

# State-dependent choice and ecological rationality

Andrew L. Nevai<sup>a</sup>, Thomas A. Waite<sup>b,c,d,\*</sup>, Kevin M. Passino<sup>c,b</sup>

<sup>a</sup>Mathematical Biosciences Institute, Ohio State University, Columbus, OH 43210, USA

<sup>b</sup>Department of Evolution, Ecology, and Organismal Biology, Ohio State University, Columbus, OH 43210, USA

<sup>c</sup>Department of Electrical and Computer Engineering, Ohio State University, Columbus, OH 43210, USA

<sup>d</sup>Department of Anthropology, Ohio State University, Columbus, OH 43210, USA

Received 25 September 2006; received in revised form 22 March 2007; accepted 23 March 2007

Available online 27 March 2007

## Abstract

Decision makers who minimize costly errors should flexibly adjust the way they trade off competing demands, depending on their current state. We explore how state (amount of hoarded food) affects willingness to take extra predation risk to obtain larger food rewards, particularly in animals that may overemphasize safety. Assuming a sigmoid fitness function, we explore how a supplement in state influences this willingness trade danger for food energy. Above a threshold, the model predicts the supplement will weaken this willingness. Incremental increases in state in the deceleratory phase yield smaller fitness gains, so it pays to increase emphasis on safety after receiving a supplement. Below this threshold, the model makes the opposite prediction because incremental increases in state yield bigger fitness gains and so it pays to decrease emphasis on safety. We use the model to explain why hoarding gray jays (*Perisoreus canadensis*) were induced by an experimental subsidy to accept greater danger. This formerly puzzling finding makes sense if the jays' effective hoard was relatively small, due to theft and decomposition. We discuss adaptive state-dependent choice as a general explanation for apparently irrational behavior.

© 2007 Elsevier Ltd. All rights reserved.

**Keywords:** Decision making; Gray jays; Impulsivity; *Perisoreus canadensis*; Rationality; State

## 1. Introduction

Decision makers must balance competing demands when choosing among options that vary along multiple dimensions. According to principles of economic rationality, humans are expected to evaluate options along relevant dimensions, assign fixed values to the alternative options available, and then make logically consistent choices based on these values. If true, humans as putatively rational cognizers would obey the principle of irrelevant alternatives (Tversky and Simonson, 1993) and express consistent preferences regardless of previously encountered options (but see Simonsohn, 2006; Simonsohn and Loewenstein, 2006). Behavioral ecologists, though, expect animals to flexibly adjust their preferences in response to recent

experiences that affect their energetic state (Houston and McNamara, 1999; Kacelnik and Marsh, 2002; Marsh et al., 2004). Consider an animal choosing between a small-and-safe versus a large-but-dangerous option. The animal's state at the moment of choice should influence its willingness to accept the extra danger to obtain bigger rewards. Under quite general conditions, the optimal response to any increase in state is to accept smaller risks of predation to obtain energy (McNamara, 1990). Thus, an animal making strictly optimal decisions should always become more cautious as its state improves.

A recent experimental test, however, revealed the opposite tendency (Waite et al., 2007). We tested whether a food-hoarding bird, the gray jay (*Perisoreus canadensis*), adjusts its tendency to choose a more valuable but also more dangerous reward after receiving a subsidy in state (i.e., an increase in hoard size). In response to the subsidy, jays tended to become more willing to trade danger for food. Why would they become less cautious when their hoard was increased? This seems suboptimal. Why not

\*Corresponding author. Department of Evolution, Ecology, and Organismal Biology, Ohio State University, Columbus, OH 43210, USA. Tel.: +1 614 292 5549; fax: +1 614 292 2030.

E-mail address: [waite.1@osu.edu](mailto:waite.1@osu.edu) (T.A. Waite).

increase emphasis on safety after receiving a subsidy? This counterintuitive result demands an adaptive, state-based explanation.

Here, we modify and apply an existing general framework of state-dependent choice (Houston and McNamara, 1999). We use the model to explore how an animal's state influences its willingness to accept extra predation risk to obtain larger rewards. We then use the model to explain why gray jays increased this willingness after receiving an experimental subsidy. We show that below a threshold on a sigmoid fitness function, incremental increases in state yield bigger fitness gains and so it pays to decrease emphasis on safety after receiving a subsidy. The jays' response thus makes sense if the effective hoard size for each jay was a relatively small proportion of its own total hoard. We discuss adaptive state-dependent choice as an explanation for various kinds of economically irrational behavior (Schuck-Paim et al., 2004).

## 2. Model

We formulate and analyze a decision-making model that applies to animals that hoard food. We describe our assumptions, establish a quantity to be maximized, introduce partial and biased preferences, choose a family of fitness functions, and show the complex ways an animal's state influences the probability of choosing a more valuable but also more dangerous option. We show that the model can account for our experimental findings.

### 2.1. Assumptions

Consider an animal with a choice of two foraging options ( $i = 1, 2$ ), where each is characterized by a positive predation rate  $\mu_i$  that applies over a short time interval  $k_i$ , and is followed by a positive net energy gain  $\gamma_i$  provided the animal survives. The better choice maximizes the individual's reproductive value (fitness), and represents a trade-off between food-energy gain and predation risk (e.g., Houston and McNamara, 1989, 1999; Waite and Passino, 2006).

