
Experimental studies in simple choice behaviour

TIAGO MONTEIRO

Pembroke College and Department of Zoology

University of Oxford



Thesis submitted for the degree of Doctor of Philosophy

Trinity Term 2012

EXPERIMENTAL STUDIES IN SIMPLE CHOICE BEHAVIOUR

Tiago Monteiro, Pembroke College and Department of Zoology

Thesis submitted for the Degree of Doctor of Philosophy, Trinity Term, 2012

ABSTRACT

This thesis addresses decision mechanisms in foraging situations, using laboratory experiments with European starlings (*Sturnus vulgaris*). Building on previous work from the Behavioural Ecology Research Group, I chose the Sequential Choice Model (SCM; reviewed in Kacelnik et al., 2011 – *Appendix 1*) as a starting point, and tested its premises and predictions generalising it to different experimental protocols. Classical decision models do not relate choice preferences to behaviour towards isolated options, and assume that choices involve time-consuming evaluations of all alternatives. However, previous work found that starlings' responses to isolated options predict preference in choices, and that response times to single-option encounters are not reliably longer than response times in choices. Since, in the wild, options are normally encountered sequentially, dealing with isolated options can be considered of greater biological, and possibly psychological, significance than simultaneous decisions. Following this rationale, the SCM postulates that when multiple simultaneous stimuli are met they are processed in parallel, each competing against the memory of background opportunities, rather than comparing present options to each other.

At the time of launching this research, these ideas had only been applied to protocols involving just two deterministic alternatives and offering no chance to explore the influence of learning history (i.e., how animals learn to choose; see *Chapter 4*). To increase their relevance and offer more rigorous tests, I generalised them to situations with multiple (see *Chapters 2, 4* and *5*), and in some cases probabilistic alternatives (see *Chapter 3*), controlling the learning regime. I combined these extensions with tests of economic rationality (see *Chapter 6*), a concept that is presently facing sustained debates.

Integrating the result of all experimental chapters (see *Chapter 7*), my results support the notion that behaviour in single-option encounters is fundamental to understand choice behaviour. The important issue of whether choices involve a decision time cost or the opposite, a shortening of response times, remains unsolved, as neither could be evidenced reliably.

For my family...

“In studying any phenomenon, dissect away everything that is not essential to it. In a word, simplify. Then study the simple system that remains, to discover the basic variables that produce the phenomenon.”

Teitelbaum¹ (1967, p.4)

¹As cited in Alberts, J.R. 2012. Observe, simplify, titrate, model, and synthesize: A paradigm for analyzing behavior. Behavioural Brain Research, 231: 250-261. doi: 10.1016/j.bbr.2012.03.007.

ACKNOWLEDGEMENTS

This dissertation would not have been possible without the help and support of many people: family, friends and co-workers. I hope I would not forget anyone, and I will try (when possible) to thank each and every one personally.

I am truly indebted and thankful to my dear Mariana, for coming along, for believing in me, and for all these years of love and patience...I would also like to thank my parents for being there for me, and not giving up...even when I did. ‘Props’ to my little brothers Miguel Dinis, future biologist, and Maria Pedro, for being truly inspirational. Warm thanks to Sofia Monteiro, for all the travels, the visits and the regular online company, and to João Ataíde and Manuela Aleixo for their logistical support. I also wish to thank my grandparents that supported this adventure one way or another. To all of whom I owe a great deal. Avó Susete: I wish you were here to see this!

I am profoundly grateful to Alex Kacelnik, for giving me the opportunity to come to Oxford and work in such a stimulating environment, full of historical meaning, within and around the *Tinbergen Building*, and for all the time we have spent together – Alex, you are, rightly, an example to follow, as a scientist and a thinker, but especially as a human being. Thanks to Marco Vasconcelos, for all the daily support, supervision and fruitful discussions. Thanks to Justine Aw, my former office mate, for teaching me my way around. Thanks to my friend Rita Sousa for the intermittent chats about the ups and downs of graduate student life, and to Ros Gloag, my ‘DPhil sister’. Thanks to all my next-door neighbours from the ‘Animal Behaviour’ corridor (Stephen Barlow, Ben Dean, Andrea Flack, Rob Holbrook, Holly Kirk, Benj Petit, Chris Rutz and more recently James St Clair and Zack Burns) for being always helpful, for all the coffee and lunch breaks, discussions, and the odd Friday evening beer.

Thanks to Graham Taylor and Teresa Burt de Perera for being in my thesis committee and for their valuable comments and remarks, and Mark Fricker, my college advisor.

Thanks to Armando Machado, my former supervisor, that motivated and encouraged my decision to pursue a research path. One evening, after a social event in the university, he told me about Alex, a guy that was doing very interesting studies with crows...in Oxford.

I am also grateful to the Biomedical Services staff, for their technical support and Simon and Jan Parry for their help in trapping my experimental participants – *The Starlings*, without their hard work and effort, none of this would have been possible.

Finally, I would like to acknowledge all the financial support: this research was funded by the Portuguese Foundation for Science and Technology (doctoral grant to the author), the Biotechnology and Biological Sciences Research Council (BBSRC research grant BB/G007144/1 to Alex Kacelnik, and doctoral training grant to the author – fees only), the 7th European Community Framework Programme (Marie Curie Intra European Fellowship to Marco Vasconcelos). In 2008 I was awarded a Pembroke College Graduate Studentship, and in 2011 a Pembroke College Lord Milles Senior Studentship. Pembroke College, through the Dean of Graduates fund, the Behavioural Ecology Research Group, the Experimental Psychology Society, and the Spanish Society for Comparative Cognition provided money to participate in conferences and meetings.

TABLE OF CONTENTS

Chapter 1.....1

General Introduction

1. Introduction.....	2
2. A brief introduction to the study of choice (or decision-making).....	4
3. The Sequential Choice Model (SCM) – a primer.....	10
4. Organisation of the thesis.....	15
5. Data chapters: summaries and keywords.....	16
6. References.....	21

Chapter 2.....27

Choice in multi-alternative environments:

A trial-by-trial implementation of the Sequential Choice Model

1. Introduction.....	28
2. Experiment	31
2.1. Materials and Methods.....	31
2.1.1. Subjects	
2.1.2. Apparatus	
2.1.3. Procedure	
2.1.3.1. Preliminary Training	
2.1.3.2. Training and Testing	
2.2. Results.....	35
2.2.1. Timing	
2.2.2. Latencies	
2.2.3. Choices	
2.2.4. Predictions from the SCM	
3. Discussion.....	39
4. Supplementary information.....	43
5. Acknowledgments.....	44
6. References.....	45

Chapter 3.....49

Cognitive mechanisms of risky choice: Is there an evaluation cost?

1. Introduction.....	50
1.1. Averaging outcomes.....	54
1.2. Variance in information processing mechanisms: the Weber-Fechner Law.....	55
2. Materials and Methods.....	57
2.1. Summary of the general procedure.....	57
2.2. Subjects.....	58
2.3. Apparatus.....	58
2.4. Detailed protocol.....	59
2.4.1. Baseline training and testing	
2.4.2. Stability criterion	
2.4.3. Data analysis	
3. Results.....	62
3.1. Preferences.....	62
3.2. Latencies to respond.....	63
3.3. Timing.....	65
3.4. Indifference points.....	66
3.5. Testing the SCM.....	67
3.5.1. Predicting choice from forced trials' latencies	
3.5.1.1. Strength of preference	
3.5.1.2. Proportion of individual choices predicted accurately	
3.5.2. Predicting shifts in latencies	
4. General conclusions.....	72
5. Acknowledgments.....	74
6. References.....	75

Chapter 4.....79

In search for the lost decision time:

The Sequential Choice Model (SCM) extended

1. Introduction.....	80
2. Experiment 1.....	85
2.1. Method.....	86
2.1.1. Subjects	
2.1.2. Apparatus	
2.1.3. Procedure	
2.1.4. Data Analysis	
2.1.5. Monte Carlo implementation of the SCM	
2.2. Results.....	91

2.2.1. Preferences	
2.2.2. Perception of time	
2.2.3. Latencies in single-option trials	
2.2.4. Latencies in simultaneous choices	
2.2.5. Monte Carlo simulations	
2.3. Discussion.....	97
3. Experiment 2.....	98
3.1. Method.....	99
3.1.1. Subjects and Apparatus	
3.1.2. Procedure	
3.1.3. Data analysis	
3.1.4. SCM simulations	
3.2. Results.....	102
3.2.1. Perception of time	
3.2.2. Latencies in single-option trials	
3.2.3. Latencies in simultaneous choices	
3.2.4. Preferences	
3.2.5. Monte Carlo simulations	
3.3. Discussion.....	107
4. General discussion.....	107
5. Supplementary information.....	110
6. Acknowledgments.....	111
7. References.....	112
Chapter 5.....	117
<i>On evolutionary and natural history constraints of decision-making:</i>	
<i>Adding function(s) to mechanism(s)?</i>	
1. Introduction.....	118
2. Methods.....	123
2.1. Subjects.....	123
2.2. Apparatus.....	124
2.3. Pre-training.....	124
2.4. General procedure.....	125
2.4.1. Trial types	
2.5. Data analysis.....	127
2.6. Simulations.....	128
2.6.1. Monte Carlo implementation of the SCM	
2.6.2. Time-constrained SCM	
3. Results.....	129
3.1. Representation of delays to food.....	129
3.2. Response latencies.....	130
3.3. Preferences.....	133

3.4. SCM predictions.....	134
4. Discussion.....	135
5. References.....	139
Chapter 6.....	145
<i>Rational choice by starlings:</i>	
<i>Transitivity and regularity for delay and probability of reward</i>	
1. Introduction.....	146
2. Results.....	150
3. Discussion.....	153
4. Methods.....	154
4.1. Preliminary training.....	155
4.2. Trial structure.....	155
4.3. Particulars of Experiment 1.....	156
4.4. Particulars of Experiment 2.....	157
4.5. Data analysis.....	157
4.6. Notation.....	158
5. Supplementary information.....	159
Supplementary Table 1.....	159
Supplementary Table 2.....	160
Supplementary Figure 1.....	161
6. Acknowledgments.....	162
7. References.....	163
Chapter 7.....	169
<i>Concluding remarks</i>	
Appendix 1.....	187
<i>Darwin's 'Tug-of-War' vs. Starlings' Horse-Racing: how adaptations for sequential encounters drive simultaneous choice.</i>	
Appendix 2.	203
<i>On the flexibility of lizards' cognition: a comment on Leal and Powell (2011)</i>	

Appendix 3.....	209
<i>Behavioural Processes Special issue – cover page word cloud</i>	

CHAPTER 1.

General Introduction

[Unpublished manuscript]

1. Introduction.....	2
2. A brief introduction to the study of choice (or decision-making).....	4
3. The Sequential Choice Model (SCM) – a primer.....	10
4. Organisation of the thesis.....	15
5. Data chapters: summaries and keywords.....	16
6. References.....	21

1. Introduction

The main objective of this doctoral dissertation is to study how animals choose between options yielding different payoffs, while developing and extending the Sequential Choice Model (SCM; Shapiro, Siller, and Kacelnik, 2008; reviewed in Kacelnik et al., 2011 – see *Appendix 1*) to new and more demanding scenarios. Ultimately it is an attempt to contribute to the broad theory of decision-making.

Building on recent work from the Behavioural Ecology Research Group (*BERG*), in general terms, all the studies presented focused on decision-making processes using operant set-ups (Fig. 1, a), and wild-caught European starlings (*Sturnus vulgaris*) as experimental models (Fig. 1, b).

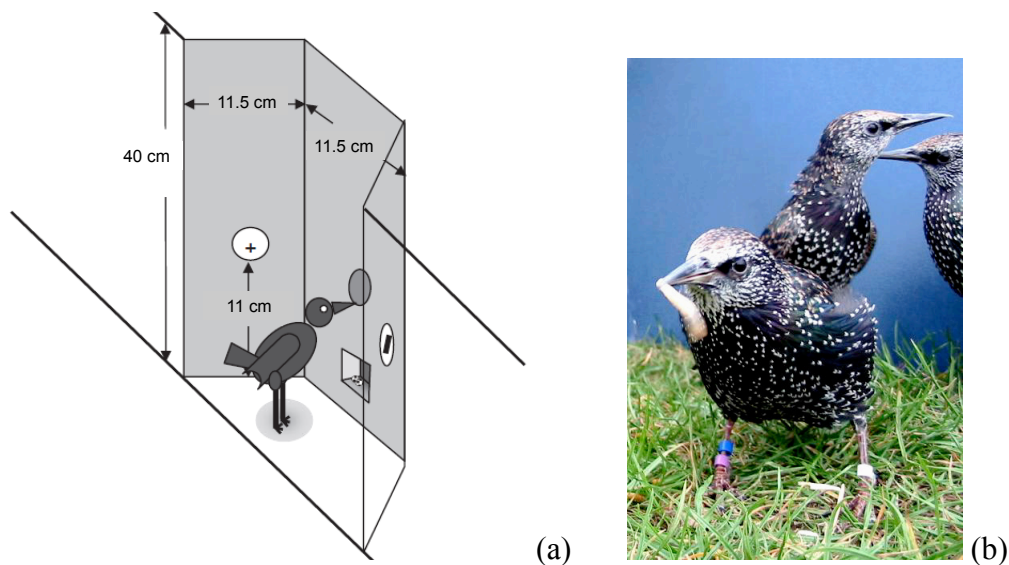


Figure 1. (a) Schematic representation of the experimental panel used in the experiments^{1,2}. (b) Group of wild-caught starlings from BERG's colony³.

¹Adapted with permission from Shapiro, Siller, & Kacelnik (2008)

²This setup was used in most experiments reported in the thesis, excluding the ones in *Chapters 2* and *3*, that were run using older equipment (i.e., in *Chapter 1*, I used a panel similar to the one shown in the figure, with only black and white symbols; for *Chapter 3* I used flat panels with 3 response keys and a food dispenser, and 3 different coloured symbols).

³Photograph taken by Cyntia Schuck-Paim and Lorena Pompilio, reproduced with permission.

In 2010, *BERG*'s behavioural laboratory was completely refurbished and re-equipped (for selected examples see Fig. 2). As a consequence, there was a substantial increase in the number of conceivable experimental situations, as well as an increase in the potential number of animals being simultaneously tested at any particular time. While initial experiments were constrained by the reduced number of options available (i.e., symbols and colours) to use as stimuli signalling food availability (cf. *Chapters 2 and 3*), as well as by the limited number of animals available for a particular experiment at any given moment (i.e., approx. 6), after the refurbishment, a total of 40 subjects could be tested simultaneously (in various experiments), and a myriad of colour-symbol combinations were also possible.

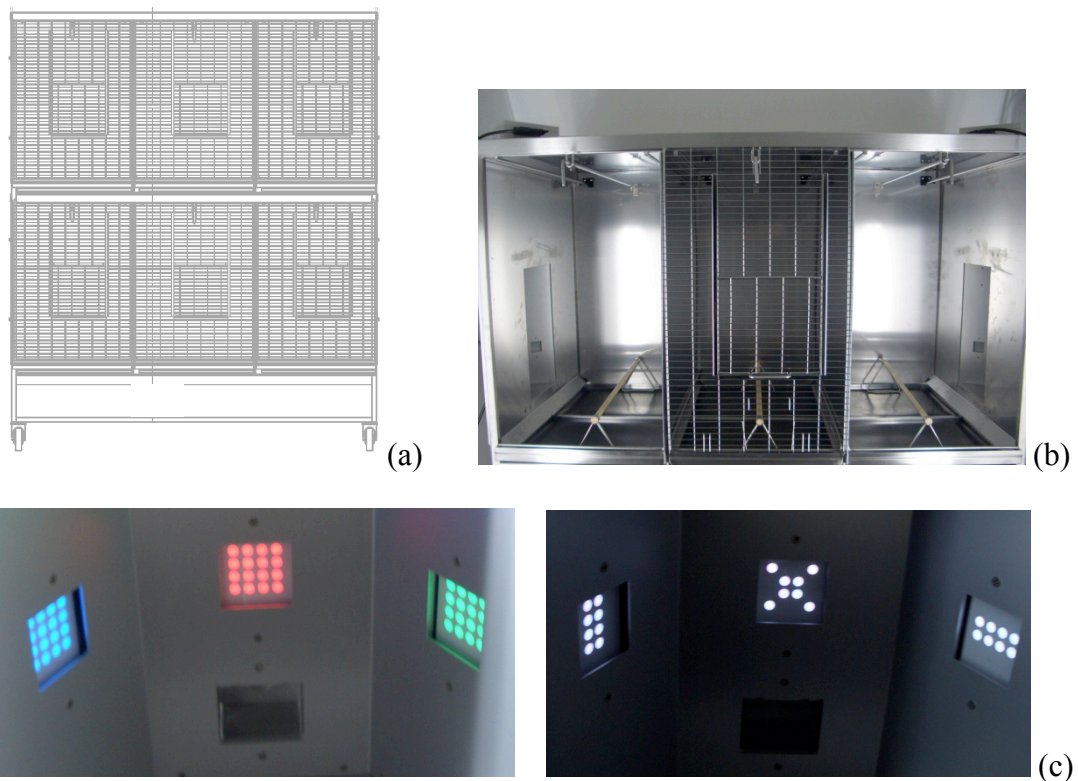


Figure 2. (a) Technical drawing of the new two-stack cages, capable of housing two birds in each stack. (b) Photograph showing top floor of an experimental cage: 2 working areas on the sides, and a communal space in the centre. (c) Sample photographs of the new pecking keys: each key was composed of a 16 LED matrix capable of displaying different combinations of colours (left) and/or symbols (right).

In the experiments reported here (a total of 7 empirical studies), choice situations varied in the number of options considered (i.e., choices between two and/or three simultaneously presented options), in their context of presentation (i.e., before, after or embedded in single-option presentations), and in the properties signalled by each option (i.e., time to food, probability of food and the ratio of amount of food per unit of time). These manipulations are described in detail in the chapter summaries that follow⁴.

All the work presented in this compendium was done in collaboration with members of the group, particularly Professor Alex Kacelnik (supervisor, head of the group) and Dr Marco Vasconcelos (co-supervisor, Marie Curie research fellow, BBSRC post-doctoral research assistant) who supervised the work, but also with Dr Justine Aw (senior graduate student and BBSRC post-doctoral research assistant). I had a substantial and leading role in all the research presented in this doctoral thesis, but naturally most of the work is (or will be) published in co-authored papers. Specifically, I actively participated in the design of the experimental protocols, I was the main person responsible for running all behavioural experiments, I had a leading role in conducting data analyses and I wrote first drafts of all manuscripts. Additionally, I had the opportunity to collaborate in other projects, not integrating this thesis but included as *Appendices*⁵. None of the presented chapters appear in any other thesis.

2. A brief introduction to the study of choice behaviour (or decision-making)

Behavioural sciences face an extremely arduous task in trying to explain why biological systems behave as they do. Even though evolution by natural selection offers a natural and solid starting point for research, it is frequently complicated (if not impossible)

⁴See section 5, below.

⁵Only published (or in press) work is included as an *Appendix*.

to follow its implications, particularly when interests are focused on behaviour or cognition, and historical or evolutionary data are non-existent.

Virtually all behaviour can be seen as the result of a decision⁶, or a choice⁷, since whenever an organism does something it cannot do something else (such as resting). In order to survive and reproduce, animals have to constantly decide what to do at a particular time, as well as where to do it. Following this logic, the study of choice (or decision-making) becomes the formal and experimental analysis of *why* and *how* animals decide to act in a certain way. As a result, decision-making research requires a constant integration of theories and facts while relating the function of behaviour (i.e., *why* do animals act the way they do) to the psychological mechanisms underlying it (i.e., *how* do they do it)⁸.

Current research and theory on animal decision-making brings together concepts from behavioural ecology, experimental psychology, microeconomics, and more recently neuroscience, just to name a few (and not counting with more recent merges such as cognitive ecology, neuroeconomics or behavioural neuroscience). Behavioural ecology (and microeconomics⁹) have had a predominantly functional approach regarding decision-making (i.e., *why* questions), while experimental psychology (and neurosciences¹⁰) explore the proximal causes of choice behaviour, or its mechanisms (i.e., *how* questions). For this

⁶*“Decision: The non-random process leading to the adoption of one of the alternative options available to an individual in a choice situation. Decision does not necessarily imply a conscious process; however, it implies the use of information concerning the alternatives. Decision theory explores the cognitive factors that can influence an individual’s decision.” (Danchin, Giraldeau, and Cézilly, 2008)*

⁷*“Choice: Refers to selection by an individual among a series of alternative options available at a given time. This choice does not necessarily imply conscious decision; however, non-random choice among alternatives implies the use of some information.” (Danchin, Giraldeau, and Cézilly, 2008)*

⁸This has been *BERG*’s main approach. For more information see <http://users.ox.ac.uk/~kgroup>.

⁹Microeconomics studies on animal decision-making focus mainly on rational behaviour – on how animals maximize a given currency according to well-defined principles (see *Chapter 6*).

¹⁰In neuroscience, the focus is on how the nervous systems enable decision-making processes. Using a combination of behavioural experiments, electrophysiology, molecular and modelling techniques it targets the biological substrate of choice behaviour (see *Chapter 5*).

reason the topic studies in each discipline also vary. A quick search on any introductory textbook for any of these disciplines exposes such differences (e.g., Krebs and Davies, 1993; Pearce, 2008 – see *Table 1* for a non-exhaustive illustrative example of dominant topics in each field).

Table 1. Common topics in behavioural ecology and experimental psychology's introductory textbooks.

<i>Behavioural Ecology</i>	<i>Experimental Psychology</i>
Prey and patch choice	Perception and attention
Sexual selection	Learning
Mate choice	Memory
Parental care	Timing
Cooperation	Numerical competence

Notice that the very titles of the topics differ: in behavioural ecology they refer to the goals of the activity, and in psychology to processes. As shown in *Table 1*, different research topics can directly or indirectly be linked and used to study choice behaviour. The differences (between columns) necessarily expose the approaches used by both disciplines. As an illustrative case, let's briefly consider two of the most classical (and preeminent) theories from each discipline, Optimal Foraging Theory (for comprehensive reviews see Pyke, 1984; Stephens and Krebs, 1986; OFT; MacArthur and Pianka, 1966) and the Matching Law (Herrnstein, 1961, 1970; Davison and McCarthy, 1988). The former was originally designed to explore time and energy resource allocation in wild animals foraging in different patches of food; the latter was developed to describe (post-hoc) behaviour of pigeons pecking at coloured keys for food rewards. Both theories are designed to make predictions as well.

OFT, in its original form, assumes that a well-adapted animal would maximize its energy intake per unit of time, in other words it postulates that, under natural selection,

behaviour has been shaped as if it had been designed to maximize the animals' fitness (rate of energy intake over time is often used as a proxy for fitness). MacArthur and Pianka (1966) clearly stated (viz. Houston, McNamara, and Steer, 2007):

“Hopefully, natural selection will often have achieved such optimal allocation of time and energy expenditures, but such “optimum theories” are hypotheses for testing rather than anything certain (...) The basic procedure for determining optimal utilization of time and energy budgets is very simple: an activity should be enlarged as long as the result gain in time spent per unit of food exceeds the loss.”

(p. 603)

The Matching Law emerged from classical experimental psychology studies, and the use of concurrent schedules of reinforcement. Typically, in a concurrent schedule, two options are simultaneously available to the animal at different spatial locations (e.g., pecking keys, levers), and each option is associated with particular (and normally different) reinforcing contingencies (originally concurrent variable interval-variable interval, or VI-VI¹¹ schedules of reinforcement). According to the Matching Law, animals distribute their responses (by allocating their behaviour differently) between options in a way that equalises the rewards experienced from each option, according to the general rule:

$$\frac{B_1}{B_1 + B_2} = \frac{R_1}{R_1 + R_2}, \quad \text{Equation 1}$$

where B_1 and B_2 are the number of responses for each of the options, and R_1 and R_2 are the number of reinforcers obtained from each option, respectively. Baum (1974) reformulated Equation 1 to accommodate systematic deviations from matching as:

¹¹In a single VI 10 seconds schedule, a response is rewarded, on average, every 10 seconds.

$$\log \frac{B_1}{B_2} = \alpha \cdot \log \frac{R_1}{R_2} + \log b, \quad \text{Equation 2}$$

with a (slope) representing the animal's sensitivity to differences in rates of reinforcement between the alternatives, and b (intercept) representing the bias toward an alternative regardless of its relative reinforcement. This is known as the Generalized Matching Law and has been shown account for most deviations of "strict matching", and across multiple species (see Belke and Belliveau, 2001, and references therein).

The reason why animals do not strictly maximize is still unclear. At mechanistic level, one possible explanation is the process of melioration (Herrnstein and Vaughan, 1980), by which subjects are supposed to bias their behavioural allocation progressively towards the option yielding higher payoffs. Naturally, such process is only at equilibrium (i.e., when allocation is stable), when both options yield the same rate of reward per unit of effort or time. However, this does not explain the functional implications. Matching is problematic when it precludes subjects to attaining the maximum possible overall reward rate. Suggestions that matching behaviour was equivalent to maximization of net intake rate (and hence in agreement with OFT) are probably not true. In several studies animals still matched (or generalised matched) even when this was not a maximizing strategy¹² (for a concise discussion see Shettleworth, 2010 and references therein).

