## ORIGINAL ARTICLE

# Thomas A. Waite Intransitive preferences in hoarding gray jays (*Perisoreus canadensis*)

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Abstract Decision makers are often assumed to assign stable fitness-based values to foraging options. Under this assumption, the tendency to prefer the more valuable of two simultaneously available options should be transitive. For example, if option *a* is preferred when paired with b, and b is preferred when paired with c, then ashould be preferred when paired with c. According to the principle of strong stochastic transitivity, the preference for a over c should be at least as strong as the stronger of the other two preferences (i.e.,  $p(a,c) \ge \max[p(a,b)]$ , p(b,c)]). Gray jays (*Perisoreus canadensis*) collecting food for storage violated this principle, and failed to support even weaker forms of transitivity. All subjects preferred option a (one raisin, 28 cm into a tube) over b(two raisins, 42 cm), and b over c (three raisins, 56 cm), but none of the subjects preferred a over c. Such paradoxical preferences are often interpreted as evidence for simple heuristics rather than complex decision mechanisms. According to bounded rationality, intransitive choice is a suboptimal byproduct of heuristics that usually perform well in real-world situations. Alternatively, intransitive choice could be a byproduct of selection favoring a complex decision process involving context-dependent assessment of each the fitness-related value of each option. From this perspective, the decision maker's subjective valuation of each option is not fixed, but rather depends on the context (i.e., the specific pairing of options). In the experiment, the subjective value of option a was apparently lower in option set  $\{a,c\}$  than in  $\{a,b\}$ . A model of context-dependent choice is used to explore conditions under which adaptive choice based on a complex decision process can lead to intransitivity.

Communicated by A. Kacelnik

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# Introduction

Natural selection is often assumed to favor choice behavior that maximizes fitness. This conventional view misleadingly suggests that decision makers assign a fixed fitness-related value to each option (Houston 1997). By extension, an animal choosing among simultaneously encountered options is expected to choose the most valuable option, based on a stable preference order. These preferences are expected to be partial rather than absolute, even under the assumption that selection favors maximization of reward rate, because the choice process is inevitably subject to error (McNamara and Houston 1987; Waite and Field 2000). Even so, according to standard theories of rational choice (Tversky and Simonson 1993) and optimal foraging (Stephens and Krebs 1986), the strength of preference should be based on the true values of the simultaneously available options. If the "attractiveness" of each option is independently evaluated, preferences should be strictly transitive. For example, if option a is preferred when paired with b, and b is preferred when paired with c, then a should be preferred when paired with c. According to the principle of strong stochastic transitivity (Fishburn 1991), the preference for a over c should exceed the stronger of the two other preferences (i.e.,  $p(a,c) \ge \max[p(a,b), p(b,c)]$ ).

Despite the intuitive appeal of this framework, preferences are not always transitive (Tversky 1969). Intransitivity is a well-documented phenomenon in humans and is the focus of considerable contemporary research (e.g., Van Zandt 1996; Monsuur and Storcken 1997; Bouyssou and Vincke 1998; Fishburn and LaValle 1998; Gass 1998; Gonzalez-Pachon and Rios-Insua 1999), but it is also known to occur in nonhuman animals. For example, in a series of elegant experiments, Shafir (1994) found intransitive preferences in some honeybees choosing between artificial flowers varying in volume of nectar and length of corolla. Such paradoxical (sensu Real 1996) preferences, when they occur in humans, are usually interpreted as evidence for the use of decision-making algorithms (heuristics) that inevitably lead to cognitive illusions (Tversky 1969; Tversky and Simonson 1993; Kahneman and Tversky 1996) or usually lead to accurate choice in naturalistic situations (Gigerenzer and Goldstein 1996; Gigerenzer 2000; see also Simon 1992). Alternatively, intransitivity may arise even in a complex decision process where the true fitness-related value of an option is not fixed, but rather depends on the local context (i.e., the specific combination of simultaneously available options) (Houston 1997). According to this view, intransitive preferences are potentially adaptive adjustments to context-dependent values of options (see Discussion).

Here, I describe an experiment designed to determine whether a nonhuman vertebrate, the gray jay (*Perisoreus canadensis*), expresses intransitive foraging preferences. Jays collecting food for storage were given binary choices between options varying along two attributes: quality (size of food reward) and price (distance into a tube). According to classical theories of rational choice and optimal foraging, the subjective (perceived utility) and true (fitness-related) value of each option should be unaffected by context and so preferences should be transitive.

