Rational Choice, Context Dependence, and the Value of Information in European Starlings (*Sturnus vulgaris*)

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Rational Choice, Context Dependence, and the Value of Information in European Starlings (*Sturnus vulgaris*)

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Both human and nonhuman decision-makers can deviate from optimal choice by making context-dependent choices. Because ignoring context information can be beneficial, this is called a "less-is-more effect." The fact that organisms are so sensitive to the context is thus paradoxical and calls for the inclusion of an ecological perspective. In an experiment with starlings, adding cues that identified the context impaired performance in simultaneous prey choices but improved it in sequential prey encounters, in which subjects could reject opportunities in order to search instead in the background. Because sequential prey encounters are likely to be more frequent in nature, storing and using contextual information appears to be ecologically rational on balance by conditioning acceptance of each opportunity to the relative richness of the background, even if this causes context-dependent suboptimal preferences in (less-frequent) simultaneous choices. In ecologically relevant scenarios, more information seems to be more.

Acquiring information involves time and energy (*1*–*3*). It follows that information-acquisition mechanisms should evolve if these costs are, on average, offset by the benefits of using knowledge to modify and improve decisions in the animal's natural environment. However, in some situations decision rules that disregard available knowledge outperform alternatives that use it—an informational "less-is-more effect" (*4*). The frequency and importance of such paradoxes in natural scenarios is not known, but they do occur in both humans and nonhumans performing experimental tasks (*5*–*15*) and can be related to well-known breaches of economic rationality. Some examples include sunk costs, state-dependent learning, and context-dependent utility. The "sunk cost fallacy" is committed when knowledge of irrecoverable, retrospective costs increases preference for alternatives known to have had greater cost, distorting cost-free choices (*5*–*8*). "State-dependent valuation learning" occurs because items obtained when in greater need yield larger benefits, so that memory for accrued benefits hinders simultaneous choices when the subject's state is identical for all options (*9*–*11*). Last, "context-dependent utility" results from the fact that perceived utility depends on background opportunities; thus, memory for context has the same hindering potential as state-dependent valuation learning, by enhancing preference for options associated with poorer contexts (*12*–*15*).

We examined the impact of contextual information on choice using a laboratory representation of foraging decision-making by European starlings (*Sturnus vulgaris*). Starlings' main foraging technique is to walk in short grass areas, briefly stopping to probe the ground searching for grubs, and then restarting their walking to cover new ground. Geographically or temporally identifiable foraging sites can be thought of as contexts that may contain a different assortment of prey of diverse quality. In a given site, upon detection of clues indicating the possible presence of a prey starlings either dig deeper to pursue the opportunity or walk on to continue searching. This involves a sequential decision in which the relative advantage of rejecting an opportunity to keep walking depends on information of both the attributes associated with each opportunity (prey species, capture time, capture probability) and the properties of the context (prey type distribution, intercapture intervals). Occasionally, a bird may simultaneously observe signs for two potential prey types and thus face a simultaneous choice. Generally, in these cases the optimal choice depends on the attributes of the prey types, regardless of the context. Thus, contextual information is irrelevant and sometimes can lead to losses. For example, if each of the items in a choice set is associated to

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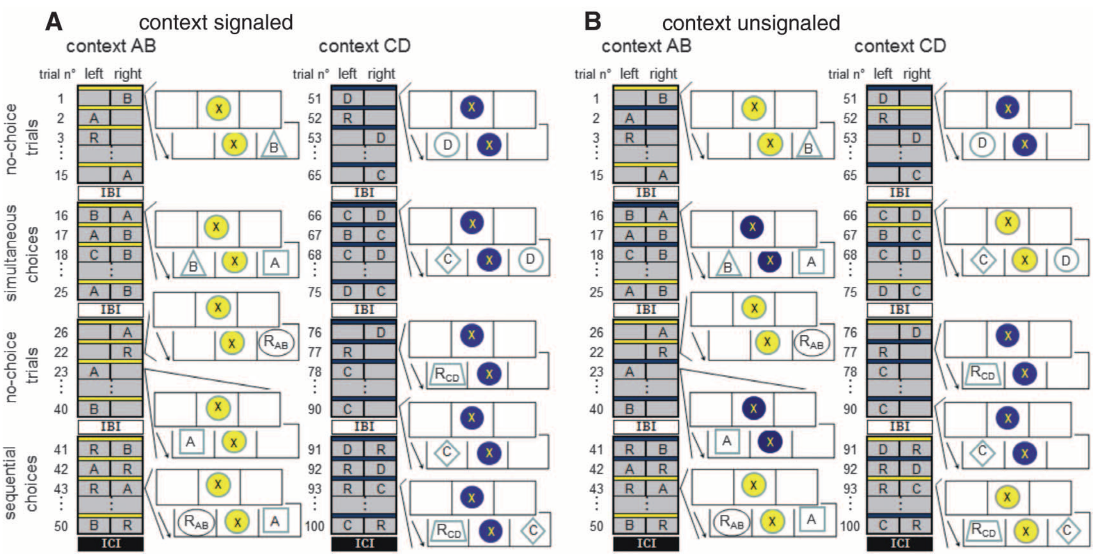