These examples illustrate why, to fully understand a given (choice) behaviour, one needs to address both the *why* and the *how* questions¹³. Krebs and Kacelnik (1991) pointed

¹²Heyman (1983) showed that different allocation of responses (e.g., indifference) might in certain situations yield the same reinforcement rate (viz. Houston, 1983).

¹³Tinbergen (1963) famously outlined that any behaviour should only be fully accounted/understood when four levels of explanation are achieved: *causation* (i.e., proximate causes), *survival value* (i.e., function and or adaptive value of a given behaviour), *ontogeny* (i.e., how a behaviour emerged in an individual's live span), and *evolution* (i.e., how a particular behaviour evolved phylogenetically) [See also Manning and Dawkins, 1998; Shettleworth, 2010]. The latter level, is

out that there has been some interchange between disciplines in terms of techniques and theory, especially in research focused on foraging behaviour in three particularly ways (all of which still apply today, two decades later):

(1) Behavioural ecology has adapted some of the operant techniques used by experimental psychology in an attempt to bring foraging studies to the laboratory (e.g., schedules of reinforcement – see *Chapters 2 to 6*).

(2) Successful integration of empirical results emerging from experimental psychology laboratories with optimal foraging theory (e.g., Risk-sensitivity theory, RST – see *Chapter 3*).

(3) Rules of choice and reinforcement schedules have been used by behavioural ecologists to study and explain behaviour that deviated from conventional fitness-maximizing models (e.g., State-dependent valuation learning¹⁴; the Sequential Choice Model, SCM – see section 1.3 for a primer and *Chapters 2 to 5* for specific implementations).

Conventional models of choice¹⁵ assume that any decision involves some kind of evaluation process, where each alternative, and its characteristics, is compared against the others. Regardless of the actual mechanism, it is natural to expect that such evaluations would necessarily take a certain amount of time. Consequently, choices should take longer than responses in the presence of a single alternative¹⁶. For instance, according to the Hick-Hyman Law¹⁷ (Hick, 1952; Hyman, 1953), the reaction-time to pick one option out of three possible options should be longer than that to pick one among two, or simply taking

hardly accessed, however as Shettleworth (2009) pointed out, studying animal cognition in its phylogenetic (and functional) context can provide hints to what animals were selected to do. And, as in the other biological sciences, it can offer a theoretical framework for meaningful comparative research into mechanisms.

¹⁴For an illustrative example see Pompilio, Kacelnik, and Behmer (2006).

¹⁵See *Appendix 1* for details.

¹⁶Throughout the thesis encounters with a single alternative might also be referred to as no-choices, single-option trials or sequential (food) encounters.

¹⁷For a more recent report, with both pigeons and humans as subjects, see Vickrey and Neuringer (2000).

an option when seen alone¹⁸. However, recent work on captive European starlings has yielded results that directly contradict this expectation: the time taken to respond in the presence of two alternatives was shorter than the time taken to respond when facing a single one (Shapiro, Siller, and Kacelnik, 2008). To account for these counterintuitive results, these authors proposed the Sequential Choice Model (or SCM for short) as an alternative way to think about decision-making. According to the SCM, the greater the number of options the shorter should the time to choose a particular one be¹⁹.

3. The Sequential Choice Model (SCM) – a primer

The SCM offers an alternative to traditional conceptions of choice behaviour that propose deliberate comparisons between options, and conceptually brings together normative and empirical reasoning. The model is inspired both by the evolution and ecology of decision makers and the empirical study of their behaviour, and is conceived by taking into account the fit between mechanisms and their environments. Its logic takes into consideration the environment under which choice might have evolved. A major consideration is that although common in the laboratory, it is unlikely that animals regularly encounter two options simultaneously. Instead, the more common choices are likely to occur between sequentially encountered options, with choices being whether to pursue a given option, or to continue searching for alternatives. Empirically, the idea can be traced to qualitative and quantitative observations, where response times (i.e., latencies) to singly-presented options were relative to the background of alternative options – the better the option relative to the alternatives, the shorter its corresponding latency (see

¹⁸According to the Hick-Hyman law, time to choose is expected to increase proportionally to the logarithm in base 2 of the number of options.

¹⁹Empirically, the relevance of the model for choices between more than two options has never been tested, but see *Chapter 4* for a recent implementation of the SCM to choices between three simultaneous options.

Freidin, Aw, and Kacelnik, 2009; Shapiro, Siller, and Kacelnik, 2008 for selected examples).

The SCM proposes that the mechanisms used by European starlings to choose between simultaneously available options is the same they use when facing each option alone, thus incorporating the idea that these mechanisms evolved as adaptations to environments in which it was rare to meet different options simultaneously, but on the contrary, meeting them sequentially was rather common. Thus, there are no special adaptations for simultaneous choices, however, the time to chase each alternative is precisely tuned to exploit the benefits it gives when compared with the opportunities in the whole environment.

Adding to the SCM's mathematical formulation, Kacelnik and collaborators (Kacelnik et al., 2011 – see *Appendix 1*) reviewed all published work (to date) on the SCM. Chronologically, Shapiro and colleagues (2008) reported the model as a new method to predict choice between simultaneous alternatives as a function of behaviour in sequential encounters. The good fit obtained supported the view that choice was driven by mechanisms adapted to sequential, rather than simultaneous encounters with feeding opportunities. Freidin and colleagues (Freidin, Aw, and Kacelnik, 2009) compared starlings' sequential and simultaneous choices using Charnov's (1976) Diet Choice Model (DCM) as well as the SCM. Notice that these models do not compete: Charnov's is a functional analysis, while the SCM proposes a mechanism of choice. Although the predictions of both models were similar, DCM does not address partial preferences, and the experimental results were close to the pattern predicted by the SCM. Vasconcelos and colleagues (Vasconcelos, Monteiro, Aw and Kacelnik, 2010 – see *Chapter 2*) implemented the model locally, to study how well the SCM could predict each individual choice, and not just the overall preference. By means of a hyperbolically decaying weighted moving

average of latencies from sequential choices, they managed to accurately predict the majority of the simultaneous choices. This manipulation was crucial in order to include the effect of temporal fluctuations in preference, as opposed to having only a single measure of overall predicted preferences. If the latency to respond to a particular option reflects its perceived value, presumably, latencies in no-choice trials and preferences in choice trials may fluctuate together along time, so that making local predictions may capture these fluctuations. Using latencies in no-choice trials that precede subsequent choices provided a clearer picture of how well the SCM could predict individual choices in time. Moreover, this implementation differentiates the SCM from the majority of choice models that usually predict only overall preference, whereas this approach provided a clear picture of local fluctuations in preference (i.e., trial-by-trial) as well as SCM's ability to predict them.

In the same review paper, Kacelnik and his team (2011) contrasted the philosophy of the SCM against a generic choice model, using the metaphor of a *horse-race* (i.e., the SCM) versus a *tug-of-war* (i.e., ToW) to discuss their formalisation and functional basis. The ToW model encompassed a competitive evaluation between the merits of each alternative option prior to action (i.e., the response), an evaluation that is likely to be time consuming. The SCM does not include a comparative evaluation between the options prior to the response, and instead of a time cost evaluation, a shortening of the time to act was predicted. The SCM postulates that in more common sequential decisions (i.e., responding in trials with only a single alternative), latencies are the result of an accumulation process that triggers a subsequent response. With successive encounters with each available option the animals form underlying distributions of latencies (for each option), with better options having (on average) faster accumulations and consequently shorter response times. Whenever two options are encountered simultaneously (in a choice), two independent accumulation processes start in parallel, with the first accumulation reaching a common

response threshold being expressed as a behavioural response to the corresponding alternative. Normally most ‘races’ will be won by the better option, due to its generally faster accumulations (and consequently average shorter latencies), resulting on only weak censoring of the richer option’s latency distributions during simultaneous choices. However, a choice of the worse option means that its accumulation out-competed the one for the better option or, in other words, its resulting latency was shorter than the sampled latency for the better option. For these worse alternatives, only samples from the left tail of the distribution out-compete the sampled latencies from the distribution of better option latencies (that are on average shorter). It is this limited expression of only the left tail of the worse option latency distribution that causes the realised distribution to be shifted to the left, and this is also the reason why censorship is more severe for the option showing longer latencies in single option trials.

According to the parallel process just described, every alternative is compared against the (remembered) background of opportunities in the environment, regardless of which other options are present at the time of each choice, and this happens for each alternative independently, while cross censorship takes place. Due to this cross censorship, when two options are simultaneously present, only the chosen option has a latency associated with it, recorded at the time of choice. No information concerning the other option(s) is(are) available since its corresponding accumulation process is terminated as soon as the alternative option is chosen²⁰.

More recently (hence not included in the review paper cited above), Mazur (2010) used the results of a series of experiments on discrete-trial choice to evaluate several theories on the topic, including the SCM. Mazur did find a shortening of the latencies in choice respect to no-choice trials, but the results were unreliable as they were marginally

²⁰See Figs 1 and 2 in Kacelnik et al. (2011) for details – *Appendix 1*.

outside conventional significance ($p=.066$). Aw and colleagues (Aw et al., 2012 – see *Chapter 3*) conducted a study to contrast and explore the applicability of both the SCM and the ToW logic to risky environments (i.e., options yielding the same average but different variances). This study found that, as postulated by the SCM, latencies to accept options in no-choice situations were, once more, relative to the background of alternatives (i.e., latencies were inversely related to the quality of a given option when compared with the background of alternative options), and that these latencies could be used to accurately predict simultaneous choices in this type of environments. However, no differences were found between latencies from no-choice and simultaneous choice trials, as predicted by both classes of model, although in opposite directions. Vasconcelos and colleagues (Vasconcelos, Monteiro, and Kacelnik, submitted) used a special procedure (Belke, 1992; Freidin and Kacelnik, 2011; Pompilio and Kacelnik, 2010), to produce context-dependent differential utilities, and evaluate the extent to which the SCM could deal with data from this specific experimental paradigm. Here, options yielding the same payoff (i.e., delay to a food reward) could have been perceived as different due to a context-dependent ranking. In order to implement the SCM to this new setup, the authors used Monte Carlo simulations²¹. Once more, the observed latencies were relative to the background of alternatives (i.e., the main assumption of the model), and some (non-significant) signs of latency shortening during simultaneous choices were observed. The Monte Carlo implementation of the SCM was overall successful in predicting choices from no-choice latencies, even though the performance varied with choice types. This difficulty exposed a limitation of the model: if latencies are very similar, the predicted bias is small and potentially undetectable. This is in fact very prevalent when latencies for all options are very short and approaching minimum reaction times.

²¹See *Chapters 4* and *5* for Monte Carlo implementations of the SCM to different experimental paradigms.

In a nutshell, the SCM postulates that: 1) the latencies to accept each source of reward upon encounter are sensitive to the option's parameters and to the background in which such option is comprised, or to the memory for the improvement in wellbeing remembered for that option; 2) shorter latencies indicate a stronger valuation for a given option and predict stronger preference if the option is met as part of a simultaneous set; 3) because options are evaluated against a common background and not against each other at the time of choice, latencies should not be longer, but rather, if anything, shorter in choices when compared to no-choice situations.

Combining these points, distributions of latencies in no-choice situations should be good predictors of both the level of preference in simultaneous presentations of stimuli and the latencies shown in such cases.

To conclude, in my view, the SCM is representative of Tinbergen's aspirations, as it involves an alternative approach to choice (and decision-making) materialized in a mechanistic model emerging from evolutionary considerations. As Kacelnik et al. (2011) pointed out, confidence in the model and its field of application grows inductively with the increase and diversification of protocols in which the approach proves efficient.

4. Organisation of the thesis

Each data chapter (*Chapters 2 to 6*) is a self-contained manuscript in preparation (*Chapters 4 and 5*), submitted to publication or under review (*Chapter 6*), in press or published (*Chapters 2 and 3*), and can be read independently of any other. As a drawback, a certain degree of overlapping and repetition is unavoidable. All chapters are incorporated as typescripts of the original papers, but for the sake of coherence all references were converted to the same standard style (i.e., *Behavioural Processes* reference style²²).

²²For details see:

http://www.elsevier.com/wps/find/journaldescription.cws_home/506046/authorinstructions#N10D52

Nevertheless, the content and organisation (i.e., sections, figures and use of first person plural throughout) was maintained as in the original papers²³, following each journal's specifications, indicated in the cover page of each chapter. All abstracts and keywords were reproduced in section 5, below.

Chapters 2 to 5 involve the empirical study of simple decision-making situations, while testing the applicability of the SCM to different scenarios. This was fulfilled using several variations of the same basic experimental procedure – birds working for food rewards, while testing the following with appropriate manipulations:

(1) If latencies to a given option, when encountered on its own, are relative to the background in which such option is embedded, or if on the contrary, they are either invariable or dependent only on the absolute properties of the option concerned.

(2) If shorter latencies in no-choice situations correlate with a stronger preference in simultaneous choices.

(3) If latencies for each option, on choice situations, differ from those in no-choice situations in the ways expected from either cross-censorship and evaluation models.

(4) If choices can be predicted with quantitative detail, from latencies in no-choice situations.

Chapter 6 is a one shot approach to rational behaviour in starlings, comprising a new empirical study and a re-analysis of data from one experiment included in *Chapter 4*.

5. Data chapters: summaries and keywords

Chapter 2 – *Choice in multi-alternative environments: A trial-by-trial implementation of the Sequential Choice Model*

The sequential choice model (SCM) proposes that latencies to accept options

²³Some footnotes were added to make reference to other section of the thesis.

presented alone can be used to predict preferences between these options when they are presented simultaneously. SCM has been proposed and tested in experiments where only two alternatives were present. To further challenge the model, we trained and tested European starlings (*Sturnus vulgaris*) in an environment with a background of four alternatives differing in delay to reinforcement. Unexpected binary choices between the six possible pairs of alternatives were used to assess preference. The model's predictions of the strength of preference roughly corresponded to the bird's choices for each of the six choice situations. More importantly, a trial-by-trial test of the model correctly predicted 84% of all individual choice trials.

Keywords: Choice; latency; starlings; Sequential Choice Model.

Chapter 3 – *Cognitive mechanisms of risky choice: Is there an evaluation cost?*

We contrast two classes of choice processes, those assuming time-consuming comparisons and those where stimuli for each option act independently, competing for expression by cross censorship. The Sequential Choice Model (SCM) belongs in the latter category, and has received empirical support in several procedures involving deterministic alternatives. Here we test this model in risky choices. In two treatments, each with five conditions, European starlings (*Sturnus vulgaris*) faced choices between options with unpredictable outcomes and risk-free alternatives. In the delay treatment the five conditions involved choices between a variable option offering two equiprobable delays to reward and a fixed option with delay differing between conditions. The amount treatment was structurally similar, but amount of reward rather than delay was manipulated. As assumed (and required) by the SCM, latency to respond in no-choice trials reflected each option's richness with respect to the background alternatives, and, crucially, preferences in simultaneous choices were predictable from latencies to each option in forced trials.

However, we did not detect reliable differences in response times between forced and choice trials, neither the lengthening expected from evaluation models nor the shortening expected from the SCM.

Keywords: Risky Choice; Sequential Choice Model; Scalar Utility Theory; Expectation of the Ratios; starlings; food delay; food amount.

Chapter 4 – *In search for the lost decision time: the Sequential Choice Model (SCM) extended*

The Sequential Choice Model (SCM) contradicts the intuition that choice between simultaneous alternatives involves a decision time. The SCM is a *horse-race* model inspired by the ecological observation that adaptations for sequential rather than simultaneous encounters shape choice mechanisms. According to the SCM, responding to single options involves a deliberation between it and the overall background, with acceptance times (i.e., latencies) negatively related to option quality. In simultaneous encounters, each option undergoes independently the same comparison with the background, so that realised latencies in choices are no longer than those observed in single-option encounters.

In this study, we focus on the effect of alternative forms of experience (i.e., with simultaneous or sequential encounters with the foraging alternatives) and on the number of alternatives experienced. In Experiment 1, response latencies in sequential encounters are compared to latencies in binary choices preceding and following them. In Experiment 2 latencies in sequential encounters are compared to those in 3- and in 2-option simultaneous choices. In both instances, our findings partly support the predictions of the SCM.

Keywords: binary, choice, decision-making, latencies, starlings, SCM, trinary.

Chapter 5 – *On evolutionary and natural history constraints of decision-making: adding function(s) to mechanism(s)?*

In this study wild-caught European starlings (*Sturnus vulgaris*) were trained and tested in a multi-alternative environment, composed of 6 bi-dimensional options, presented either sequentially (in no-choice trials) or in binary-choice trials (i.e., 15 different pairings). Each option was associated with one out of three possible reward rates (defined as amount/delay ratios), and within each of the three rates various alternatives offered different amount of/delay to reward combinations. In most previous studies, starlings were tested in multi-alternative environments composed of options differing only in delay (Freidin, Aw, and Kacelnik, 2009; Vasconcelos et al., 2010). In one case (Shapiro, Siller, and Kacelnik, 2008), bi-dimensional differences between options were considered, but in each treatment the environment was composed of only two options at any particular time, so that in comparing a present option against the background the subject only had to consider one of the alternatives. The main purpose here was twofold: to test the ecological validity of the Sequential Choice Model (SCM) using a more complex environment in which the background to each decision was a mixture of many possible alternatives; and to stress the importance of sequential food encounters to the study of foraging decisions, by comparing the SCM's rationale with other sequential sampling models (SSMs) from both mathematical psychology and neuroscience, that are normally applied to binary-choice situations. The first goal was achieved, since the SCM successfully predicted the birds' choices using single-option trials, even in the present more complex background conditions. This was true both using a Monte Carlo version of the model and after adding a discounting memory rule. Since the ecological rationale for the SCM is the ecological prevalence of such single-option encounters, these findings constitute further validation of its biological credentials.

Keywords: binary, choice, decision-making, latencies, starlings, Sequential Choice Model, SSM, Starlings.

Chapter 6 – *Starlings uphold principles of economic rationality for delay and probability of reward.*

Rationality principles are the bedrock of normative theories of decision-making in biology and microeconomics, and their violations are sometimes invoked against optimality reasoning. Reported violations in non-humans include intransitivity (i.e., circular preferences) and lack of independence of irrelevant alternatives (changes in relative preference between options when embedded in different choice sets). We tested these principles of rationality with starlings (*Sturnus vulgaris*), training subjects either with 5 options differing in food delay (Exp. 1) or with 6 options differing in reward probability (Exp. 2), before letting them choose repeatedly one out of binary and trinary sets of options. The starlings conformed to economic rationality by showing strong stochastic transitivity and no violation of the independence principle. These results endorse the rational choice and optimality approaches used in behavioural ecology, and highlight the need for functional and mechanistic enquiring on observed violations.

Keywords: choice; decision-making; foraging; transitivity; IIA

6. References

- Aw, J., Monteiro, T., Vasconcelos, M. and Kacelnik, A. 2012. Cognitive mechanisms of risky choice: Is there an evaluation cost? *Behavioural Processes*, 89: 95-103.
- Baum, W.M. 1974. On two types of deviation from the matching law: Bias and undermatching. *Journal of the Experimental Analysis of Behavior*, 22: 231.
- Belke, T.W. 1992. Stimulus preference and the transitivity of preference. *Animal Learning and Behavior*, 20: 401-406.
- Belke, T.W. and Belliveau, J. 2001. The general matching law describes choice on concurrent variable-interval schedules of wheel-running reinforcement. *Journal of the Experimental Analysis of Behavior*, 75: 299.
- Charnov, E.L. 1976. Optimal Foraging: Attack Strategy of a Mantid. *American Naturalist*, 110: 141-151.
- Danchin, É., Giraldeau, L.A. and Cézilly, F. 2008. *Behavioural ecology*. Oxford University Press.
- Davison, M. and McCarthy, D. 1988. *The matching law: A research review*. Lawrence Erlbaum Associates, Inc.
- Freidin, E., Aw, J. and Kacelnik, A. 2009. Sequential and simultaneous choices: Testing the diet selection and sequential choice models. *Behavioural Processes*, 80: 218-223.
- Freidin, E. and Kacelnik, A. 2011. Rational Choice, Context Dependence, and the Value of Information in European Starlings (*Sturnus vulgaris*). *Science*, 334: 1000-1002.
- Herrnstein, R.J. 1961. Relative and absolute strength of response as a function of frequency of reinforcement. *Journal of the Experimental Analysis of Behavior*, 4: 267.

- . 1970. On the law of effect. *Journal of the Experimental Analysis of Behavior*, 13: 243.
- Herrnstein, R.J. and Vaughan, W., Jr. . 1980. Melioration and behavioral allocation. In: J.E.R. Staddon (Editor), *Limits to action*, Academic Press., New York.
- Heyman, G.M. 1983. Optimization theory: Close but no cigar. *Behaviour Analysis Letters*, 3: 17-26.
- Hick, W.E. 1952. On the rate of gain of information. *Quarterly Journal of Experimental Psychology*, 4: 11-26.
- Houston, A.I. 1983. Optimality theory and matching. *Behaviour Analysis Letters*, 3: 1-15.
- Houston, A.I., McNamara, J.M. and Steer, M.D. 2007. Do we expect natural selection to produce rational behaviour? *Philosophical Transactions of the Royal Society B-Biological Sciences*, 362: 1531-1543.
- Hyman, R. 1953. Stimulus information as a determinant of reaction time. *Journal of Experimental Psychology*, 45: 188–196.
- Kacelnik, A., Vasconcelos, M., Monteiro, T. and Aw, J. 2011. Darwin's "tug-of-war" vs. starlings' "horse-racing": how adaptations for sequential encounters drive simultaneous choice. *Behavioral Ecology and Sociobiology*, 65: 547-558.
- Krebs, J.R. and Davies, N.B. 1993. *An introduction to behavioural ecology*. Blackwell Scientific Publications, Oxford.
- Krebs, J.R. and Kacelnik, A. 1991. Decision-making. In: J.R. Krebs and N.B. Davies (Editors), *Behavioural Ecology*, Blackwell Scientific Publications, Oxford.
- MacArthur, R.H. and Pianka, E.R. 1966. On Optimal Use of a Patchy Environment. *The American Naturalist*, 100: 603-609.
- Manning, A. and Dawkins, M.S. 1998. *An introduction to animal behaviour*. Cambridge University Press, Cambridge.

- Mazur, J.E. 2010. Distributed Versus Exclusive Preference in Discrete-Trial Choice. *Journal of Experimental Psychology-Animal Behavior Processes*, 36: 321-333.
- Pearce, J.M. 2008. *Animal learning & cognition: an introduction*. Psychology Press.
- Pompilio, L. and Kacelnik, A. 2010. Context-dependent utility overrides absolute memory as a determinant of choice. *Proceedings of the National Academy of Sciences of the United States of America*, 107: 508.
- Pompilio, L., Kacelnik, A. and Behmer, S.T. 2006. State-dependent learned valuation drives choice in an invertebrate. *Science*, 311: 1613-1615.
- Pyke, G.H. 1984. Optimal Foraging Theory: A Critical Review. *Annual Review of Ecology and Systematics*, 15: 523-575.
- Shapiro, M.S., Siller, S. and Kacelnik, A. 2008. Simultaneous and sequential choice as a function of reward delay and magnitude: Normative, descriptive and process-based models tested in the European Starling (*Sturnus vulgaris*). *Journal of Experimental Psychology: Animal Behavior Processes*, 34: 75-93.
- Shettleworth, S.J. 2009. Cognition: theories of mind in animals and humans. *Nature*, 459: 506-506.
- . 2010. *Cognition, Evolution, and Behavior*. Oxford University Press, New York.
- Stephens, D.W. and Krebs, J.R. 1986. *Foraging Theory*. Princeton University Press, Princeton, New Jersey.
- Tinbergen, N. 1963. On aims and methods in ethology. *Zeitschrift für Tierpsychologie*, 20.
- Vasconcelos, M., Monteiro, T., Aw, J. and Kacelnik, A. 2010. Choice in multi-alternative environments: A trial-by-trial implementation of the Sequential Choice Model. *Behavioural Processes*, 84: 435-439.
- Vasconcelos, M., Monteiro, T. and Kacelnik, A. submitted. Mechanisms of choice and context-dependent preferences in starlings.

Vickrey, C. and Neuringer, A. 2000. Pigeon reaction time, Hick's law, and intelligence. Psychonomic bulletin & review, 7: 284-291.

Choice in multi-alternative environments: A trial-by-trial implementation of the Sequential Choice Model

[Vasconcelos¹, M., Monteiro¹, T., Aw, J. and Kacelnik, A. 2010. Choice in multi-alternative environments: A trial-by-trial implementation of the Sequential Choice Model. Behavioural Processes, 84: 435-439.²]

1. Introduction.....	28
2. Experiment	31
2.1. Materials and Methods.....	31
2.1.1. Subjects	
2.1.2. Apparatus	
2.1.3. Procedure	
2.1.3.1. Preliminary Training	
2.1.3.2. Training and Testing	
2.2. Results.....	35
2.2.1. Timing	
2.2.2. Latencies	
2.2.3. Choices	
2.2.4. Predictions from the SCM	
3. Discussion.....	39
4. Supplementary information.....	43
5. Acknowledgments.....	44
6. References.....	45

¹Authors contributed equally to this work

²doi: 10.1016/j.beproc.2009.11.010

1. Introduction

Choice is usually taken as the result of a rather elaborative and time consuming process (Hick, 1952). When humans are presented with two or more options, introspection may create the perception that decisions are driven by careful evaluation of each alternative. If this were true, choosing would require information-processing effort and time: more options, more time to choose. One might thus expect the time difference between acting when facing two options and acting when facing a single possibility to reflect the temporal cost of the evaluation process.