We assume the animal's reproductive value  $V$  (which takes unitless values between 0 and 1) depends on its state  $x$ , which we take to be the perceived total number of hoards it has made in some time window. This perceived hoard size  $x$  may be less than the actual hoard size  $x_{actual}$  (i.e., the total number of hoarded food items in place), and the distinction between  $x$  and  $x_{actual}$  arises when  $x_{actual}$  is large, as seems plausible for the gray jays we tested. In this case, an individual with a short-term window will perceive  $x$  to be far less than  $x_{actual}$ , an individual with an intermediate-term window will perceive  $x$  to be moderately less than  $x_{actual}$ , and an individual with a long-term window will perceive  $x$  to be near  $x_{actual}$ . The effective reproductive value of a jay with a short-, intermediate-, or long-term window may reflect the number of hoards made in an hour, a day, or an entire season, respectively. We assume  $V$  does

not depend directly on time, so the background foraging strategy has zero cost.

### 2.2. Choice equation

Let  $V(x)$  be the reproductive value of an animal with state  $x$  at the moment of choice. The individual's expected reproductive value after selecting option  $i$  is

$$(1 - \mu_i k_i)V(x + \gamma_i) + \mu_i k_i \cdot 0,$$

where  $1 - \mu_i k_i$  and  $\mu_i k_i$  represent the probabilities that the animal will survive or die, respectively, while obtaining the food items associated with option  $i$ , and  $V(x + \gamma_i)$  and 0 represent the animal's resulting (perceived) reproductive value. If we assume net energy gain of option  $i$  is small and reproductive value  $V$  changes slowly as a function of  $x$ , then we have the following approximation (cf. Houston and McNamara, 1999):

$$(1 - \mu_i k_i)V(x + \gamma_i) \approx (1 - \mu_i k_i)[V(x) + \gamma_i V'(x)],$$

where we ignore terms of  $\gamma_i^2$  or higher in the Taylor expansion of  $V$  around  $x$ . Multiplication yields

$$(1 - \mu_i k_i)[V(x) + \gamma_i V'(x)] \approx V(x) + \gamma_i V'(x) - \mu_i k_i V(x),$$

where we assume capture time  $k_i$  is so short that we can drop the product  $\mu_i k_i \gamma_i$ . Moreover, this approximation works only if both  $\mu_i k_i$  and  $\gamma_i$  are small (i.e., of order  $O(\epsilon^2)$ ). It follows that an individual should select option  $i$  provided this choice maximizes

$$V_{i(x)} = \gamma_i V'(x) - \mu_i k_i V(x). \quad (1)$$

This expression has a straightforward interpretation. The first term on the right-hand side (RHS) represents the net energy gain from choosing option  $i$ ,  $\gamma_i$ , multiplied by the rate at which reproductive value increases with state,  $V'(x)$ . This term represents the (unitless) increase in reproductive value resulting from choosing option  $i$ . The second term represents the product of the predation rate,  $\mu_i$ , and time interval,  $k_i$ , which equals the probability that the animal will die if it chooses option  $i$ , multiplied by its reproductive value. This term represents the (unitless) decrease in reproductive value resulting from choosing option  $i$ . The RHS thus represents the net increase in reproductive value resulting from choosing option  $i$ . This expression differs from Houston and McNamara's (1989, 1999). Our Eq. (1) is a discrete-time version of their equation (6.3) in Houston and McNamara (1999). According to their expression, the best choice is the one that maximizes the net *rate* of increase in reproductive value. According to our expression (Eq. (1)), the best choice is the one maximizes the net increase in reproductive value.

### 2.3. Partial preferences with bias towards safety

All decision processes are intrinsically subject to error, so we include so-called partial preferences (McNamara and Houston, 1987; Houston, 1997). This incorporation of

partial preferences captures the notion that natural selection should not be expected to lead to decision-making perfection. Instead, selection should favor decision processes that tend to minimize costly errors. We assume the probability of choosing option 2 in the choice task described above is given by

$$P_2 = \frac{\exp[b\theta(x) - a]}{1 + \exp[b\theta(x) - a]}, \quad (2)$$

where  $b$  is a positive scaling constant that reflects the relative benefit of choosing option 2,  $\theta(x) = V_2(x) - V_1(x)$ , and  $a$  is a constant that characterizes the animal's bias against the more dangerous option 2, even when neither option confers a clear fitness advantage (i.e., when  $V_2 = V_1$  and hence  $\theta(x) = 0$ ). We emphasize that  $P_2$  is not the optimal probability of choosing option 2, in the conventional sense where choice behavior is assumed to be unconstrained and error-free (e.g., McNamara, 1990). Instead,  $P_2$  represents the strength of preference for option 2, where adaptive choice behavior is subject to error and bias.

Observe from Eq. (1) that  $V_2(x) - V_1(x) = \gamma V'(x) - dV(x)$ , where  $\gamma = \gamma_2 - \gamma_1$  is the differential net energy gain, and  $d = \mu_2 k_2 - \mu_1 k_1$  is the differential predation risk, between the two options. We assume  $\gamma$  and  $d$  are both positive, which implies that option 2 is the more rewarding ( $\gamma_2 > \gamma_1$ ) yet more dangerous option ( $\mu_2 k_2 > \mu_1 k_1$ ). We also assume  $a$  is non-negative. For positive values of  $a$ , the less valuable but safer option 1 is preferred when neither option confers a distinct fitness advantage ( $V_2 = V_1$ ). Observe from Eq. (2) that for the special case where  $a = 0$ , an animal would be a rational decision maker (i.e., if  $\theta(x) > 0$ , then  $P_2(x) > \frac{1}{2}$ ; if  $\theta(x) = 0$ , then  $P_2(x) = \frac{1}{2}$ , and if  $\theta(x) < 0$ , then  $P_2(x) < \frac{1}{2}$ ). Where  $a > 0$ , the animal will tend to prefer the less valuable but safer option, unless  $\theta(x)$  is sufficiently positive. That is, according to Eq. (2), any bias towards safety (i.e.,  $a > 0$ ) leading to a preference for the option yielding lower  $V(x)$  can be overcome if the fitness advantage for the more dangerous but also more valuable option becomes large enough. We incorporated the parameter  $a$  to capture the idea that natural selection may favor preference for safer options.