## Methods

#### Subjects and study area

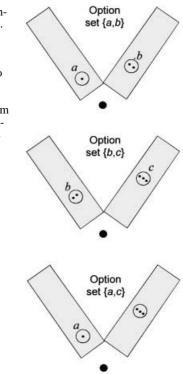
The gray jay (*P. canadensis*), a year-round resident of boreal and subalpine forests of North America (see Strickland and Ouellet 1993 for a detailed account), lives in social groups on all-purpose territories and occasionally breeds cooperatively (Waite and Strickland 1997). Outside the breeding season, the mated pair is often accompanied by a retained offspring or an immigrant evicted from the natal territory by its dominant sibling (Strickland 1991). Routinely during summer and autumn, and opportunistically during winter and spring, individual jays make hundreds of food caches per day, placing each saliva-coated bolus in a separate arboreal site (Waite and Reeve 1993, 1994). Their decisions tend to maximize hoarding rate (e.g., Waite and Ydenberg 1994a, 1994b, 1996) or minimize costly errors (Waite and Field 2000). The jays rely on these caches throughout the winter and even use them to provision nestlings and fledglings.

Twelve semi-tame, free-ranging gray jays, identifiable by unique color-band combinations, were used as subjects in the present experiment. These subjects, representing seven territorial social groups, comprised four adult females, seven adult males, and one retained juvenile male.

The experiment was conducted in Algonquin Provincial Park, Ontario, Canada (45°33' N, 78°38' W). A detailed description of the study area has been published elsewhere (Strickland 1991). The experiment was conducted between 23 October and 1 November 1997. All tests were conducted between 0750 and 1810 hours. Air temperature varied between -5 and 6°C. Light snow fell during one test; no precipitation occurred during the remaining tests.

#### Experimental procedure

The experiment was designed to measure the preference between simultaneously available paired options. Options varied along two attributes, quality (number of raisins) and price (distance into a **Fig. 1** Top view of experimental set-up for three option sets. *Dots* represent raisins placed on white plastic discs (*open circles*). Option *a*: one raisin, 28 cm into tube; option *b*: two raisins, 42 cm; option *c*: three raisins, 56 cm. *Shaded circles* represent a standard perch from which the subject could simultaneously inspect the contents of both tubes



tube). Presumably, the jays perceived greater danger (predation hazard) with greater distance into the tube. The binary-choice task (Fig. 1) measured the jays' tendency to choose one option versus a higher-quality but higher-price option, as influenced by local context (i.e., the specific pairing of simultaneously available options). To determine whether such preferences were transitive, each subject was given repeated choices between option *a* paired with *b*, *b* paired with *c*, and *a* paired with *c*.

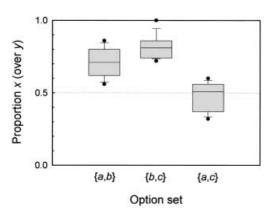
The experimental set-up consisted of two tubes, both containing food (Fig. 1). Subjects were required to hop into one or the other of these tubes during each visit to obtain the food reward (one, two, or three raisins). These 1.2-m-long tubes, made of 1-cm welded wire mesh (hardware cloth), were semi-cylindrical (radius 25 cm) and closed at one end. The open ends were situated equidistantly from a standard 25-cm-high perch. From this perch, subjects could inspect the contents of the two tubes simultaneously. Food was placed on white plastic discs (diameter 17.8 cm), positioned at specified distances into the tubes. The subject could choose between the two options immediately upon each arrival. The food was replenished (as described below) as soon as the jay collected the food and flew to hoard it in nearby trees. Detailed descriptions of hoarding behavior in this species are published elsewhere (Waite and Ydenberg 1996 and references therein).

To test a particular individual, I positioned myself near the known core of its territory and whistled to attract the jay. As soon as the jay arrived, I began a performance test in which the prospective subject was given a choice between identical options (one raisin, 28 cm into tube) during 12 consecutive visits to the set-up. To train jays to treat the task as an exclusive binary choice, I flushed any individual that attempted to enter both tubes during a given visit. No individual attempted to do so more than twice. All individuals passed the performance test, entering one of the tubes during each visit, collecting the raisin and transporting it to a nearby arboreal site for storage. Throughout this and subsequent tests, raisins were offered to all jays accompanying the subject to minimize the influence of interference competition on the subject's choice behavior. Following this test, the set-up was moved ~50 m to minimize the influence of density-dependent cache theft on the subject's choice behavior (see Waite and Ydenberg 1996 for the rationale for each of the last two details of the protocol).

