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Paradoxical preferences when options are identical

Abstract Normative models of choice predict no preference when unequally priced options of identical quality are temporarily offered for the same low price, yet several studies using nonhuman subjects have found a preference in this context. Paradoxically, subjects have preferred the stimulus associated with typically *higher* acquisition cost. Here, preference tests were conducted for gray jays (*Perisoreus canadensis*) choosing between temporarily identical options, which were color coded to represent typical conditions. During no-choice trials, subjects were offered either a cheap or an expensive food reward, by positioning the reward either 1.9 or 60 cm into a tunnel. During intermittent free-choice trials, subjects chose between color-coded but otherwise identical options (same reward, both cheap). Jays preferred the stimulus associated with *lower* cost, unlike subjects in previous studies. To reconcile these conflicting findings, we model choice as a trade-off between state and predation. We explore how alternative mechanisms of valuation may lead to preference in either direction (i.e., for greater workload vs lower predation risk). Our models accommodate observed paradoxical preferences in both directions.

Keywords Choice · Predation risk · Preference · Rationality · State

Introduction

Classic rationality theory assumes that decision-makers consistently choose the most profitable option among those

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available. According to the principle of irrelevant alternatives, only those options that are locally (currently) available should influence choice behavior (Tversky and Simonson 1993; Kahneman and Tversky 1996; cf. Roe et al. 2001). Therefore, if options are identical in quality and price, the decision-maker should show no preference. Likewise, models from foraging theory assume animals make choices that tend to maximize some currency such as long-run net rate of energy gain (Stephens and Krebs 1986). These models also predict no preference when options are identical. Yet, several experimental studies have found preferences when options typically differing in cost are made to be identical at the moment of choice (e.g., Belke 1992; Gibbon 1995; Kacelnik and Marsh 2002).

Paradoxically, these studies have found a preference for stimuli associated with higher-cost options. For example, captive starlings (*Sturnus vulgaris*) were exposed to series of hard and easy no-choice trials (Kacelnik and Marsh 2002). In hard trials, subjects were required to make 16 flights to obtain a food reward. In easy trials, they were required to make just four flights to receive the same reward. In intermittent free-choice trials, subjects could choose between two stimuli, one associated with high cost or the other associated with low cost. In these trials, there was no cost (i.e., no flights required) and the reward was fixed (i.e., independent of choice). Remarkably, starlings tended to prefer the stimulus associated with greater work.

Conventional explanations (e.g., Curio 1987; Elliot and Devine 1994; Inglis et al. 1997; Aloysius 2003) cannot satisfactorily account for the starlings' preference, but a promising explanation has been offered. Preference for stimuli associated with high cost may be the by-product of state-dependent choice (Clement et al. 2000; Kacelnik and Marsh 2002). Starlings might have preferred the stimulus associated with higher cost not because it was associated with harder work per se, but because greater effort caused a greater reduction in energetic state and hence a greater fitness gain could be accrued from a given reward. In general, selection should favor mechanisms that assign higher value to stimuli usually associated with higher payoffs. Such mechanisms could lead to preferences when options are locally identical because it is adaptive to prefer options whose attributes are

usually reliable cues of superior payoff (Todd and Gigerenzer 2003).

Here we describe an experiment designed to evaluate whether the gray jay (*Perisoreus canadensis*) would show any preference when the cost differential was eliminated during free-choice trials. This experiment differs from Kacelnik and Marsh (2002) in a key way. It was designed to create cost differential primarily based on predation risk rather than workload. The jays exhibited a preference where normative models would predict none, but it was in the opposite direction from the starlings' preference. Seeking to reconcile these findings, we develop a model to explore whether alternative mechanisms of valuation may account for preferences in both directions.

Methods

Subjects and study area

The gray jay, a nonmigratory bird of boreal forest, hoards food intensively throughout group-held territories (for a detailed description see Strickland and Ouellet 1993; Strickland and Waite 2001). Outside the breeding season, social groups typically comprise a mated pair often accompanied by a philopatric offspring or an unrelated immigrant (evicted from its natal territory by a dominant sibling). Members of the social group routinely make hundreds of scattered caches per day during summer and autumn, placing each cache in an arboreal site. They rely on these caches during winter and use them to provision nestlings and fledglings.

We tested 11 semi-tame jays in six territories. These subjects comprised 10 members of mated pairs (six adult females and four adult males) and one extra (juvenile male retained on his natal territory). None of the adults had participated in any experiment for at least 1 year, and the juvenile had never participated in an experiment. Every subject was identifiable by a unique combination of color bands.

We conducted the experiment in Algonquin Provincial Park, Ontario (45°33′N, 78°38′W), between 14 October and 2 November 2002. Tests were conducted between 0920 and 1809 hours. Air temperature varied between −2 and 9°C. Light rain or snowfall occurred during three tests and no precipitation occurred during the other eight tests.

Procedure

The experiment was designed to determine whether subjects show a preference for the color associated with either a low- or high-cost foraging opportunity when tested in a binary-choice task, where the cost differential has been temporarily removed. Each subject was exposed to 50 series of four forced (no-choice) visits, with each series followed by one binary, free-choice visit. Each subject thus collected 250 food rewards (one raisin per visit). Immediately upon collecting each raisin, the jay flew to a nearby tree to hoard it and then returned to the experimental setup, where the next reward was already available. Subjects completed the 250 visits and hoarding trips in 6.4 h, on average, within a single day. For detailed descriptions of hoarding, see Waite and Ydenberg (1996).