But why would selection favor such a bias? Why would animals show an apparently irrational, inflated preference for options that entail lower hazard? We argue that a tendency to prefer the safer option (i.e.,  $a > 0$ ) may be adaptive where the true underlying predation risk is incalculable (i.e., especially in novel, including experimental, contexts). In our experiment (Waite et al., 2007), the subjects were required to travel into tunnels to collect food rewards. It is inconceivable that the hazard associated with this novel task could be translated into a precise or accurate estimate of the resulting decrement in reproductive value. In situations characterized by such high uncertainty, it may often pay to overestimate predation risk (Abrams, 1994; Welton et al., 2003).

Selection could favor bias in the same direction due to a nonexclusive, alternative mechanism that we have not incorporated into the model. In our experiment (Waite et al., 2007), option 1 was not just safer but also more immediate, and it is well known that animals often show a strong preference for immediacy. Experimental subjects, across a variety of taxa, exhibit a pervasive tendency to prefer small-immediate rewards to larger-but-delayed rewards, even when their net rate of return suffers as a consequence. This tendency to prefer the more immediate option, despite being economically irrational in experimental contexts, may be adaptive under ecologically relevant conditions (reviewed by Stephens, 2002; Stephens and Anderson, 2001). This preference for immediacy in experimental subjects could reflect an adaptive tendency in nature, where a forager is less likely to be interrupted (e.g., by a dominant competitor or a predator) while collecting a more immediately available reward. By assuming  $a > 0$ , we attempted to capture the idea that natural selection might favor a preference for safer options, not to incorporate any bias due to preference for immediacy. Our model would require an extension to incorporate the idea that selection may also favor bias in the form of preference for immediacy.

#### 2.4. Sigmoidal fitness functions

Fitness functions may often be sigmoidal rather than monotonically decelerating (e.g., Jaenike, 1996; Cotton et al., 1999; Kuznar and Frederick, 2003). We assume an animal's reproductive value (fitness) increases as a function of state according to

$$V(x) = \frac{x^m}{x^m + c^m}, \quad (3)$$

where  $m > 1$  and  $c > 0$  are parameters that influence the way  $V$  increases from 0 to 1 as  $x$  increases from 0 to  $\infty$  (Fig. 1). The restriction of  $m$  to values exceeding unity implies a sigmoidal graph for any member of this family of fitness functions. We assume this functional form here (cf. Waite and Passino, 2006) to capture the idea that incremental increases in hoard size will do little to improve a gray jay's prospects for overwinter survival and subsequent reproduction when the total hoard size is quite small (or quite large). These jays rely almost exclusively on their hoards throughout the winter and, to a lesser degree, even during the breeding season. Each jay stores tens of thousands of food items in preparation for the winter. We reason that a small hoard will typically be inadequate for overwinter survival, and it seems plausible that the total hoard must exceed some quasi-threshold size for overwinter survival to be likely. Eventually, we assume, the total accumulated hoard becomes so large that additional items have diminishing effects of fitness.

The parameter  $c$  has a simple interpretation. It is the half saturation constant (i.e., the value of  $x$  at which  $V = 0.5$ ). These graphs imply maximal fitness is approached at high

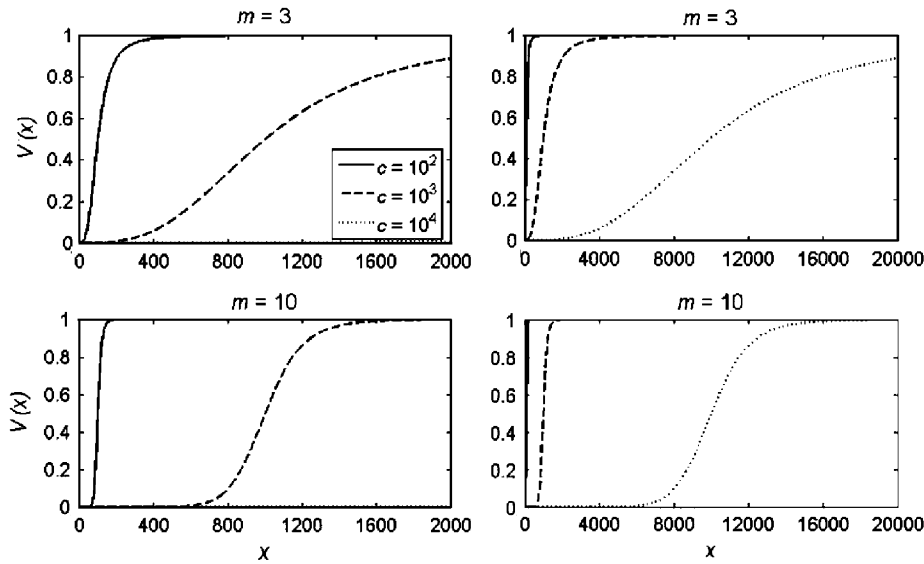


Fig. 1. Fitness  $V(x)$  for various values of  $m$  and  $c$  over multiple ranges of state. Small, intermediate, and large values of  $c$  represent gray jays with short-, intermediate-, and long-term windows, respectively.

state regardless of the values of  $m$  and  $c$ . The ascent parameter  $m$  reflects the steepness of  $V$  at  $x = c$ , with larger values of  $m$  producing a more step-like function. For a fixed value of  $m$ , Fig. 1 shows that individuals requiring small, intermediate, or large states to approach maximal fitness are best represented by small, intermediate, or large values of  $c$ , respectively. Thus, small, intermediate, and large values of  $c$  describe individuals with short-, intermediate-, and long-term windows, respectively. Specific ranges for  $c$  and  $m$  depend on the species under consideration.