Following a 5-min hiatus, the first of three successive 50-visit choice tests was conducted. Across the three tests, the subject was given all three choices:  $\{a,b\}$ ,  $\{b,c\}$ , and  $\{a,c\}$  (Fig. 1), where option *a*=one raisin at 28 cm, *b*=two raisins at 42 cm, and *c*=three raisins at 56 cm. To avoid an order effect, the order of contexts was randomly assigned without replacement for the first six subjects and this order was then repeated for the next six subjects. To avoid a side bias, the positioning of the rewards was randomized initially and then switched after each visit. After the 50th (last) visit in each of the first two tests, the subsequent test. The experiment was thus a within-subjects design in which each of 12 subjects was tested in all three contexts ( $\{a,b\}$ ,  $\{b,c\}$ ,  $\{a,c\}$ ), and each of the six possible orders was used for an equal number of subjects (2).

#### Data analysis

Analyses used SigmaStat (SPSS 1997) routines. Wilcoxon signedranks tests were used to evaluate any preference for each of the three contexts. Binomial probabilities were calculated to evaluate preferences across all subjects. Binomial probabilities were also calculated to evaluate each subject's preferences. Spearman's rank correlation was used to evaluate the degree of autocorrelation (lag=1) in each subject's 50 consecutive choices of option x versus y in each of the three contexts: {a,b}, {b,c}, and {a,c}. For each series of choices (where x=0 and y=1),  $C_{1, 2,..., 50}$ , the correlation between  $C_t$  and  $C_{t-1}$  was calculated. For any subject whose choices were autocorrelated, logistic regression was used to evaluate



**Fig. 2** Measured choice behavior in gray jays. Proportion of 50 choices of option *x* versus *y* for three option sets:  $\{a,b\}$ ,  $\{b,c\}$ , and  $\{a,c\}$ . *Horizontal lines* represent medians, *boxes* encompass the 25–75th percentiles, *whiskers* indicates the 10th and 90th percentiles, and *circles* show values falling below the 10th or above the 90th percentile

whether the subject's tendency to choose x versus y increased or decreased across the 50 consecutive choices. Bonferroni adjustments were invoked where multiple tests were performed.

### Results

Figure 2 shows that subjects tended to prefer option aover b and option b over c (Wilcoxon signed-ranks test, both W=-78.0, P<0.001), but not option a over c (W=13.0, P=0.58). In fact, both p(a,b) and p(b,c) exceeded 0.5 for all subjects (binomial Ps=0.00024). Moreover, 9 of 12 subjects showed a significant preference for aover b, and all 12 subjects showed a significant preference for b over c (nominal binomial Ps<0.016; Table 1). [Six of the 12 subjects showed a significant preference for a over b following Bonferroni adjustment (critical  $\alpha$ level=0.05/12 tests=0.004).] By contrast, while none of the subjects showed a significant preference for a over c, three subjects (GOSLROBR, WOSLBOYR, POW-LGOSR) showed a significant preference for c over a (nominal binomial Ps<0.032; Table 1). None of the 12 subjects showed a significant preference for c over a following Bonferroni adjustment.

No significant autocorrelation in the tendency to choose *x* versus *y* was detected for any of the 12 subjects in context  $\{a,b\}(-0.27 \le r_s \le 0.16$ , nominal  $Ps \ge 0.06)$  or context  $\{b,c\}(-0.23 \le r_s \le 0.27$ , nominal Ps > 0.06). Only one significant autocorrelation was found among the subjects in context  $\{a,c\}$  ( $r_s=0.51$ , Bonferroni-adjusted P<0.01; for the other 11 subjects:  $-0.16 \le r_s \le 0.26$ , Ps>0.07). Logistic regression revealed a trend in this subject's tendency to choose *a* versus *c* across the 50-visit test. The 95% confidence interval (0.04, 0.47) of the odds ratio (0.14), an estimate of the odds of choosing *a* in the next visit, did not encompass 0.5, which implies that the subject's tendency to choose *a* decreased significantly during the test.

