting-delay condition did not differ significantly: a repeated-measures ANOVA with condition and block as factors revealed no significant effect of condition,  $F(1, 7) = .264$ ,  $p = .623$ ,  $\eta_G^2 = .006$ , or block,  $F(2, 14) = .063$ ,  $p = .939$ ,  $\eta_G^2 = .001$ . The Bayes factors yielded by a Bayesian repeated-measures ANOVA suggested that the data were 3.13, 6.30, and 19.55 times more likely to occur under the null hypothesis relative to the alternative models assuming an effect of condition only, block only, and session + block, respectively.

In summary, this experiment showed that pigeons strongly prefer an option that provides information about the delivery of food, even when 80% of the trials with such an option are spent in the presence of a signal for the absence of food for more than 3 min. This indicates that the bad-news stimulus does not function as a punisher or as a conditioned inhibitor, in the sense that it does not seem to affect preference for the informative option. Assuming the same parameters and constraints used in Experiment 1, according to Equation 1, the preferred, informative option yielded about 0.074 reinforcements per minute, whereas the noninformative option yielded 2.609, a 35-fold difference favoring the latter. If, however, the bad-news delay is not considered, the rates become consistent with the pigeons' preference, with the informative and noninformative options yielding approximately 4.615 and 2.609 reinforcers per minute, respectively.

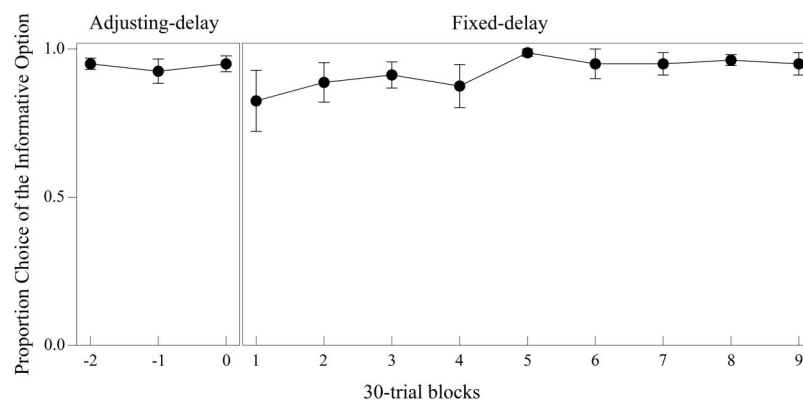


Figure 6. Mean proportion of choices of the informative option ( $\pm 1$  SEM) in the last three blocks of the adjusting-delay condition and during the nine blocks of the fixed-delay condition.



Previous studies already hinted at our findings, but used much shorter durations (Mazur, 1995; Spetch et al., 1994; Pisklak, McDevitt, Dunn, & Spetch, 2015). For instance, Spetch et al. (1994) did not find differences in preference when the bad-news duration was either 5 or 55 s, while the good-news stimulus and the single-discriminative stimulus on the other option were kept constant at 30 s. In other words, the longest bad-news duration tested by Spetch and collaborators was less than two times the other terminal-link durations, compared to the 20-fold difference in our experiment (200 s vs. 10 s). In terms of rates, and using the same assumptions as before, in Spetch et al.'s experiment the noninformative option was at most *only* 2.7 times richer than the preferred, informative option.

One could argue that increasing the bad-news delay did not affect choice because pigeons avoided being in the presence of this stimulus (e.g., turning around). In fact, we did observe that the birds usually turned their back to the keys when the bad-news stimulus appeared. However, previous research has shown that avoidance of the negative discriminative stimulus per se cannot account for our findings. Stagner, Laude, and Zentall (2011), for example, replaced the bad-news stimulus by the houselight (a diffuse stimulus difficult to avoid) and found no changes in preference relative to the usual protocol.

In short, by letting subjects control the bad-news delay and consequently testing extremely long durations, we compellingly showed that the bad-news delay does not affect preference on this task. Our educated guess is that the bad-news duration would continue to increase had we not been forced to include an upper bound.

## General Discussion

When offered a choice between options with signaled versus unsignaled outcomes, animals have systematically shown a strong preference for the former (e.g., Bower, McLean, & Meacham, 1966; Prokasy, 1956; Roper & Zentall, 1999) even when the signaled option is the less profitable of the two (for reviews, see McDevitt et al., 2016; Zentall, 2014, 2016). This preference for an option that, although informative, yields a lower rate of reinforcement has been repeatedly asserted as a violation of optimal foraging theory. In this paper, we show how an optimal foraging model incorporating ideas from the natural foraging ecology of the model species and from learning theory can account for such paradoxical preferences.