Shapiro, Siller, and Kacelnik (2008) found the opposite to be true in starlings (*Sturnus vulgaris*): they took longer to take a lonely alternative than to take the same alternative in a choice situation. To explain this finding, Shapiro and colleagues proposed the Sequential Choice Model (SCM) whose basic assumption is that contemporary choice mechanisms evolved as adaptations to environments in which choices between simultaneously presented options are rare, and are driven by mechanisms adapted to more common sequential encounters.

SCM states that choices made when facing alternatives simultaneously can be predicted by behaviour during sequential encounters where one alternative occurs at a time. The model captures the fact that when animals face single options, they do not accept them immediately, but instead express a 'latency', which reflects a tendency to skip the option in favour of continuing to forage. This provides a mechanism for Charnov's (1976a) prey selection model, which identifies the rejection policy that maximises overall rate of intake in sequential encounters. Latencies to accept lonely options are, however, not a rigid function of each option's properties, but sensitive to the background of alternative opportunities present in the environment. Hence, they are a decreasing function of the improvement in fitness that the decision maker may expect

from the present option relative to lost opportunity in the whole environment. Repeated sequential encounters with each option result in a specific probability density function of latencies for each. When two or more options are met simultaneously, each elicits a sample from its own distribution of latencies and the shortest sample is expressed as a choice. Crucially, there is no comparative evaluation of the merits of each option at the time of choice; instead each option elicits a latency, just as in sequential encounters, but the slowest one is not expressed because it is censored by the alternative.

The significance of sequential encounters and of lost opportunity date back to the early days of optimal foraging theory through Charnov's Diet Choice model (Charnov, 1976a) and the Marginal Value Theorem (Charnov, 1976b), both of which inspired empirical tests (Fantino & Abarca, 1985; Krebs, Erichsen, Webber, & Charnov, 1977) that are now considered classical. The present focus on the interaction between the properties of options and their background context offers an opportunity to link these functional ideas to precise mechanistic modelling.

SCM emerged from experimental results obtained with starlings in two-alternative environments facing single-option encounters and binary choices, with options differing in amount and delay to reward (Freidin, Aw, & Kacelnik, 2009; Shapiro et al., 2008). Latencies observed in single-option trials very accurately predicted how long birds took to accept an option in binary-choice trials and which option was chosen. Here, to further challenge the model, we trained and tested starlings in a four-alternative environment, still using binary choices to assess preference. This is a stricter test of the model, as birds are required to adjust latencies to a more complex background resulting from a larger set of options, and face six rather than just one type of binary choices. Thus the same option can be the better or the worse alternative depending on its pairing. This, together with the low density of choices relative to no-choice trials, firmly

excludes the possibility of the animals learning to respond towards or against a given option. The expectation is that the mechanism that determines the latency to accept each option (which depends on its value with respect to the background opportunities) also underlies choices in binary encounters.

We add a further refinement in the model testing by moving closer to a local (trial-by-trial) test of the predictions. In previous studies, SCM's predictions of choices were tested either by computing the model's predictions for each condition across the subject population (Shapiro et al., 2008, Fig. 8f) or within-individual but averaged over blocks of trials (Freidin et al., 2009, Fig. 5; Shapiro et al., 2008, Fig. 12). However, by these methods we can only know how close the overall prediction (the predicted preference strength) is to the overall actual preference and have no indication of how well SCM can predict each individual choice.

To generate local predictions we predicted the outcome of each binary choice using the latency to accept each of the presented options during the nearest preceding single-option trial with each of the two options. The option which had shown the shorter latency in the most recent trial was the predicted winner. As an example, let us consider ten choice trials where the latencies in preceding single-option trials predicted the choices AAAAAABBBB, where A and B identify each option. Suppose further, that the observed choices in the same set of trials are AAAABBBBBB. Here the observed proportion of choices for A is 40%, while the predicted preference strength for A is 60%. The model is seen to perform badly because it predicted the wrong preference. However, on a trial-by-trial basis, the model agreed with the observations 80% of the time. The difference emerges because it matters which individual choices one is addressing.

This local approach is preferable both because it reflects more directly the putative mechanism being modelled and because it captures potential local fluctuations in preference. Besides, this is a feature that differentiates this model from the majority of algorithms predicting choice. For instance, a hyperbolic discounting model would compute some value of each option using programmed delays and then predict global proportion of choices for each option by a stochastic matching of the ratio of the option's values, but it has no inherent process to deal with temporal fluctuations in choice probabilities. Most choice models simply do not make local predictions. Our present method offers two quantitative indicators of the model's performance: a prediction of preference strength (global) and the proportion of individual choices accurately predicted (local).

2. Experiment

Starlings were trained and tested in an environment consisting of four options, each signalling a different *fixed-interval* (FI) schedule (FI 3, 6, 12, or 24 s). Infrequent trials with the six possible pairwise choices between the four options were used to assess preference since the outset of the experiment.

2.1. Materials and Methods

2.1.1. Subjects

Eight adult wild-caught European starlings participated in the experiment (Natural England licence 20073610). All subjects were naïve to experimentation. Prior to the experiment, birds were socially housed in a large outdoor aviary (3m high x 3.2m wide x 4m long) with *ad libitum* food (a mixture of turkey crumbs, Orlux© pellets and mealworms, *Tenebrio sp.*) and continuous access to fresh drinking and bathing water.

For experimental participation, starlings were transferred to individual cages (160 cm long x 45 cm high x 40 cm deep) that were visually, but not acoustically isolated. These served both as home and experimental cages. Indoor temperatures ranged from 13°C to 15°C and lights followed a 12:12 day-night cycle with lights on at 07h00. We used 20 mg precision pellets (BioServ®) as rewards throughout. This was supplemented with three hours of free access to turkey crumbs (14h00-17h00) and 10 mealworms daily. This regime is known to maintain starlings at approximately 90% of their free-feeding body weight (Bateson, 1993). Birds had continuous access to drinking water and received bathing trays every other day.

2.1.2. Apparatus

Each cage had an operant panel attached to the centre of the back wall and two perches, one at each side of the cage. The panel was as tall as the cage with three sections: a middle subpanel, facing the cage (10 cm wide), and two side subpanels (each 10 cm wide) attached to the cage at a 110 degree angle from the centre subpanel. The bottom of the panel was the same level as the floor of the cage (see Shapiro et al., 2008, Fig. 1). The middle subpanel had one response key in the centre (11 cm from the bottom) that could be illuminated with a green light, and a food hopper (2 cm from the bottom), that was connected to a pellet dispenser (Campden Instruments®) which delivered 20 mg dustless precision pellets (BioServ®). Each side subpanel had a centrally located response key (11 cm from the bottom), which could display nine black and white symbols. Trials were controlled by custom software running on the Microsoft® Windows® operating system and attached to an Animal Behaviour Environment Test System (Campden Instruments®) via WhiskerServer.

2.1.3 Procedure

2.1.3.1. Preliminary Training

After magazine training, the birds were trained to peck a flashing green centre key (700ms ON, 300ms OFF). A single peck to this key delivered four precision pellets, extinguished the keylight, and initiated a 120-s inter-trial-interval (ITI). Failing to peck the key within 30-s from the onset of flashing resulted in the same events as a peck. Training thus combined autoshaping with an operant response. Once birds were reliably pecking the centre key, the lateral keys were introduced. Trials again began with the flashing green centre key. A peck to this key turned its light off and caused one of the side keys to start flashing with a designated symbol (not used in subsequent phases). A peck to the flashing lateral key turned it off and produced two food pellets followed by a 90-s ITI. During this phase, failing to peck the centre key within 30 s from trial onset resulted in a 10-s blackout followed by the ITI. Failing to peck the flashing side key during the same time period was followed by food 75% of the time. This program was maintained 5 hours per day until the birds reliably pecked the centre and side keys on at least 80% of the trials.

Next, birds received preliminary, response-initiated FI training. In this phase two pecks to the side key were required to deliver food. The first peck turned the symbol steadily on and began a delay, the duration of which was progressively increased from 1 to 25 s. The first peck after the delay lapsed extinguished the symbol, delivered two food pellets and initiated a 45-s ITI. Once birds were reliably obtaining food on FI 25 trials, the experimental sessions began.

2.1.3.2. Training and testing

This phase involved three intermixed trial types: single-option trials, peak trials, and binary-choice trials, all separated by a 45-s ITI.

Single-option trials began with the green centre key flashing (700ms ON, 300ms OFF). A single peck to this key switched its light off and caused one of the side keys to start flashing one of four possible symbols (for details, see Supplementary Figure 1, pp. 43)³ at the same rate used for the centre key. A peck to this key turned it steadily on and initiated the FI associated with the displayed symbol (FI 3, 6, 12, or 24 s). The time between pecking the green centre key and pecking the flashing side key is hereafter referred to as the latency to respond. The first peck after the delay elapsed turned the side key symbol off and produced two food pellets followed by the ITI.

Peak trials were identical to single-option trials except that once the flashing side key was pecked, the symbol remained continuously on for three times its typical delay, and then extinguished without reinforcement. These trials were used to determine the animals' knowledge of the delay to reward associated with each particular option (Catania, 1970).

Binary-choice trials involved simultaneous presentations of two of the four options arranged in the 6 possible pairs. These trials were similar to single-option trials with the exception that pecking the flashing centre key caused two different symbols, one on each side key, to begin flashing simultaneously. A single peck to one of these keys turned the selected symbol continuously on, triggered the appropriate delay, and extinguished the unselected option. Thus, a bird committed itself to one of the options with its first peck to a flashing symbol. Once an option was selected, the trial proceeded as a regular single-option trial.

In all trial types, if the bird failed to peck the flashing centre or side keys within 20 s from their onset, all key lights were turned off for 10 s. Afterwards, the trial was repeated a maximum of four times. In single-option and binary-choice trials, if the bird

³Not included in the published paper.

failed to peck the steady side key within 20 s after its associated delay had elapsed, the next trial began after the intervening ITI.

Starlings received one session per day for 30 days. Sessions ended after 176 trials or 5 hours from the session start, whichever came first. Each completed session consisted of 144 single-option trials (36 per option), 24 binary-choice trials (4 per pair of options) and 8 peak trials (2 per option), all with side key allocation counterbalanced across trials. There was a 45-minute break after half a session was completed, to avoid potential satiation effects. Trials occurred in pseudorandom order with the constraint that no two peak or two binary-choice trials could occur consecutively. Symbol/delay pairings were partially counterbalanced across birds.

2.2. Results

Pecks in all trials were recorded in 250-ms bins. Only the last 10 days of the experiment are considered in the analysis, as visual inspection of the daily peak trials indicated that prior to this stage birds were still learning the timing properties of each option⁴. One bird was excluded from all analyses due to showing a strong side preference.

2.2.1. Timing

Figure 1a shows the relative number of pecks per second for peak trials with each option averaged across subjects. The pecking rate reached its maximum near the reward time associated with each option; although, not surprisingly, absolute peak rates

⁴The SCM is a steady-state performance model, not designed (in its present form) to deal with data from acquisition of new behaviour. The SCM takes learning about the properties of each option for granted (i.e., acquired through principles at least similar to the ones proposed in reinforcement-driven models) and it is built under the assumption that the animals knowledge about the properties of each option is reflected both on the typical performance on peak trials (for timing-related contingencies - see Catania, 1970) and in differential latencies (or response times) to accept options associated with different contingencies. For these reasons, only data after stability were included in the analyses and model testing.

decreased (not shown in figure) and spreads increased with longer delays. This confirms that birds accurately discriminated between the delays associated with each option.

2.2.2. Latencies

According to SCM, latencies to accept each option when encountered alone (i.e., in single-option trials) should be sensitive both to the option's properties and to the properties of the background of alternatives in the environment. As such, SCM predicts that single-option latencies should be an increasing function of the options' associated delays. Figure 1b shows the median latencies for each option during single-option trials averaged across subjects. As predicted, latencies increased with increasing delays. A repeated-measures analysis-of-variance (ANOVA) conducted on natural log transformed latencies (Grafen & Hails, 2002) confirmed a significant effect of delay [$F(3,18) = 82.27$, $p < 0.001$]. Planned paired samples t -tests showed that, for all six pairwise comparisons, the latency for the shorter option was significantly shorter than the latency for the longer one [all $ts(6) < -3.15$, $p < .021$].

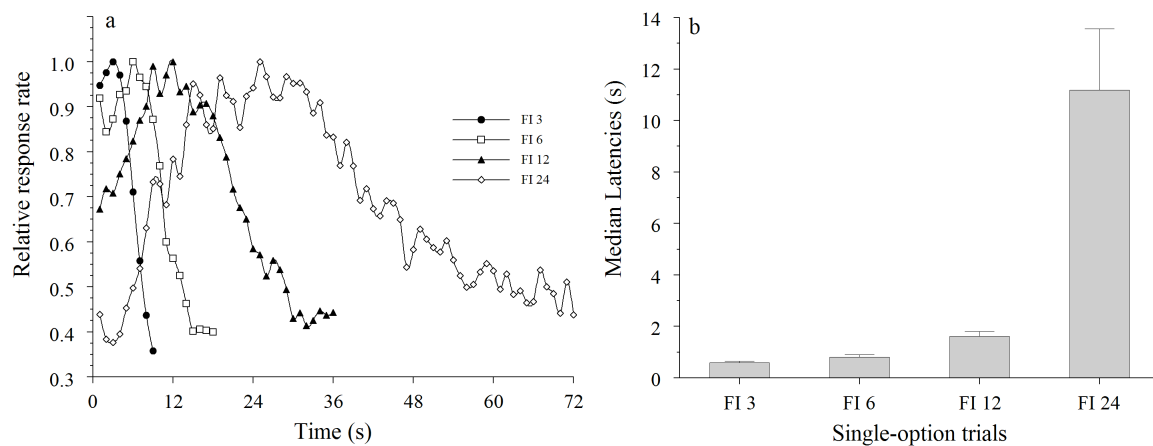


Figure 1. (a) Relative number of pecks per second during peak trials for each option, averaged across subjects. Response rate curves were normalized by dividing each value by the curves' maximum rate; (b) Median latencies for each singly presented option, averaged across subjects (+SEM). For data analysis, trials in which birds failed to peck the flashing side key yielded a 20-s latency.

2.2.3. Choices

When given a choice between two options, birds chose the option associated with the shorter delay almost exclusively (range across binary-choice pairs: .87 - .99). The bars in Figure 2a plot the average proportion of choices of the shorter programmed delay in each binary-choice pair. A repeated-measures ANOVA conducted on arcsine square-root transformed proportions (Grafen & Hails, 2002) showed no significant difference in preference for the shorter FI across the six treatments [Greenhouse-Geisser adjusted $F(1.618, 9.705)=2.92$, $p=.108$]. This reflects the extremity of choice in all pairings. This was also observed when binary choices were grouped by ratio of shorter to longer delays (not shown in figure). Here, however, a repeated-measures ANOVA revealed a significant effect of ratio [$F(2,12)=14.44$, $p<.01$], with planned t -tests indicating that preferences were significantly lower when one option was twice as long as the other compared to when one option was four or eight times as long as the other [smallest absolute $t(6)=3.90$, $p<.01$]. In summary, choices for the shorter delay increased from 89% to 98% and 99% as the ratio between the options' FI changed from 1:2 to 1:4 to 1:8, respectively. Taken together these results indicate that, for the values used, preferences were extreme, reducing the scope for the analysis of partial preferences. These extreme preferences make it impossible to test one of the predictions of SCM: that latencies for the least favoured option should be shorter in choice than in single-option trials. This cannot be tested here simply because there were not enough choices of the less-preferred options to run the analysis.

2.2.4. Predictions from SCM

To test SCM, we predicted the outcome of each choice trial, using the latencies shown for each option in its most recent single-option trial. For instance, when animals faced a choice between the options leading to a 3 and a 6-s delay, we considered the latencies from the most recent FI 3 and FI 6 single-option trials. The predicted choice was

the option with the shorter latency. For each binary-choice pair, we then calculated the proportion of trials for which the model predicted that birds would choose the option signalling a shorter delay and used this proportion as the overall preference strength predicted by the model (i.e., our measure of global performance). These data are represented by the dots in Figure 2a. Overall, preferences for the shorter FI were more extreme than predicted. Under-prediction of preferences seemed to relate to the ratio of the FIs involved. This is perhaps unsurprising as for FI ratios of 1:4 and 1:8, both observed and predicted values reached a ceiling of absolute preference. Although the model consistently underestimated observed preferences, its predictions capture the observed pattern of preference (compare dots with bars). Visual inspection of the data indicates no substantial differences between observed and predicted values except in the 3 vs. 6 condition. This was, nonetheless, expected as these were the options with the smallest difference in median latencies during single-option trials (cf. Figure 1a)

Figure 2b shows the predictive performance of the model in the local analysis. In this case the overall measure of predictive accuracy is the proportion of choice trials for which the prediction of the SCM agreed with the animal's selection.

Overall, the model correctly predicted 84% of all individual choices (range across treatments: 71 – 99%). One-sample t-tests confirmed that the proportion of correct predictions for each binary-choice pair was significantly above chance [smallest absolute $t(6)=688.33$, $p<.001$].

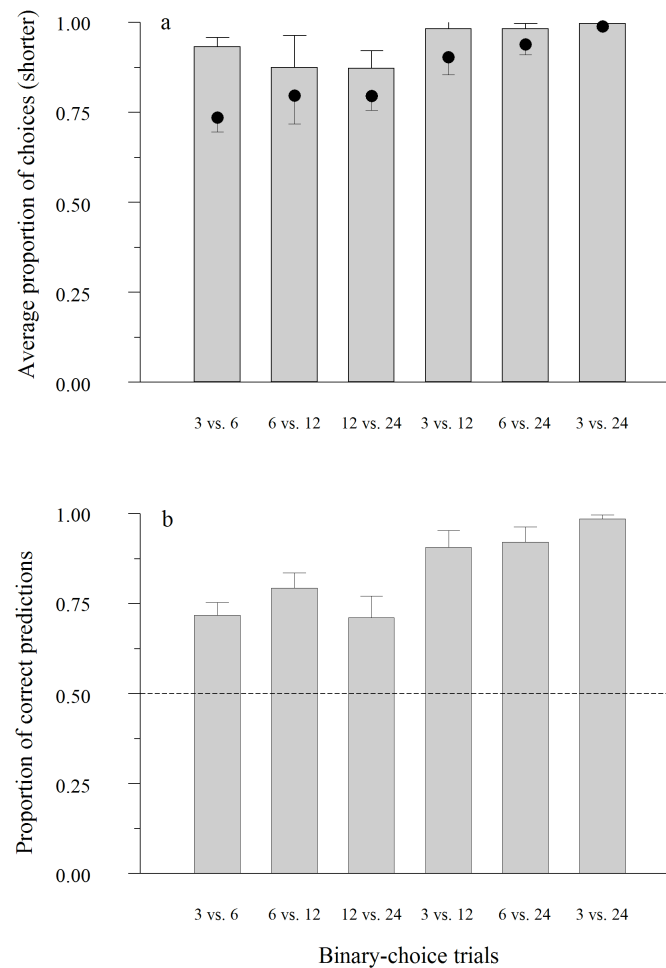


Figure 2. (a) Bars represent average proportion of choices for the shorter delay in each binary-choice pair (+SEM); Dots show the strength of preference for the shorter delay predicted by SCM for each binary-choice pair (-SEM); (b) Proportion of choices accurately predicted by SCM for each choice pair. The horizontal dashed line indicates chance level. Notice that the first three bars refer to contrasts where the shorter delay was half the longer one, the next 2 bars when they were one quarter and the last bar when they were one eighth.

3. Discussion

SCM proposes that, at least under laboratory conditions, when animals make choices between simultaneously present alternatives they do not comparatively evaluate the different options. Instead, choice is generated by the same mechanism that controls responding when options are faced alone. Differences in subjective value of an option relative to its environmental background determine the readiness (immediacy) to respond

to it, expressed as a distribution of latencies in single-option encounters. The latencies on which the model is based are conceived as distinct from reaction times, reflecting the sum of the subjects' ability to respond as swiftly as possible (the reaction time) and a predominantly motivational component expressing willingness to act towards that opportunity. If two options are met simultaneously, this mechanism acts independently (i.e., in parallel) on the stimulus associated with each option. The option that generates a shorter latency is 'chosen' at a behavioural level.

Choices can be predicted under the SCM rationale through various methods. One option, that could be called global, uses the overall distribution of latencies from single-option trials with each option to predict the overall proportion of choices. This has the cost of ignoring the temporal structuring of the data. Temporally local fluctuations in motivation can unfairly reduce the predictive power of the model. An alternative, that we preferred to use here, predicts each choice using latencies from the immediately previous single-option trials for each option under consideration.

Using this method, SCM correctly predicted 84% of all individual choices, with some variance between treatments and subjects. This suggests that choices can be predicted from latencies observed during no-choice situations but it is not immediately obvious how it can be compared with the performance of other potentially competing models, as few models generate trial-by-trial predictions. In the rare cases when they do, models that perform well over aggregates of trials often fail when tested trial-by-trial (e.g., Prokasy & Gormezano, 1979) found that although the Rescorla-Wagner model was a good global predictor it failed when responding was analysed trial-by-trial). SCM showed the opposite trend: it had a good performance on the local analysis, but a poorer one on the aggregate. Since the latter is actually discarding information (about temporal fluctuations) it would seem that local testing offers stronger support.

It may be argued that considering only the latencies (one per option) of the two most recent single-option trials previous to each choice neglects potentially valuable information. If the success of local predictions is due to temporal fluctuations in the subject's state spanning over groups of trials, then better estimates of the latencies in a given trial may in fact be computable as weighted averages of trials in the temporal neighbourhood of the choice, including both preceding and forthcoming trials.

As an exploratory exercise we tried making predictions using a weighted average of past single-option trials, including 2, 4, 8, 16, or 32 single-option trials (per option) to predict the subsequent binary-choice. To account for recency, we used a hyperbolically weighted moving average, with each latency's weight inversely proportional to its distance from choice. As shown in Figure 3, the accuracy of predictions for both preference strength (right axis) and individual choices (left axis) significantly improved as the number of trials considered increased [smallest $F(5,30)=28.22$, $p<.001$]. But this observation raises familiar problems in model testing. Using an estimator of latencies from a set of single option trials in the temporal vicinity of each choice (we only used the past, but there is no reason why this estimator could not include the following trials) is better than using exclusively the most recent single option trials. It would seem that temporal aggregation of trials is a good idea, but the precise algorithm to do this is yet to be defined. However, ad-hoc trial averaging to make predictions has its own problems, as it necessarily includes using the same single-option latencies to predict more than one choice, affecting the independence between predictions as well as adding new assumptions about the steepness of discounting. This can only be obtained by parameter fitting, which we aim to avoid as much as possible.

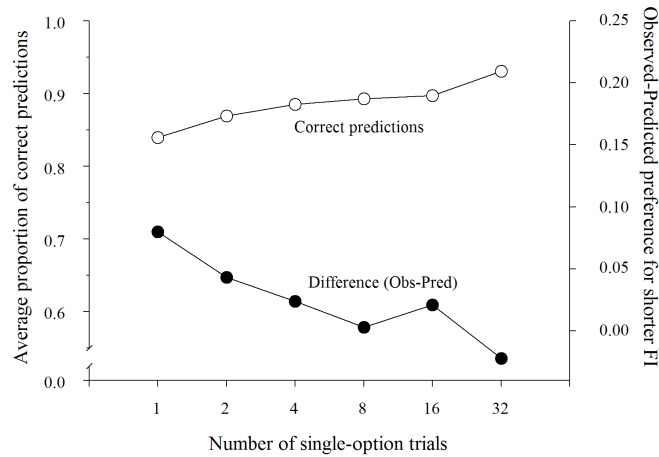
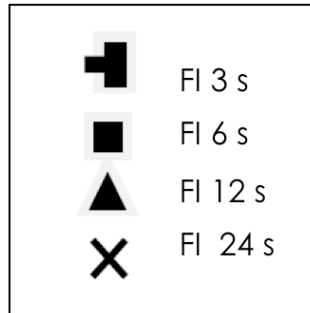


Figure 3. Proportion of choices accurately predicted by SCM (open circles, left axis) and difference between observed and predicted preference strengths (solid circles, right axis) as a function of the number of single-option trials considered. Both are averages across subjects and binary-choice pairs. The weighted moving average was calculated as follows:

$$\frac{\sum_{i=1}^n l_{-i} \cdot i^{-1}}{\sum_{i=1}^n i^{-1}}$$

where $n = 1, 2, 4, 8, 16$ or 32 , i corresponds to the i th place preceding the current choice and l =latency.

In short, SCM predicts individual choices with considerable success, whether choices occur in a two- or multi-alternative environment. Although the extreme preferences observed in this experiment prevent us from testing the prediction that latencies for the least favoured option should be shorter in choice than in single-option trials, results strongly support the predictive power of single-choice latencies on subsequent choices. Experiments yielding less extreme preferences permit more direct evaluation of the SCM's claim that animals do not compare the merits of each option at the time of choice. In the meantime, these results add to a growing body of evidence supporting the view that latencies and choices are behavioural expressions of the same valuation process acting independently on each option during both multiple and single option encounters.

