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Cost can increase preference in starlings

ALEX KACELNIK & BARNABY MARSH
Behavioural Ecology Research Group, Department of Zoology, University of Oxford

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We used European starlings, *Sturnus vulgaris*, to investigate the relationship between the cost paid to obtain food rewards and preference between stimuli associated with the resulting rewards. In no-choice trials either 16 1-m flights (high effort) or four 1-m flights (low effort) gave access to differently coloured keys. Pecking at these keys resulted in identical food rewards. When subjects were given choices between the coloured keys in choice trials without having paid any effort, the majority preferred the coloured key that was paired with the higher level of work in no-choice trials. We relate our findings to results in animal behaviour, psychology and economics, and give a theoretical account that has implications for phenomena variously recognized as the 'sunk cost fallacy' (the tendency to invest more in something after much has already been invested), 'work ethics' (valuing an option more as a result of physical effort), 'cognitive dissonance' (making mental effort to overlook or re-evaluate information that does not accord with a dominant internal representation) and the 'Concorde Fallacy' (the readiness to forego more fitness for something that has been responsible for greater fitness compromise in the past).

The vast majority of normative behavioural models predict action based on the premise that behaviour should maximize some increasing function of expected benefit and decreasing function of expected cost. In the literature on foraging, for instance, benefit is often associated with energy gains and cost with the use of time or energy, leading to models that predict preferences between food sources according to the maximization of either net rate of gain ((Gain − Expenditure)/Time) or efficiency (Gain/Expenditure). In the case of our study animal, the European starling, *Sturnus vulgaris*, net rate of gain successfully predicts decisions such as patch residence time (Kacelnik 1984) or the choice between flying and walking as a foraging mode (Bautista et al. 2001). There are, however, reports of behavioural findings that cannot be accounted for easily within these schemes.

One example is provided by Clement et al. (2000), who reported that in binary choice tasks, pigeons, *Columba livia*, preferred secondary reinforcers that had previously been more expensive in terms of time and effort. This finding appears to conflict directly with conventional foraging models, which assume that foragers should prefer options that yield the greatest absolute payoff relative to time and effort. While Clement et al. (2000) remarked that their results seem related to various contrast effects, or the finding that payoff values are influenced not only by absolute effort and payoff amounts but also by relative changes in these dimensions (for an overview and discussion see Clement et al. 2000; see also Flaherty 1996), no single model neatly accommodated their results. One hypothesis Clement et al. (2000) offered is that the state of the animal at the time of reward might play a part in the development of value preferences. This idea is supported by studies of incentive learning, which have shown that the value of a reward can depend on factors such as the difference in the subject's state between the time of acquisition and the time of expressing its preference (Balleine et al. 1995; Balleine & Dickinson 1998).

Another case is the phenomenon known as 'contrafreeloading', where subjects prefer food sources that are associated with greater rather than lower work requirements (e.g. Neuringer 1969, 1970; Osbourne 1977; Inglis & Ferguson 1986; Inglis et al. 1997; Bean et al. 1999). One line of argument in the literature on contrafreeloading (e.g. Inglis & Ferguson 1986; Inglis et al. 1997; Bean et al. 1999) is that it is not work itself, but additional information of some kind, that is being valued by the subjects. In this view, more demanding food sources may be associated with more information gain and this offsets the extra cost of working when the animal is not in too great a need for food. Hence, the argument goes, owing to 'information primacy' animals should prefer food that is harder to obtain when not very hungry and the opposite as energetic state declines, but the preference for work is only a side effect of the 'hunger for information'. Tasks requiring extra work but not yielding information

Correspondence: B. Marsh, Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, U.K. (email: barnaby.marsh@zoo.ox.ac.uk).

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because of their monotonous structure should not produce the effect and there is evidence that supports this view.