2.5. Effect of state on choice

We now explore how  $\theta(x)$  varies as a function of state  $x$ . The function  $\theta(x)$  is obtained by substituting the  $V(x)$  of Eq. (3) and

$$V'(x) = \frac{mx^{m-1}c^m}{(x^m + c^m)^2}$$

into  $\theta(x) = V_2(x) - V_1(x)$  to get

$$\theta(x) = \frac{x^{m-1}}{x^m + c^m} \left[ \frac{\gamma mc^m}{x^m + c^m} - dx \right]. \tag{4}$$

It is straightforward to show that there exists a positive state  $x^*$  (depending on values of both  $m$  and  $c$ ) such that the continuous function  $\theta(x)$  increases from 0 to a maximum  $\theta^*$  (which also depends on both  $m$  and  $c$ ) as  $x$  increases from 0 to  $x^*$ , and then decreases from  $\theta^*$  to  $-d$  as  $x$  continues to increase beyond  $x^*$  to  $\infty$ . It can be shown also that  $x^*$  occurs within the acceleratory phase of  $V(x)$ , as shown in Fig. 2. (Proofs are available upon request from the authors.)

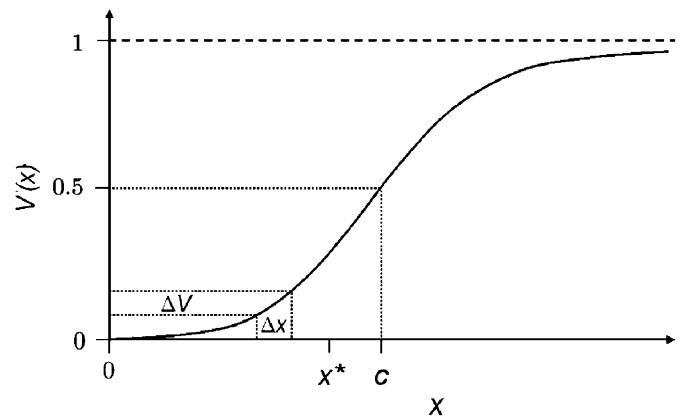


Fig. 2. Fitness function  $V(x)$  showing that  $x^*$  occurs within the acceleratory phase of  $V(x)$  and so  $x^* < c$ , the state at which  $V(x) = 0.5$  (i.e., inflexion point where  $V(x)$  changes concavity). The function  $\theta(x)$  (Eq. (5)) increases from 0 to a maximum as  $x$  increases from 0 to  $x^*$ , and then decreases to  $-d$  as  $x$  increases beyond  $x^*$  to  $\infty$ .

It follows from these properties of  $\theta(x)$  and Eq. (2) that the continuous function  $P_2(x)$  increases from

$$P_2^{\text{low}} = \frac{\exp(-a)}{1 + \exp(-a)}$$

to

$$P_2^* = \frac{\exp(b\theta^* - a)}{1 + \exp(b\theta^* - a)}$$

as  $x$  increases from 0 to  $x^*$ , and then decreases from  $P_2^*$  to

$$P_2^{\text{high}} = \frac{\exp(-bd - a)}{1 + \exp(-bd - a)}$$

as  $x$  continues to increase beyond  $x^*$  to  $\infty$ . The function  $P_2(x)$  is shown in Fig. 3 for various values of  $m$  and  $c$  and ranges of state  $x$ .

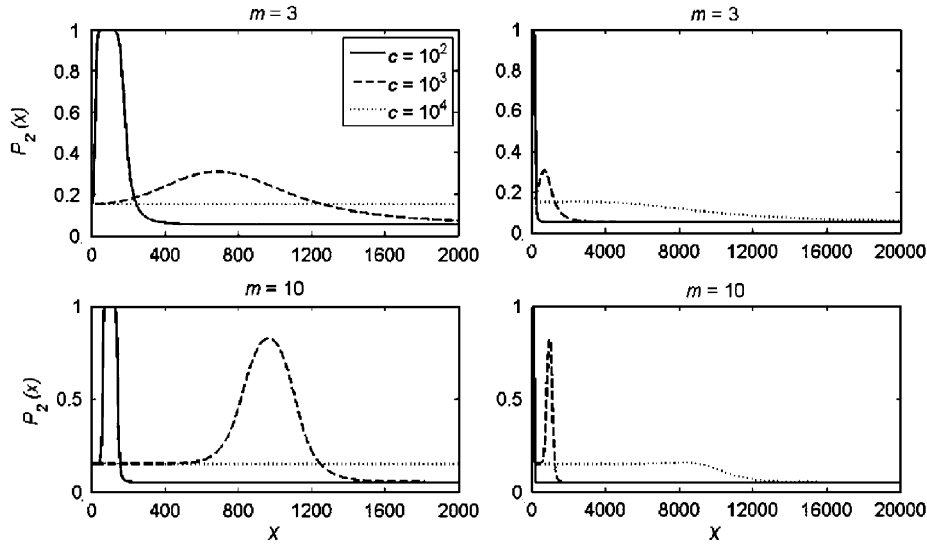


Fig. 3. Probability  $P_2(x)$  of selecting the more valuable but also more dangerous option 2 for different values of  $m$  and  $c$  over multiple ranges of state. Small, intermediate, and large values of  $c$  represent gray jays with short-, intermediate-, and long-term windows, respectively. All curves are plotted with the same values:  $\gamma = 2$ ,  $b = 756$ ,  $d = 0.0016$ , and  $a = 1.73$ .