Before testing a particular individual, we attracted the jay to the core of its territory, usually by whistling. As soon as the jay arrived, we began a preliminary performance test in which the prospective subject was given a choice between identical options (one raisin, 60 cm into tunnel; see below) during 10 consecutive visits to the setup. To train the jay to treat the task as an exclusive binary choice, we flushed it if it attempted to enter both tunnels during any single visit. All individuals passed the performance test, entering one of the tunnels during each visit, collecting the raisin and transporting it to a nearby arboreal site for storage. Throughout this performance test and the subsequent experimental test, raisins were offered to all jays accompanying the subject to minimize any influence of interference competition on the subject's choice behavior (Waite and Ydenberg 1996). Following the performance test, we immediately began the experiment as described below.

In each no-choice visit, the subject obtained a single raisin placed either 60 cm (high cost) or 1.9 cm (low cost) into a single 1.2-m-long tunnel (made of welded wire, 1-cm mesh; semi-cylindrical [radius 25 cm], closed at one end). In high-cost visits, subjects were required to hop into the tunnel to collect the food. In low-cost visits, subjects collected the food without entering the tunnel. Entering the tunnel reduces the subject's ability to escape a surprise attack. Subjects in related experiments have always behaved as if the perceived predation risk increases with distance into the tunnel (e.g., Waite 2001a,b; Shafir et al. 2002). Within each series of four no-choice visits, the placement of the food alternated between the high- and low-cost positions, with the order alternating across series. For each forced-choice visit, we recorded the subject's latency to collect the food reward.

These foraging opportunities were color-coded. In each no-choice visit, the food (one raisin) was placed within a plastic cup (diameter 8.9 cm, depth 3.8 cm). The cup was either white or blaze orange, depending on its placement within the tunnel (low- vs high-cost position). The color associated with the low-cost position was randomly assigned (orange) for the first subject and alternated across successive subjects.

In each free-choice visit, the subject obtained a single raisin by choosing between a white cup and an orange cup. The cups were placed in the low-cost position of tunnels arranged to be adjoining at the open end and angled at 45°. The cups were randomly assigned to a side (left or right tunnels). Thus, the two options were identical both in quality (reward=one raisin) and price (same placement in opening of tunnels). They differed only in color, which encoded price (distance into tunnel) during no-choice visits.

We recorded the subject's choice for each of 50 free-choice visits, 25 in each of two consecutive sessions. After completing the first session (i.e., immediately following the 25th free-choice visit), we moved the experimental setup 80 m (to minimize density-dependent shifts in hoarding strategy; Waite and Ydenberg 1996) and repeated the procedure following a 5-min hiatus. The proportion of

choices for the color associated with the low-cost option was used as the measure of preference.

Data analysis

Analyses were performed using SPSS (2002) routines. Generalized linear method (GLM) repeated-measures analysis of variance (ANOVA) (on arcsine square-root-transformed proportions of low-cost option) was used to test the effects of time (choices 1–25 [session 1] vs 26–50 [session 2]; within-subjects factor) and color (white vs orange associated with low-cost option; between-subjects factor) on preference during free-choice visits. Linear mixed-model, repeated-measures ANOVA was used to test the effects of time (100 visits in session 1 vs 100 visits in session 2) and cost (low vs high), both within-subjects factors, on median latency to collect the food reward during forced (no-choice) visits.

Binomial tests (two-tailed) were used to evaluate preference in individual subjects. To compensate for the multiplicity of tests performed, we evaluate the significance of these results using the Benjamini–Hochberg method (Benjamini and Hochberg 1995). Any nominally significant (i.e., $P<0.05$) test is considered to remain significant if the following condition is met: $p_i \leq (iq)/m$, where $p_1 \leq p_2 \leq ... \leq p_m$ are the observed P values in ascending order, q is the assigned False Discovery Rate (FDR) (0.05), and m is the number of subjects (11). We also report whether any nominally significant test remains significant following sequential Bonferroni adjustment (Rice 1989), with the Family-wise Error Rate (FWER) set at 0.05.

Results

Results of the preference tests are summarized in Table 1. Repeated-measures ANOVA revealed: (1) a significant increase in preference for the color associated with the low-cost option from the first session (free choices 1–25) to the second session (26–50) ($F_{1,9}=7.851$, $P=0.021$, power=0.704), (2) no significant effect of color ($F_{1,9}=4.349$, $P=0.067$, power= 0.461), and (3) no significant interaction ($F_{1,9}=1.747$, $P= 0.219$, power=0.220) (in a follow-up analysis, no significant effect of territory was found [$F_{5,4}=0.151$, $P=0.969$, power= 0.063]). In free-choice tests for the two sessions combined, all 11 subjects chose during most visits the color usually (80% of visits) associated with low cost (binomial $P<0.001$). Ten of the subjects showed a nominally significant ($P<0.05$) preference for the color associated with low cost (Table 1). All 10 of these results remain significant at FDR=0.05, and more conservatively, nine of these 10 results remain significant at FWER=0.05 (Table 1).