4. Supplementary information (not included in the publish paper)

Supplementary Figure 1. Illustrative example of symbol/delay pairings used in the experiment (all pairings were partially counterbalanced across birds).

5. Acknowledgments

This research was supported by BBSRC Grant BB/G007144/1 to AK. MV, TM and JA were supported by an Intra-European Marie Curie Fellowship, a doctoral grant from the Portuguese Foundation for Science and Technology, and a BBSRC Grant BB/G007144/1, respectively.

6. References

- Bateson, M. 1993. Currencies for decision-making: the foraging starling as a model animal. Unpublished D. Phil dissertation. University of Oxford, Oxford, 143p.
- Catania, A.C. 1970. Reinforcement schedules and psychophysical judgments: A study of some temporal properties of behavior. *The Theory of Reinforcement Schedules*: 1-42.
- Charnov, E.L. 1976a. Optimal Foraging: Attack Strategy of a Mantid. *American Naturalist*, The, 110: 141-151.
- Charnov, E.L. 1976b. Optimal foraging, the marginal value theorem. *Theoretical population biology*, 9: 129-136.
- Fantino, E. and Abarca, N. 1985. Choice, optimal foraging, and the delay reduction hypothesis. *Behavioral and Brain Sciences*, 8: 315-329.
- Freidin, E., Aw, J. and Kacelnik, A. 2009. Sequential and simultaneous choices: Testing the diet selection and sequential choice models. *Behavioural Processes*, 80: 218-223.
- Grafen, A. and Hails, R. 2002. *Modern statistics for the life sciences*. Oxford University Press, Oxford, 351 pp.
- Hick, W.E. 1952. On the rate of gain of information. *Quarterly Journal of Experimental Psychology*, 4: 11-26.
- Krebs, J.R., Erichsen, J.T., Webber, M.I. and Charnov, E.L. 1977. Optimal prey selection in the great tit (*Parus major*). *Animal Behaviour*, 25: 30-38.
- Prokasy, W.F. and Gormezano, I. 1979. The effect of US omission in classical aversive and appetitive conditioning of rabbits. *Animal learning & behavior*, 7: 80.

Shapiro, M.S., Siller, S. and Kacelnik, A. 2008. Simultaneous and sequential choice as a function of reward delay and magnitude: Normative, descriptive and process-based models tested in the European Starling (*Sturnus vulgaris*). Journal of Experimental Psychology: Animal Behavior Processes, 34: 75-93.

Cognitive mechanisms of risky choice: Is there an evaluation cost?

[Aw, J., Monteiro, T., Vasconcelos, M. and Kacelnik, A. 2012. Cognitive mechanisms of risky choice: Is there an evaluation cost? Behavioural Processes, 89: 95-103¹.]

1. Introduction.....	50
1.1. Averaging outcomes.....	54
1.2. Variance in information processing mechanisms: the Weber-Fechner Law.....	55
2. Materials and Methods.....	57
2.1. Summary of the general procedure.....	57
2.2. Subjects.....	58
2.3. Apparatus.....	58
2.4. Detailed protocol.....	59
2.4.1. Baseline training and testing	
2.4.2. Stability criterion	
2.4.3. Data analysis	
3. Results.....	62
3.1. Preferences.....	62
3.2. Latencies to respond.....	63
3.3. Timing.....	65
3.4. Indifference points.....	66
3.5. Testing the SCM.....	67
3.5.1. Predicting choice from forced trials' latencies	
3.5.1.1. Strength of preference	
3.5.1.2. Proportion of individual choices predicted accurately	
3.5.2. Predicting shifts in latencies	
4. General conclusions.....	72
5. Acknowledgments.....	74
6. References.....	75

¹doi: 10.1016/j.beproc.2011.09.007

1. Introduction

The present study deals with two aspects of foraging decisions: how do subjects attribute value to sources of reward, and what is the process by which they arrive at individual choices. With regard to the first issue, we consider propensities to under- or over-value food sources with respect to their mean rate of reward as a function of the variability of their outcomes (see further discussion of this topic in Shapiro, Schuck-Paim, and Kacelnik, 2012). With regards to the second, we examine how animals use valuations acquired and expressed in sequential encounters (i.e., when meeting one food source at a time) to make choices when more than one opportunity is simultaneously present. Both topics have been discussed on their own elsewhere, but here we treat them jointly for the first time. Our basic question is: when animals make choices between stochastic sources of reward, do they, at the time of choice, evaluate the properties of each alternative, using time for the cognitive operation, or do they treat each alternative independently? If the latter, a choice would simply reflect action towards the option eliciting the fastest response time. Risky choice should *a priori* be a better arena to compare the models because evaluating an option with variable outcomes may be more complex, and then involve longer evaluation times, if they exist at all.

We focus on two classes of choice models, labelled the Tug-of-War model (ToWM) and the Sequential Choice model (SCM; for a review see Kacelnik et al., 2011 – *Appendix 1*²). Both assume that subjects value options as a function of factors experienced during learning, notably the profitability of each outcome (defined, following foraging theory, as the ratio of amount of food over delay to food), the profitability of alternatives present in the same environment (e.g., Shapiro, Siller, and Kacelnik, 2008), and the state of the subject at the time of acquisition (e.g., Kacelnik and Marsh, 2002; Pompilio and

²For a primer, see *Chapter 1*, section 3.

Kacelnik, 2005; Vasconcelos and Urcuioli, 2008). However, the models differ in how these values control choice.

According to the ToWM, when an agent faces an opportunity for reward it simply acts on it, but when it faces two or more simultaneous opportunities it undergoes an evaluation to compare them, then acts on whichever is more favourable. This evaluation may be expected to have a time cost, so that acting towards each option may take longer when an alternative is present than when the same option is encountered alone (where no time-consuming comparisons would be necessary). In the case of risky choice, the subject may know that each option yields a characteristic mean and variance in outcomes, and to make a choice it may need to contrast both measures. For instance, a risk prone subject may be caricatured as thinking, “option A yields higher mean returns, but it has a lower chance of a jackpot, hence I will prefer B”. For normative considerations, the evaluation mechanism can be assumed to implement an adaptive trade-off between the time and processing costs of such evaluations and the advantages of increasing the chance of choosing the best option.

The SCM postulates that no such evaluation occurs, because simultaneous choices are rare in nature and no special adaptations exist to deal with them. Instead, it assumes that the circumstances that have influenced the evolution of action have predominantly been choosing between pursuing a single option and the overall environmental background. Charnov (1976) identified the conditions under which the overall rate of gain would be maximized by rejecting leaner options to pursue more profitable ones. The SCM proposes a mechanism that could be appropriate to maximize rate of intake in single-option situations such as those foreseen by Charnov (for details regarding the relation between Charnov’s Diet Choice Model and the SCM, see Freidin, Aw, and Kacelnik, 2009).

According to SCM, options encountered on their own are acted upon faster the richer they are respect to background opportunities, probably reflecting time taken to scan the environment for alternatives. Due to different sources of external and internal noise, the presence of each option elicits a frequency distribution of times to act (i.e., latencies). Critically, the SCM further postulates that when two opportunities are faced simultaneously, they elicit samples from the same latency distributions as when they are met sequentially (for a similar approach to this last point, see Blough, 2011; Ratcliff, Van Zandt, and McKoon, 1999). The joint expression of two distributions of latency to act means that they cross-censor each other, so that whichever distribution yields a shorter value in a particular simultaneous encounter is translated into action, the other one being masked and remaining unobserved. Such a cross-censorship process should result in shorter latencies to act towards each of the alternatives in a simultaneous choice than when the same alternatives are faced in isolation, because the left tails of each distribution (which yield short latencies) would produce more “winners” than right tails (which yield longer latencies), so that all observed latency distributions would be shifted to the left. Consequently, the distributions of latencies collected during simultaneous choices would be necessarily composed of shorter latencies (i.e., winners) when compared with the latency distributions from the same options when acted upon in isolation.

Several experimental studies have tested the contrasting predictions of these mechanisms. All of them (e.g., Freidin, Aw, and Kacelnik, 2009; Mazur, 2010; Shapiro, Siller, and Kacelnik, 2008; Vasconcelos et al., 2010) failed to detect a time cost for decision in simultaneous choice, and two reported either a significant (Shapiro, Siller, and Kacelnik, 2008) or marginally significant (Mazur, 2010) latency shortening during choices, thus favouring the SCM over the ToWM. However, these published tests used deterministic protocols, so that little evidence exists so far to favour one or the other when

the relation between actions and outcomes is probabilistic (but see Aw, 2008 for an exception). Since stochastic problems involve greater complexity because of the possible additional role of the second moment of outcome distributions, evaluations may be more time consuming, so that distinctions between the two categories of models may be more obvious.

Here we compare the models' performance in probabilistic (risky) environments, using European starlings as subjects. Firstly, we looked at how well SCM can predict the level of preference in simultaneous choices from the latency distributions observed in forced trials (in which only a single option is present); the ToWM and all other models of risky choice are mute in this respect, so this type of evidence supports or contradicts the SCM without addressing the alternatives. While predicting choice proportions from latencies in no-choice situations does not amount to establishing a causal link between latencies to act and choices, it is more informative than a mere correlation, because the reverse (predicting latencies in no-choice situations from choices) is never possible. Lastly, we compared latencies in choice trials against latencies towards the same options in single-opportunity (or forced) trials. While the ToWM predicts that latencies to choose should be longer due to the time of cognitive evaluation, the SCM predicts that they should be shorter due to cross-censorship.

Although we study the mechanisms underlying risky choice here, it is relevant to refer to other perspectives of risk sensitivity, because different theories make specific predictions about preferences between fixed and variable sources of reward, and we use these predictions to examine the data. As these theories are well described elsewhere, we only touch on them here, briefly dealing with two issues that are relevant to the present study: how animals compute averages of foraging information and how they perceive and represent this information in memory. Both issues affect predictions for how the values of

fixed and variable sets of outcomes are compared, and hence will be relevant to our analyses.

1.1. Averaging outcomes

Classical foraging studies reasonably start from the assumption that everything else being equal, natural selection should favour organisms that collect more food per unit of time (Stephens and Krebs, 1986). Thus, food sources should be preferred according to the ratio of the expected gains to expected time that a forager using each source exclusively for a given period would experience. For short, this currency is known as the Ratio of the Expectations, or RoE. Since only mean gains and mean times enter the equation, variance in outcomes has no impact on RoE. Empirical work however has suggested that RoE is not the most successful predictor of choice. An alternative postulates that foragers compute the ratio of gains to time cost (known as profitability) after each foraging event (say a prey capture) rather than across a given foraging period, and that time components other than those between the act of choosing a target and receiving the outcome play a negligible role in how options are ranked (Bateson and Kacelnik, 1996). This currency is known as the Expectation of the Ratios (EoR, Equation 1).

$$EoR = \frac{\sum_{i=1}^n \left(\frac{G_i}{T_i} \right)}{n}, \text{ Equation 1}$$

where i identifies an event, G_i is the amount of food gained and T is the time between the beginning of the event (say starting to chase an identified prey) and its end (eating the item), excluding time components such as search time that are common to all prey types. Notice that a disadvantage of this currency is that events with the same ratio of gain to time have identical impact on the valuation of the source regardless of the absolute gains and

times involved. Choosing food sources according to EoR leads to overvaluation of sources that are more variable in time, and can objectively lead to preference for options that, over an extended period, yield lower rates of return. The reason why EoR is the rate index that best predicts choices by animals may be found in the process for acquisition of associative strength by the stimuli that identify each source of reward (see further discussions in Killeen, 1968; Bateson and Whitehead, 1996; Shapiro, Schuck-Paim, and Kacelnik, 2012; Kacelnik, 2003).

What matters to the present study is that Equation 1 shows that when an option delivers two equiprobable delays to reward (say T_1 and T_2), the EoR of that option is equivalent to that of a fixed option always delivering a delay equal to the harmonic mean of the two equiprobable delays (for the original proposal of averaging schedule times by the harmonic mean, see Killeen, 1968). If, on the other hand, unpredictability is introduced in the amount of food offered by a variable option (say by delivering equiprobably G_1 and G_2), with no variance in times, then EoR is the same as that of an option always delivering a gain equal to the arithmetic mean of these two amounts.

1.2. Variance in information processing mechanisms: the Weber-Fechner Law

The second issue has to do with how preference between fixed and variable options depends not only on the variability of the food sources, but also on additional variance introduced by the information-processing mechanisms, an approach known as Scalar Utility Theory (SUT; Reboresda and Kacelnik, 1991). A ubiquitous property of such mechanisms is the Weber-Fechner law, which results in error (i.e., perceived variance) in internal representations being proportional to the magnitude of objective stimuli. Functionally, the Weber-Fechner law is likely to be a common biological solution to the need to cope with large ranges in data values by encoding information using logarithmic or

power law transformations and decoding this information with a constant error in the transformed values. The reason why this matters in the present case is that when two options with the same mean but different variance in outcome are compared, preference should favour the less variable alternative if bigger outcomes are preferred (as for food) but favour the more variable one if smaller outcomes are preferred (as with delays to food). For full justifications of this prediction see Reboresda and Kacelnik (1991), Bateson and Kacelnik (1995; 1996) and Kacelnik and Brito e Abreu (1998). Under some special plausible assumptions (i.e., Gaussian memory representations with constant coefficient of variation), when one option delivers two equiprobable outcomes and the other a fixed one, if one assumes that each choice is based on a single random sample from the memory distribution for each option, SUT predicts indifference when the fixed option is at the geometric mean of the two values of the variable one.

Summarising, the main differences between models discussed in this study in relation to choices between a fixed and a variable option with two equiprobable outcomes are as follows: i) EoR predicts points of indifference for delay and amounts hypothesising an averaging process derived from associative learning. When the fixed delay is shorter than the harmonic mean of the two possible delays of the variable option, the fixed option yields a higher EoR, and the same occurs when the fixed amount is larger than the arithmetic mean of the variable set. This model predicts the sign but not the strength of preference. ii) SUT makes its predictions on the bases of psychophysics and memory processes. For SUT (with some restrictive assumptions) the fixed option should be preferred when its delay is shorter or its amount larger than the geometric mean of the variable set. Variance in delay should add value while variance in amount should decrease it. iii and iv) ToWM and SCM make predictions based on hypotheses about how the subjective value of each option acts at the time of choice. The variables used to make

predictions about choice are not the amounts and delays of the options directly, but the times to respond that they cause. The crucial relation is that between latencies to respond in sequential and in simultaneous encounters. ToWM argues that when two options are met simultaneously preference is constructed through a time-consuming comparison, while SCM states that the value of each option influences action independently: the observed action reflects the option eliciting a shorter latency. Regarding the point of indifference, SCM does not predict its location, but states that the indifference point marks the condition under which the medians of the distribution of latencies to take both options in sequential encounters is equal. The ToWM in its present form does not make precise quantitative predictions but expects latencies in choice trials to be longer than those in single-option trials.

2. Materials and Methods

2.1. Summary of the general procedure

Starlings were pseudorandomly assigned to one of two treatments (amount or delay), each of which consisted of 5 separate conditions. In all cases, we first trained starlings to encounter two foraging options in separate trials, one (Variable) that delivered two equiprobable outcomes, and another (Fixed) that within a treatment and condition delivered the same outcome in every trial. Once the birds were acquainted with these options in sequential random alternation, we offered them choices between them by presenting both options simultaneously. The variable option offered either variable delays to food or variable amounts of food, depending on the bird's treatment (i.e., amount or delay treatment). Within each of these two treatments, the parameters of the variable option were constant across all conditions, while the value of the fixed one varied across five conditions ranging between the smallest and largest of the two outcomes of the

variable alternative. Our dependent variables were the latencies to accept options in forced and choice trials, as well as the proportion of choices for the fixed option.

2.2. Subjects

Twelve experimentally naïve adult wild-caught European starlings (*Sturnus vulgaris*), captured and held in captivity under Natural England license 20073610, participated in the experiment. Prior to testing, birds were housed socially in an outdoor aviary (3m high x 3.2m wide x 4m long) where they received *ad libitum* food (a mixture of turkey crumbs, Orlux© pellets and mealworms, *Tenebrio sp.*) and continuous access to fresh drinking and bathing water.

During the course of the experiment, starlings were moved to individual indoor cages, which were visually, but not acoustically isolated. Indoor temperatures ranged from 13 to 15°C and lights followed a 12:12 light:dark schedule with daylight from 0700 to 1900, and gradual transitions at dawn and dusk. Starlings were rewarded with BioServ 20mg precision pellets throughout the experimental session (0800-1300) and provided with three hours of free access to turkey crumbs (1400-1700) and 10 mealworms daily. This regime maintains starlings at approximately 90% of their free-feeding weight (Bateson, 1993) and was conducted in accordance with the University of Oxford ethical protocols. Birds had continuous access to drinking water and received bathing trays every other day.

2.3. Apparatus

Tests took place in the home cages (120 cm long × 60 cm wide × 50 cm high), which were equipped with two perches, one at each side. The back wall of each cage contained an operant panel with a central food hopper and three circular response keys (3 cm in diameter), one central and two lateral, that could be transilluminated with distinct

colour cues³. The hopper had an entrance 4 cm wide $\times$ 3.5 cm high and was illuminated whenever food was delivered. Trials were governed by custom software running on the Microsoft® Windows® operating system attached to an Animal Behavior Environment Test System (Campden Instruments®) via WhiskerServer©.

2.4. Detailed protocol

Each individual received one experimental session per day, beginning at 08h00 and ending after 176 trials or 5 hours, whichever came first.

Birds were randomly assigned to either the amount or delay treatment. Each treatment consisted of 5 conditions, representing different values for the fixed option. Transitions between conditions occurred between sessions when stable preferences were observed (see section 2.4.2). The order of conditions was pseudorandomized using a modified Latin square.

In the delay treatment, subjects chose between a fixed option, F, that offered a fixed delay to food, D_F , and a variable option, V, that offered a mix of two equiprobable delays, D_{VS} and D_{VL} . The two equiprobable delays in option V remained constant across all conditions at $D_{VS} = 5$ s and $D_{VL} = 25$ s. The delays in the fixed option were, in the five experimental conditions, 5, 10, 15, 20 and 25 s. Note that the central condition is located at the arithmetic mean (15 s) of the two variable delays and that 10 s falls between their harmonic and geometric means (8.33 and 11.18 s, respectively). Both F and V delivered the same amount of reward (2 pellets).

In the amount treatment, subjects made choices between a fixed option, F, that offered a fixed amount of food, A_F , and a variable option, V, that offered a mix of two equiprobable numbers of pellets, A_{VS} and A_{VL} . In this treatment, all rewards were

³For this experiment, red and green cues signalled the fixed and variable options, counterbalanced across individuals.

delivered after the same fixed delay (22.5 s). The two outcomes of option V remained constant across all conditions at $A_{VS} = 1$ pellet and $A_{VL} = 5$ pellets. The number of pellets in the fixed option remained constant within each condition, but varied between A_{VS} and A_{VL} across conditions, taking the values of 1, 2, 3, 4, or 5 pellets. In this case, the geometric and arithmetic means of the two equiprobable amounts were 2.24 and 3 pellets, respectively.

2.4.1. Baseline training and testing

All starlings were pre-trained to peck the keys using autoshaping as described by Aw et al. (2011). To ensure birds learnt the options' properties before experiencing choices, at the start of each condition (both in the delay and the amount treatment), subjects received 2 sessions where each trial had a single option available, either F or V. These sessions were composed of 176 trials: 168 forced trials (84 per option) and 8 probe trials (4 per option). Forced trials began with the flashing illumination of the white central attention key. A peck to this key turned the central key off and began the flashing transillumination of one of the two lateral keys, counterbalanced across trials. A peck to the illuminated key turned it steadily on and initiated the programmed delay during which pecks were recorded in 500-ms bins. Once this interval elapsed, a single peck to the key turned the keylight off and delivered the programmed number of pellets, after which a 45 s inter-trial interval (ITI) was initiated. Half of these trials involved the presentation of option F (a fixed delay to or a fixed amount of food in the delay and amount treatments, respectively) and the other half involved the presentation of option V (one of the two equiprobable delays to or amounts of food in the delay and amount treatments, respectively). The two options were signalled with different coloured transillumination of the keys (red or green). Pairings of colours and treatments was balanced between subjects. The position of colours was pseudorandomized with options appearing equiprobably on

each side. If a bird failed to peck the key during the time it was flashing (a maximum of 20s) all keylights turned off and the ITI began after a 10 s delay. If the animal failed to peck the central key the same option was offered in the next trial after the ITI. Probe trials were identical to forced trials except that once the flashing side key was pecked, the light remained continuously on for three times the typical fixed option delay, and then extinguished without reinforcement. Probe trials were used to determine the animals' knowledge of the delay to reward associated with each option (Catania, 1970). Due to experimenter error, probe trials for the variable option in the delay treatment were only three times the length of the fixed delay in each condition.

After the two initial sessions in each condition, choice trials were introduced. These sessions included 144 forced (72 per option), 8 probe (4 per option) and 24 choice trials offering individuals choices between options F and V. Choice trials were structurally similar to forced trials except that once the central attention key was pecked, both lateral keys started flashing, one displaying the cue associated with option F and the other displaying the cue associated with option V, with side allocation counterbalanced across trials. A single peck to one of the flashing keys turned it steadily on and turned the unselected key off. The first peck after the programmed delay in the selected key elapsed turned its light off and delivered the programmed number of pellets for that particular option.

2.4.2. Stability Criterion

Subjects received a minimum of 4 testing sessions per condition and continued testing on a given condition until they were judged to be stable in their preferences. Stability was assumed after recording 3 consecutive sessions showing no trend in the proportion of choices for the fixed option, and a standard deviation in this proportion of less than 0.1.

2.4.3. Data analysis

Prior to analysis, all proportion and latency data were successfully normalized using an arcsine square root and a natural log transformation, respectively (Grafen and Hails, 2002). Following the procedure described in Vasconcelos et al. (2010), trials in which an animal failed to respond to an option were coded as having the maximum possible latency (which was 20 s). This may lead to a conservative estimate as it represents a latency to respond which is shorter than what would actually have been expressed if the trial had not been stopped. The last 3 days of testing (i.e., sessions at stability) in each condition were included in the analyses. A Type-1 error rate of 0.05 was adopted for all reported statistical comparisons.

3. Results

All subjects completed all conditions. The mean number of days per condition was 5.07 ± 0.34 (mean $\pm$ SE, range: 4-11 sessions) in the delay treatment, and 7.03 ± 0.32 (mean range $\pm$ SE, range: 6-13 sessions) in the amount treatment. A general linear model of number of sessions to stability with subject ($n=6$) as a random factor and condition ($n=5$) as a fixed factor found no significant effect of condition in the delay treatment [$F(4,20) = 1.48$, $p = 0.247$], and a significant effect in the amount treatment [$F(4,20) = 2.98$, $p = 0.044$], with subjects taking longer to complete conditions as the fixed amount increased.

3.1. Preferences

The average proportion of choices for the fixed option in each condition is shown in the top panels of Figure 1. As expected, in the delay treatment (top left), starlings showed a monotonically decreasing preference for the fixed option as its associated delay

to reward increased, and in the amount treatment (top right) a monotonically increasing preference for the fixed option as the number of pellets it delivered increased.

To examine the effect of condition on preferences in the delay treatment, we fitted a general linear model with the fixed option's delay to reward as a fixed factor and subject as a random factor, which found a significant effect of condition [$F(1.294, 6.471) = 36.483$, $p=0.001$, Greenhouse-Geisser correction for sphericity]. The corresponding analysis conducted in the amount treatment also yielded a significant effect of condition [$F(4,20) = 24.740$, $p < 0.001$].

In the delay treatment, Student's t -tests revealed that subjects significantly preferred the fixed option when $D_F = 5$ s [$t(5)=4.11$, $p=.009$] and V when $D_F = 15$, 20 and 25 s [smallest absolute $t(5)=8.32$, $p<.001$]. Preference at $D_F = 10$ s was below 50% but marginally outside conventional statistical significance [$t(5)=-2.44$, $p=.059$]. In the amount treatment, preference for the fixed option was significantly above chance when $A_F = 5$ [$t(5)=3.89$, $p=.011$] and below chance when $A_F = 1$ and 2 pellets [$t(5)=-19.65$, $p<.001$ and $t(5)=-4.06$, $p=.01$, respectively]. Preference in the remaining conditions, $A_F = 3$ and 4, did not differ significantly from chance [$t(5)=-.64$, $p=.549$ and $t(5)=0.57$, $p=0.591$, respectively].

3.2. Latencies to Respond

Means of each individual's median latencies to respond to options F and V when faced alone (i.e., in forced trials) are shown in the bottom panels of Figure 1. In the delay treatment (bottom left), latencies to respond to the fixed option were longer when this option had a longer programmed delay to reward. More interestingly, however, although the variable option did not change in its programmed properties, latencies to respond to it were longer when the alternative, fixed option was shorter. A general linear model with

option and condition as factors yielded a significant effect of option [$F(1, 5)=106.237$, $p<.001$] and a significant interaction [$F(4, 20)=37.418$, $p<.001$]. To further explore the effect of condition, separate general linear models were conducted for each option with latency as dependent variable and condition and subject as fixed and random factors, respectively. These analyses revealed that latencies to accept the fixed option significantly increased [Greenhouse-Geisser adjusted $F(1.537, 7.684)=17.056$, $p<.001$] and that, on the contrary, latencies to accept the variable option significantly decreased [$F(4, 20)=4.181$, $p=.013$] as the fixed delay increased.