Fig. 1. Schematic of the sequence of trials in a session in which the context was (**A**) signaled or (**B**) unsignaled by the color of the trial-initiating light (*x*). On the right of each of the main columns, there are amplified representations of exemplar trials. Trials started with the *x*-light flashing. A peck to *x* led to either a no-choice trial or a choice (either simultaneous or sequential) after a 2-s random interval (β in Eqs. 1 and 2). Pecking options A_3, B_8, C_{13}, and D_{35} yielded two food pellets after the delays indicated in the suffixes (in seconds). Pecking R_{AB} or R_{CD} caused the next trial to start immediately, hence choosing the R-option served to reject the food option available on that trial. Sessions consisted of two consecutive contexts (AB and CD), each comprising blocks of no-choice, simultaneous-choice, and sequential-choice trials. A simultaneous choice trial in context AB consisted of B_8 paired against A_3 (8 out of 10 choices) or against C_{13} (2 out of 10 choices), and in context CD of C_{13} paired against D_{35} (8 out of 10 choices) or B_8 (2 out of 10 choices). A sequential choice trial in context AB consisted of either A_3 or B_8 paired against R_{AB}, and in context CD of either C_{13} or D_{35} paired against R_{CD}. As soon as subjects pecked at an option in a choice, the other one was turned off and disabled for that trial. IBI, inter-block interval (~10 min long); ICI, inter-context interval (45 min long) (*20*).

the memory for a different background, then using background-relative information in a simultaneous choice may lead to preference for the worse item. Experimental animals are known to fall for this (*12*, *14*, *15*). Sequential encounters are different. According to rate-maximizing models in optimal foraging theory (OFT) [and profit maximization in microeconomics (*16*)], optimal sequential decisions depend on the attributes of the present opportunity and its background. To maximize foraging rate of gain, an individual should pursue each opportunity if doing so confers a higher expected outcome than foraging in the background. For this reason, far from being a potentially confusing factor, in sequential encounters contextual information is at the core of optimal decision-making. The lost-opportunity rationale is the basis of the two main paradigms in OFT, the marginal value theorem (*17*) and the diet choice model (*18*, *19*).

The fundamental difference in the role of contextual information between sequential encounters (in which it is crucial) and simultaneous encounters (in which it is irrelevant or harmful) gives us an opportunity to investigate the apparent paradox of context-dependent decision-making, in which agents gather contextual information but can experience losses by using it. We show that providing more contextual information leads to stronger context-dependent valuation of prey types, helping decision-makers (DMs) in sequential foraging but hindering them in simultaneous prey choices.

Eight European starlings made both sequential and simultaneous decisions while we manipulated the availability of contextual information. The basic procedure was as follows: Four arbitrary stimuli were consistently paired with specific time intervals between the animal's choice and food delivery (an analog of the pursuit time for each potential prey item). They were arranged in two pairs. The objective profitabilities of each of them ranked as follows: $A_3 > B_8 > C_{13} > D_{35}$, with the suffixes indicating the delays (seconds) in each option (Fig. 1). Because all options provided the same amount of food, profitability comparisons are based on immediacy, the reciprocal of the delay between responding and food delivery. The two pairs appeared in two temporal contexts, hereafter referred to as "contexts" AB and CD (Fig. 1). For options B_8 and C_{13}, this arrangement causes the ranking of their objective profitabilities ($B_8 > C_{13}$) to be the opposite of the memory for their respective within-context ranking ($B_8 < A_3$, $C_{13} > D_{35}$). Thus, any bias toward favoring C_{13} over B_8 reflects the influence of contextual information. We manipulated the amount of contextual information in two conditions: In condition "context signaled," the color of the trial-initiating light signaled whether the present time block (context) was AB or CD. In condition "context unsignaled," this light was uncorrelated with context (Fig. 1). We examined sequential and simultaneous choices in each context. See further details in the caption of Fig. 1 (*20*).