Mixed-model, repeated-measures ANOVA revealed a significantly longer median latency to collect the food reward in high-cost (marginal mean=3.6±0.23 s [SE]) than low-cost visits (1.4±0.12; $F_{1,19.35}=83.383$, $P<0.001$), but no

Table 1 Results of preference tests in gray jays choosing between two locally identical options, where a typical cost differential during no-choice trials is encoded by color of the food container

Subject (Age, Sex)	Proportion of choices for stimulus (color) associated with typically lower cost	Binomial P
1 (AHY, ♀)	0.56 (o)	0.32
2 (AHY, ♂)	0.88 (w)	<0.001[a,b]
3 (AHY, ♀)	0.66 (o)	0.015[a,b]
4 (AHY, ♂)	0.96 (w)	<0.001[a,b]
5 (AHY, ♂)	0.66 (o)	0.015[a,b]
6 (AHY, ♀)	0.94 (w)	<0.001[a,b]
7 (AHY, ♀)	0.74 (o)	<0.001[a,b]
8 (AHY, ♂)	0.82 (w)	<0.001[a,b]
9 (HY, ♂)	0.88 (o)	<0.001[a,b]
10 (AHY, ♀)	0.64 (w)	0.033[a]
11 (AHY, ♀)	0.74 (o)	<0.001[a,b]

Proportion of low-cost choices calculated for sessions 1 and 2 combined. Color associated with low-cost option indicated in parentheses

AHY After hatching year=adult, *HY* hatching year=juvenile, *o* orange, *w* white

[a]Significant at False Discovery Rate=0.05 (Benjamini–Hochberg method)

[b]Significant at Family-wise Error Rate=0.05 (see "Data analysis")

significant change in latency from the first (2.6±0.23) to second session (2.4±0.12; $F_{1,19.35}=0.911$, $P=0.352$) (in a follow-up analysis, no significant effect of territory was found [$F_{5,5}=1.535$, $P=0.325$, power=0.233]). Across the two sessions, all 11 subjects showed a tendency toward longer latency in the high-cost than low-cost treatment (binomial $P<0.001$).

Model

Here we explore how mechanisms of valuation could lead to preferences, although the options are economically identical at the moment of choice. Consider an animal with i foraging options, each characterized by a net rate of energy gain γ_i and a predation rate M_i. The animal must trade γ_i against M_i, where reproductive value V_i increases with γ_i and decreases with M_i. By choosing option i, an animal with energetic state x increases its reproductive value by net rate:

$$\dot{V}(i) = \gamma_i \frac{\partial V_i}{\partial x_i} - M_i V_i \qquad (1)$$

(Houston and McNamara 1999). Defining state as energy available either internally or externally (hoarded food), $\gamma_i = \partial x_i / \partial t$ is the rate at which state increases as a result of choosing option i, $\partial V_i / \partial x_i$ is the rate at which V_i increases with x_i, and so $\gamma_i \partial V_i / \partial x_i$ is the rate at which reproductive

value increases due to the increase in state. $M_i V_i$ is the rate at which reproductive value decreases due to predation risk. We assume $V=V_i$ for all options. The best option maximizes Eq. (1). For a binary choice, the animal should choose option 1 if:

$$\dot{V}(1) = \gamma_1 \frac{\partial V}{\partial x} - M_1 V > \gamma_2 \frac{\partial V}{\partial x} - M_2 V = \dot{V}(2). \quad (2)$$

Consider a discrete choice where $\partial x_i / \partial t$ is replaced with values meant to mimic the experimental task. We express the rate of energy gain when option i is chosen as $\gamma_i = \partial x_i / \partial t = e_i / h_i$, where e_i is energy value and h_i is time required to acquire this payoff. In our experiment, h_i was the time required to hoard the food and return to the source.

Now consider that all decision processes are intrinsically subject to error and hence partial rather than absolute preferences are inevitable (McNamara and Houston 1987). We assume the probability of choosing option 1 to be described by:

$$P_1 = \frac{\exp\left[\beta\left(\dot{V}(1) - \dot{V}(2)\right)\right]}{1 + \exp\left[\beta\left(\dot{V}(1) - \dot{V}(2)\right)\right]}, \quad (3)$$

where $\beta > 0$ is a scaling constant. The probability of choosing option 1 depends on the fitness-related advantage of choosing this option (Houston 1997; Waite 2002).

Substituting e_i / h_i for γ_i and then the right-hand side of Eq. (1) into Eq. (3) and rearranging yields:

$$P_1 = \frac{\exp\left\{\beta\left[\left(\frac{e_1}{h_1} - \frac{e_2}{h_2}\right)\frac{\partial V}{\partial x} + (M_2 - M_1)V\right]\right\}}{1 + \exp\left\{\beta\left[\left(\frac{e_1}{h_1} - \frac{e_2}{h_2}\right)\frac{\partial V}{\partial x} + (M_2 - M_1)V\right]\right\}}. \quad (4)$$

This expression predicts P_1 when two simultaneously available options differ in energetic gain and/or predation risk at the moment of choice. However, the two options were never simultaneously available under these conditions in our experiment. We tested jays choosing between stimuli associated with options that typically differed in energetic gain and/or predation risk (i.e., when only one option was available). Our objective is to model preference when such options have become simultaneously available and economically identical.