Vasconcelos et al.'s (2015) fundamental assumption is that foragers were sculpted by natural selection assuming that information is usable. Therefore, under natural foraging circumstances, animals use the available information and avoid paying the opportunity costs when they are not justified (i.e., when certain that no prey is attainable), never experiencing clearly avoidable delays. Conversely, in the laboratory preparations used in the experiments reported here, animals are forced to experience such delays because the information imparted by the informative option cannot be used, rendering the evolved mechanism of pursuing other foraging opportunities inappropriate. In short, if animals use the same strategy under natural and artificial choice situations, a preference for the lower probability, informative option ought to develop.

In two experiments, we tested two counterintuitive predictions that follow from these assumptions, namely that: (a) preference for the informative option should always be observed regardless of the values of  $p_{\text{Info}}$ , except when  $p_{\text{Info}} = 0$ , and (b) the duration of the bad-news stimulus should have no effect on preference because it is not included in the rate functions. In Experiment 1, we increased the probability of the bad-news stimulus, from 0.80 to 1.00, and found that most of the animals only reversed preference when the bad-news stimulus was always presented. More specifically, animals clearly preferred the informative option when it provided bad news 80, 90, and 95% of the time. When the probability increased to 97.5% we obtained mixed results caused by order effects that preclude firm conclusions. Finally, when the bad news was always presented, all pigeons preferred the noninformative option. Even though preference only reversed with very high probabilities of bad news, most birds showed a slight decrease in preference for the informative option as  $p$  increased. Upon further reflection, this unforeseen finding seems sensible: when the bad-news stimulus is presented, animals must first attend to it for a short period of time before disregarding it. This minimum engagement time with the bad-news stimulus imposes an additional opportunity cost. Consequently, as the probability of bad news increases so does the cost of choosing the informative option, leading to slight decreases of its value. The auxiliary assumption would be that natural selection favored agents with a behavioral allocation strategy not completely oblivious to the ratio of expected profitabilities, perhaps because exclusive preferences deprive the animal of information about changes in the environment.

In Experiment 2, we let pigeons control the bad-news duration making it dependent on their own choices. Even though choices of the informative option were even more detrimental than in previous preparations, because they resulted in increases of the bad-news delay, all pigeons inflexibly preferred the informative option. Eventually, we had to introduce an upper limit of 200 s for this duration. Importantly, because  $p_{\text{Info}}$  was kept constant, the aforementioned possibility of a minimum engagement time with the bad-news stimulus does not affect the original prediction that the duration of this stimulus ought to be irrelevant vis-à-vis preference.

Altogether, the results of the two experiments corroborate the predictions of Vasconcelos et al.'s (2015) model and suggest that animals do "ignore" the time spent in the presence of the stimulus signaling the absence of food. By ignore, we mean only that the stimulus does not influence choice of the informative option because it clearly influences other behaviors of the animals: They turn their back to the stimulus and do not peck at it. Semantics aside, the animals' preference for the low-probability but informative option was immune to a ninefold (Experiment 1) and a 35-fold (Experiment 2) difference in rates of reward, always favoring the noninformative option.

Although Vasconcelos et al.'s (2015) model is mute about the psychological mechanism(s) underlying the observed preferences, one could argue that, in the presence of a stimulus associated with the absence of food, no conditioning takes place. Without conditioning, the animal does not pay attention to the stimulus (i.e., it does not associate the costs of waiting in the presence of the bad-news stimulus with the choice of the informative option). As a result, the animal does not devalue the informative option even though the bad-news stimulus is presented frequently. In the non-

informative option, because both signals are associated with food, conditioning takes place and the animal pays the cost of waiting half of the trials for no food. As a consequence, the informative option is perceived as more profitable and therefore preferred.

In fact, other researchers have theorized that animals do not take into account the negative stimulus, and behave as if they were in a situation without bad news (Laude, Stagner, & Zentall, 2014; Mazur, 1991, 1995, 1996; McDevitt, Spetch, & Dunn, 1997; Spetch et al., 1994; Stagner et al., 2012; Zentall et al., 2015). Interestingly, the model developed by Vasconcelos and colleagues (2015) based on an optimality account leads to similar predictions as other models emphasizing proximate causes. Mazur (1995, 1996) and Dunn and Spetch (1990), for instance, developed different accounts emphasizing the relevance of conditioned reinforcers. Even though these latter accounts do not always make the same predictions, both assume that a stimulus that is never followed by food is “ignored.” Mazur’s hyperbolic discounting model states, for example, that the current value of a delayed reward decreases hyperbolically as the delay to reward increases. However, only delays in the presence of conditioned reinforcers (i.e., stimuli associated with food) are taken into account. This means that when a stimulus is never followed by food it should not be considered and it should not affect the option’s value. Thus, Mazur’s (1995, 1996) model predicts that the value of the informative option in our study has the same value as an option that always delivers food after 10 s.