The expressions for  $P_2^{\text{low}}$  and  $P_2^{\text{high}}$ , together with the assumed positivity of benefit  $b$ , differential predation risk  $d$ , and bias towards safety/immediacy  $a$ , imply that an individual whose current state is very low or very high will prefer the less valuable but safer option 1, regardless of differential energy gain  $\gamma$  or values of  $m$  and  $c$ . (Recall the proper interpretation of  $P_2$ . It represents the strength of preference for a decision process that is subject to error and bias, not the conventional optimal strategy.) Furthermore, the expression for  $P_2^*$  implies that if  $\theta^* < a/b$ , then an individual may prefer option 1 regardless of its state. By contrast, if  $\theta^* > a/b$ , then there exists an intermediate range of states  $(x_1, x_2)$  within which an individual may prefer the more valuable but also more dangerous option 2, and outside of which an individual should prefer option 1. That is, if  $\theta(x) < a/b$ , then  $P_2(x) < \frac{1}{2}$ ; if  $\theta(x) = a/b$ , then  $P_2(x) = \frac{1}{2}$ ; and if  $\theta(x) > a/b$ , then  $P_2(x) > \frac{1}{2}$ . (For the case  $a = 0$ , there exists a single state  $x^{**}$  at which  $\theta(x) = 0$ . In this case, the animal should be a rational decision maker: if  $x > x^{**}$ , then  $P_2(x) < \frac{1}{2}$ . If  $x = x^{**}$ , then  $P_2(x) = \frac{1}{2}$ ; and if  $x < x^{**}$ , then  $P_2(x) > \frac{1}{2}$ . That is, where  $a = 0$ , there is a single predicted switching point.) This preference switching will be examined in detail elsewhere. Here, because just one of our subjects exhibited any preference for option 2 (Table 1 in Waite et al., 2007), we do not consider such preference switching. Instead, we consider state-dependent adjustments in the tendency to choose option 2.

### 2.6. Effect of supplements in state on choice

An animal provided with a supplement  $\Delta x$  in state before the moment of choice may adjust its preference  $P_2(x)$  for the more valuable but also more dangerous option 2. It is clear from the properties of the partial preference function  $P_2(x)$ , and from Fig. 4, that  $P_2(x + \Delta x)$  will exceed  $P_2(x)$

when both  $x$  and  $x + \Delta x$  are less than  $x^*$ , and that the reverse inequality will hold when both  $x$  and  $x + \Delta x$  are greater than  $x^*$ . The relative values of  $P_2(x)$  and  $P_2(x + \Delta x)$  when  $x^*$  is within the interval  $(x, x + \Delta x)$  can be difficult to establish without direct computation.

### 2.7. Model validation

In our experiment (Waite et al., 2007), subjects were required to enter one of two tunnels to obtain food. Upon each visit to the experimental setup, subjects could obtain either a safe-but-small (5 cm into tunnel, 1 raisin) or a dangerous-but-large reward (45 cm into adjacent tunnel, 3 raisins). Here, we explore whether the conditions of our experiment favored adjustment in the tendency to choose the dangerous-but-valuable option 2 after receiving a supplement in state.

### 2.8. Parameter values

The values of these options were  $\gamma_1 = 1$  raisin and  $\gamma_2 = 3$  raisins. We assume hoarding imposes no additional costs, which implies that the differential gain  $\gamma = 2$  raisins. For option  $i$ , distance from entrance of the tunnel to food was  $D_1 = 5$  cm and  $D_2 = 45$  cm. We assume that predation rate  $\mu_i$  is the same for both options, but that capture time  $k_i$  is proportional to the distance  $D_i$  that an animal must enter the tunnel to collect the reward. Thus,  $\mu_2 = \mu_1$  and  $k_2 = 9k_1$ . It follows that differential predation risk is given by  $d = \mu_2 k_2 - \mu_1 k_1 = 8\mu_1 k_1$ .

We assume the less valuable but safer option 1 has predation rate  $\mu_1 = 10^{-4} \text{ s}^{-1}$  and capture time  $k_1 = 2$  s, so the differential predation risk was  $d = 0.0016$  (Fig. 5). In view of the minimum measured value of  $P_2$  (Table 1 in Waite et al., 2007), we assume  $P_2^{\text{low}} = 0.15$  and solve for  $a$

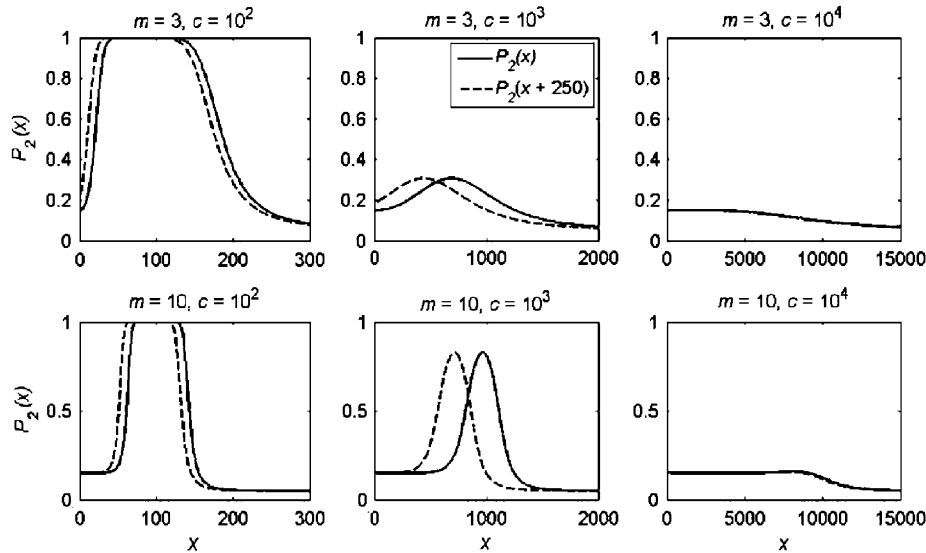


Fig. 4. Effect of supplement in state on the probability  $P_2(x)$  of selecting the more valuable but also more dangerous option 2 for various values of  $m$  and  $c$  over multiple ranges of state. Small, intermediate, and large values of  $c$  represent gray jays with short-, intermediate-, and long-term windows, respectively. All curves are plotted with the same values:  $\gamma = 2$ ,  $b = 756$ ,  $d = 0.0016$ , and  $a = 1.73$ .