We assume selection favors mechanisms of valuation that lead to preferences for stimuli associated with options typically conferring higher V. In doing so, we predict preference based on which option *appears* to confer greater V. Thus, we expect subjects to prefer the option yielding higher net rate of increase in subjective value, or utility $\dot{U}(i)$, not necessarily the option yielding higher net rate of increase in actual reproductive value $\dot{V}(i)$. We modify Eq. (4) accordingly. To simplify, we let $\theta = e_1/h_1 - e_2/h_2$ and $M = M_2 - M_1$.

Next we subdivide the scaling constant into two components, where $\beta_e > 0$ scales the effect of differential energetic gain and $\beta_p > 0$ scales the effect of differential predation risk. Incorporating these changes yields an expression for the probability of choosing the stimulus associated with option 1, s_1:

$$P(s_1 | \text{locally identical conditions}) \quad (5)$$
$$= \frac{\exp\left(\beta_e \theta \frac{\partial V}{\partial x} + \beta_p M V\right)}{1 + \exp\left(\beta_e \theta \frac{\partial V}{\partial x} + \beta_p M V\right)}.$$

Here, θ and M refer to differential profitability and predation risk under typical conditions, not at the moment of choice. For brevity, we write $P(s_1 | \text{locally identical conditions})$ as P_{s_1}.

We assume reproductive value increases as a negative exponential function of state:

$$V = 1 - exp(-ax), \quad (6)$$

where $a > 0$ is a scaling constant and x is state. For our study, we define x to be total hoard size (we assume that our subjects' internal state was chronically high during the experiment because they maintained a high net self-feeding rate; Waite and Ydenberg 1996). Reproductive value is zero for a hoard size of zero because the animal has no external energy reserves. We assume a gray jay would maximize its probability of over-winter survival and successful reproduction at $V=1$ (i.e., as $x \to \infty$).

Based on Eq. (6), the partial derivative of V with respect to x is:

$$\frac{\partial V}{\partial x} = a \cdot \exp(-ax). \quad (7)$$

This equation represents an increase in reproductive value associated with an increase in state. To explore how preference depends on the trade-off between θ and M, we substitute Eqs. (6) and (7) into Eq. (5) and solve for P_{s_1}.

To predict preference for conditions like those faced by our subjects, we must specify parameter values. Under typical conditions (i.e., during no-choice visits), subjects were required to enter a tunnel to obtain food. These visits alternated between low and high cost, where a one-raisin reward ($e_1 = e_2 = 1$) was positioned either 1.9 or 60 cm into the tunnel. The time required to hoard the item differed between successive no-choice visits ($h_1 \approx 25$ s, $h_2 \approx 28$ s; Waite and Ydenberg 1996). Next, we define predation rate parameters M_1 and M_2. For low- and high-cost visits, the distances from the entrance of the tunnel to the food were $D_1 = 1.9$ cm and $D_2 = 60$ cm. We assume predation risk to be proportional to D, $M_1 = D_1/(D_1 + D_2)$ and $M_2 = D_2/(D_1 + D_2)$, and choice to depend on the difference, $M_2 - M_1 = M = 0.94$. Finally, we specify values for β_e and β_p. Consider the

boundary condition when x is large and hence P_{s_1} is small. When x is large, $\partial V/\partial x \to 0$ and $V \to 1$. Substituting into Eq. (5) and rearranging gives:

$$\ln\left(\frac{P_{s_1}^{large}}{1 - P_{s_1}^{large}}\right) = \beta_p M. \tag{8}$$

We assume $P_{s_1}^{l\arg e} = 0.95$ (based on prior experiments; Shafir et al. 2002) and solve for β_p so that our model generates plausible values of P_{s_1} under large hoard size x. Next, consider the boundary condition when $x=0$ and thus P_{s_1} is relatively large. We arbitrarily assume P_{s_1} when total hoard size is small, $P_{s_1}^{small} = 0.99$. Because $V=0$ when $x=0$ (Eq. 6) and $\partial V/\partial x=a$ when x is small (Eq. 7), from Eq. (5) we see that:

$$P_{s_1}^{small} = \frac{\exp\left(\beta_e \theta a(i)\right)}{1 + \exp\left(\beta_e \theta a(i)\right)},$$

and thus

$$\ln\left(\frac{P_{s_1}^{small}}{1 - P_{s_1}^{small}}\right) = \beta_e \theta a(i). \tag{9}$$

We solve for β_e for assumed values of a (see below) so that our model generates plausible values of P_{s_1} under small x, an extrapolation because our subjects had large x.

Now we predict preference for animals facing conditions like our subjects did. Because our subjects had already hoarded tens of thousands of food items, we begin by solving Eq. (5) for $x=50,000$, and we assume $a=0.001$ (note that for small values of a, V increases slowly with hoard size (Eq. 6)). These values translate into the assumption that the subjects' reproductive value was ~99% of the asymptotic value. To consider a case toward the other end of the continuum, we assume our subjects might have behaved as if their reproductive value were maximized for a very small hoard. We assume $x=10$ and $a=0.1$. From Eq. (6), we thus assume the subjects' reproductive value was ~63% of the asymptotic value. This assumption acknowledges the possibility that jays could make decisions based on number of hoards made during a short interval such as a hoarding bout (i.e., within an hour).