A different account for preference for the informative option (Dunn & Spetch, 1990) comes from a modified version of the delay-reduction theory (Fantino, 1969; see also Ward, Gallistel, & Balsam, 2013 for a similar idea). The core of Dunn and Spetch’s (1990) account lies on the idea that a signal has greater conditioned-reinforcement value when it signals a greater reduction in the delay to reinforcement. Specifically, using the task depicted in Figure 1, when the animal chooses the informative option, the expected delay to food is 50 s. When it sees the good-news stimulus, that cue signals a large reduction in the delay to food (from 50 s to 10 s) so the good-news stimulus becomes a strong conditioned reinforcer; if, on the contrary, it sees the bad-news stimulus, no food is given and therefore this stimulus does not become a conditioned reinforcer. When the noninformative option is chosen the expected delay to food is 20 s, and when the terminal-link stimuli appear, they do not signal a reduction in delay to food (the expected delay remains 20 s) and thus do not become strong conditioned reinforcers. In other words, the noninformative option provides delayed primary reinforcement, whereas the informative option provides delayed primary reinforcement and an immediate and strong conditioned reinforcement.

The fundamental difference between the models developed by Mazur (1995, 1996) and Dunn and Spetch (1990), on the one hand, and the model developed by Vasconcelos et al. (2015), on the other hand, is commonly overlooked, which may lead to the deceptive interpretation that they are competing models. They are, in fact, complementary: whereas the former two originate from the analysis of the contemporary mechanisms controlling behavior, the latter originates from a functional analysis of the ancestral causes of such behavior (Tinbergen, 1963; for recent discussions, see Bateson & Laland, 2013; Dawkins, 2014). The failure to notice this distinction has plagued unreasonable critiques of the optimality approach to behavior by incorrectly assuming that the optimi-

zation agent is the behaving organism when, in reality, the optimization agent is natural selection. Considering the experimental task at hand, the optimality model takes the rate of reward as a proxy for the long-term fitness consequences of foraging activities. Also, it assumes that organisms were pruned by natural selection to use information to determine the optimal course of action; it, however, does not specify the contemporary mechanisms underlying behavior. Conversely, the mechanistic models pinpoint the psychological processes underlying behavior but overlook the adaptive reasons for such behavior. Put simply, functional and mechanistic models are detachable but not independent: function and mechanism must inform each other if we are to achieve coherence between levels of analysis.

To conclude, the pattern of choice reported here is still another example of irrational behavior arising from a mismatch between the experimental and the selection environments (the problem of the domain of testing vs. the domain of selection; see, e.g., Stevens & Stephens, 2010). In other words, the so-called “suboptimal” choice is essentially a consequence of using a mechanism that is advantageous in the wild but suboptimal in a controlled, artificial environment like the operant box. It is assumed nowadays that, as animals’ bodies evolved through natural selection, the same happened with behavior and cognition. We should thus try to understand behavior in light of the selective pressures and the evolutionary environment in which it supposedly evolved. Such an analysis frequently reveals that some apparently irrational behavior is, in fact, adaptive under certain circumstances.

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(Appendix follows)

## Appendix

### Experiment 2: Individual Data

*Individual Preferences for the Informative Option in the Last Three Sessions of the Adjusting-Delay Condition and in the Fixed-Delay Condition*

| Condition       | 30-trial block | Pigeon |      |      |      |      |      |      |      | Mean |
|-----------------|----------------|--------|------|------|------|------|------|------|------|------|
|                 |                | P463   | PG13 | P665 | P022 | P876 | P748 | P948 | PG35 |      |
| Adjusting-delay | −2             | 1.00   | .90  | .90  | 1.00 | 1.00 | 1.00 | .90  | .90  | .95  |
|                 | −1             | 1.00   | 1.00 | 1.00 | 1.00 | .70  | 1.00 | .90  | .80  | .93  |
|                 | 0              | 1.00   | 1.00 | 1.00 | 1.00 | .90  | 1.00 | .90  | .80  | .95  |
| Fixed-delay     | 1              | 1.00   | 1.00 | 1.00 | 1.00 | .60  | 1.00 | .80  | .20  | .83  |
|                 | 2              | 1.00   | 1.00 | 1.00 | 1.00 | .70  | 1.00 | .90  | .50  | .89  |
|                 | 3              | 1.00   | 1.00 | 1.00 | 1.00 | .80  | .80  | 1.00 | .70  | .91  |
|                 | 4              | 1.00   | 1.00 | 1.00 | 1.00 | .80  | .90  | .90  | .40  | .88  |
|                 | 5              | 1.00   | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | .90  | .99  |
|                 | 6              | 1.00   | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | .60  | .95  |
|                 | 7              | 1.00   | 1.00 | 1.00 | 1.00 | .90  | 1.00 | 1.00 | .70  | .95  |
|                 | 8              | 1.00   | 1.00 | .90  | .90  | 1.00 | 1.00 | 1.00 | .90  | .96  |
|                 | 9              | 1.00   | 1.00 | .70  | 1.00 | 1.00 | .90  | 1.00 | 1.00 | .95  |

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