The assignment of extra value to a food source simply because it scores lower in its yield per unit of effort sounds as perverse as a liking for high taxes. A similar (but not identical) perversity has been discussed in evolutionary biology in the context of the so-called 'Concorde Fallacy' (Dawkins & Carlisle 1976; Boucher 1977; Maynard Smith 1977), which in its original form described a hypothetical maladaptive decision maker that would increase the help offered to a conspecific as a function of having already assigned effort to the recipient in previous history. Such behaviour is regarded as maladaptive because sound decisions should be based on the expected values of available options at the present time, irrespective of what has been invested in them in the past. Nevertheless, there has been much debate about whether animals behave as if they commit this fallacy and, if so, what might be the evolutionary explanation for it. There are recurrent reports of animals appearing to fight harder or take greater risks in defending resources after greater investments (e.g. Robertson & Biermann 1979; Weatherhead 1979, 1982; Dawkins & Brockman 1980; Coleman et al. 1985; Curio 1987; Winkler 1990; Rytkönen et al. 1996), but in natural circumstances it is often impossible to separate past investment from future prospects, making the existence of a valuation mechanism based on past investment speculative. Even when animals are in a situation where a difference in future value can be excluded by experimental design, if the subject usually faces recurrent choices it is reasonable to postulate the existence of adaptive psychological mechanisms that would increase the subjective value of a resource when more has been invested in acquiring it. An obvious candidate to explain the existence of such mechanisms is the possibility that, under most ecologically relevant circumstances, a subject's previous investment may in fact offer good guidance for estimating expected future benefits (or a good estimate of the expected cost of acquiring the same resource in the future) and that experimental situations, by decoupling investment from payoff, simply expose this mechanism.

The tendency to assign higher value on account of past investment is equally suboptimal but empirically less controversial in economics, where such behaviour is observed regularly in consumers and investors and is referred to as the 'sunk cost effect' (Thaler 1980). A typical instance of sunk cost behaviour is provided by an experiment by Arkes & Blumer (1985), who randomly gave discounts to students buying season tickets to the theatre. Students who received no discount attended the most plays, followed by those who received small discounts. Students given the largest discounts missed the greatest number of plays. In this experiment and others, individuals behaved as if something was more valuable if more had been invested to acquire it. Thaler (2000) accounted for sunk cost effects in terms of mental accounting, while making the implicit assumption that people expect to get more out of something as they invest more in it (for examples and discussion see Thaler 1980; Garland 1990; Sutherland 1992). However, the tendency to value something more on the basis of cost also seems to extend beyond actual investment to more abstract notions of what an item or goal would ordinarily cost. For instance, in one study that systematically manipulated the prices of otherwise equal textbooks, students rated textbooks with higher prices as being more desirable and more interesting (Piehl 1977).

Valuing something more on the basis of investment has also been reported in experimental psychology contexts, although different explanatory frameworks are used. For instance, working hard for something that turns out to have little value is said to cause unpleasant cognitive dissonance, resulting in mental effort to eliminate discomfort, either by changing the way the outcome is framed or by altering beliefs (Festinger 1957; Elliot & Devine 1994). Several studies that have invoked the reduction of cognitive dissonance as a causal factor in behaviour are of interest here; for example, Aronson (1961) found that human subjects reported that stimuli associated with specific rewards (colours, in this case) seemed more intense when a task was difficult, suggesting that increased effort was associated with an increase in the salience of associated stimuli. Similarly, increased task difficulty can result in subjects rating the task itself as more interesting, meaningful and valuable (e.g. Aronson & Mills 1959; Gerard & Mathewson 1966; Rosenfeld et al. 1984). Despite these findings, cognitive dissonance as a theoretical framework has several major limitations. For instance, it is well known that information not fitting expectations and events with small probabilities are not overlooked or disregarded, as would be predicted by cognitive dissonance theory but, in contrast, are overweighted (see Allais 1953; Kahneman & Tversky 1979).

We explored these issues further in subjects that are not suitable for explanatory frameworks based on assuming that individual preferences are aimed at maintaining an internal image of consistency or self-justification of previous actions. Our specific interest was in determining whether costs have a way of systematically 'colouring' the subjective value of behavioural outcomes and our more general interest was in integrating the discussion of related phenomena in different literatures, both nonhuman and human. We did this by training starlings to obtain two otherwise identical food rewards that were associated with differently coloured lights after different work demands, and then testing whether they showed a preference between the coloured lights.