As shown in Fig. 1, jays should prefer the stimulus typically associated with option 1 when tested in free-choice trials. Assuming large x, choice is independent of state (Fig. 1a) because the energy gain makes an infinitesimal contribution to reproductive value. Thus, the jay should prefer the stimulus associated with the typically safer option (i.e., $P_{s_1}>0.5$). Assuming small x (Fig. 1b), the jay should also prefer this stimulus (i.e., $P_{s_1}>0.5$), but preference should depend on both the typical profitability ($\theta>0$) and safety advantages ($M>0$) of option 1. Because $\theta=0.0043$ and $M=0.94$ in our experiment, subjects should have preferred the stimulus associated with option 1.
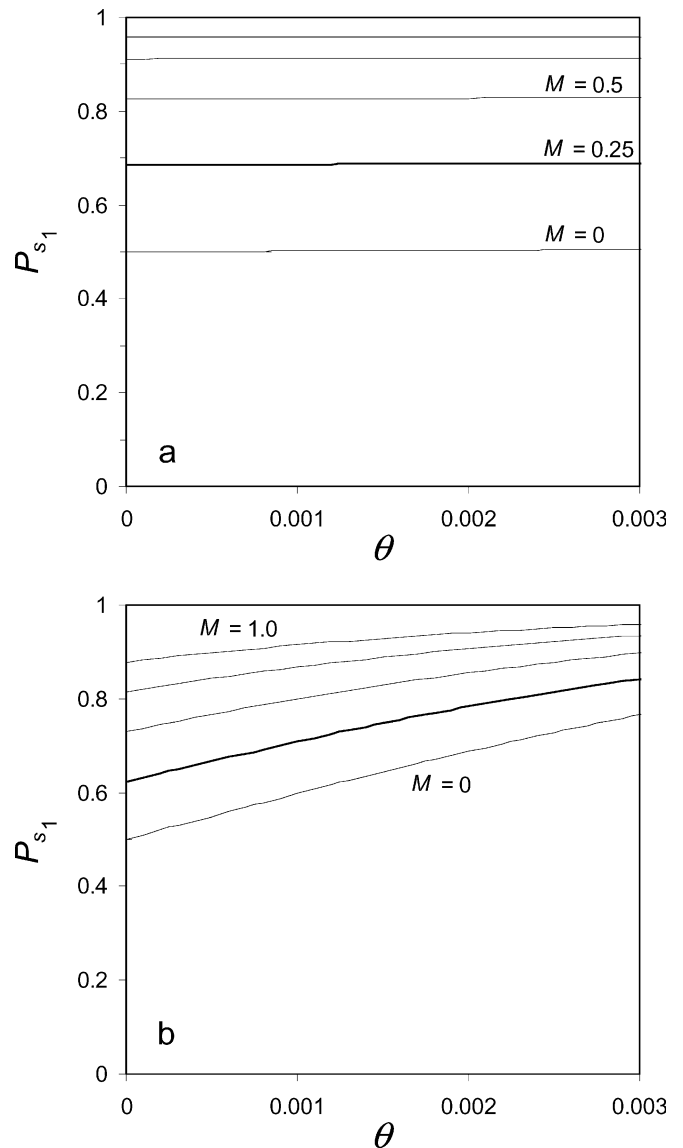

Fig. 1 Predicted preference for stimulus associated with option 1, P_{s_1}, when two options are identical at the moment of choice, as influenced by differential profitability, $\theta = e_1/h_1 - e_2/h_2$, and differential predation risk, $M=M2-M1$, under typical conditions. Predictions generated by solving Eq. (5) (for $M=0, 0.25,..., 1.0$). Preference is never predicted for stimulus associated with the typically less profitable and/or more dangerous option 2 (i.e., $0.5 \leq P_{s_1} \leq 1.0$ and hence $0 \leq P_{s_2} \leq 0.5$). Under no conditions does this model predict preference for the stimulus associated with the option typically yielding lower reproductive value. Where preference is predicted (i.e., $P_{s_1} \neq 0.5$, it is for the stimulus s_1 typically associated with higher profitability ($\theta>0$, $M \geq 0$), lower predation risk ($M>0, \theta \geq 0$) or both ($\theta>0$, $M>0$). Panels show how relative influence of θ vs M depends on state x. **a** P_{s_1} for decision-maker with high state is strongly influenced by M but virtually insensitive to θ. Assumed parameter values: $a=0.0001$, $x=50,000$, $\beta_e=1.55 \text{H} 10^7$ (calculated from Eq. (12) assuming $\theta=e_1/h_1-e_2/h_2=[(\text{item}/25\text{s})-\text{item}/28\text{s}]= 0.00429$ and $P_{s_1}^{small} = 0.99$(arbitrary)]), and $\beta_p=3.13$ (calculated from Eq. (11) assuming $P_{s_1}^{large} = 0.95$[arbitrary] and $M = .94$). **b** P_{s_1} for decision-maker with low state is strongly influenced by both M and θ. Assumed parameter values: $a=0.1$, $x=10$; other values as in (**a**)

This model can predict preference in one direction only, for the stimulus associated with the typically safer and/or more profitable option 1. It thus could have predicted the observed preference in gray jays, but cannot predict a preference for the stimulus associated with the typically more costly option 2, as observed in previous studies. Therefore, we modify key assumptions of our model to uncover a mechanism of valuation that could lead to preference in the opposite direction.