For the amount treatment (Fig.1, bottom right panel), a general linear model with option and condition as factors yielded only a significant interaction [$F(4, 20)=36.106$, $p<.001$]. Separate general linear models for each option with condition and subject as fixed and random factors respectively showed that the effect of condition was significant for both options: latencies to accept the fixed option significantly decreased [$F(4, 20)=6.627$, $p=.001$] and, on the contrary, latencies to accept the variable option significantly increased [$F(4, 20)=15.684$, $p<.001$] as the number of pellets offered by the fixed option increased.

To summarize, the latency data confirm that our subjects were sensitive to the properties of each option in both treatments. They were affected both by the intrinsic quality of each option (the amount of or delay to reward) and the quality of the alternative present in the same environment (i.e., condition) as a background.

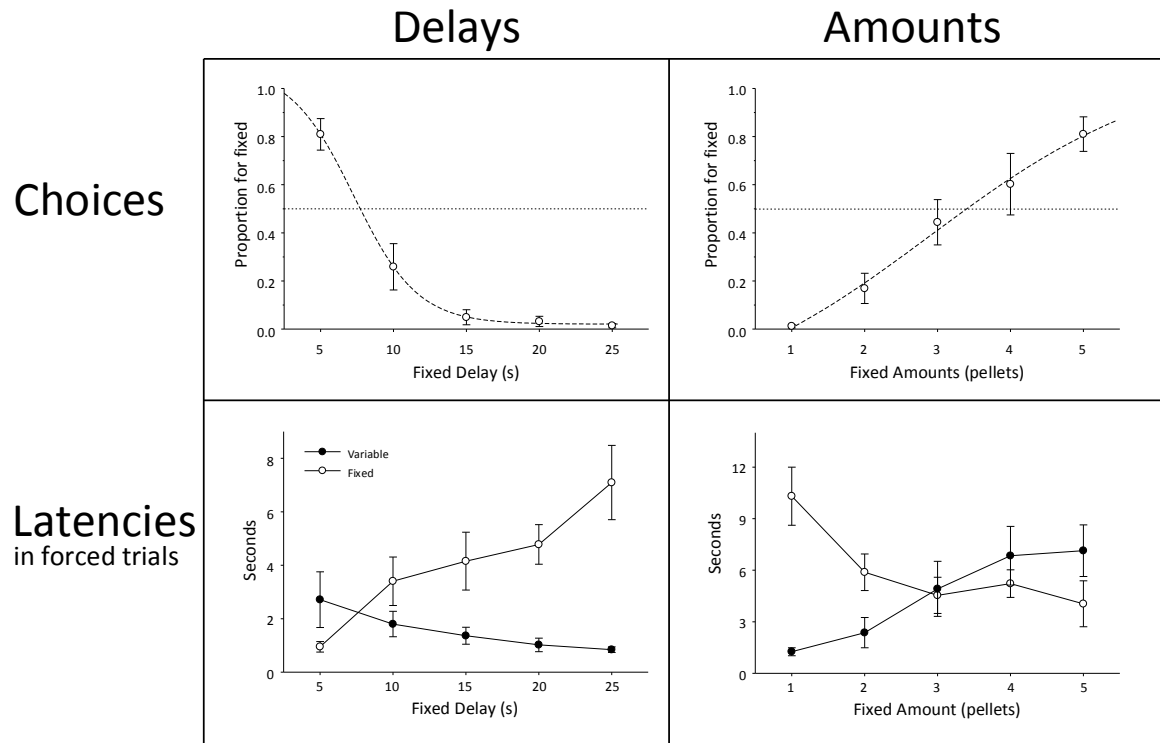


Figure 1. Preferences expressed as proportion of choices for the fixed option (top) and latencies during forced trials (bottom) in the delay (left) and amount (right) treatments. Where proportions are shown, data points represent mean proportions of choice in each condition ($n=6$). The dashed lines represent logistic functions fitted using an unbounded nonlinear least-squares method. Where latencies are shown, data points represent means of individuals' median latencies ($n=6$) to accept the fixed and variable when presented alone in forced trials. Error bars denote one standard error of the mean.

3.3. Timing

Evidence that starlings had an accurate perception of each option's temporal properties comes from probe trials. The top panel of Figure 2 shows the average number of pecks per second for both options in each condition of the delay treatment. For the fixed option (top left panel), the pecking rate reached its maximum near the programmed reward time in each condition, with peak rates decreasing and spreads increasing with longer delays. For the variable option (top right panel), starlings exhibited a bimodal distribution with peaks close to the two equiprobable delays. The position of these peaks did not seem to be affected by condition, suggesting that the preference and latency effects are unlikely to be mediated by distortions in timing. The bottom panel of Figure 2 shows the corresponding data for the amount treatment. Despite some variability, the birds'

maximum pecking rate was near the programmed delay both for the fixed (bottom left panel) and variable (bottom right panel) options. Overall, the timing results confirm that the birds had accurate representations of the delays associated with each option in both treatments.

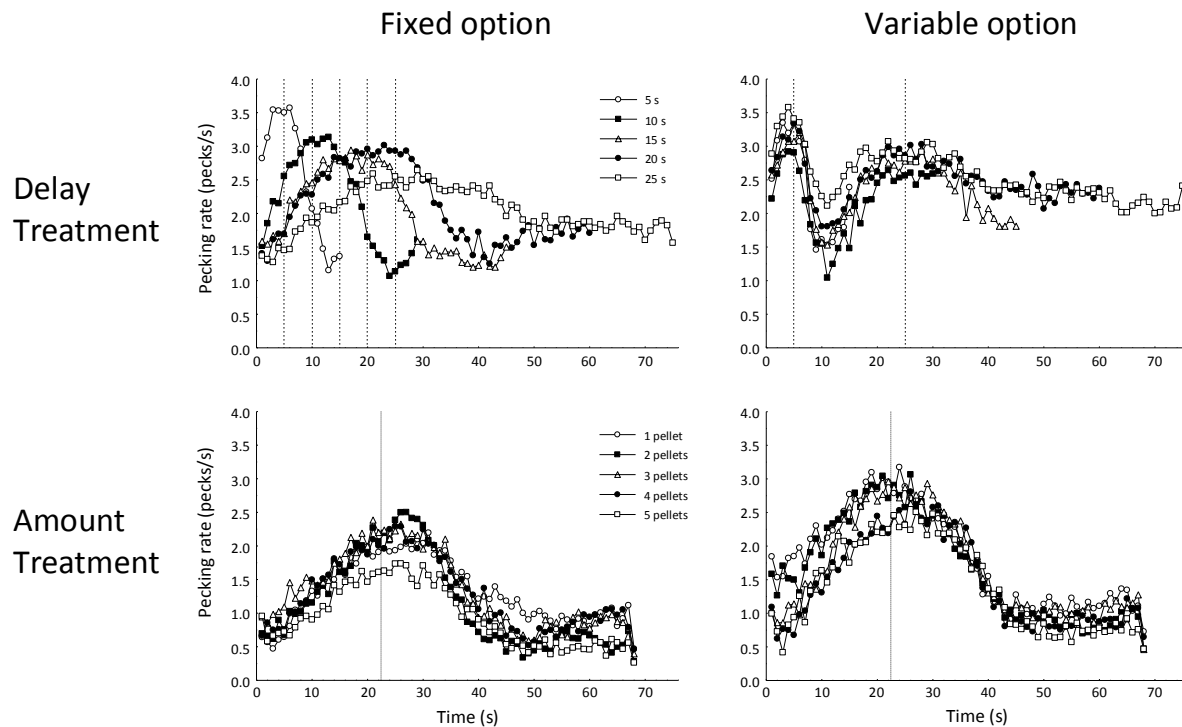


Figure 2. Average number of pecks per second for the fixed (left panels) and variable (right panels) options during probe trials for each condition in the delay (top panels) and amount (bottom panels) treatments.

3.4. Indifference Points

As mentioned in the Introduction, EoR and SUT make distinct predictions regarding the indifference points (i.e., the points at which animals are indifferent between the fixed and the variable option, also known as certainty equivalents or points of subjective equality). When variability is in delays, the two algorithms predict indifference at the harmonic and geometric means of the two possible delays in the variable option, respectively. When variability is in amounts, the predictions fall at the arithmetic and geometric means of the two possible numbers of pellets in the variable option, respectively. Figure 3 shows the harmonic, geometric and arithmetic means and the

estimated indifference point for each bird in the delay and amount treatments. Individual indifference points were obtained through nonlinear least-squares fitting of a logistic function to each bird's preference versus condition data. When variability was in delays (left panel), the mean indifference point was close to the harmonic mean and significantly below the geometric mean as revealed by one-sample t -tests [$t(5)=0.775$, $p=0.473$ and $t(5)=-3.510$, $p=0.017$, respectively]. The corresponding analyses in the amount treatment (right panel) revealed that the indifference point was close to the arithmetic mean and significantly above the geometric mean [$t(5)=0.610$, $p=0.569$ and $t(5)=-2.612$, $p=0.048$, respectively]. In summary, indifference point results from both treatments are consistent with the predictions of EoR but not with those of a version of SUT based on Gaussian representations and single sampling from memory.

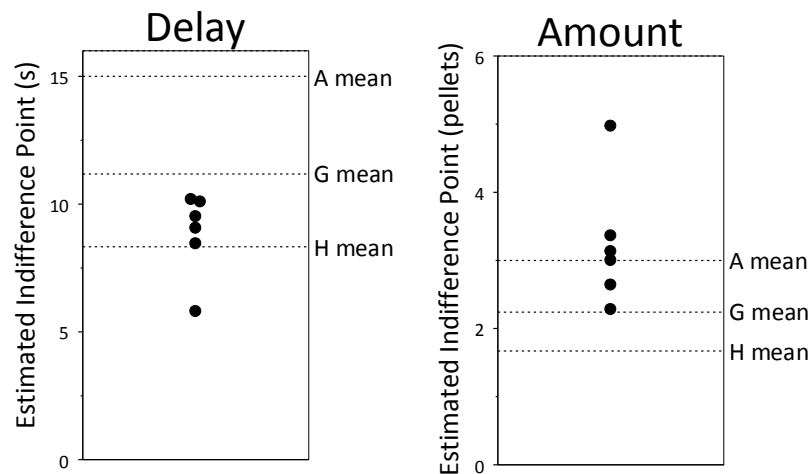


Figure 3. Predicted and observed indifference points in the delay (left) and amount (right) treatments. Each data point represents the estimated indifference point for each of the six subjects. To facilitate visualization, superimposed data points were horizontally offset. Horizontal lines represent the harmonic, geometric and arithmetic means of the two possible variable outcomes.

3.5. Testing the SCM

The SCM makes predictions about preference and latency in choice trials based on latencies in no-choice trials. We examine these two kinds of predictions next.

3.5.1. Predicting choice from forced trials' latencies

According to the SCM, choices should map latencies in forced trials, as both express the same mechanism. This can be tested by comparing latencies during forced trials against choices in both treatments (Fig.1). Whether options differed in delays or in amounts, the points at which preference crossed 50% (top panels) were close to the points at which the sign of the difference between latencies in no-choice trials (bottom panels) reversed. This observation supports the logic behind SCM in terms of the overall (molar) pattern of preference. The model can be stretched further by looking at its ability to predict individual choices from the latencies in temporally close forced trials. To do this, we predicted the outcome of each choice from the option with shorter latency in the most recent pair of forced trials. This method controls for potential temporal fluctuations in preference and provides two quantitative tests of the model: (1) a test of the strength of preference between the options, achieved by comparing the predicted and observed proportions of choices across trials and test sessions and (2) a test of the predictive accuracy of the model, captured by the proportion of choices successfully predicted by the difference in sign between the latencies in the two preceding forced trials (one for each option).

3.5.1.1. *Strength of preference*

Since every subject experienced 5 conditions in which both latencies and preferences varied, it is possible to compute the correlation between preferences predicted according to the pairs of forced trials preceding choices and observed preferences for each subject, with 5 data points per subject. These correlations were significant for all subjects in the delay treatment (largest $p=.003$) and five out of six subjects in the amount treatment (largest significant $p=.042$; non-significant $p=.072$). In the delay treatment, the mean $\pm$ SE of the individual correlation coefficients was 0.991 ± 0.003 (range: 0.981 – 0.999) and the

mean $\pm$ SE slope was 1.043 ± 0.035 (range: 0.904-1.139). In the amount treatment, the mean $\pm$ SE of the individual correlation coefficients was 0.923 ± 0.022 (range: 0.844-0.970) and of the slopes 1.465 ± 0.082 (range: 1.213-1.770). Figure 4 presents Deming regressions for both treatments.

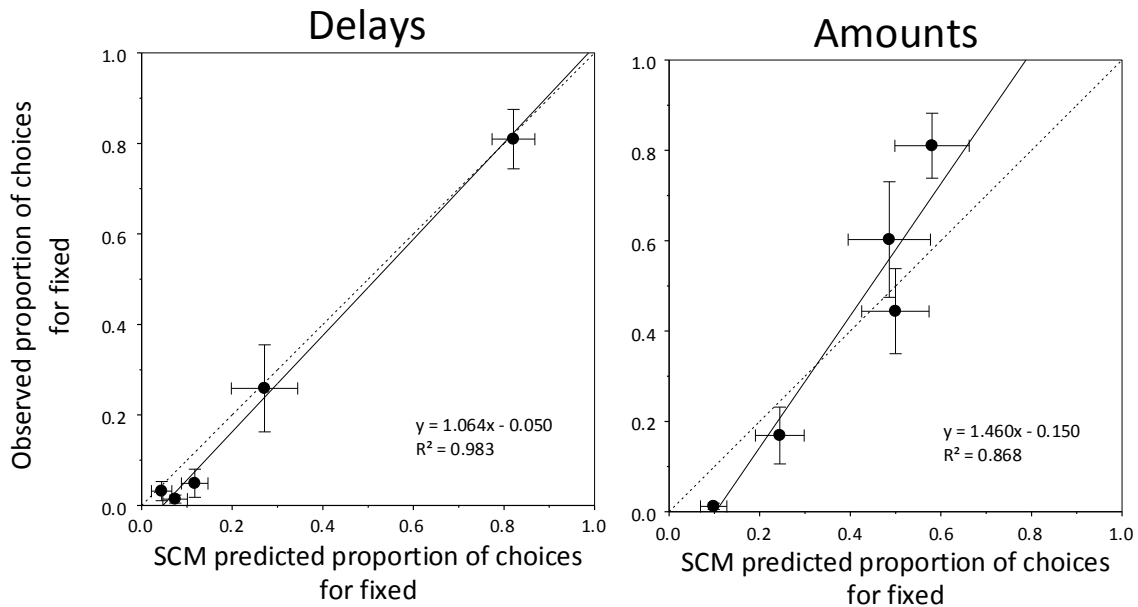


Figure 4. Obtained (ordinate) versus predicted (abscissa) proportion of choices for the fixed option according to SCM in the delay (left) and amount (right) treatments. Each data point represents the mean predicted and observed levels of preference in a given condition (proportions at stability averaged across six individuals). Error bars denote one standard error of the mean. Solid lines depict Deming regressions whose equations and coefficients of determination are shown in the inset.

3.5.1.2. Proportion of Individual Choices predicted accurately

Here we compare observed choices in individual trials against the sign of the difference in latency in the most recent pair of forced-trials. SCM accurately predicted 82.55% of all choices (ranging from 67.41 to 92.40% across individuals) in the delay treatment and 67.24% in the amount treatment (ranging from 50.49 to 89.56% across individuals). Notice that this analysis is not independent of that of the overall accuracy of proportion of choices, since the performance of the model in predicting overall proportion of preference establishes boundaries to how accurate and/or inaccurate individual trial

predictions can be. At the extreme, if a model accurately predicts near-exclusive preference, it cannot get many individual choices wrong. In spite of this caveat it is worth pointing out that other predictors of choice are mute with respect to individual choices. For instance, EoR, the most successful algorithm for predicting the indifference point, does not address partial preferences at all unless supplemented by an allocation assumption such as matching, and SUT, which has the strongest psychophysical bases, is also mute in this respect. The Matching Law (Davison and McCarthy, 1988; Herrnstein, 1961, 1970) is in a similar position regarding individual choices (but see Mark and Gallistel, 1994 for an approach that relates individual choices to local response rates).

3.5.2. Predicting shifts in latencies

In addition to predicting choices from no-choice trials, the SCM argues that latencies during choice trials should be shorter than those observed in forced trials (Kacelnik et al., 2011 – *Appendix 1*; Shapiro, Siller, and Kacelnik, 2008). In contrast, the ToWM predicts that latencies should be longer in choice than in forced trials. To test these predictions, we summarized each individual latency distribution by means of a cumulative frequency score of latencies both in forced and choice trials (see Shapiro, Siller, and Kacelnik, 2008 for details), provided that a minimum of five latencies were recorded for a particular option and subject. The general idea is that the larger the area under the cumulative (i.e., higher cumulative scores), the sooner the distributions peak and so the shorter the overall latencies. We also calculated such scores for the latencies dictating choice in our simulations (i.e., the shortest latencies in each pair of forced trials prior to a choice) and used such scores as an index of the shortening predicted by SCM.

For the delay treatment, we were unable to detect any signals of shortening or lengthening during choice relative to forced trials for any option or condition [all t s $\geq$ -.883 and $\leq$ 2.685, smallest $p=.075$] despite predicting a significant shortening in some

conditions for both the fixed [10 and 15-s delays; smallest $t=3.789$, $p=.019$] and variable options [5-s delay; $t(4)=3.132$, $p=.035$]. For the amount treatment, again a significant shortening was predicted both for the fixed [all conditions; smallest $t=3.517$, $p=.017$] and variable options [3, 4, and 5 pellets; smallest $t=2.621$, $p=.047$], but once more no significant shortening was observed. In fact, for the fixed option, we found a significant lengthening during choices relative to forced trials in condition 5 [$t(5)=-3.042$, $p=.029$].

These results contrast with those of Shapiro et al. (2008), who did find a shortening, and partially with those of Vasconcelos et al. (2010)⁴, where neither shorter nor longer latencies were observed. Here, in 20 opportunities for a shift, we observed no cases of shortening and only one instance of lengthening. The latter contradicts the predictions of the SCM but such low incidence does not boost our confidence in the ToWM. In any event, the present paradigm may have a limited ability to observe a generalized shortening, as subjects had a maximum of 20 s to respond before a trial was terminated. The effect observed by Shapiro et al. (2008) was largely driven by the differential presence of extremely long latencies, which would have been artificially censored and then equalised across the options by the present design. It is also possible that the contrast with Shapiro et al.'s results is due to the difference between their deterministic protocol against our risky choice. The addition of outcome variance in the present experiment may have caused an increase in cognitive evaluation time at the time of choice, moving the results a notch away from the SCM process towards the ToWM.

Overall, the available evidence suggests that the SCM is more successful in predicting choice than in predicting latency shifts. It is possible that the correlation between latency differences in forced and choice trials that makes the latter predictable from the former (but not *vice versa*), is not revelatory of a causal link, but reflects a

⁴See Chapter 2.

common underlying process by which options are given value that is later used in both sequential and choice situations (see discussions in Kacelnik et al., 2011 – *Appendix 1*; Vasconcelos et al., 2010 – *Chapter 2*). This is a distinct possibility that we cannot confirm or refute with the available data at the moment.

4. General Conclusions

The present experiments test the predictions of several models of risky choice that differ in logic, background and the behavioural variables dealt with. We observed that when choice involved delays to reward, starlings were typically indifferent when the fixed delay fell close to the harmonic mean of the variable set of outcomes, and when it involved amounts, they were typically indifferent when the fixed option fell close to the arithmetic mean of the variable set. Further, we corroborated that, similarly to previous observations using non-risky paradigms, the strength of preference between options in choice trials could be predicted from the latency to respond to the same options in forced trials. While in the vast majority of cases no time cost of choosing was identified, we could not support the prediction that latencies in choice trials should be shorter than those in forced trials. The most successful predictor of indifference points as a function of programmed parameters was the algorithm known as Expectation of the Ratios, which computes the gain per unit time in each foraging event (or trial) and then averages these values.

Neither these nor other available experiments allow for a definitive rejection or confirmation of any of these models. Further studies are required to better understand the relationship between latencies and the preferences expressed by animals during simultaneous choices. The use of a maximum response time may have obscured extremely long latencies that may be where latency shifts are more evident, or there may be genuine differences between risky and deterministic choice processes. The introduction of choice

situations with more than two options available might be revealing since, according to the SCM, the greater the number of options, the shorter should be the time to choose. The step between two and more options may seem minor, but it is conceptually a very significant leap. For instance, Schuck-Paim and Kacelnik (2007) showed that starlings that behaved as risk-prone in binary choices were, overall, risk-averse when (in the same sessions) were tested in trinary choices. This means that the nearly-universal approach of using binary choices may be, in fact, misleading in characterizing the underlying behaviour of the subjects.

5. Acknowledgments

This work was supported by Biotechnology and Biological Sciences Research Council Grant BB/G007144/1 to AK. TM was supported by a doctoral grant from the Portuguese Foundation for Science and Technology. MV was supported by a Marie Curie Intra European Fellowship within the 7th European Community Framework Programme followed by a post-doctoral grant from the Portuguese Foundation for Science and Technology. We thank Simon and Jan Parry for their assistance in trapping our participants.

6. References

- Aw, J. 2008. Decisions under uncertainty: common processes in birds, fishes and humans. Unpublished D. Phil dissertation. University of Oxford, Oxford, 297 p.
- Aw, J., Vasconcelos and Kacelnik, A. 2011. How costs affect preferences: Experiments on state-dependence, hedonic state and within-trial contrast in starlings. *Animal Behaviour*, 81: 1117-1128.
- Bateson, M. 1993. Currencies for decision-making: the foraging starling as a model animal. Unpublished D. Phil dissertation. University of Oxford, Oxford, 143 p.
- Bateson, M. and Kacelnik, A. 1995. Preferences for fixed and variable food sources: variability in amount and delay. *Journal of the Experimental Analysis of Behavior*, 63: 313-329.
- Bateson, M. and Kacelnik, A. 1996. Rate currencies and the foraging starling: the fallacy of the averages revisited. *Behav. Ecol.*, 7: 341-352.
- Bateson, M. and Whitehead, S.C. 1996. The energetic costs of alternative rate currencies in the foraging starling. *Ecology*, 77: 1303-1307.
- Blough, D.S. 2011. A random-walk model of accuracy and reaction time applied to three experiments on pigeon visual discrimination. *Journal of Experimental Psychology: Animal Behavior Processes*, 37: 133-150.
- Catania, A.C. 1970. Reinforcement schedules and psychophysical judgments: A study of some temporal properties of behavior. *The Theory of Reinforcement Schedules*: 1-42.
- Charnov, E.L. 1976. Optimal Foraging: Attack Strategy of a Mantid. *American Naturalist*, 110: 141-151.
- Davison, M. and McCarthy, D. 1988. *The matching law: A research review*. Lawrence Erlbaum Associates, Inc.

- Freidin, E., Aw, J. and Kacelnik, A. 2009. Sequential and simultaneous choices: Testing the diet selection and sequential choice models. *Behavioural Processes*, 80: 218-223.
- Grafen, A. and Hails, R. 2002. *Modern statistics for the life sciences*. Oxford University Press, Oxford, 351 pp.
- Herrnstein, R.J. 1961. Relative and absolute strength of response as a function of frequency of reinforcement. *Journal of the Experimental Analysis of Behavior*, 4: 267.
- . 1970. On the law of effect. *Journal of the Experimental Analysis of Behavior*, 13: 243.
- Kacelnik, A. 2003. The evolution of patience. In: G. Loewenstein (Editor), *Time and Decision: Economic and Psychological Perspectives on Intemporal Choice*, Russell Sage, New York.
- Kacelnik, A. and Abreu, F.B.E. 1998. Risky choice and Weber's law. *Journal of Theoretical Biology*, 194: 289-298.
- Kacelnik, A. and Marsh, B. 2002. Cost can increase preference in starlings. *Animal Behaviour*, 63: 245-250.
- Kacelnik, A., Vasconcelos, M., Monteiro, T. and Aw, J. 2011. Darwin's "tug-of-war" vs. starlings' "horse-racing": how adaptations for sequential encounters drive simultaneous choice. *Behavioral Ecology and Sociobiology*, 65: 547-558.
- Killeen, P. 1968. On the measurement of reinforcement frequency in the study of preference. *Journal of the Experimental Analysis of Behavior*, 11: 263.
- Mark, T.A. and Gallistel, C. 1994. Kinetics of matching. *Journal of Experimental Psychology: Animal Behavior Processes*, 20: 79.