METHODS

Subjects and Apparatus

We used 12 wild-caught adult European starlings (six males, six females) caught with a funnel trap, under licence from English Nature in Oxfordshire, U.K. Throughout the experiment the birds were housed in individual flight cages measuring 120 × 50 cm in area and 53 cm high, stacked in groups of three in rooms maintained at 18 ± 3°C. Automatic timers maintained laboratory lighting on a 14:10 h light:dark cycle with gradual transition periods at 0700 hours and 2100 hours, respectively. Each cage was fitted with an operant panel which had two circular response keys (3 cm diameter) and a centrally mounted food hopper (4 × 3.5 cm). The response keys were opaque and could be transilluminated by orange or white lamps. There were two perches, at the far ends of each cage, which were fixed to switches, enabling perch use to be monitored by computer, and two coloured lamps at each end of the cage, near each perch ('perch lamps'). Perch lamps were red and green, with each colour later paired with a given response key of a different colour (e.g. orange or white). Specific colour-pairings were counterbalanced across subjects to control for possible colour preferences. Experimental trials were governed by an Acorn A5000 microcomputer running Arachnid experimental control language (Paul Fray Ltd., Cambridge, U.K.). Food rewards were fixed at two units of turkey starter crumbs (0.011 ± 0.001 g per unit) delivered at a rate of one unit/s by automatic pellet dispensers (Campden Instruments, Leicester, U.K.) situated above the cages.

We pretrained birds using an operant schedule that rewarded pecks to lit pecking keys. Later, pecking keys were illuminated only after subjects flew between perches several times in a trial, guided by perch lamps. When several flights were required for the pecking keys to be lit, for each individual flight a perch lamp was lit at either end of the cage and automatically switched off when the bird occupied the perch nearest to the lamp. This resulted in a lamp of the same colour being lit at the opposite end of the cage, a process that continued until a predetermined number of flights between perches was satisfied. The number of flights required was gradually increased until the birds would fly 10 times to activate the response key. The colours of perch lamps and keys were balanced between treatments and selected randomly across individuals. Pretraining lasted 7 days. During pretraining and experimental trials birds were given access to free food for 1 h at the beginning and at the end of each day. We cleaned the cages each morning before experimental trials began, to remove any spilled food. Externally mounted water flasks supplied fresh drinking water at all times. We weighed all birds periodically to ensure that body mass was relatively stable throughout and none of the birds evidenced signs of ill health during their period of captivity. After ca. 18 months in captivity participating in this and similar experiments they were kept in an outside aviary for a week and released near the place of capture in midsummer.

Experimental Design

The schedule consisted of a series of trials arranged in sets. Each set consisted of five 'work' trials followed by one 'free choice' trial. In work trials subjects needed to fly between the travel perches at the far ends of the cage either four or 16 times (we label these Easy or Hard trials, respectively) to illuminate a corresponding coloured pecking key on the operant panel. A single peck to the key extinguished the lamp and released the food reward. Both trials were presented in a random sequence and food deliveries were followed by an intertrial interval (ITI) of 45 s. In the free choice trials both coloured keys on the operant panel were lit immediately after the ITI (that is, there was no flight requirement). Pecking either key extinguished both keys and released the reward. This was to test which coloured key the birds preferred when given a cost-free choice. There were four 2-h sessions throughout the day, beginning 2 h after lights on. As session length was determined by duration, the number of trials completed per session was variable. Each session was separated by 1 h of rest, when food was not available. Experimental trials were given for 15 consecutive days.