Figure 2A shows that varying the amount of contextual information affected subjects' preference in simultaneous B_8-versus-C_{13} choices. Starlings preferred B_8 over C_{13} (the rate-maximizing choice) when context was unsignaled (*t* test against indifference: $t_7 = 3.84$, $P < 0.004$) but not when context was signaled ($t_7 = 0.82$, $P = 0.22$). A Wilcoxon matched pairs test showed a significant effect of context signaling on the proportion of choices for B_8 over C_{13} ($n = 8$ starlings, $z = 2.24$, $P = 0.025$), but neither the context in which preference was measured (whether AB or CD) nor its interaction with condition were significant [analysis of variance (ANOVA), condition: $F_{1,7} = 5.67$, $P = 0.049$; context: $F_{1,7} = 2.36$, $P = 0.17$; and condition *x* context interaction: $F_{1,7} < 1$, $P = 0.87$), proving that the effects were mediated by contextual memory and not by context at the time of choice [supporting online material (SOM) text].

We discuss sequential decision-making following Charnov's diet choice model (*18*). We assume that a forager encounters food options on average every β seconds of searching and can meet either of two option types, *X* and *Y*, with probabilities p_X and $1 - p_X$, respectively. If attacked, option *X* delivers α_X food units after δ_X seconds, whereas option *Y* yields α_Y after δ_Y seconds. Arbitrarily, we set option *X* as having greater profitability, defined as the ratio α/δ. Equations 1 and 2 present the rate of intake of an ideal forager that is either a generalist (accepts all options; Eq. 1) or a specialist [only takes the option with the highest payoff in each context, rejecting the lower-profitability option upon encounter (we assume that identifying, handling, and if appropriate, rejecting items takes no time at all); Eq. 2]. To identify which of these is the rate-maximizing strategy, we plugged the experimental parameters into Eqs. 1 and 2 and compared the resulting rates (SOM text).

$$\text{Generalist rate} = \frac{p_X\alpha_X + (1-p_X)\alpha_Y}{p_X\delta_X + (1-p_X)\delta_Y + \beta} \quad (1)$$

$$\text{Specialist rate} = \frac{p_X\alpha_X}{p_X\delta_X + \beta} \quad (2)$$

The comparison shows that a specialist that took only the better option in each context (accepted A_3 and C_{13} but rejected B_8 and D_{35}) would obtain a mean rate of intake 17% higher than would a generalist that consumed all options (averaging across contexts). Intuitively, this happens because the specialist uses the time that the generalist dedicates to exploit poorer options to search for the most profitable alternatives in the context. In terms of our experimental situation, optimal (rate-maximizing) sequential choices consist of always accepting option A_3 and rejecting B_8 in context AB (choose R_{AB} over B_8) and always accepting option C_{13} and rejecting D_{35} (choose R_{CD} over D_{35}) in context CD (Fig. 1).

In contrast with the results in simultaneous choices, observed preferences in sequential choices came closer to the predictions of the rate-maximizing model just described when more contextual information was available: Signaling the context increased the proportion of choices of

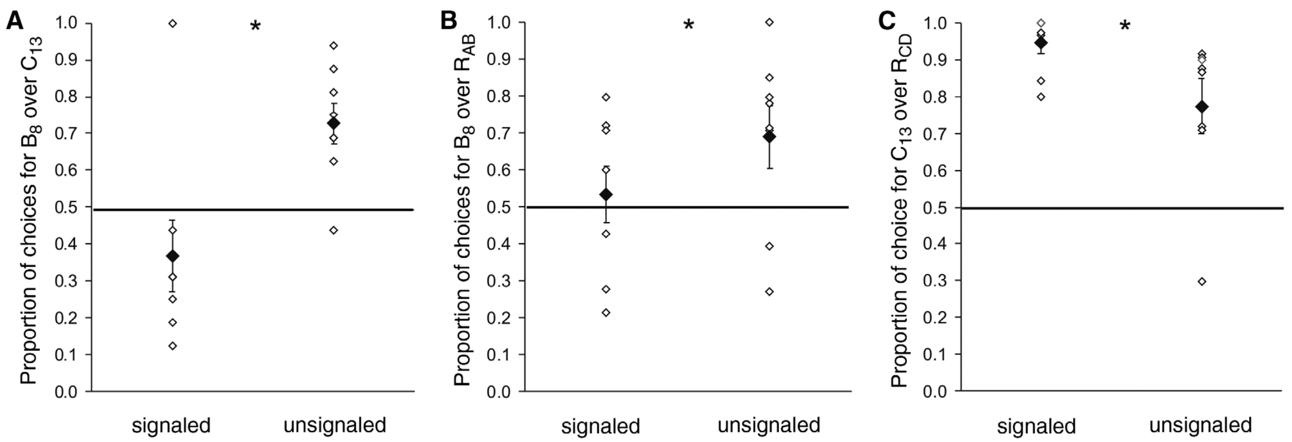
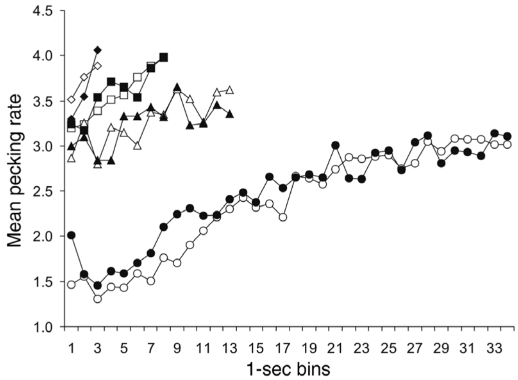