- Mazur, J.E. 2010. Distributed Versus Exclusive Preference in Discrete-Trial Choice. *Journal of Experimental Psychology-Animal Behavior Processes*, 36: 321-333.
- Pompilio, L. and Kacelnik, A. 2005. State-dependent learning and suboptimal choice: when starlings prefer long over short delays to food. *Animal Behaviour*, 70: 571-578.
- Ratcliff, R., Van Zandt, T. and McKoon, G. 1999. Connectionist and diffusion models of reaction time. *Psychological review*, 106: 261.
- Reboreda, J.C. and Kacelnik, A. 1991. Risk sensitivity in starlings: variability in food amount and food delay. *Behavioral Ecology*, 2: 301-308.
- Schuck-Paim, C. and Kacelnik, A. 2007. Choice processes in multialternative decision making. *Behavioral Ecology*, 18: 541-550.
- Shapiro, M.S., Schuck-Paim, C. and Kacelnik, A. 2012. Risk sensitivity for amounts of and delay to rewards: Adaptation for uncertainty or by-product of reward rate maximising? *Behavioural Processes*, 89: 104-114.
- Shapiro, M.S., Siller, S. and Kacelnik, A. 2008. Simultaneous and sequential choice as a function of reward delay and magnitude: Normative, descriptive and process-based models tested in the European Starling (*Sturnus vulgaris*). *Journal of Experimental Psychology: Animal Behavior Processes*, 34: 75-93.
- Stephens, D.W. and Krebs, J.R. 1986. *Foraging Theory*. Princeton University Press, Princeton, New Jersey.
- Vasconcelos, M., Monteiro, T., Aw, J. and Kacelnik, A. 2010. Choice in multi-alternative environments: A trial-by-trial implementation of the Sequential Choice Model. *Behavioural Processes*, 84: 435-439.
- Vasconcelos, M. and Urcuioli, P.J. 2008. Deprivation level and choice in pigeons: A test of within-trial contrast. *Learning & Behavior*, 36: 12-18.

In search for the lost decision time: The Sequential Choice Model (SCM) extended

[Monteiro, T., Vasconcelos, M., Kacelnik. A. (in prep.)]

1. Introduction.....	80
2. Experiment 1.....	85
2.1. Method.....	86
2.1.1. Subjects	
2.1.2. Apparatus	
2.1.3. Procedure	
2.1.4. Data Analysis	
2.1.5. Monte Carlo implementation of the SCM	
2.2. Results.....	91
2.2.1. Preferences	
2.2.2. Perception of time	
2.2.3. Latencies in single-option trials	
2.2.4. Latencies in simultaneous choices	
2.2.5. Monte Carlo simulations	
2.3. Discussion.....	97
3. Experiment 2.....	98
3.1. Method.....	99
3.1.1. Subjects and Apparatus	
3.1.2. Procedure	
3.1.3. Data analysis	
3.1.4. SCM simulations	
3.2. Results.....	102
3.2.1. Perception of time	
3.2.2. Latencies in single-option trials	
3.2.3. Latencies in simultaneous choices	
3.2.4. Preferences	
3.2.5. Monte Carlo simulations	
3.3. Discussion.....	107
4. General discussion.....	107
5. Supplementary information.....	110
6. Acknowledgments.....	111
7. References.....	112

1. Introduction

Most foraging decisions in vertebrates involve previously acquired information. Animals accumulate experience relating environmental stimuli and/or their own actions to specific outcomes, and later choose between actions by processing this previously acquired information. This account is uncontroversial and coincident with learning theory's account of operant conditioning, but the specifics of how information about food sources interacts to generate actions is subject to diverse modelling alternatives. In particular, we focus on the effect of alternative forms of experience (i.e., with simultaneous or sequential encounters with the foraging alternatives) and on the number of alternatives experienced.

In humans, introspection creates the perception (often inaccurate) that one's own decisions are driven by a reasoned evaluation of each alternative. It follows that choosing is expected to take information-processing effort and time: more options, more evaluation, and hence more time. Technically, this is implemented in the Hick-Hyman Law (Hick, 1952; Hyman, 1953), which states that the time to take a decision is proportional to the logarithm in base 2 of the number of alternatives. It is often assumed that other species should also choose by comparing attributes of simultaneous alternatives, and that such evaluation must be time-costly. Shapiro, Siller and Kacelnik (2008) found that such view was inconsistent with results of experiments with European starlings (*Sturnus vulgaris*): rather than taking extra time to choose, the birds took longer to respond to an isolated alternative compared to responding to the same alternative in a simultaneous choice. To account for this counterintuitive observation they proposed the Sequential Choice Model (SCM), an evolutionarily inspired mechanistic model with ancestry in other *horse-race* models from mathematical psychology [Ratcliff (1978), Ratcliff, Van Zandt, and McKoon

1999), Ratcliff, Carpenter, and Reddi (2001), Smith and Ratcliff (2004)^{1]} and, functionally, on diet-choice model of optimal foraging (Charnov, 1976).

The SCM incorporates the expectation that cognitive mechanisms reflect adaptations to the environments in which they are typically used. It assumes that although simultaneous choices are common in the laboratory, it is unlikely that animals would encounter them very frequently in nature. Instead, common decisions are assumed to involve sequentially encountered alternatives, with animals opting between pursuing a given option (e.g., a food patch or prey item) or continuing to search for better alternatives. This hypothetical ecology implies that mechanisms that improve performance in such cases would be favoured by selection, even if they are suboptimal on rare simultaneous encounters.

In sequential decisions the profitability of the option in sight must be compared against the remembered profitability of the common background (rather than against other options present at the moment of choice). This comparison may take time, but the process is the same regardless of whether the option is alone or in the presence of other alternatives, hence the horse-race dynamics to cause action. An option whose profitability is vastly superior to its background would be pursued immediately after identification (a reaction time delay), but a leaner one would be either rejected or taken after a longer delay. The existence of such delays is not derived from rate maximising principles (an unconstrained performer would take or reject options without any delay, upon identification) but they are universally present in decision studies and they have been shown to contain useful information.

We refer to the time between encountering an option and responding to it as ‘latency’, and differentiate them from reaction times (RTs). RTs (see Blough, 2006) are

¹Blough (2011) applied a similar modelling approach to hue discrimination experiments in pigeons.

also operationally defined as the duration of the interval beginning with the onset of a stimulus and ending with a response (e.g., a pigeon's peck directed at the stimulus). However, classical RTs are typically assessed with paradigms that minimise motivational variation and where such intervals last well below one second. For instance, Vickrey and Neuringer (2000) tested and confirmed predictions from the Hick's Law in pigeons, their reaction times were typically below 500 ms, while the intervals measured and discussed by Shapiro et al. (2008)² range, on average, between 1 and 10 seconds. Such long latencies are best interpreted as encompassing the RTs plus a longer, strategic, component that reflects the likelihood of a free-ranging animal rejecting an option to continue searching in the overall environment. More specifically, while in their natural habitats animals have the opportunity to reject poor quality options in favour of searching the environment for better alternatives, in our experimental setup this course of action is not possible (for an alternative design see Freidin et al., 2009) - a response is always necessary to advance to the next trial (and to a potentially different option). This is reflected in longer latencies to accept low quality options. The leaner the option, in relation to the background environment, the longer the latency to accept it. This may be seen as psychologically intuitive but it is challenging for rate-maximising accounts: time waiting is time lost.

Informative latencies in the seconds or even tens of seconds range are observed in most foraging-inspired, closed-economy, protocols. For instance, in a risk-sensitivity experiment Reboresda and Kacelnik (1991) found that latencies to respond in no-choice trials ranged roughly between 5 and 40 s. Such latencies were more orderly (i.e., better at defining preference between fixed and variable amounts or delays to food) than choices in simultaneous encounters.

²See also *Chapters 2 and 3*.

Kacelnik et al. (2011) formalised the SCM and reviewed relevant published work while contrasting it against a generic choice model inspired by simultaneous encounters, using the metaphors of a *horse-race* (i.e., the SCM) versus a *tug-of-war* (ToW). The ToW model involves a competitive evaluation between the merits of each alternative option prior to action (i.e., the response) so that the presence of alternatives at the time of choice delays the time taken to process each option (as postulated by the Hick-Hyman law). In contrast, the SCM assumes that each present option triggers a response depending on a comparison against the common, and remembered, richness of the background. For this reason, the number of options at the time of choice does not cause an increase in the latency, just as the presence of additional horses in a race may not slow down a particular competitor. If anything, (perhaps belabouring the metaphor) if the time a given horse takes to complete a course is only recorded on the occasions when it wins the race, under the non-interference hypothesis, the recorded mean completion times will be shorter in the presence of competitors, because slow days will not enter the computations [See Figs. 1 and 2 in Kacelnik et al. (2011) – *Appendix 1* for details, and Mazur (2010) and Aw et al. (2012) – *Chapter 3*, for more recent implementations of the SCM]. In such *horse-race* models (i.e., the SCM), the outcome of races can be predicted from the performance of each horse when training on its own, while in ToW models the competitors interact in a way that slows each other down, and who is the winner is not directly predictable from training times.

Notice that this account is independent on whether decision processes are relatively rigid hereditary adaptations or honed through experience. If they are learned, sequential encounters should favour the organism to form representations of the attractiveness of each option and of the background environment, as these variables are crucial in driving decisions respect to lost opportunity. In simultaneous encounters the subject may learn to

respond to the complex of stimuli present, as “in the presence of complex AB, go towards A” without necessarily storing information about A or B independently. It may be argued that the existence of cognitive representations of the parameters of each option is consistent with the view that sequential encounters are more influential than simultaneous ones in the design of decision processes, because for the latter, such representations are incidental. An animal whose experience is exclusively with simultaneous encounters might conceivably save the effort of forming option representations, and might then not respond to each option if encountered alone, as one with a predominance of sequential encounters in its past. For an animal with a simultaneous history, performance on sequential encounters might not produce sufficient information to predict preference in simultaneous choices. We address this issue experimentally later on.

In summary, the SCM postulates that animals evolve or develop in environments where sequential encounters with isolated opportunities predominate, and as a consequence display decision processes designed to cope with such situations. The model’s specific predictions are that:

(1) Choice behaviour in simultaneous encounters should be predictable from performance when each alternative is met on its own, but not the other way around.

(2) In sequential encounters, the latency to accept a given option reflects lost opportunity and should decrease as a function of each option’s profitability relative to the common background.

(3) Latencies should not be longer when an option is encountered simultaneously with other(s). If anything, average responding times to an option, when others are present, should be shorter because latency distributions cross-censor each other.

So far, predictions (1) and (2) have been well supported by experimental data (Aw et al., 2012 – see *Chapter 3*; Freidin, Aw, and Kacelnik, 2009; Vasconcelos et al., 2010 –

see *Chapter 2*). Regarding prediction (3) the evidence is inconclusive: neither a lengthening nor a shortening of latencies has been universally documented when comparing simultaneous with sequential decisions (Shapiro, Siller, and Kacelnik, 2008; Kacelnik et al., 2011 – see *Appendix 1*; Mazur, 2010). The influence of history with either sequential or simultaneous encounters has not yet been tested, and constitutes an aim of the present study.

In addition to examine the effect of learning on choice behaviour, we extend our analyses to simultaneous choice involving three (not only two) options (Fig. 1), gathering further evidence as to whether choosing encompasses a time cost.

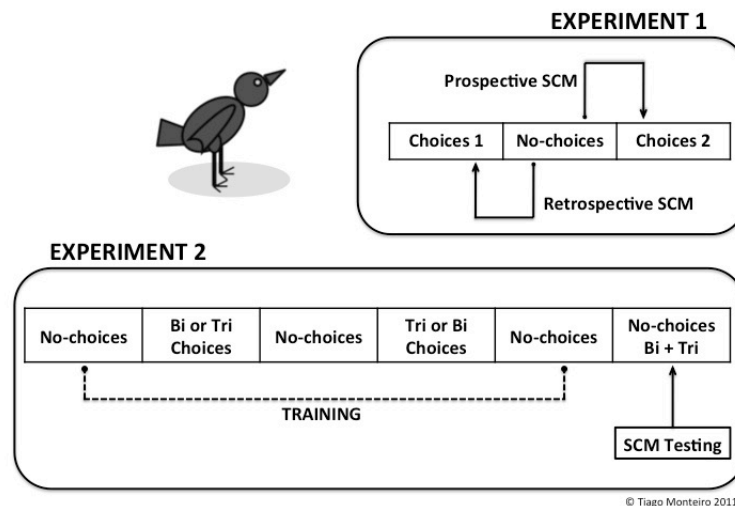


Figure 1. Experimental methods. Schematic representation of Experiment 1 and Experiment 2 procedure and analysis, top and bottom panels, respectively.

2. Experiment 1

Understanding the relation between choice and learning is difficult since the training procedure can drive later results (i.e., the choices). For instance, an animal trained with single options may learn that there are no simultaneous choices in its world, and behave inappropriately when facing one. In contrast, an animal trained exclusively with choices (i.e., no encounters with singly presented options) may learn where to respond,

rather than the properties of each option). Previous tests of the SCM used animals trained with single options before (or concomitantly) measuring preference in choices, the underlying assumption being that single-option trials emulate sequential food encounters in natural environments, thus offering the animals information about the properties of each option. The main objective of Experiment 1 was to test the SCM using a design in which the animals were firstly trained with choices between pairs of different options, and were subsequently exposed to the different options on their own (i.e., in single-option or no-choice trials). Finally, and as previous experiments, choices were reintroduced (see Fig. 1, top panel). Using a Monte Carlo implementation of the SCM, we used the latencies to accept each option during the *No-choices* phase to predict behaviour in both choice phases (i.e., retrospective and prospective predictions, for *Choices 1* and *2*, respectively – see Fig. 1, top panel).

2.1. Method

2.1.1. Subjects

Twelve adult wild-caught European starlings (*Sturnus vulgaris*) participated in the current experiment. Animals were captured and held in captivity under Natural England license 20083718.

All subjects were naïve to experimentation. Prior to testing, birds were housed communally in a large outdoor aviary (3 m high x 3.2 m wide x 4 m long) where they received *ad libitum* food (a mixture of turkey crumbs, and mealworms (*Tenebrio sp.*) and had continuous access to fresh drinking and bathing water.

For the experiment, starlings were moved in pairs to indoor cages, which were visually, but not acoustically isolated. Indoor temperatures ranged from 13 to 15°C and lights followed a 12 hour cycle with lights on at 07h00, and gradual transitions at dawn and

dusk. Starlings were rewarded with BioServ® 20 mg precision pellets throughout the experimental session and provided with four hours (13h00-17h00) of free access to turkey crumbs, Orlux© remiline universal granules and 10 mealworms daily, and social interaction with the respective pair. This regime maintains starlings at approximately 90% of their free-feeding weight (Bateson, 1993) and was conducted in accordance with Oxford University's ethical protocols. After the experiment, starlings were reintroduced into the communal aviary and eventually released into the wild.

2.1.2. Apparatus³

Each indoor cage [1350 mm x 784 mm x 800 mm (l x w x h)] was composed of two units, vertically mounted (800 mm each). Each unit included two experimental areas separated by a common middle section. Each experimental area had a panel attached 100 mm above the floor. The panel was 400 mm tall with three sections: a middle sub panel, facing the cage (115 mm wide), and two side subpanels (same length) attached to the cage at a 120 degree angle from the centre subpanel. The middle subpanel had one response key in the centre (110 mm from the bottom), and the food hopper (25 mm from the bottom), that was connected to the pellet dispenser (Campden Instruments®) containing 20 mg precision dustless pellets. Each side subpanel had one response key in the centre (110 mm from the bottom). Every key was composed of a 16 LED⁴ light matrix that could display 16 different symbols in seven possible colours. Trials were controlled by custom software running on the Microsoft® Windows® operating system and attached to an Animal Behavior Environment Test System (Campden Instruments®) via WhiskerServer (Cardinal and Aitken, 2010).

³See Figs. 1 and 2, *Chapter 1*.

⁴Light-emitting diode.

2.1.3. Procedure

2.1.3.1. Preliminary Training. Following magazine training, the birds were trained to peck a flashing white centre key (700ms ON, 300ms OFF). A single peck to this key delivered four precision pellets, extinguished the keylight, and initiated a 120-s inter-trial-interval (ITI). Failing to peck the key within 30-s from the onset of flashing resulted in the same events as a peck. Training thus combined autoshaping with an operant response. Once birds were reliably pecking the centre key, the lateral keys were introduced. Trials again began with the flashing white centre key. A peck to this key turned its light off and started a flashing white lateral key. A peck to the flashing lateral key turned it off and produced two food pellets followed by a 90-s ITI. During this phase, failing to peck the centre key within 30 s from trial onset resulted in a 10-s blackout (i.e., all keys OFF) followed by the ITI. Failing to peck the flashing side key during the same time period was followed by food 75% of the time. This program was maintained 5.5 hours per day until the birds reliably pecked the centre and side keys on at least 80% of the trials.

Next, birds received response-initiated *fixed-interval* (FI) training. In this phase two pecks to the side key were required to deliver food. The first peck turned the symbol steadily on and began a delay, the duration of which was progressively increased from 1 to 20 s. The first peck after the delay lapsed extinguished the keylight, delivered two food pellets and initiated a 45-s ITI. Once birds were reliably obtaining food on FI 20-s trials, the experimental sessions began. For the experimental sessions, a different set of symbols-colours was used for each bird (Supplementary Figure 1, pp. 110).

2.1.3.2. General Procedure. In the phase *Choices 1*, starlings were trained for 15 days in an environment consisting of 15 pairs of two different stimuli [270 binary-choice trials, 18 per binary-choice type, half of those in each possible location]. In total, there were six different options signalling five different delays to food (6s, 9s, 12s, 12s, 15 or

18s), each option counterbalanced across birds and identified by a particular LED pattern⁵. In the later *No-choices* phase birds were exposed for 15 days to single-option trials with each of the trained stimuli, as well as infrequent peak trials (Catania, 1970; Roberts, 1981) designed to expose the animals' knowledge of the delay to reward associated with each particular option [204 single-option trials, 34 per option, 17 in each side key, 12 peak-trials, 2 per option, 1 in each possible location]. Finally, the phase *Choices 2* was identical to *Choices 1* and lasted for 6 days.

2.1.3.3. Trial types. Choice trials offered simultaneous choices between all combinations of two different stimuli (among the 15 possible combinations). Trials began with a flashing centre attention key. A peck to this key turned it off and began the flashing of two side keys (each one displaying a different symbol/delay pairing at a random location). A peck to one of the flashing keys turned the unselected key off, while the selected key was turned continuously on and its programmed delay initiated. Once this interval elapsed, the first peck to the key turned the keylight off and delivered 2 pellets of reward (at a rate of 200 ms per pellet), after which a 40-s ITI was initiated. If the bird failed to peck any of the flashing keys during 120 s the key was turned off, and the ITI started, followed by the next trial. The birds had 10 s to peck the steady key after the programmed delay elapsed. Failure to do so moved them to the ITI. Single-option trials were similar to choice trials with the exception that a peck to the centre key (turned the key off and) caused only one of the side keys to begin flashing (randomly assigned). Probe trials proceeded similarly to single-option trials, but once pecked, a given option remained on for three times its typical delay. At the conclusion of this interval, the light extinguished without reward or requiring a peck, followed by the ITI.

⁵Note that two of the options signalled the same delay, 12 s, but were associated with different stimuli.

In all trial types, latencies are defined as the time difference between pecking the centre key (t_0) and a peck to a flashing side key (t_1).

2.1.4. Data analysis

All proportional (i.e., choice preference) and latency data were successfully normalized for statistical analyses using arcsine square root and natural log transformations, respectively (Grafen and Hails, 2002). An alpha level of 0.05 was adopted for all statistical comparisons.

There was an experimental criterion of 70% completion of all daily trials for a session to be included in the analysis. Six birds were excluded from all analyses after failing to reliably reach the experimental criterion.

2.1.5. Monte Carlo implementation of the SCM

The theoretical core of the SCM is that choices are generated by sampling the same latency distributions as when options are encountered alone. To test the predictive power of this proposal it is necessary to identify a distribution of latencies for each option alone, and then implement a sampling process that could lead to choices. The latency distributions can be inferred from sequential encounters, but the sampling process must remain hypothetical. One option is to find the parameters of theoretical distributions fitting the latency data for each option, and then sample such distributions randomly before each experimentally set choice. One difficulty is that observed latency distributions are often irregular, so that fitting theoretical distributions requires additional assumptions. To circumvent this, we stored the whole set of available latencies and sampled this set. Each simultaneous choice was predicted by picking a random sample from each observed distribution, and identifying the shorter latency as belonging to the chosen option. Notice, however, that there was one period of sequential choices sandwiched between a preceding (*Choices 1*) and a following (*Choices 2*) period of choices. If the performance of the SCM

depends on the learning sequence, *Choices 1* should be less accurately predicted than *Choices 2*, because at the time of the former phase, the subject has no experience with each option alone.

We thus ran two Monte Carlo simulations. A *retrospective* simulation used latencies from the first 6-day block of *No-choices* to generate predictions (or post-dictions) regarding the last 6-day block of *Choices 1*. The *prospective* simulation proceeded in the same way but used latencies from the last 6-day block of *No-choices* to estimate behaviour from the first 6-day block of *Choices 2* (see Fig.1, top panel). Both simulations included 100,000 runs of 1620 trials each (108 predictions per binary-choice type, the equivalent of 6 days of *Choices 1* or 2, for the *retrospective* and *prospective* simulations, respectively). For every choice trial, the simulation drew two latencies (i.e., one for each option) from the latencies recorded during *No-choices*, and predicted that the option yielding the shorter latency would be chosen.

2.2. Results

2.2.1. Preferences

Figure 2 shows the average preference for the better option in every binary-choice pair. *Filled dots* show the average preference (+SEM) during the last 6-day block of *Choices 1* and *open dots* depict the average preference (-SEM) during *Choices 2*. Differences in preference between choice phases were significant across all pairings and individuals (all binomial $p < .001$), with preferences for the richer option being more extreme in *Choices 1* (i.e., before exposure to sequential encounters) than in the *Choices 2*.

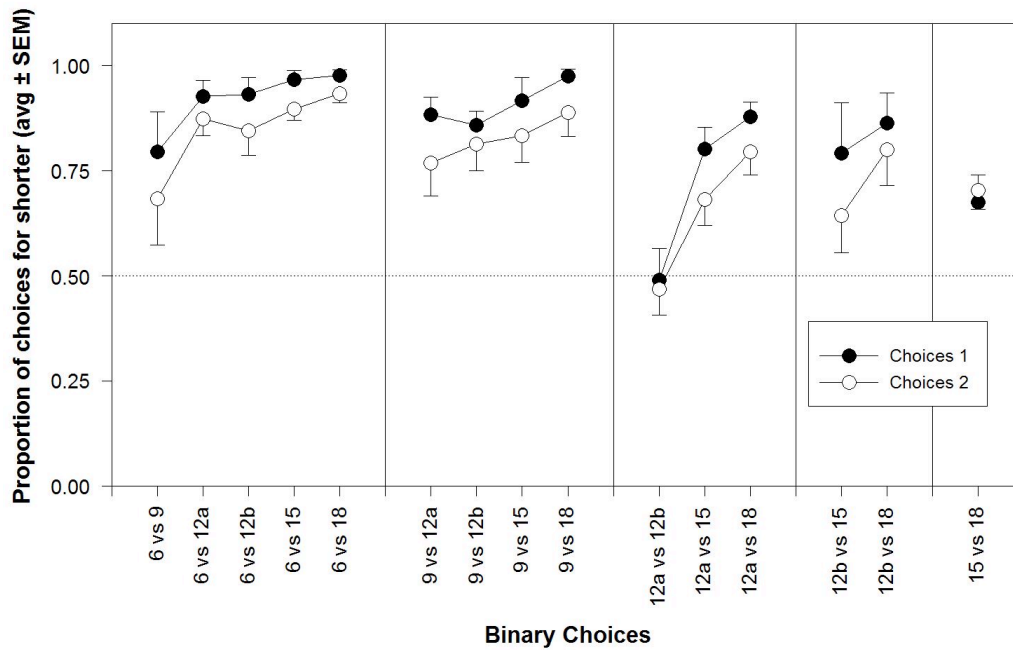


Figure 2. Preference data for phases Choices 1 and 2. Filled dots show the average proportion of choices for shorter option (+SEM) during the last 6-day block of *Choices 1*; opened dots show average proportion of choices for shorter option (-SEM) during the first 6-day block of *Choices 2*.

2.2.2. Perception of time

Figure 3 shows the performance (i.e., response rate in pecks per second) in peak trials during the first (left panel) and the last (right panel) 6-day blocks of the *No-choices* phase. A visual inspection of this figure shows that animals were accurately discriminating each option since the maximum response rates were on or near the corresponding reward time. A repeated-measures ANOVA with block and option as fixed factors, subject as random factor and peak time (the 1-s bin with maximum response) as dependent variable, showed significant main effects of block [$F(1, 5)=26.661$, $p=.004$] and option [Greenhouse-Geisser adjusted $F(1.751, 8.757)=21.868$, $p<.001$], but no significant interaction between the two factors [$F(5, 25)=.961$, $p=.46$].