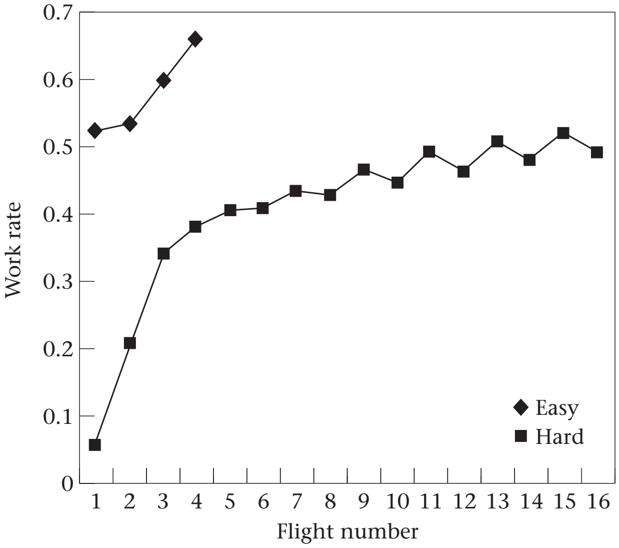

Figure 1. Work rate (1/interflight interval) for consecutive flights separated by trial type. Work rate for each flight number was computed as the between-subject mean of within-subject medians. In the section of the trials that can be compared between trial types (up to the fourth flight) all birds worked faster in Easy (four-flight) trials than in Hard (16-flight) trials.

RESULTS

Trial Type Discrimination

We first examined flight rate data from work trials for evidence that birds differentiated between Easy and Hard trials using perch-lamp colour. There was a significant effect of trial type on both median latency to start (Mann–Whitney *U* test: $U=79.0$, $N_1=N_2=6$, $P<0.001$) and median flight rate for the first four flights (Wilcoxon signed-ranks test: $T=78$, $N=12$, $P=0.0004$), meaning that the birds discriminated between the two types of trials on the basis of lamp colour. For the first four flights, all 12 birds worked faster in Easy trials than in Hard trials (binomial test on flight rates: $P<0.001$; Fig. 1).

Choice Preferences

We tallied pecking key data from free choice trials for each bird. Because sample sizes varied between

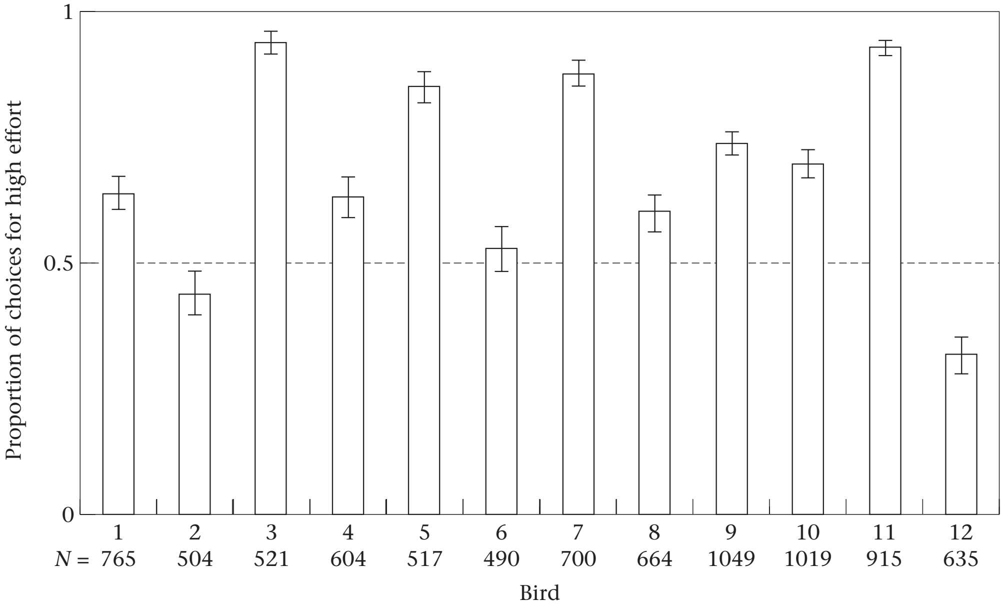

Figure 2. Proportion (±95% confidence intervals) of choices for the outcome associated with greater cost for all 12 starlings.

individuals ($\bar{X} \pm \mathrm{SD}=699 \pm 199$, range 490–1049), we converted the total number of pecks to either key type into proportions for each bird (sample sizes and resulting proportions are given in Fig. 2). Ten out of 12 birds preferred the key normally associated with Hard trials (binomial test: $N=12$, $P=0.016$). There was no effect of colour side (Mann–Whitney U test: $U=42.0$, $N_1=N_2=6$, $P=0.69$).