## Discussion

According to standard theories of optimal foraging and rational choice, animals should prefer the most valuable of simultaneously encountered options, and the strength

Subject	p(a,b)	Р	p(b,c)	Р	p(a,c)	Р
GOYLOOSR	0.58	0.16	0.74	4.7×10-4	0.50	0.56
ROTLROSR	0.86	$1.0 \times 10^{-7}$	0.74	$4.7 \times 10^{-4}$	0.58	0.16
YOSLWOBR	0.82	$2.8 \times 10^{-6}$	0.92	$2.2 \times 10^{-10}$	0.56	0.24
GOSLROBR	0.76	$1.5 \times 10^{-4}$	0.80	1.1×10-5	0.36	0.03
GOOLWOSR	0.68	0.008	0.82	$2.8 \times 10^{-6}$	0.38	0.05
WOSLBOYR	0.56	0.24	0.86	$1.0 \times 10^{-7}$	0.34	0.01
POWLGOSR	0.58	0.16	0.74	4.7×10-4	0.32	0.00
GOSLTOPR	0.66	0.016	0.72	0.001	0.52	0.44
YORLWOSR	0.74	4.7×10-4	0.82	$2.8 \times 10^{-6}$	0.54	0.34
ROSLGOYR	0.78	$4.5 \times 10^{-5}$	1.00	$1.0 \times 10^{-15}$	0.48	0.44
GOSLTOYR	0.84	5.8×10-7	0.86	$1.0 \times 10^{-7}$	0.60	0.10
LOPLOOSR	0.66	0.016	0.80	$1.2 \times 10^{-5}$	0.56	0.24

**Table 1** Measured choice be-<br/>havior by gray jays in three op-<br/>tion sets

Table 2 Symbols used in model of context-dependent simultaneous choice with error (Houston 1997)

Symbol	Definition
β	Positive scaling constant (probability of choosing option with higher payoff increases as $\beta$ increases)
γ	Future (potential) rate of energetic return
$\dot{d}_i$	Energetic equivalence of distance associated with choosing option <i>i</i>
ei	Energetic value of option <i>i</i>
$\dot{h_i}$	Handling time (round-trip hoarding time) of option <i>i</i>
$\dot{H_i}$	Payoff (rate of energy return) of option <i>i</i>
$p_i$	Probability of choosing option <i>i</i>
p(x,y)	Probability of choosing option x when paired with option y
t	Time at which choice is made
Т	Time horizon over which choices can be made
τ	Delay in the hoarding cycle (preceding each choice)

of this preference should be based on stable fitness-related values. By extension, preferences should be transitive. If option a is preferred to b, and b is preferred to c, then a should be preferred to c. According to the principle of strong stochastic transitivity (SST), the preference for a over c should be at least as strong as the stronger of the other two preferences (i.e.,  $p(a,c) \ge \max[p(a,b), p(b,c)]$ . In violation of SST, every subject showed a significant preference for option aover b, and for b over c, but none of the subjects showed a preference for *a* over *c* exceeding  $\max[p(a,b)]$ , p(b,c)] (Table 1, Fig. 2). In violation of weaker forms of stochastic transitivity (Fisburn 1991), none of the subjects showed a preference for a over c exceeding  $\min[p(a,b), p(b,c)]$  or even significantly exceeding 0.5 (Table 1). This intransitivity implies that the jays' subjective valuation of options was not fixed. Instead, their perception of the value of an option apparently depended on local context (i.e., the specific pairing of simultaneously available options). In particular, the subjective value of option a was apparently lower in option set  $\{a,c\}$  than in  $\{a,b\}$ .

Such intransitive preferences, especially when they occur in humans, are often interpreted as evidence for simple heuristics rather than complex decision mechanisms. According to the heuristics-and-biases view, intransitivity is a byproduct of quick-and-dirty heuristics that not only fall short of producing rational choice in a complex environment, but lead to systematically erroneous choice (i.e., cognitive illusions: Tversky and Kahneman 1974; Tversky and Simonson 1993; Kahneman and Tversky 1996). According to the competing bounded-rationality view, intransitivity is a byproduct of fast-and-frugal heuristics that usually perform well in nature (see Gigerenzer 2000 for a review of heuristics that lead to intransitive preferences; see also Goodrich et al. 2000). In the present experiment, intransitivity could have arisen from a simple algorithm where the probability of choosing the higher-price (presumably more dangerous) option was some positive function of the difference in the size of the rewards. The jays might have preferred a over b and b over c because the additional reward to be gained was small, but not a over c because the difference in rewards was large (see also Shafir 1994). Superficially, intransitivity arose because the jays, with limited knowledge about the predation hazard of each option, preferred the safer option except when the dangerous option was much more valuable. While this view considers the ecological relevance of choice, it differs from the conventional approach in behavioral ecology because the decision maker is assumed to satisfice (using simple heuristics) rather than optimize (using a complex decision process).