Fig. 2. Results of (**A**) simultaneous choices for B_8 over C_{13} and (**B**) sequential choices for B_8 (over R_{AB}) and for (**C**) C_{13} (over R_{CD}). Solid diamonds indicate the mean (±1 SEM). Empty diamonds indicate individual subjects. Asterisks indicate significant statistical differences between conditions.

Fig. 3. Subjects reward expectation as a function of delay, expressed as mean pecks per second in no-choice trials (open symbols, context signaled; solid symbols, context unsignaled; *n* = 8 starlings) for options A_3 (◆,◇), B_8 (■,□), C_{13} (▲,△), and D_{35} (●,○).



R_{AB} over B_8 and of C_{13} over R_{CD}. (Wilcoxon matched pairs tests of the proportion of choice with condition as a factor; *n* = 8 starlings; R_{AB} over B_8, $z = 1.96$, $P = 0.049$; C_{13} over R_{CD}, $z = 2.38$, $P = 0.017$) (Fig. 2, B and C, and SOM text).

Context effects could be mediated either by context dependence for the memory of the options' utility or for the memory of the options' physical attributes (*15*). These possibilities can be differentiated when, as here, options only differ in delay to outcome because there is an independent measure of attribute knowledge. Key pecking during options' delay to food indicates the subjects' expected time of reward (*21*, *22*). Options B_8 and C_{13} were the alternatives with the most similar profitabilities, and choices involving these options were the most affected by manipulation of contextual information. We were particularly interested in testing first, whether subjects discriminated between them, and second, whether contextual information influenced memory of reward immediacy. The answers were yes and no, respectively (Fig. 3). Pecking patterns during the delay to food prove that they discriminated between B_8 and C_{13} and knew that B_8 involved a shorter delay. This can be inferred from the higher pecking rate toward B_8 than C_{13} during the initial 8 s of responding to each stimulus (ANOVA, $F_{1,7} = 15.12$, $P = 0.006$); after that, B_8 delivered its food reward and was turned off (Fig. 3). Also, timing discrimination was not affected by the differential amount of contextual information (ANOVA, condition and option *x* condition interaction, both *F*s < 1, $P = 0.98$, and $P = 0.90$, respectively) (Fig. 3), implying that the effect of contextual information was not mediated by distortions of memory for physical attributes of the alternatives.

In the wild, memory for contextual information may be highly adaptive because it enhances sensitivity to background opportunities. For starlings in their typical foraging settings, simultaneous choices are rare, and the occasional loss caused by context influence in such cases is likely to be overridden by the benefit they confer in sequential decisions. From a reverse engineering perspective, the widespread finding of context dependence across many species supports the inference that sequential decision-making has probably been a strong influence in the evolution of valuation and choice mechanisms across a majority of taxa. Thus, although the costs that these mechanisms cause in controlled experiments seem highly relevant to modern-day shopping decisions (*13*, *23*), they are likely to have been less important in nature (*24*, *25*). So far, however, it has not been possible to quantify the relative importance of different kinds of decisions in the ecological circumstances of any species. In conclusion, the advantageous influence of context dependence in sequential choices may be relevant for a variety of decision issues in which the relative value of incentives has been highlighted, from the study of heuristics and biases in animal (*7*–*12*, *14*, *15*) and human (*4*, *13*, *23*) decision-making to research on incentive relativity in behavior (*26*) and brain functioning (*27*).

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Supporting Online Material

www.sciencemag.org/cgi/content/full/334/6058/1000/DC1
Materials and Methods
SOM Text
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