Work Trial After-effects

Because there were five work trials before each free choice trial, and since work trial type was binary and selected randomly, there were 32 possible sequences of work trial types before each free choice. We tested for effects of preceding sequences of work trials on preference. There was no effect of the last work trial type on subsequent choice (Wilcoxon signed-ranks test: $T=46$, $N=12$, $P=0.62$). We also pooled and compared between runs in which Easy and Hard trials had randomly repeated two, three or four consecutive times immediately before a free choice trial. Even in the most extreme case, when comparing choices after four consecutive Easy trials versus choices after four consecutive Hard trials, there was no evidence of an effect of trial type run on preference (Wilcoxon signed-ranks test: $T=43$, $N=12$, $P=0.78$).

DISCUSSION

Our results suggest that increased cost enhances the value starlings attribute to a secondary reinforcer. Why should this be, and how does this relate to standard foraging results? One possible line of analysis arises from both utility and fitness perspectives: what is important is not the physical value of the outcome of an action, but how the outcome modifies the subject's state in some relevant dimension, such as the consumption function in economic contexts and the energetic state in foraging scenarios. We refer to either subjective utility or fitness as 'value' in the discussion that follows, because our argument could be applied to either. It is possible that the reinforcing properties of an outcome are dependent on the state of the animal at the time that the outcome is realized, and that a food reward after a Hard trial is more valuable than its same-sized counterpart after an Easy trial because it is normally associated with a greater change in state. This idea is developed graphically in Fig. 3.

Let us assume that the subject initiates trials at a given energetic state, and that because of the cost of work, energetic reserves decline linearly with the number of flights. When a work requirement is completed and the reward is consumed, the magnitude of the change in state is a function of the physical properties of the outcome and it is hence independent of the amount of work and hence the state at the time of the reward (see Fig. 3b). We can further assume, as it is usually the case, that it is not the change in state but the change in fitness or utility that should affect choice, and that the utility or fitness change caused by an improvement in state is a declining function of initial state. This was made clear by Bernoulli (1738) who wrote that 'a gain of one thousand ducats is more significant to a pauper than to a rich man though both gain the same amount' and that the 'determination of the value of an item must not be based on its price, but rather on the utility it yields'. The theoretical equivalent of utility for biologists is of course fitness, but otherwise Bernoulli was anticipating the emergence of state dependency in the analysis of decision making. To indicate the role of fitness or utility, we add Fig. 3a, which has its abscissa drawn vertically to the right of the plot (this way of plotting is to emphasize that that the independent variable in Fig. 3a is the dependent variable in Fig. 3b)