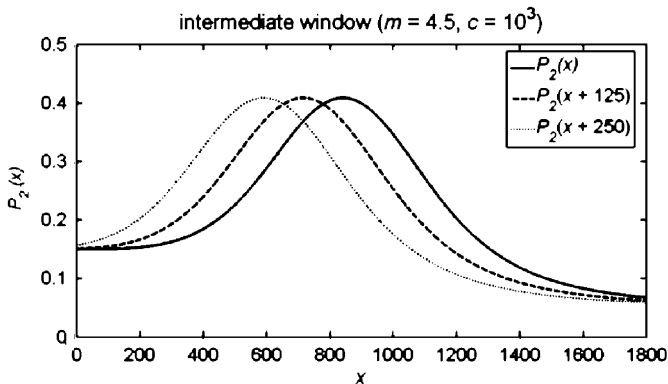


Fig. 5. Effect of range of supplements in state on the probability  $P_2(x)$  of selecting the more valuable but also more dangerous option 2 for a gray jay with an intermediate-term window ( $m = 4.5$  and  $c = 1000$ ). All curves are plotted with the same values:  $\gamma = 2$ ,  $b = 756$ ,  $d = 0.0016$ , and  $a = 1.73$ .

so that our model produces appropriate probabilities of choosing the dangerous-but-valuable option 2 at very low state,

$$a = \ln\left(\frac{1 - P_2^{\text{low}}}{P_2^{\text{low}}}\right) = 1.73.$$

We assume  $P_2^{\text{high}} = 0.05$  and now solve for benefit  $b$  so that our model produces appropriate probabilities of choosing option 2 at very high state,

$$b = \frac{1}{d} \left[ -a + \ln\left(\frac{1 - P_2^{\text{high}}}{P_2^{\text{high}}}\right) \right] = 756.$$

We can thus study how perceived state  $x$  influences choice, despite the presumption that all of our subjects had large background hoards  $x_{\text{actual}}$ .

Individual gray jays hoard tens of thousands of food boli each year (Waite, 1991), so we include fitness functions in Fig. 1 with values of  $c$  up to 10,000. A function  $V(x)$  with  $c = 10,000$  suggests the biologically relevant definition of state is actual size of the hoard  $x_{\text{actual}}$ , which is collected over an entire season, and that a jay’s probability of overwinter survival and successful reproduction would be 0.99 at a total hoard size of  $x_{99\%} = 46,300$  if  $m = 3$  or  $x_{99\%} = 15,800$  if  $m = 10$ . We would consider a jay to possess a long-term window if its fitness function were described by such a large value of  $c$ . Based on observation, we also include fitness functions as if jays possess short-term windows ( $c = 100$ ) and so make decisions based on the number of hoards made during an hour-long hoarding bout, and as if they possess an intermediate-term window ( $c = 1000$ ) and so make decisions based on the number of hoards made during a day-long hoarding bout.

2.9. Effect of supplements in state on choice

In the experiment (Waite et al., 2007), we explored whether a gray jay’s tendency to choose the dangerous-but-valuable option 2 might be state-dependent. We supplemented the hoard  $x_{\text{actual}}$  of each individual with  $\Delta x = 250$  raisins prior to the experimental trial. Upon receiving this supplement, subjects, on average, increased their tendency to choose option 2.

2.10. Model validation

Since an individual with a short-term window ( $c = 100$ ) may not perceive its hoard to be incremented by the full supplement of 250 raisins, we assume that its state was supplemented by  $\Delta x = 250\varepsilon$ , where  $\varepsilon$  was chosen between 0

and 1. In Fig. 3, we establish the relative magnitudes of  $P_2(x)$  and  $P_2(x + \Delta x)$  for various values of  $m$  and  $c$  to determine whether a supplement in state could ever increase an individual's tendency to choose the dangerous-but-valuable option 2. An individual of any window type could follow such a pattern, but it is clear from Fig. 3 that results in Fig. 1 are most plausible if gray jays have intermediate-term windows. Consider the perceived states that produce probabilities  $P_2(x)$  and  $P_2(x + \Delta x)$  falling largely within the range 0.2–0.4. These states are most consistent with intermediate-term windows (i.e., for jays whose biologically relevant window consists of about a day, during which jays routinely make up to ~1000 hoards). In Fig. 4, we show how one such hypothetical individual (whose fitness curve is given by  $m = 4.5$  and  $c = 1000$ ) would adjust its tendency to choose the dangerous-but-valuable option 2 in response to various supplements in state.

### 3. Discussions

Our model of adaptively imperfect (cf. McNamara, 1990), state-dependent choice reveals some complex ways an animal's perceived state may influence its choice behavior. If reproductive value were a monotonically decelerating function of state, then any reduction in state would induce an increased willingness to accept great danger to obtain a larger reward. However, by assuming a sigmoid fitness function (Fig. 2), we have revealed how an animal may respond to changes in its state by adjusting the tendency to accept an extra predation risk to obtain a bigger reward—upward, downward, or not at all.