The possibility that intransitivity could arise from an adaptively complex decision process should be fully explored before abandoning the optimality approach in favor of this bounded-rationality approach. Intransitive preferences can clearly arise when a decision maker has limited knowledge and uses simple heuristics, but intransitivity could also arise even if a decision maker uses a complex decision process that evaluates the fitness-related value of each alternative along every relevant attribute (e.g., size of reward, handling time, distance). In fact, Houston (1997) recently argued that adaptive choice may lead to intransitive preferences because the fitness-based value of an option depends on local context. To explore this possibility, he considered an animal faced with a repeated-choice task, where two simultaneously available options varied in energetic content  $e_i$  and handling time  $h_i$  (see Table 2 for definitions). Here, I incorporate a third attribute, the distance  $d_i$  associated with option *i*. Assuming selection favors rate-maximizing choice subject to inevitable errors in the decision-making process, the probability of choosing the option with the higher payoff  $H_i$  depends on the difference between the two payoffs (Houston 1997):

$$P_1 = \frac{\exp[\beta(H_1 - H_2)]}{1 + \exp[\beta(H_1 - H_2)]},$$
(1)

where the effect of this difference increases as the scaling constant increases. This model incorporates constraints on the decision maker's perception of the payoff associated with choosing an option by adding a random variable with a double exponential distribution to the value of each option (McNamara and Houston 1987). That is, suboptimal choice is an explicit feature of this model. **Table 3** Numerical example of<br/>predicted violation of transitivi-<br/>ty (Eqs. 2, 4) ( $\beta$ =0.1,  $\tau$ =0)

Option	Assumptions				Predictions	
	e	d	h	( <i>e</i> - <i>d</i> )/ <i>h</i>	Option set	p(x,y)
a b	$\frac{1}{2}$	$0.25 \\ 1.00$	20 35	0.038 0.029	a,b b,c	0.608 0.641
<i>c</i>	3	2.15	45	0.019	$\{a,c\}$	0.500

Because the decision maker has repeated opportunities for choice until time T, the payoff for choosing option i at time t,

$$H_i = (e_i - d_t) + \gamma (T - t - h_i), \tag{2}$$

depends on the future rate of foraging,

$$\gamma = \frac{P_{1}(e_{1} - d_{1}) + P_{2}(e_{2} - d_{2})}{P_{1}h_{1} + P_{2}h_{2} + \tau}$$

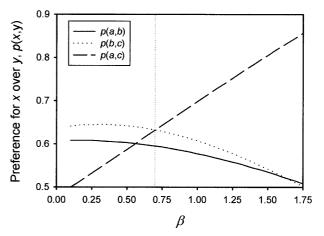
$$= \frac{P_{1}(e_{1} - d_{1}) + (1 - P_{1})(e_{2} - d_{2})}{P_{1}h_{1} + (1 - P_{1})h_{2} + \tau},$$
(3)

which in turn depends on the probability  $p_1$  of choosing the option with the higher payoff. Generating an expression for  $H_1$ – $H_2$  based on Eq. 2 and substituting this expression into Eq. 1 yields:

$$P_1 = \frac{\exp\{\beta[(e_1 - d_1) - (e_2 - d_2) - \gamma(h_1 - h_2)]\}}{1 + \exp\{\beta[(e_1 - d_1) - (e_2 - d_2) - \gamma(h_1 - h_2)]\}}.$$
 (4)

To explore whether SST holds under all conditions, Houston (1997) exploited the equivalence of SST and substitutability (Tversky and Russo 1969). Choice satisfies the condition of substitutability if two options, *a* and *b*, that are equally likely to be chosen when paired with a "standard" option, *c*, are equally attractive when paired with each other (i.e., p(a,c)=p(b,c) and p(a,b)=0.5). For several standard options, substitutability was violated (i.e., although p(a,c)=p(b,c)=0.2,  $p(a,b)\neq 0.5$ ), which implies that SST does not necessarily hold.