Paradoxical preference for costliness

Consider an animal choosing between j simultaneous options, where options are identical in energetic gain per unit time at the moment of choice but usually differ in acquisition cost and/or predation risk. Acquisition costs reduce the animal's state, where state is now defined to be internal energetic state rather than hoard size. Specifically, we redefine:

$$x = x_0 - x_j, \tag{10}$$

where x_0 is initial state at the moment of choice (i.e., before incurring the acquisition cost), x_j is state reduction incurred while acquiring the reward, and $x_0 - x_j$ is state at the moment of obtaining the reward. We assume that valuation of an option is impacted by the rate at which reproductive value typically increases as a function of choosing that option (Kacelnik and Marsh 2002). That is, preference for a stimulus depends on the animal's state at the moment of reward $x_0 - x_j$, not just its initial state at the moment of choice x_0. An option with heavier workload entails a larger state reduction, and so the animal may value the reward more highly because it provides a higher rate of increase in V. By choosing option j, an animal with initial state x_0 experiences an *apparent* increase in reproductive value, or utility, by net rate:

$$\dot{U}(j) = \gamma_j \left.\frac{\partial V}{\partial x}\right|_{x=x_0-x_j} - M_j V(x_0). \tag{11}$$

Energetic gain per unit time, $\gamma = \partial x / \partial t$, is the rate at which state increases as a result of choosing an option. This rate is assumed to be identical for the two options because they are economically identical at the moment of choice, so we let $\gamma_j = \gamma$ for convenience. The partial derivative is the rate at which reproductive value increases with x under typical conditions, where it is evaluated for the state at the moment of reward, $x = x_0 - x_j$. $M_j V(x_0)$ is the rate at which reproductive value decreases due to predation risk at the moment of choice (i.e., when the animal's state=x_0 and hence regardless of which option is chosen). The apparently better option in a binary-choice task maximizes Eq. (11).

Incorporating partial preferences, we assume the probability of choosing the stimulus associated with option 1, P_{s_1}, to be described by Eq. (3), where we replace scaling constants β_e and β_p with φ_e and φ_p and replace $\dot{V}$ with $\dot{U}$. Next,

we substitute the right-hand side of Eq. (11) for $\dot{U}$ and substitute e/h for γ. Rearranging yields:

$$P_{s_1} = \frac{\exp\left[\varphi_e\gamma\left(\left.\frac{\partial V}{\partial x}\right|_{x=x_0-x_1} - \left.\frac{\partial V}{\partial x}\right|_{x=x_0-x_2}\right) + \varphi_p MV(x_0)\right]}{1 + \exp\left[\varphi_e\gamma\left(\left.\frac{\partial V}{\partial x}\right|_{x=x_0-x_1} - \left.\frac{\partial V}{\partial x}\right|_{x=x_0-x_2}\right) + \varphi_p MV(x_0)\right]} \tag{12}$$

This expression predicts preference when options are locally identical but typically differ in state-reducing cost of acquisition and/or predation risk.

Equation (12) predicts preference for the stimulus associated with the typically safer option (i.e., $0.5 < P_{s_1} < 1.0$) if an individual's current state is high (i.e., if x_0 is large, $\partial V / \partial x \to 0$ and $V \to 1$, and hence $\partial P_{s_1} / \partial x = 0$) or if options are typically identical in energetic cost of acquisition (i.e., substituting zero for the quantity in rounded brackets in Eq. (12) yields $P_{s_1} = \left\{\exp\left[\varphi_p MV(x_0)\right]\right\} / \left\{1 + \exp\left[\varphi_p MV(x_0)\right]\right\}$). Under these conditions, the decision-maker should prefer the stimulus associated with the typically safer option and this preference should be independent of state reduction incurred during acquisition.

By contrast, the decision-maker should prefer the stimulus associated with the typically more energetically costly option 2 if initial state x_0 is low and options are typically identical in predation risk ($M=0$). To see this, substitute zero for M in Eq. (12). Because the partial derivative of V with respect to x (calculated at $x=x_0-x_j$) is greater for the more costly option 2, the quantity in rounded brackets is negative, and so P_{s_1} can take values between 0 and 0.5. As we show below, if state is low enough, the animal may prefer the stimulus associated with the typically more costly option, even if that option is typically more dangerous.

Here, we solve Eq. (12) to explore conditions favoring preference when options are locally identical. Fig. 2a shows predictions where initial state x_0 is high and reproductive value is maximized at large x. Under these conditions, animals should prefer the stimulus associated with the typically safer option 1 and this preference should be insensitive to differential cost of acquisition.