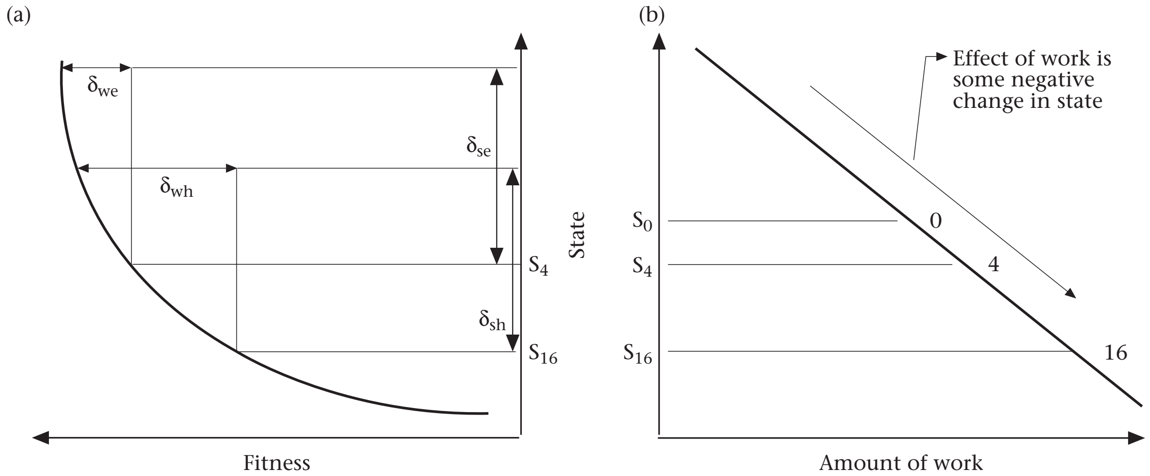

Figure 3. A graphical model of state dependency in value assignment. Figure 3b shows some dimension of state (it is easiest to think in terms of energy reserves) that drops linearly with amount of work (indicated by the numbers of flights 0, 4 and 16 along the negatively sloped straight line). All trials are assumed to start at the same initial state S_o, hence leading to lower states at the end of trials requiring high effort (S_{16} for 16 flights) than in those requiring low effort (S_4 for four flights). Outcome magnitude is independent of trial type and thus it produces the same change in state ($\delta_{sh}=\delta_{se}$). Figure 3a shows fitness (or some other positively valued dimension) as a concave function of state, the latter plotted along the vertical axis on the right). Although equal in magnitude, the improvement in fitness caused by the outcome is greater for subjects in the poorer state resulting from high-effort trials ($\delta_{wh}>\delta_{we}$). If the mechanism for value assignment depends on fitness gain and not on state gain or on final state, the outcome of Hard trials (16 flights) and any stimulus associated with it would acquire greater value than those of Easy trials (four flights).

and shows a concave function relating utility (or fitness) to state. Linking the two plots we can see that the expected improvement in value resulting from an identical outcome after a small work cost is less than after a larger one. If the subject attributes value to stimuli associated with each outcome on the basis of the change in utility or fitness and not on the basis of the magnitude of the change in state or the final state achieved, one might expect the development of preference for the more costly outcome. In nature this mechanism should lead subjects to prefer actions that yield a greater experience of state improvement, and thus the mechanism would be functional provided that the cost is paid before the choice, so that the subject is not choosing a greater cost but choosing the outcome of a greater cost.

Although this argument offers a qualitative account of our results and hence is worth considering, it cannot be the whole story, because the model predicts an accumulated effect of runs of trials, and our analysis of sequences yielded no support for this. If this negative result is included, our argument would need to consider that the 'state' in Fig. 3b is reset every trial; this could not be energetic reserves but it may be some cognitive measure of effort for a particular reward. We still believe that such a mechanism would be evolutionarily stable when competing with other putative value assignment mechanisms under most natural ecological situations, but further theoretical work needs to be done to explore this matter.

Another line of argument that deserves to be discussed, because it is in line with several accounts of contrafreeloading (Inglis & Ferguson 1986; Inglis et al. 1997; Bean et al. 1999), is that the option that is associated with more work is preferred because it is perceived as yielding more information, and that such information has a value other than that conferred by the immediate reward. While it is impossible to reject this argument in general because in nature heavier loads may be associated with either greater or smaller information gains, nothing in our results supports this view. In our set-up, both work trial types used the same foraging process (flying between perches), and it seems reasonable to expect that the same type of information (if any) would have been gathered in each trial type. Latency to start and work rate comparisons between trial types did not suggest that Hard trials were being valued more, but only that the outcomes associated with these trial types were valued differently. We have no reason to assume that the birds would have chosen harder work, and our previous experience in related experimental situations makes us expect the opposite. Even in the present experiment, if it is assumed that work rate and latency to start flying relate to motivation, the opposite is observed: birds paused for longer before starting long flights.

A final point, which is a more anthropomorphic presentation of the idea discussed in our graphical model, is that the tendency of an individual to value more highly something for which it has worked harder may be a by-product of the ways that representational systems work. Although this is a speculative argument, it is possible that a prolonged representation of a specific goal during work may lead to a higher build-up of tension or expectancy that, when released by experiencing the outcome, gives higher satisfaction. If so, this might play a part in reward assessment. In other words, effort may increase the salience of a focal point of effort (e.g. Aronson 1961), implicitly serving to enhance the valuation of the outcome itself, with implications both at the time of reward and in how the value of the reward is represented in memory. Such mechanisms could be reflected in terms of a general evaluation bias; namely, that as more is invested in a goal that is desirable, the more it is valued.

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