To explore the possibility that adaptive context-dependent choice could lead to intransitive preferences in a scenario like that faced by the jays, I chose parameter values that were rank ordered to resemble the experimental conditions (i.e.,  $e_1 < e_2 < e_3$ ,  $d_1 < d_2 < d_3$ , and  $h_1 < h_2 < h_3$ ; see Waite and Ydenberg 1996). The specific values chosen (Table 3) yielded payoffs  $[(e_i-d_i)/h_i]$  for the three options suggesting preferences consistent with SST:  $p(a,b) \ge 0.5$ ,  $p(b,c) \ge 0.5$ , and  $p(a,c) \ge \max[p(a,b), p(a,c) \ge \max[p(a,c), p(a,c) \ge \max[p(a,c), p(a,c) \ge \max[p(a,c), p(a,c) \ge \max[p(a,c), p(a,c), p(a,c) \ge \max[p(a,c), p(a,c), p(a,c) \ge \max[p(a,c), p(a,c), p(a,c), p(a,c), p(a,c) \ge \max[p(a,c), p(a,c), p(a,$ p(b,c)]. Using these values, I performed a sensitivity analysis by solving simultaneous Eqs. 3 and 4 over a range of values for  $\beta$ . Contrary to conventional theory, this analysis revealed conditions under which natural selection could favor intransitive choice. Overall, SST is expected to hold for large values of  $\beta$  (i.e., when the fitness cost of erroneous choice is most severe; Waite and Field 2000). In the example shown in Fig. 3, violation of SST is predicted for  $\beta < 0.7$ . Violation of even the weakest form of transitivity is predicted for  $\beta < 0.1$  (Table 3). Thus, while I do not claim that the intransitivity observed in the present experiment was locally adaptive,



**Fig. 3** The hypothetical effect of scaling constant (see Table 2 for definition) on the preference for option *x* when paired with *y* [i.e., p(x,y)] for three option sets:  $\{a,b\}$ ,  $\{b,c\}$ , and  $\{a,c\}$ . Choice satisfies the principle of strong stochastic transitivity (SST) if p(a,b) and  $p(b,c)\geq 0.5$  and  $p(a,c)\geq \max[p(a,b), p(b,c)]$ . In this numerical example, SST holds for  $\beta\geq 0.7$  and is violated for  $\beta<0.7$ . This threshold is indicated by the *vertical dotted line*. Corresponding to the example in Table 3, no preference for option set  $\{a,c\}$  [i.e., p(a,c)=0.5] is predicted for  $\beta=0.1$ . Assumed parameter values (units arbitrary):  $e_1=1$ ,  $e_2=2$ ,  $e_3=3$ ,  $d_1=0.25$ ,  $d_2=1.25$ ,  $d_3=2.15$ ,  $h_1=20$ ,  $h_2=35$ ,  $h_3=45$ , and  $\tau=0$ . Curves were generated by solving simultaneous Eqs. 2 and 4

this model can generate predictions qualitatively consistent with the finding that gray jays preferred option awhen paired with b, and b when paired with c, but did not prefer a when paired with c. In principle, this analysis reinforces Houston's (1997) interpretation of intransitive choice. Rather than viewing intransitivity as the byproduct of simple yet usually accurate (satisficing) algorithms (e.g., Gigerenzer and Goldstein 1996), he recognized that intransitivity can also arise in a complex decision process where cognitive constraints inevitably lead to errors and where the fitness value of an option depends on the context.

Other recent experiments have revealed related effects of context. Gray jays and honeybees (S. Shafir, T.A. Waite, B. Smith, unpublished data) responded to the introduction (removal) of an unattractive third option by increasing (decreasing) their subjective valuation of the more similar of the two original options (see also Hurly and Oseen 1999). In another experiment, gray jays that could initially obtain a large reward for the same price (distance) as a small reward devalued the large reward in subsequent choice (Waite 2001). Additional experimentation could help resolve the conflict (Gigerenzer 2000; Goodrich et al. 2000; see also Dukas 1998) between the

views that such effects are byproducts of efficient heuristics (Gigerenzer and Goldstein 1996; Gigerenzer 2000) versus complex decision mechanisms involving adaptive context-dependent valuation of options (Houston 1997).

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