By contrast, Fig. 2b shows predictions for conditions meant to resemble those in the experiment of Kacelnik and Marsh (2002), where initial state x_0 is low and reproductive value is maximized at low x. Our initial model (Eq. 5) could not predict $P_{s_1} < 0.5$ and hence could not account for observed preferences for stimuli associated with higher cost, but the modified model (Eq. 12) can predict P_{s_1} across the full range, 0 to 1. The bold curve shows that animals should always prefer the stimulus associated with the typically more costly option 2 (i.e., $P_{s_1} < 0.5$ or $P_{s_2} > 0.5$) if the two options are typically identical in predation risk ($M=0$). The curves for $M=0.25$ and $M=0.5$ show that animals should sometimes prefer the stimulus associated with the typically more costly option 2, even if this option is also typically more dangerous.
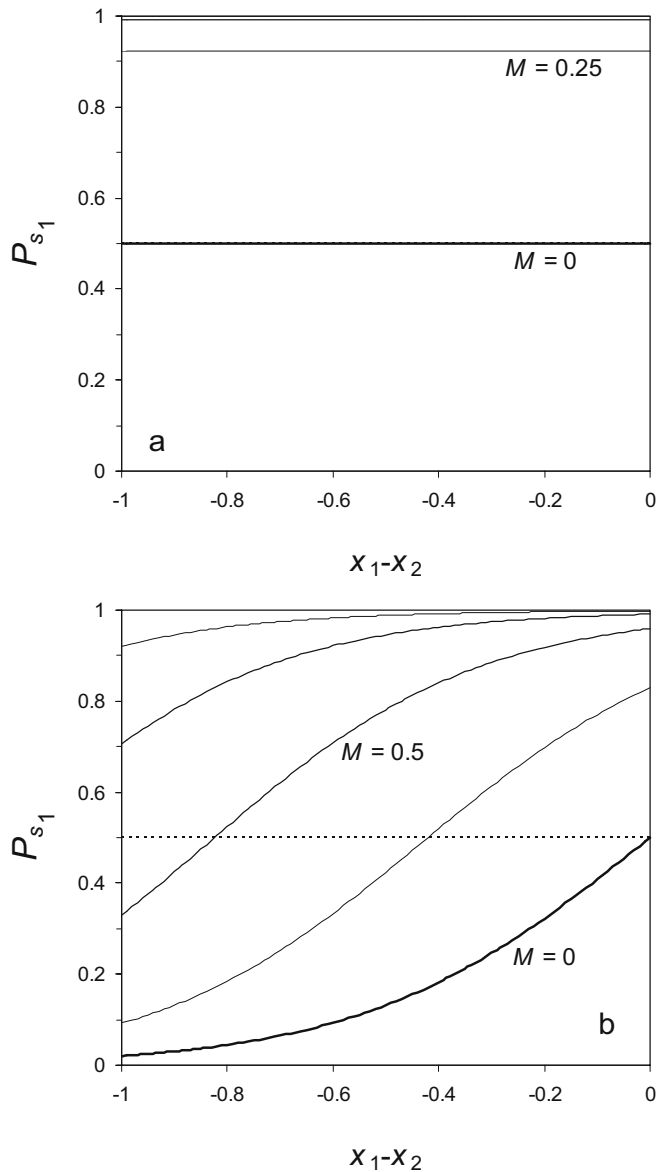
Fig. 2 Predicted preference for stimulus associated with option 1, P_{s_1}, when two options are identical at the moment of choice, as influenced by differential reduction in state from the moment of choice to the moment of reward, x_1-x_2, and differential predation risk, $M=M_2-M_1$, under typical conditions. Predictions generated by solving Eq. (12) (for $M=0, 0.25,..., 1.0$). Under some conditions, preference is predicted for stimulus associated with option 2 that typically entails a greater state-reducing acquisition cost (i.e., $P_{s_1}<0.5$). Panels show how relative influence of x_1-x_2 vs M depends on decision maker's state x_0 at the moment of choice. **a** P_{s_1} for decision-maker with high state is strongly influenced by M but virtually insensitive to x_1-x_2. Assumed parameter values: $a=0.0001$, $x_0=50,000$, $x_1=0$, $\varphi_e=100$. **b** P_{s_1} for decision-maker with low state is strongly influenced by both M and x_1-x_2. Preference for stimulus associated with typically greater state-reducing acquisition tends to increase for smaller M (i.e., P_{s_2} increases with differential acquisition cost, x_1-x_2, and decreases with differential predation risk, M). Assumed values: $a=0.1$, $x_0=10$, $x_1=0$, $\varphi_p=10$

However, preference should shift to the other stimulus if the typical difference in acquisition cost is small enough. The remaining curves show that if the typical difference

in predation risk is large enough, animals at low state should prefer the stimulus associated with the typically safer option 1. Thus, this model can predict preference for the stimulus associated with the typically safer option and preference for the stimulus associated with the typically more costly option.

Discussion

Our results constitute evidence for violation of economic rationality in hoarding gray jays (see also Waite 2001a,b; Shafir et al. 2002; cf. Schuck-Paim and Kacelnik 2002). Normative cost–benefit rules predict no preference when competing options are locally identical, yet our subjects routinely expressed a preference. Unlike subjects in previous studies (e.g., Belke 1992; Gibbon 1995; Clement et al. 2000; Kacelnik and Marsh 2002), ours tended to prefer the stimulus associated with the typically *lower*-cost option when choosing between options that were made to be identical at the moment of choice (Table 1, Fig. 1). Beyond simply asking why animals would show any preference in this context, we attempt to reconcile these conflicting findings. Why would some subjects prefer stimuli associated with high cost while others prefer stimuli associated with low cost?