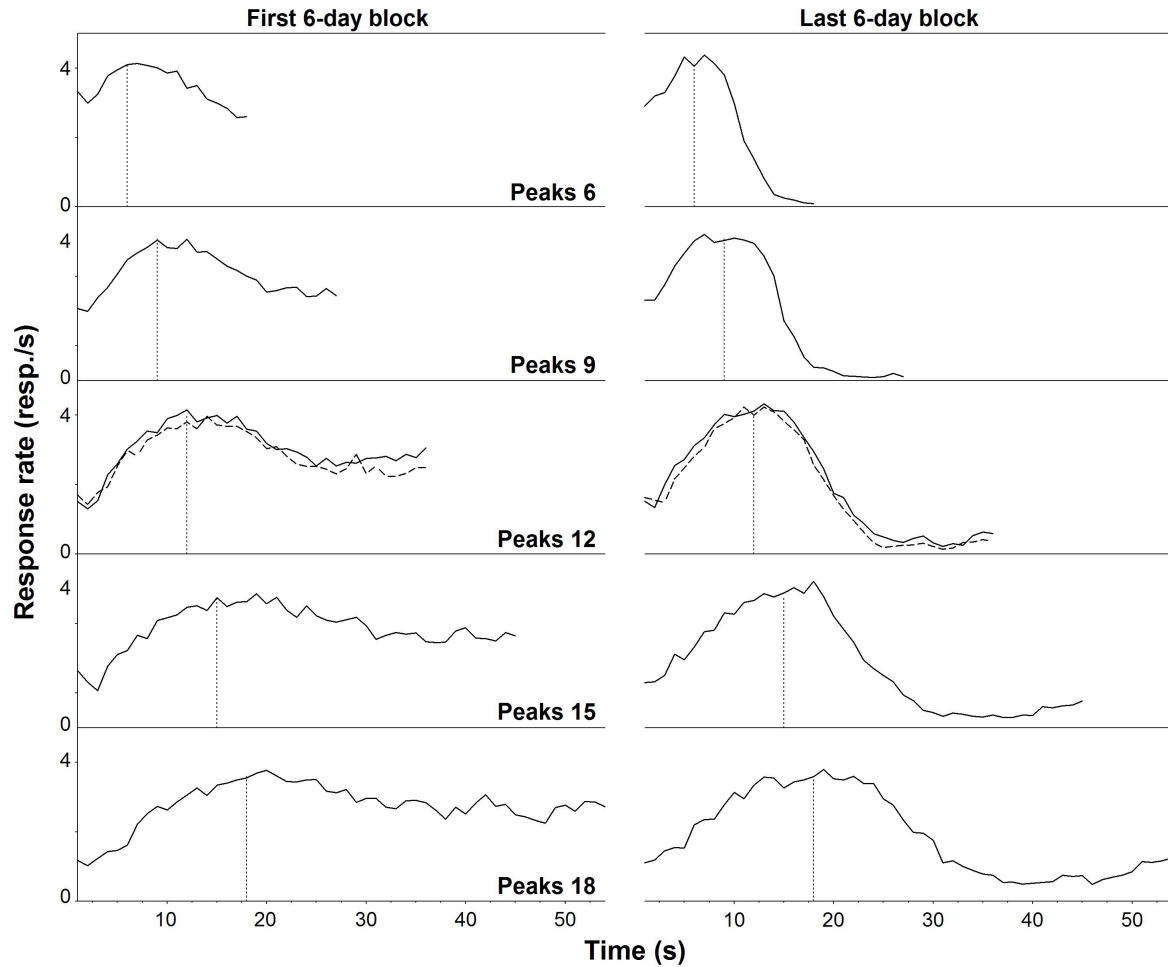


Figure 3. Response rate (pecks per second) during peak trials. Left panel shows data from the first 6-day block of the phase *No-choices* (i.e., days 1 to 6), right panel shows data from the last 6-day block of the same phase (i.e., days 10 to 15). Horizontal lines indicate 0 pecks per second for each particular option, vertical dashed lines signal usual time of reinforcement availability. Data are averaged across subjects.

In the last sessions of *No-choices* (Fig. 3, right panel), a decrease in the average response rates can be clearly observed after the trained reward time (signalled by the vertical dashed lines). This decrease is not as evident during the first few sessions when peak trials were introduced, reflecting that some experience with unrewarded trials was necessary for the observed decrease in the average response rate after the trained reinforcement time (Kaiser, 2008; Balci et al., 2009). In other words, with accumulated experience the animals became more accurate regarding the usual reinforcement time, hence they responded less whenever food was not delivered at the expected time.

2.2.3. Latencies in single-option trials

According to the SCM, the attractiveness of a given option is relative to its background. This relative quality is related to the latency to accept it, reflecting a tendency to skip particular options (in single-option trials) in favour of continuing searching the environment for better alternatives. In other words, the SCM postulates that the latency for a particular option should be inversely related to its relative quality. Figure 4 shows the median latencies (mean + SEM) to accept each option during the first (*grey bars*) and last (*white bars*) 6-day blocks of *No-choices*. A repeated-measures ANOVA with block and option as fixed factors, and latencies as dependent variable, revealed a significant effect of the option [$F(5, 25)=43.865$, $p<.001$]. Planned paired sample *t*-tests also showed that median latencies were different between all options [largest $p = .047$], except between options 6 s and 9 s [$p=.112$] and between the two options associated to a 12-s delay to food [$p=.865$]. Latencies collected during the first 6-day block were not statistically different from those collected during the last 6-day block [$F(1, 5)=1.798$, $p=.238$], and there was no interaction [$F(5, 25)=1.819$, $p=.145$].

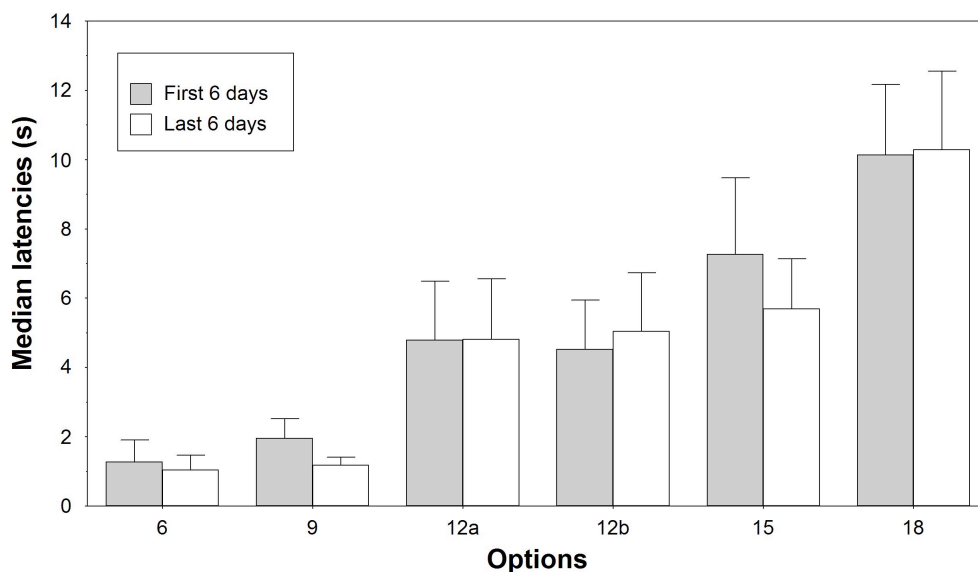


Figure 4. Latency data from *No-choices* phase. Grey bars represent the median latencies in seconds averaged across subjects (+SEM) for the first 6-day block, white bars show the same results for the last 6-day block *No-choices*.

2.2.4. Latencies in simultaneous choices

According to the SCM, latencies in choices should be shorter than in no-choices, particularly for the worse option in any given binary-choice. Figure 5 shows cumulative frequency scores for latencies collected during choices (each data point represents a given chosen option, averaged across subjects) as a function of the same statistic during no-choice trials ($\pm$ SEM). Cumulative frequency scores are given by the total area under each cumulative distribution, with high scores capturing shorter latencies to respond (i.e., in such cases most latencies must occur in the first few time-bins). Data points above the main diagonal indicate that latencies for a particular option were on average shorter during choices when compared to no-choice situations, data points below the main diagonal show that latencies for a given option were on average longer on choices, when compared to no-choice trials. As shown in Figure 5, most data points fell close to the main diagonal. Paired-sample *t*-tests revealed one case of significant lengthening of latencies to accept an option during choice trials in *Choices 1* [12b-s option: $t(5)=4.091$, $p<.001$] and two cases in *Choices 2* [6-s option: $t(5)=3.818$, $p=.012$; 12a-s option: $t(5)=3.348$, $p=.02$]. Two cases of significant shortening were also observed during *Choices 2* [9-s option: $t(5)=3.102$, $p=.027$; 15-s option: $t(5)=4.522$, $p<.001$]. All the remaining comparisons yielded non-significant results.

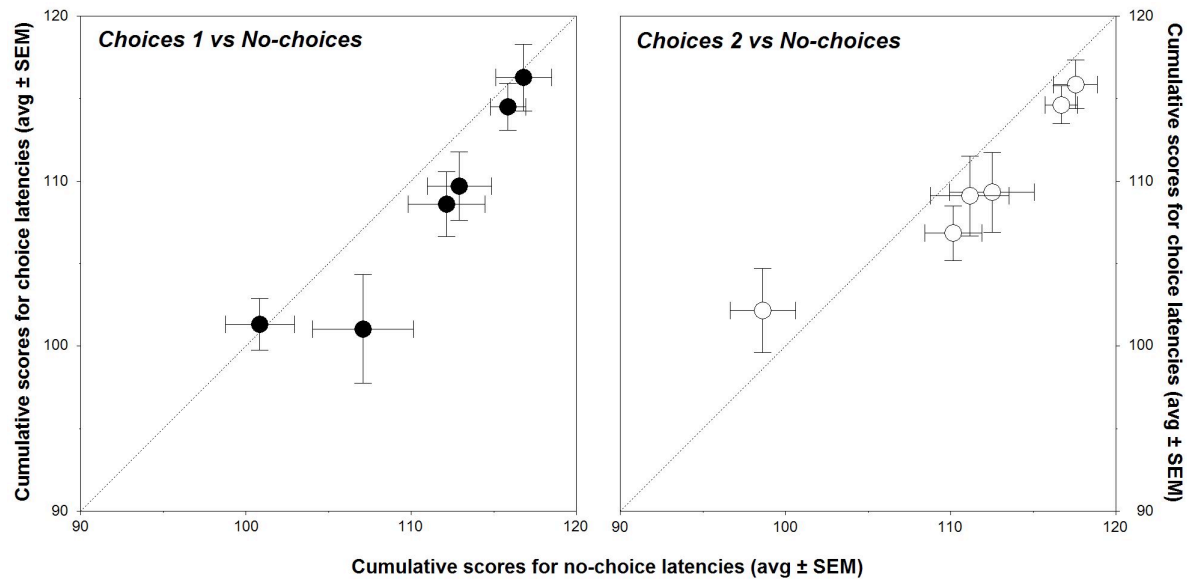


Figure 5. Cumulative frequency scores for choice and no-choice latencies. Each dot represents the score for choosing a particular option in a no-choice situation and over the different binary-choice combinations where that option was included (averaged across individual subjects, $\pm$ SEM). Points above the diagonal lines indicate that choice latencies were shorter than corresponding no-choice latencies. Left panel shows data from the last 6-day block of *Choices 1* as a function of data from the first 6-day block of *No-Choices*. Right panel depicts data from the first 6-day block *Choices 2* as a function of data from the last 6-day block of *No-Choices*.

2.2.5. Monte Carlo simulations

Figure 6 shows the predictions of the SCM (*white dots*, averaged across subjects, $\pm$ SEM). To contrast with the predictions, Figure 6 also shows the observed preference (*black dots*, averaged across subjects, $\pm$ SEM), already shown in Figure 2, but now decomposed into two panels, for both *Choices 1* (top panel) and *Choices 2* (bottom panel), respectively. As shown, the model's predictions followed quite closely the recorded preference, especially in the *Prospective* simulation ($r=.984$, $n=15$, $p<.001$). Regarding the *Retrospective* implementation of the model, the predictions followed the same trend as the observed preferences but the model consistently under-predicted preference ($r=.957$, $n=15$, $p<.001$), consistently with the more extreme preferences displayed in phase *Choices 1*.

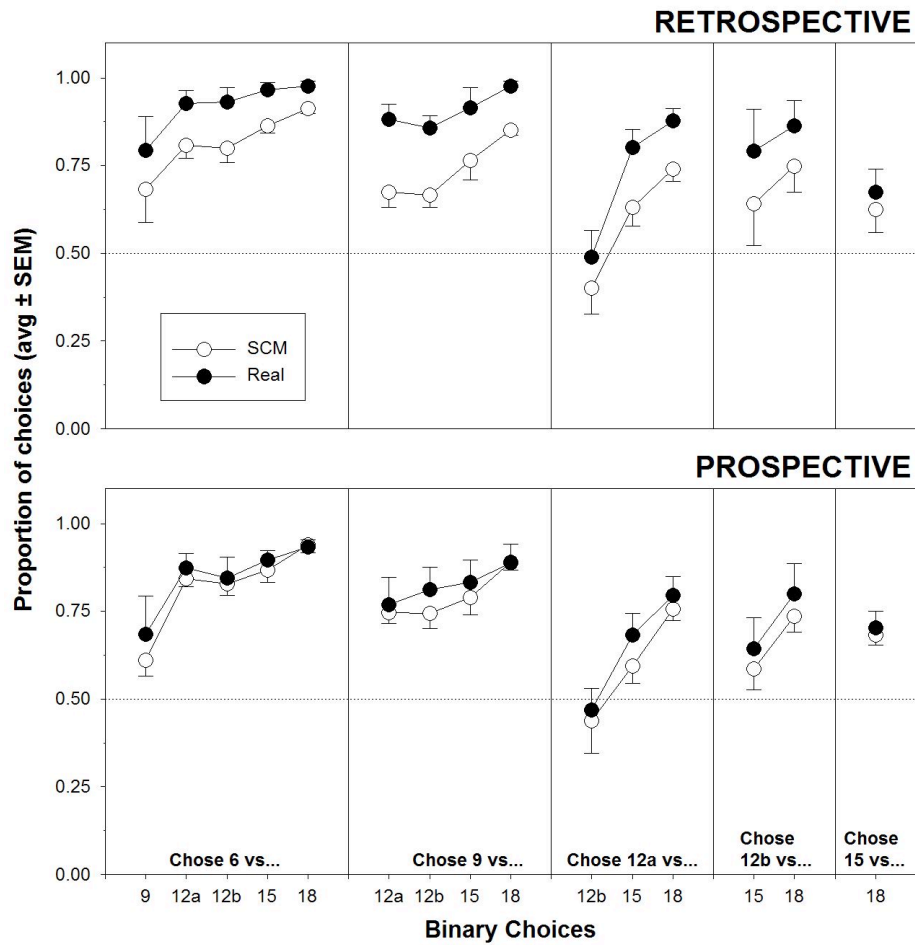


Figure 6. Observed and predicted preference. Top panel shows the observed proportion of choices for the last 6-day block of *Choices 1* (black dots; avg +SEM), and the SCM's predictions, using as input data latencies from the first 6-day block *No-choices* (white dots; avg -SEM). Bottom panel shows the corresponding data for the first 6-day block of *Choices 2* and the SCM's corresponding predictions, using as input data latencies from the last 6-day block of *No-choices*.

2.3 Discussion

Consistently with previous studies, we found that latencies to respond to single options were sensitive to the background of alternatives. In this respect two points are worth mentioning: 1) as observed by Vasconcelos et al. (submitted), the quality of the option might sometimes cause latencies to be as short as the minimum time required for the animal to respond to it (i.e., a floor effect). This might have been the reason why no differences were found in the latencies to accept the two best available options. For such high quality options, the animals might have been responding to the better options in the

shortest amount of time possible, so that latencies are reduced to conventional reaction times; 2) options yielding the same properties (i.e., delay to a food reward) but signalled by different cues, were associated to the same time to act (i.e., latency), hence no differences were statistically significant/detectable.

The prediction of the SCM for a latency shortening in choices respect to single-option encounters was thus not supported, but neither did we find evidence for a deliberation time: out of 12 potential instances, we found two cases of shortening, 3 of lengthening and no differences in the remaining 7.

In line with previous research, latencies to accept individual options could be successfully used to predict both past and future simultaneous choices (i.e., *retrospective* and *prospective* implementation of the SCM, respectively), adding support to the notion that the SCM might be emulating, at least in principle, the actual decision mechanism, rather than being a spurious (or correlational) effect of the training regime.

3. Experiment 2

The SCM was developed and tested using comparisons between actions in front of a single option versus choices between two simultaneously presented (and different) options. An important generalisation would be to extend the model to situations where an animal is facing more than two options at a given time (or in the environment). By increasing the number of options in simultaneous choices, our goal was to detect whether evaluation times and latencies proceed differently when more than 2 options are simultaneously available, while exploring a new implementation of the SCM. The step between two and more options is procedurally simple, but conceptually very significant to expose the process of choice. Different underlying processes may lead to substantial differences in the effect of an additional option to the choice set. For instance, Schuck-

Paim and Kacelnik (2007) showed that, in a risk sensitivity experiment, starlings that behaved as risk-prone in binary choices turned risk-averse when (in the same sessions) were tested in trinary choices. This means that the nearly universal approach of using binary choices is, in fact, misleading in characterizing the underlying behaviour of the subjects.

In Experiment 2, choices between three simultaneous options were introduced for the first time in a SCM testing context (Fig. 1, bottom panel). Here, we simulated the animals' preferences using the same Monte Carlo method as in Experiment 1, but using latencies for no-choice trials to predict simultaneous choices between three (as well as two) different options.

This experiment was first reported in Monteiro, Vasconcelos and Kacelnik (Experiment 1, submitted⁶), where these authors compared the effect of adding options to the preference between two pre-existent and different options (i.e., preference in binary-choice trials versus relative preference in trinary-choice trials). Their analysis aimed at testing some of the most common principles of economic rationality⁷. Here we use the latency data (not included in the previous report) to make independent predictions for both binary and trinary-choice trials, respectively.

3.1. Method

3.1.1. Subjects & Apparatus

Eight adult wild-caught European starlings (*Sturnus vulgaris*) participated in this experiment (captured and held under Natural England license 20093673). All subjects had previous experience participating in laboratory experiments with unrelated contingencies. The animals were kept in the same conditions as described in Experiment 1. After the

⁶See Chapter 6.

⁷For details see Chapter 6.

experiment, starlings were reintroduced into the communal aviary and eventually released into the wild.

The same equipment described for Experiment 1 was used.

3.1.2. Procedure

3.1.2.1. Pre-training. FI training only, as described in Experiment 1.

3.1.2.2. Trial types. There were three types of trial: single-option, choice and peak trials. Single-option trials began with a flashing attention key (location randomly assigned). Pecking at the flashing key turned it off, and caused one of the three available keys (randomly assigned) to begin flashing (700 ms ON, 300 ms OFF). A peck to the illuminated flashing key either turned the key steadily on and initiated a delay to food. Choice trials offered simultaneous choices between two or three options. All combinations of two and three different options were used. Trials began with a flashing attention key at a random location. A peck to it turned it off and began the flashing of two (binary choices) or three (trinary choices) randomly located keys (each displaying a different symbol). A peck to one of the flashing keys initiated its programmed contingency, and turned the unselected key(s) off. Peak trials were similar to single-option trials and were used to determine the animals' knowledge of the delay to reward associated with each. In these trials, the chosen option remained on for three times its typical delay and then extinguished without reward. Successive trials were separated by a 45-s.

3.1.2.3. Training and Testing. Two groups of starlings were trained during 35 days in an environment consisting of five different options (for details, see Supplementary Figure 1, pp. 110), each signalling a different delay to reward (6, 9, 12, 15 and 18 s). No-choice training encompassed 150 daily single-option trials [30 per option, 10 in each possible location], in choice-training infrequent trials with the 10 possible binary or trinary choices between the five options were interspersed with more common single-option trials

[90 single-option trials, 18 per option, 6 in each possible location, and 60 choice trials, 6 per pair or trio combination, one in each possible location, daily]. After training, both groups were tested for 7 days, with binary, trinary and no-choice trials interspersed within the same session [75 single-option trials, 15 per option, 5 in each possible location, and 60 binary-choice trials and 60 trinary-choice trials, 6 per binary and trinary combination, one in each possible location].

In summary (see Monteiro et al., submitted, for details⁸), one group received the sequence: Training → Binary → Training → Trinary → Training → **Binary+Trinary**⁵; while the other the sequence: Training → Trinary → Training → Binary → Training → **Binary+Trinary**⁹

Infrequent peak trials (3 times the delay of the respective option and no reinforcement in the end) were included in all phases except in the testing phase.

3.1.3. Data analysis

All data was transformed as described in Experiment 1. An alpha level of 0.05 was adopted for all statistical comparisons.

There was an experimental criterion of 80% completion of all daily trials for a session to be included in the analysis. Three birds were excluded from the experiment after failing to reliably reach the experimental criterion.

3.1.4. SCM simulations

To test if the SCM could predict simultaneous choices with three, as well as just two, simultaneously presented options (i.e., trinary and binary choice trials) from latencies recorded in single-option trials, we ran virtual experiments. As described in Experiment 1, in Monte Carlo simulations, randomly sampled latencies from the empirical data recorded in single-option trials, were compared in order to predict potential choices between two

⁸See *Chapter 6*.

⁹Bold highlights the testing phase, equal for both groups.

and three different options. The choice rule was to predict a particular choice whenever the latency for a given option, was shorter than the latency of the alternative(s) option(s), all recorded during no-choice trials. Two different Monte Carlo simulations were run. One to predict binary choices from forced trial latencies collected during the 7 days of testing, and another to predict trinary choices from those same latencies. In both cases, 100 000 ‘virtual experiments’ were run, with each experiment comprising 420 choices per choice type (42 choices per binary or trinary choice type, the equivalent to the 7 days of testing). Similarly to the simulations ran for Experiment 1, for every trial, the simulation would draw two (or three) latencies (i.e., one for each option present in a particular binary or trinary choice combination, respectively) from the latencies recorded during forced trials. The option yielding the shortest latency was the predicted choice.

3.2. Results

3.2.1. Perception of time

Figure 7 shows the response rate in peak trials (averaged across individuals) during the last 5 sessions of the last phase of no-choice training (see Fig 1, bottom panel).

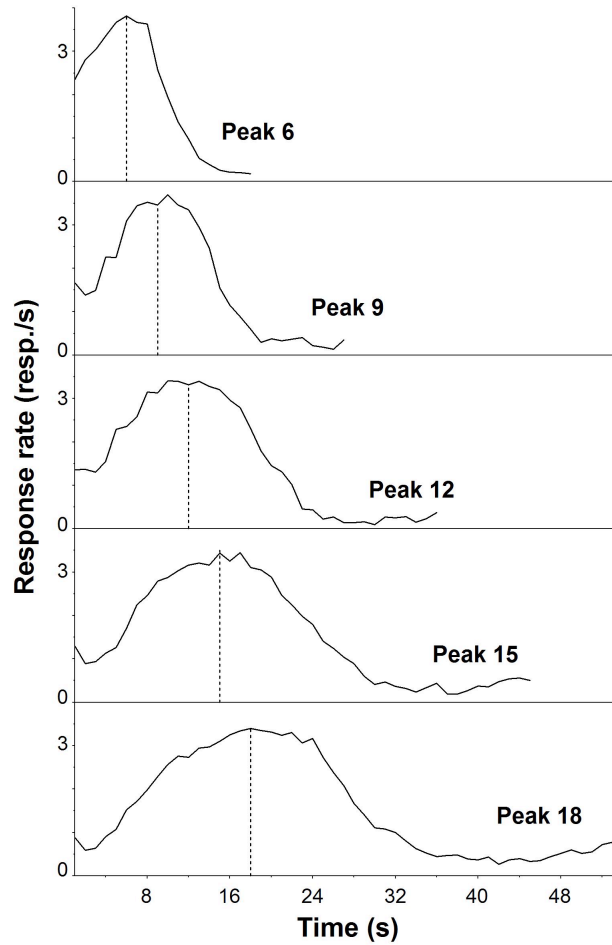


Figure 7. Response rate (pecks per second) during peak trials. Data from the last 5 days of no-choice training (i.e., days 3 to 7) prior to the start of testing (averaged across subjects). Horizontal lines indicate 0 pecks per second for each option, vertical dashed lines signal usual time of reinforcement availability.

Visual inspection of the data shows that prior to the start of testing, the animals had already learned the temporal properties of each option: maximum response rates were at or near the reward time associated with each option (vertical dashed lines signal usual reinforcement time, omitted in peak trials). A repeated measures ANOVA with option as single factor and *peak times* (i.e., 1-s bin with maximum response) as dependent variable supported our qualitative analysis, showing a significant effect of the delay associated with each option [$F(4, 16)=30.285, p<.001$].

3.2.2. Latencies in single-option trials

Figure 8 shows the median latencies in no-choice trials for each option (mean +SEM) during the 7 testing sessions. As postulated by SCM, the latencies were generally inversely related to the quality of the option, or, in other words, directly related to the delay associated to each option – the shorter the delay of an option, the shorter the latency associated with it. A repeated-measures ANOVA with option as single fixed factor and latencies as dependent variable confirmed this prediction [$F(4,9)=11.050$, $p<.001$], with a significant linear trend showing that the shorter the delay of a given option the shorter its corresponding latency [$F(4,9)=12.045$, $p<.01$].