We make the following observations, which are based on the assumptions that selection favors the minimization of costly errors and a bias towards overemphasizing safety (additional assumptions detailed in Section 2.5). If an animal's current state is very high, the animal may show a strong preference for the safer option, even if this option yields a much smaller energy gain. The extra energy obtained by choosing the more valuable option would have minimal influence on reproductive value and so it pays to minimize predation risk. Likewise, if its current state is very low, the animal may show a strong preference for the safer option, even if it yields a much smaller energy gain. Again, owing to the sigmoid functional form, the extra energy obtained by choosing the more valuable option would have minimal influence on reproductive value and so it pays to minimize predation risk. However, for some intermediate range of state where reproductive value increases faster with increases in state, the animal may show the opposite preference. That is, an animal may sometimes prefer the dangerous option, not because it entails a greater mortality risk but because it provides a bigger fitness-enhancing reward. Our model, because it incorporates error and bias (cf. McNamara, 1990), thus predicts state-dependent preference reversals.

#### 3.1. State subsidies can induce dangerous choice

We used the model to explore effects of supplements in state on an animal's willingness to accept extra predation risk to obtain a bigger reward. The model makes predictions in both directions. Above a threshold state, the animal should respond to a supplement by decreasing its willingness to take a bigger predation risk to obtain a more valuable reward. Any incremental increase in state after having received a supplement has a smaller fitness-enhancing effect and so it pays to increase emphasis on safety. Below this threshold, the animal should respond by increasing this willingness because any incremental increase in state after having received a supplement has a bigger fitness-enhancing effect. Thus, if the animal's state is relatively high, then it should respond to improvements in state by increasing its tendency to play it safe; conversely, if its state is relatively low, then it should respond to improvements in state by increasing its tendency to accept danger.

According to the model, our subjects (Waite et al., 2007) should have been insensitive to the experimental supplement in state if their perceived state were equivalent to the total hoard. But what if their perceived state were “computed” for a smaller window than the preceding weeks of intense hoarding? According to our model, the jays should have decreased their willingness to take the extra predation risk for the bigger reward if their perceived state was equivalent to a relatively large proportion of the total hoard, and they should have increased this willingness if their perceived state was a relatively small proportion of the total hoard. Our manipulation had no significant effect for any individual subject, but subjects, on average, responded to the supplement by increasing this tendency. This adjustment is consistent with the model provided the subjects' perceived state was relatively low. The measured effect was consistent with the possibility that jays' perceived state was something on the order of 1000 hoards (i.e., the number of hoards made during the last few days). This level of perceived state places the jays in the accelerating portion of the fitness function, where it pays to accept greater danger to obtain larger rewards.

#### 3.2. Is it ecologically rational to devalue the hoard?

Why would the jays behave as if their effective hoard was smaller than their total hoard? We contend that devaluing the hoard in this way makes good biological sense. Such “ecological discounting” seems plausible in this case because the effective hoard is inevitably smaller than the total hoard. Unlike financial investments, which may accrue value over time, the jays' investment inevitably diminishes over time. Many items are stolen daily. All items are subject to decomposition, which may be exaggerated in our study area, at the extreme southern edge of the species range. This population has undergone a dramatic demise in recent decades, apparently because jays

have poor reproductive success following warm autumns (Waite and Strickland, 2006). Warmer autumns in recent years represent hostile conditions because the jays ordinarily rely on cold storage to preserve their hoards. Waite et al. (2007) conducted the experiment during autumn, before the onset of food-preserving conditions. Thus, the subjects might have behaved in an ecologically rational way by discounting their prior investment.

### 3.3. Adaptive state-dependent choice can violate economic rationality

Our work has implications for how to interpret violations of economic rationality. In recent years, several studies have uncovered context-dependent violations of economic rationality (Bateson, 2002; Bateson et al., 2002, 2003; Hurly and Oseen, 1999; Shafir, 1994; Shafir et al., 2003; Waite, 2001a,b). We previously interpreted such violations as evidence that animals use comparative valuation based on context (i.e., array of options available) (Shafir et al., 2002, 2003; Waite, 2001a,b). It remains clear that our subjects do not assign fixed values to options. However, we have now formalized the claim (Schuck-Paim et al., 2004) that any unintended experimental manipulation of state could induce adjustments in choice behavior. Seemingly irrational behavior could arise in any experiment in which the procedure manipulates the subjects' state (e.g., Kacelnik and Marsh, 2002; Marsh et al., 2004). Definitive tests of our model will require dramatic manipulations of effective hoard size, perhaps by temporarily holding some subjects in captivity or by giving them chronic access to superabundant food.

### 3.4. State-dependent choice in hoarders versus nonhoarders

Experiments using nonhoarding species such as hummingbirds should be performed as well. Such species may be especially prone to state-dependent effects (e.g., Bateson et al., 2003; Hurly and Oseen, 1999). These tiny birds, with their high metabolic demands and minimal energetic reserves, may be strongly responsive to manipulation of state. They may be prime candidates for testing state-dependent preference reversals as predicted by our model.

### 3.5. Conclusions and future needs

To conclude, our model shows how animals should trade off danger for food, depending on their own perceived state. If relatively high, they should emphasize safety; if relatively low, they should de-emphasize safety. Experimental findings (Waite et al., 2007) agree with the possibility that supplemented gray jays were more inclined to take extra predation risk to obtain larger rewards because their perceived state was in the accelerating portion of the fitness function. These findings suggest that previously observed violations of rationality might have been a byproduct of state-dependent choice (Schuck-Paim

et al., 2004). Whether state dependence can account for other apparent violations of economic rationality (e.g., Waite, 2001b; Shafir et al., 2003; reviewed by Roe et al., 2001) awaits future experiments.