Kacelnik and Marsh (2002) interpreted their subjects' preference for stimuli associated with greater effort as a form of state-dependent choice (see also Schuck-Paim et al. 2004). In their experiment, starlings were required to make either 4 or 16 flights to obtain a food reward in no-choice trials. Because rewards were identical, the increase in state (nutritional condition) should have been identical in the two kinds of trials. The fitness gain, however, should have been greater
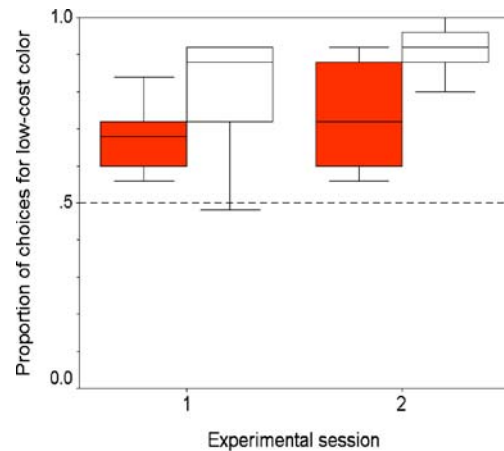

Fig. 3 Proportion of jays' choices in free-choice trials for stimulus (*color*) associated with low cost in no-choice trials. *Color of box* represents color associated with low-cost option during no-choice visits (gray box = orange stimulus; white box = white stimulus). *Thick lines* indicate median, *boxes* encompass interquartile deviation, and *whiskers* show extremes. *Pair of boxes* on left represents choice during visits 1-25 (session 1) and *pair on right* represents preference during visits 26-50 (session 2)

following 16 flights than 4 flights, provided fitness is a concave function of state. By preferring the stimulus associated with greater effort when tested in free-choice trials, the starlings preferred the stimulus associated with typically greater state reduction and hence greater fitness rebound. Their preference is paradoxical because the rewards were identical at the moment of choice. However, in nature, it should be adaptive to develop preferences for stimuli that are usually associated with greater fitness gains. Thus, the presumed mechanism of valuation may have adaptive value, although it led to a preference under experimental conditions where none was predicted by normative rules.

This form of state-dependent choice, however, cannot account for our findings because gray jays expressed the opposite preference. They preferred the stimulus associated with typically lower cost (Fig. 3). These conflicting findings reflect a key difference between the choice tasks. Our experiment differed in one important respect from that of Kacelnik and Marsh; the choice task was designed to create a cost differential that was mainly due to predation risk rather than state reduction. In no-choice trials, jays could obtain a food reward either without entering the tunnel (low cost) or by traveling (60 cm) into the tunnel (high cost). Thus, the jays expressed a preference for the stimulus associated with the typically safer option.

How do we reconcile these conflicting findings? Our models reveal how mechanisms of valuation can lead to preference between locally identical options in either direction, depending on how competing options typically differ in acquisition cost and predation risk. We assume selection favors stronger preference for stimuli associated with typically smaller fitness decrement due to predation risk or typically higher fitness enhancement due to energy gain. If an animal's state is high, the energetic consequence of choice will have a trivial impact on reproductive value (fitness), so it pays to play it safe. For conditions like those faced by our subjects, we predict a preference for the stimulus associated with the typically safer option (Fig. 1a). Conversely, if an animal's state is low, both energetic and predation-risk consequences of choice may impact fitness. For conditions like those faced by the starlings of Kacelnik and Marsh, we predict a preference for the stimulus associated with the typically more energetically costly option (Fig. 2b) because the apparent impact of a given reward on fitness is greater after paying a higher acquisition cost. Thus, our model accommodates the opposing preferences observed in gray jays and starlings. Both sets of findings appear to be by-products of an adaptive decision process, where mechanisms of valuation lead to paradoxical preferences under experimental conditions.

To conclude, gray jays persistently preferred one option to a locally identical alternative. In conflict with previous findings, jays preferred the stimulus associated with lower cost. We have argued that such preferences can be bidirectional, depending on the mechanism of valuation. Our models provide a plausible explanation for opposing preferences in starlings (Kacelnik and Marsh 2002) and pigeons (Belke 1992; Gibbon 1995; Clement et al. 2000) vs gray jays (this study). Future experiments should manipulate both workload and predation risk and should test alternative explanations for our findings. First, it is conceivable that the observed preference was a by-product of a neophobic response to atypical placement of the high-cost stimulus during free-choice trials. We could test this possibility by positioning stimuli at the same *intermediate* distance during free-choice trials. Second, it is conceivable that the observed preference was not for lower predation risk but rather for greater immediacy (Stephens and Anderson 2001). However, this possibility received no support in a recent experiment in which stimuli, during no-choice trials, were positioned at a common distance, but in tunnels of differing diameter (Waite et al., unpublished results).

Finally, future work should explore the importance of state vs predation risk in generating "irrational" choice in hoarders vs nonhoarders. Some violations of rationality in nonhoarders may be the outcome of adaptive state-dependent choice (Schuck-Paim et al. 2004), but our work suggests violations in hoarders (Waite 2001a,b; Shafir et al. 2002) may be less attributable to state dependence. We recognize, though, that internal state (e.g., lipid stores) and external state (hoarded food) are not simply substitutable (e.g., Day et al. 1999). We also recognize that hoard value may be a stochastic function of hoard size (Hitchcock and Houston 1994), not a deterministic function as we have assumed (Eq. 6). Future work could explore these complexities. In general, it will be of interest to explore whether recently reported violations of rationality (Shafir 1994; Hurly and Oseen 1999; Waite 2001a,b; Bateson 2002, 2004; Bateson et al. 2002, 2003; Shafir et al. 2002, 2003) can be interpreted as adaptive by-products of a state–predation trade-off.

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