### Acknowledgments

We thank C. Schuck-Paim, A. Kacelnik, L. Pompilio, and other participants at the Limits to Rationality workshop held at the Institute for Advanced Study for inspiring this study; and M. Bateson, A. Hurly and S. Shafir for discussion; and Stauf's and Soul Sistas for providing pleasant workspace. Supported by OSU Office of Research, Large Interdisciplinary Grant Program; Mathematical Biosciences Institute, and National Science Foundation.

### References

- Abrams, P., 1994. Should prey overestimate the risk of predation? *Am. Nat.* 144, 317–328.
- Bateson, M., 2002. Context-dependent foraging choices in risk-sensitive starlings. *Anim. Behav.* 64, 251–260.
- Bateson, M., Healy, S.D., Hurly, T.A., 2002. Irrational choices in hummingbird foraging behaviour. *Anim. Behav.* 63, 587–596.
- Bateson, M., Healy, S.D., Hurly, T.A., 2003. Context-dependent foraging decisions in rufous hummingbirds. *Proc. R. Soc. B* 270, 1271–1276.
- Cotton, P.A., Wright, J., Kacelnik, A., 1999. Chick begging strategies in relation to brood hierarchies and hatching asynchrony. *Am. Nat.* 153, 412–420.
- Houston, A.I., 1997. Natural selection and context-dependent values. *Proc. R. Soc. B* 264, 1539–1541.
- Houston, A.I., McNamara, J.M., 1989. The value of food: effects of open and closed economies. *Anim. Behav.* 37, 546–562.
- Houston, A.I., McNamara, J.M., 1999. Models of adaptive behaviour: an approach based on state. Cambridge University Press, Cambridge, UK.
- Hurly, T.A., Oseen, M.D., 1999. Context-dependent, risk-sensitive foraging preferences in wild rufous hummingbirds. *Anim. Behav.* 58, 59–66.
- Jaenike, J., 1996. Population-level consequences of parasite aggregation. *Oikos* 76, 155–160.
- Kacelnik, A., Marsh, B., 2002. Cost can increase preference in starlings. *Anim. Behav.* 63, 245–250.
- Kuznar, L.A., Frederick, W.G., 2003. Environmental constraints and sigmoid utility: implications for value, risk sensitivity, and social status. *Ecol. Econ.* 46, 293–306.
- Marsh, B., Schuck-Paim, C., Kacelnik, A., 2004. Energetic state during learning affects foraging choices in starlings. *Behav. Ecol.* 15, 396–399.
- McNamara, J.M., 1990. The policy which maximises long-term survival of an animal faced with the risks of starvation and predation. *Adv. Appl. Prob.* 22, 295–308.
- McNamara, J.M., Houston, A.I., 1987. Partial preferences and foraging. *Anim. Behav.* 35, 1084–1099.
- Roe, R.M., Busemeyer, J.R., Townsend, J.T., 2001. Multialternative decision field theory: a dynamic connectionist model of decision making. *Psych. Rev.* 108, 370–392.
- Schuck-Paim, C., Pompilio, L., Kacelnik, A., 2004. State-dependent decisions cause apparent violations of rationality in animal choice. *PLoS Biol.* 2, 2305–2315.
- Shafir, S., 1994. Intransitivity of preferences in honey-bees: support for comparative-evaluation of foraging options. *Anim. Behav.* 48, 55–67.



- Shafir, S., Waite, T.A., Smith, B., 2002. Context-dependent violations of rational choice in honeybees (*Apis mellifera*) and gray jays (*Perisoreus canadensis*). *Behav. Ecol. Sociobiol.* 51, 180–187.
- Shafir, S., Bechar, A., Weber, E.U., 2003. Cognition-mediated coevolution: context-dependent evaluations and sensitivity of pollinators to variability in nectar rewards. *Plant Syst. Evol.* 238, 195–209.
- Simonsohn, U., 2006. New Yorkers commute more everywhere: contrast effects in the field. *Rev. Econ. Stat.* 88, 1–9.
- Simonsohn, U., Loewenstein, G., 2006. Mistake #37: the effect of previously encountered prices on current housing demand. *Econ. J.* 116, 175–199.
- Stephens, D.W., 2002. Discrimination, discounting and impulsivity: a role for an informational constraint. *Philos. Trans. R. Soc. B* 357, 1527–1537.
- Stephens, D.W., Anderson, D., 2001. The adaptive value of preference for immediacy: when shortsighted rules have farsighted consequences. *Behav. Ecol.* 12, 330–339.
- Tversky, A., Simonson, I., 1993. Context-dependent preferences. *Manage. Sci.* 39, 1179–1189.
- Waite, T.A., 1991. Economics and consequences of scatterhoarding in the gray jay, *Perisoreus canadensis*. Ph.D. dissertation, Ohio State University, Columbus, USA.
- Waite, T.A., 2001a. Intransitive preferences by hoarding gray jays. *Behav. Ecol. Sociobiol.* 50, 116–121.
- Waite, T.A., 2001b. Background context and decision making in hoarding gray jays. *Behav. Ecol.* 12, 318–324.
- Waite, T.A., Passino, K.M., 2006. Paradoxical preferences when options are identical. *Behav. Ecol. Sociobiol.* 59, 777–785.
- Waite, T.A., Strickland, D., 2006. Climate change and the demographic demise of a hoarding bird living on the edge. *Proc. R. Soc. B* 273, 2809–2813.
- Waite, T.A., Nevai, A.I., Passino, K.M., 2007. State subsidies induce gray jays to accept greater danger: an ecologically rational response? *Behav. Ecol. Sociobiol.*, in press, doi:10.1007/s00265-007-0356-8.
- Welton, N.J., McNamara, J.M., Houston, A.I., 2003. Assessing predation risk: optimal behaviour and rules of thumb. *Theor. Pop. Biol.* 64, 417–430.