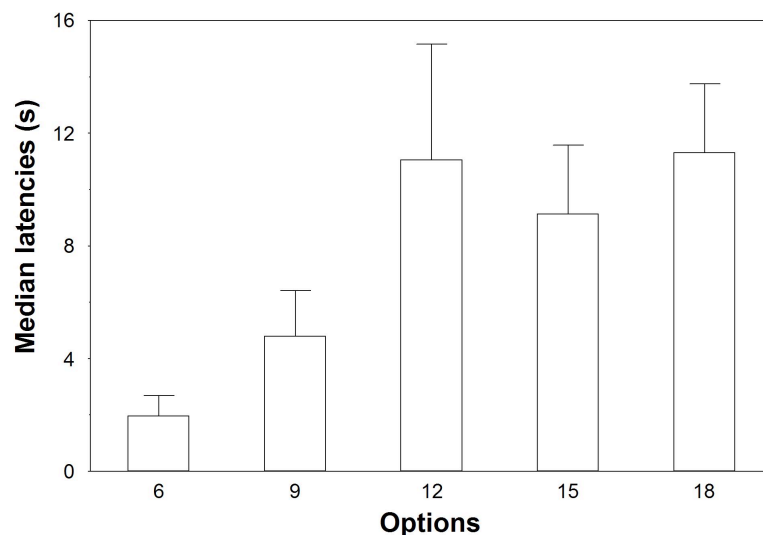


Figure 8. Latencies in single-option trials. Median latencies in seconds averaged across subjects (+SEM) during testing (7 sessions).

3.2.3. Latencies in simultaneous choices

As in Experiment 1, in order to evaluate the relation between latencies in no-choice trials and latencies either in binary- or in trinary-choice trials, we plot the cumulative frequency latency scores for options in choice trials as a function of the cumulative score for latencies to accept the same option in no-choice trials (averaged across subjects, $\pm$ SEM). Figure 9 shows this relation. Out of 10 comparisons (5 binary- and 5 trinary-

choice latencies versus 5 single-option latencies), no shortening was detected for either type of choice trials (Fig. 9, left and right panels, respectively). We were also unable to find any lengthening of latencies, in any of the two choice situations, since most values fell on the main diagonal. Paired-sample t -tests corroborate this observation revealing no significant differences between choice and no-choice latencies [binary vs. single-option: all $t(4) > -.568$ and < 2.487 , smallest $p=.068$; trinary vs. single-option: all $t(4) > -.407$ and < 1.698 , smallest $p=.165$].

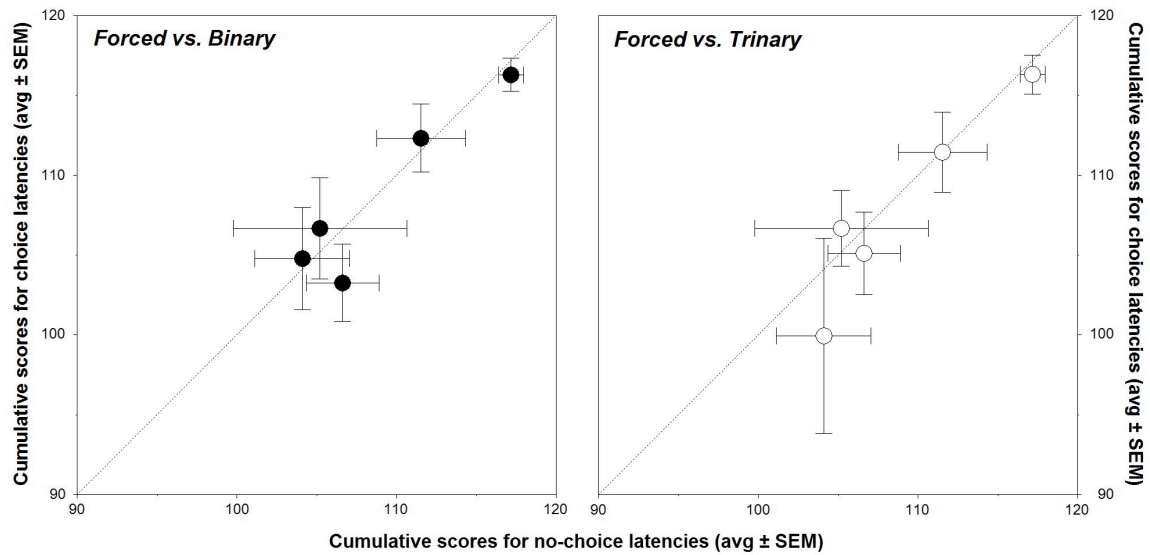


Figure 9. Cumulative frequency scores for choice and no-choice latencies. Each dot represents the score for choosing a particular option in a no-choice trial and the score for choosing the same option over the different binary- and trinary-choice combinations where that particular option was included (averaged across subjects, $\pm$ SEM). Points above the diagonal line indicate that choice latencies were shorter than the corresponding no-choice latencies. Left panel shows cumulative scores for no-choice versus binary-choice data (*filled dots*). Right panel depicts the same results for no-choice versus trinary-choice data (*open dots*).

3.2.4. Preferences

Figure 10 (top panel) shows the proportion of choices for the best option in every binary-choice pairing (*black dots*) during the experimental testing sessions (averaged across subjects $\pm$ SEM). A repeated-measures ANOVA with binary combination as single fixed factor, subject as random factor and choice proportion for the best of two options as dependent variable showed a significant effect of the options' combination in each the

binary-choice trials [$F(9, 36)=6.298, p<.001$]. Figure 10 (bottom panel) shows the corresponding data for trinary-choice trials, with *black dots* depicting the observed preference for every option (averaged across subjects, $\pm$ SEM). A single factor repeated-measures ANOVA showed a significant effect of the options' combination in each the trinary-choice trials [$F(9, 36)=9.267, p<.001$].

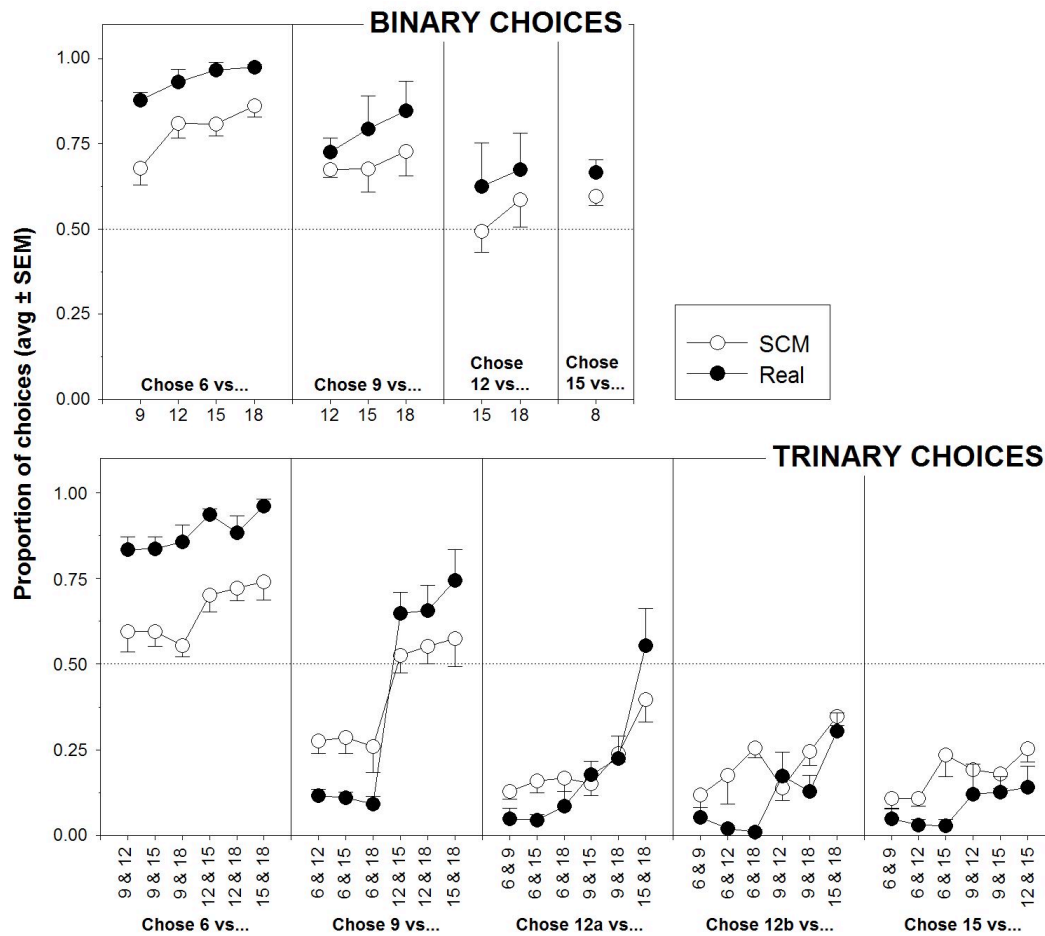


Figure 10. Observed and predicted preference. Top panel shows the observed proportion of choices in binary-choice trials (*black dots*; $\pm$ SEM) and the predictions of the Monte Carlo implementation of the SCM (*white dots*; $\pm$ SEM), bottom panel shows observed proportion of choices in trinary-choice trials (*black dots*; $\pm$ SEM) and the corresponding predictions of the Monte Carlo implementation of the SCM (*white dots*; $\pm$ SEM). All data was averaged across subjects.

3.2.5. Monte Carlo simulations

Figure 10 (top panel) also shows the predicted proportion of choices for the best option in every binary-choice pairing (*White dots*), according to the Monte Carlo implementation of the SCM (averaged across subjects, $\pm$ SEM). As seen in the figure, the

SCM consistently under predicted preference in all binary-choice pairings, even though the predictions followed quite closely the pattern of observed preferences ($r=.952$, $n=10$, $p<.001$). Figure 10 (bottom panel) also shows the corresponding data for trinary-choice trials (*White dots*, -SEM). Again, the model's predictions were less extreme than the observed preference, but as observed for binary-choice trials, the predicted outcome followed quite closely the observed performance ($r=.946$, $n=30$, $p<.001$).

3.3. Discussion

In this experiment, we aimed to explore the effect of adding more options to simultaneous choices on deliberation time, while extending the applicability of the SCM to choices with three simultaneously presented options, drawn from a multiple-alternative environment. In line with previous work, the SCM's main requirement was fulfilled, as latencies to accept singly presented options were relative to the quality of a particular option and the background alternatives. Once more, and as previously reported, no substantial shortening or lengthening was detectable between choice and no-choice latencies.

Nonetheless, the results reported here, where we extended the model's implementation to choices between three simultaneous options, added considerable support to the SCM's generality and its potential to be extended to more than two option choice scenarios.

4. General Discussion

The real value of a theoretical model is only exposed when it works for situations different from those that led to its inception. In this report, we extended the SCM to two new scenarios:

1) In Experiment 1, we tested a potential effect of learning about choice by presenting the animals with pairs of options prior to giving them experience with each alternative on its own. Still, we observed that the SCM's main assumptions and predictions upheld, namely that latencies were inversely related with the quality of each option, and that subsequently recorded latencies could be used to predict (i.e., post-dict) earlier choices. This retrospective implementation of the SCM exposed the importance of experience with single options. The SCM's predictions were similar (both derived from no-choice data) but there were differences in the strength of preference of both choice phases, according to whether animals had experience only with choices (i.e., *Choices 1*) or also with single-option trials (i.e., *Choices 2*). The model had a less good fit in the former case not because its predictions changed considerably, but because preference changed (as a result of accumulated experience with choice and no-choice trials), and the model could not capture this difference in the predictions. The fact that earlier choices showed more extreme preferences than later ones is somewhat surprising as it goes against the accumulation of information about the options. From a functional viewpoint, the higher the subjects' confidence, in the values of the options, the more extreme one would expect the behavioural allocation to be, the opposite of what we found.

2) In Experiment 2, in order to assess the ability of the SCM to deal with trinary-choice situations, we used the latency data to apply the model to choices between 3 simultaneously available options. However, the task of predicting choices between three different options is considerably harder than just between two [i.e., when only two options are present (e.g., A and B), knowing the proportion of choices allocated to one of the options (e.g., $p(A)$) immediately gives away the proportion allocated to the other one (i.e., $p(B) = 1 - p(A)$); when considering preference between three different options (e.g., A, B, and C), this is not the case (i.e., $p(A) = 1 - (p(B) + p(C))$)]. As in Experiment 1, the SCM's

predictions followed closely the observed preferences both for binary-choice (as shown in previous tests) and trinary-choice scenarios.

Put together, the findings from the experiments reported here are supportive of the view that choice mechanisms probably evolved from sequential (as opposed to simultaneous) encounters, but the detailed predictions of SCM are not invariably supported.

The good news for the SCM are that, using its rationale as a baseline for making behavioural predictions, we managed to predict choices from latencies to accept individually presented options retrospectively and prospectively (Exp. 1), and between sets of two (Exps. 1 and 2) and three different options (Exp. 2). No competing model can do that.

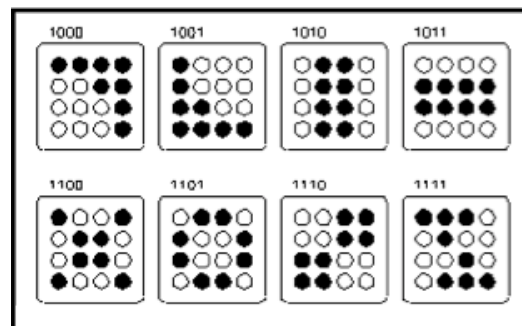
The fact that neither the latency shortening, one of the SCM's more idiosyncratic predictions, or lengthening (predicted by alternative models) were observed (in Exp. 1 some instances of lengthening and some of shortening were observed) deserves further research and theoretical reflection.

A final word should be said regarding the similarities between the current proposal and a number of *drift diffusion* or *race* models explored in the fields of mathematical psychology and more recently in neuroscience (e.g., Bogacz, 2007; Gold and Shadlen, 2007; Smith and Ratcliff, 2004, and references therein)¹⁰. None of those models use the subjects' behaviour facing individual options, as proxies for predicting choices between simultaneously available options in multiple combinations. Moreover, our proposal, though not perfect, does not use any curve fitting techniques to improve predictive power. Instead we adopt a functional standpoint, taking into account the evolutionarily inspired theoretical assumption that choice mechanisms evolved from sequential foraging

¹⁰See *Chapter 5* for a more in-depth discussion.

decisions, where animals either take a given option or skip it in favour of continuing searching the environment for alternatives. Using simplified laboratory settings, our goal is to put these assumptions under empirical scrutiny hoping to add to the understanding of general decision-making mechanisms.

5. Supplementary information



Supplementary Figure 1. Schematic representation of the symbols used in the experiments. Each symbol was an singly coloured eight LED combination (black dots), presented in red, green, lilac, turquoise, orange or blue). For each bird (and experiment) different symbol and colour pairings were used (i.e., partially counterbalanced). The attention key was composed of 16 white coloured LEDs.

6. Acknowledgements

We thank Simon and Jan Parry for trapping our participants. This research was supported by Grant BB/G007144/1 from the UK Biotechnology and Biological Sciences Research Council to AK. TM was supported by a doctoral grant from the Portuguese Foundation for Science and Technology and a Pembroke College Graduate Scholarship. MV was funded by the abovementioned BBSRC grant followed by post-doctoral grant SFRH/BPD/79311/2011 from the Portuguese Foundation for Science and Technology.

7. References

- Aw, J., Monteiro, T., Vasconcelos, M. and Kacelnik, A. 2012. Cognitive mechanisms of risky choice: Is there an evaluation cost? *Behavioural Processes*, 89: 95-103.
- Balci, F., Gallistel, C.R., Allen, B.D., Frank, K.M., Gibson, J.M. and Brunner, D. 2009. Acquisition of peak responding: What is learned? *Behavioural Processes*, 80: 67-75.
- Bateson, M. 1993. Currencies for decision-making: the foraging starling as a model animal. Unpublished D. Phil dissertation. University of Oxford, Oxford, 143 p.
- Blough, D.S. 2006. Reaction-Time Explorations of Visual Perception, Attention, and Decision in Pigeons. In: E.A. Wasserman and T.R. Zentall (Editors), *Comparative Cognition: Experimental Explorations of Animal Intelligence*, Oxford University Press, New York.
- Blough, D.S. 2011. A random-walk model of accuracy and reaction time applied to three experiments on pigeon visual discrimination. *Journal of Experimental Psychology: Animal Behavior Processes*, 37: 133-150.
- Bogacz, R. 2007. Optimal decision-making theories: linking neurobiology with behaviour. *Trends in Cognitive Sciences*, 11: 118-125.
- Cardinal, R.N. and Aitken, M.R.F. 2010. Whisker: A client—server high-performance multimedia research control system. *Behavior research methods*, 42: 1059-1071.
- Catania, A.C. 1970. Reinforcement schedules and psychophysical judgments: A study of some temporal properties of behavior. *The Theory of Reinforcement Schedules*: 1-42.
- Charnov, E. 1976. Optimal foraging: The marginal value theorem. *Theoretical population biology*, 9: 129.

- Freidin, E., Aw, J. and Kacelnik, A. 2009. Sequential and simultaneous choices: Testing the diet selection and sequential choice models. *Behavioural Processes*, 80: 218-223.
- Gold, J. and Shadlen, M. 2007. The neural basis of decision making. *Annual Review of Neuroscience*, 30: 535-574.
- Grafen, A. and Hails, R. 2002. *Modern statistics for the life sciences*. Oxford University Press, Oxford, 351 pp.
- Hick, W.E. 1952. On the rate of gain of information. *Quart. Journal of experimental psychology*, 4: 1.
- Hyman, R. 1953. Stimulus information as a determinant of reaction time. *Journal of Experimental Psychology*, 45: 188–196.
- Kacelnik, A., Vasconcelos, M., Monteiro, T. and Aw, J. 2011. Darwin's "tug-of-war" vs. starlings' "horse-racing": how adaptations for sequential encounters drive simultaneous choice. *Behavioral Ecology and Sociobiology*, 65: 547-558.
- Kaiser, D.H. 2008. The proportion of fixed interval trials to probe trials affects acquisition of the peak procedure fixed interval timing task. *Behavioural Processes*, 77: 100-108.
- Mazur, J.E. 2010. Distributed Versus Exclusive Preference in Discrete-Trial Choice. *Journal of Experimental Psychology-Animal Behavior Processes*, 36: 321-333.
- Ratcliff, R. 1978. A theory of memory retrieval. *Psychological review*, 85: 59-108.
- Ratcliff, R., Van Zandt, T. and McKoon, G. 1999. Connectionist and diffusion models of reaction time. *Psychological review*, 106: 261.
- Ratcliff, R. 2001. Putting noise into neurophysiological models of simple decision making. *Nature Neuroscience*, 4: 336-337.

- Reboreda, J.C. and Kacelnik, A. 1991. Risk sensitivity in starlings: variability in food amount and food delay. *Behavioral Ecology*, 2: 301-308.
- Roberts, S. 1981. Isolation of an internal clock. *Journal of Experimental Psychology: Animal Behavior Processes*, 7: 242-268.
- Schuck-Paim, C. and Kacelnik, A. 2007. Choice processes in multialternative decision making. *Behavioral Ecology*, 18: 541-550.
- Shapiro, M.S., Siller, S. and Kacelnik, A. 2008. Simultaneous and sequential choice as a function of reward delay and magnitude: Normative, descriptive and process-based models tested in the European Starling (*Sturnus vulgaris*). *Journal of Experimental Psychology: Animal Behavior Processes*, 34: 75-93.
- Smith, P.L. and Ratcliff, R. 2004. Psychology and neurobiology of simple decisions. *Trends in Neurosciences*, 27: 161-168.
- Vasconcelos, M., Monteiro, T., Aw, J. and Kacelnik, A. 2010. Choice in multi-alternative environments: A trial-by-trial implementation of the Sequential Choice Model. *Behavioural Processes*, 84: 435-439.
- Vasconcelos, M., Monteiro, T. and Kacelnik, A. submitted. Mechanisms of choice and context-dependent preferences in starlings.
- Vickrey, C. and Neuringer, A. 2000. Pigeon reaction time, Hick's law, and intelligence. *Psychonomic bulletin & review*, 7: 284-291.

On evolutionary and natural history constraints on decision-making: Adding function(s) to mechanism(s)?

[Monteiro, T., Vasconcelos, M., Kacelnik, A. (in prep.)]

1. Introduction.....	118
2. Methods.....	123
2.1. Subjects.....	123
2.2. Apparatus.....	124
2.3. Pre-training.....	124
2.4. General procedure.....	125
2.4.1. Trial types	
2.5. Data analysis.....	127
2.6. Simulations.....	128
2.6.1. Monte Carlo implementation of the SCM	
2.6.2. Time-constrained SCM	
3. Results.....	129
3.1. Representation of delays to food.....	129
3.2. Response latencies.....	130
3.3. Preferences.....	133
3.4. SCM predictions.....	134
4. Discussion.....	135
5. References.....	139

1. Introduction

We present a study of choice processes in the European starling (*Sturnus vulgaris*) aimed at increasing the ecological validity of the work of Shapiro, Siller and Kacelnik (2008). These authors developed a choice model that predicted choices from no-choice behaviour and also, as a consequence of its architecture, sought to account for the elusive nature of so called deliberation time, namely the time an animal may be expected to spend before deciding between simultaneously present alternatives. Their model, in fact, predicts shorter response times in choices relative to no-choice situations. This last prediction is at odds with most classical (if not all) choice models [e.g., the Hick-Hyman law; (Hick, 1952; Hyman, 1953; see also Schwartz, 2004)]. The Sequential Choice Model (SCM; reviewed in Kacelnik et al., 2011 - see *Appendix 1*; Shapiro, Siller, and Kacelnik, 2008) postulates that the mechanism(s) used by European starlings to choose is (are) the same they use when facing each option alone, incorporating the idea that such mechanism(s) evolved as adaptations to environments in which it was rare to meet different options simultaneously, but instead, sequential encounters were common. Empirically, the model was a response to laboratory observations showing that response times (i.e., latencies) to singly presented options were longer than minimal reaction times, and were relative to the background environment. In other words, while the rate-maximising strategy would be to respond to every option either in the shortest amount of time possible or not at all, latencies to respond to singly presented options showed a variable and orderly pattern. Responses to the better options in the environment elicited shorter response latencies (Freidin, Aw, and Kacelnik, 2009; Shapiro, Siller, and Kacelnik, 2008)¹, even when there were no alternatives present at the time of choice.

¹See also *Chapters 2 to 4*.

Formally², the SCM assumes that in common sequential encounters with food-signalling stimuli, prior to a response, an accumulation process takes place in unspecified structures of the central nervous system. Better options have faster accumulations (on average) and consequently shorter response latencies, than poorer alternatives. Whenever two options are simultaneously available, a parallel accumulation process occurs and the first option reaching a decision threshold elicits a directed response (i.e., a choice). Hence, in simultaneous encounters only latencies from winning options are recorded. This happens because no information concerning alternative options is recorded – choosing a particular option triggers the contingencies associated with it, while immediately removing the alternative option from the environment; the corresponding accumulation process for the non-chosen option, terminates and is reset as soon as the winning alternative is chosen. In summary, latencies are the end product of an underlying parallel accumulation process that is reflected in the time to respond to each particular option, when encountered alone³.

In most previous studies⁴ aimed at testing the model, starlings faced multi-alternative environments composed of options differing only in delay (Freidin, Aw, and Kacelnik, 2009; Vasconcelos et al., 2010). In one case (Shapiro, Siller, and Kacelnik, 2008), bi-dimensional differences between options were considered, but in each successive treatment the environment was composed of only two options, so that when comparing a present option against the background the subjects only had to consider one of the alternatives (they could respond away or towards a given option, regardless of its pairing). The main purpose here was: (1) to test the ecological validity of the Sequential Choice Model (SCM) by using a more complex environment in which the background to each decision was a mixture of many possible alternatives, and (2) to stress the importance of sequential food encounters to the study of foraging decisions, by comparing the SCM's

²For the analytical formalization of the model see *Appendix 1*.

³See Figs. 1 and 2 in Kacelnik et al. (2011) – *Appendix 1*, for details.

⁴See *Chapters 2 and 4*.

rationale with other sequential sampling models (SSMs) from both mathematical psychology and neuroscience, that are normally applied to binary-choice situations.

In mathematical psychology, SSMs also encompass underlying accumulating process(es), and have been used to discuss putative processes of how human subjects reach a particular decision in simple choice situations (see Ratcliff and Smith, 2004; Bogacz et al., 2006 and references therein for comprehensive reviews). In these models, prior to a particular choice, noisy perceptual information accumulates until a threshold is reached and a decision is made. This is often described by saying that a decision is made when sufficient evidence favouring a particular option is acquired⁵.

SSMs encompass two major categories: *random-walks* (or diffusion models) and *accumulator* (or counter) models. The fundamental difference between these two classes is how accumulation of perceptual information takes place. *Random-walk* models use a relative stopping rule, proposing the accumulation of the net evidence between the alternatives; alternatively, in *accumulator* models evidence for each particular option accumulates independently, and an absolute stopping rule determines when a decision is made⁶. Several examples of each class can be found in the literature (e.g., Ratcliff and Rouder, 1998; Usher and McClelland, 2001), however a thorough review is beyond the scope of this report

In recent years, there has been a growing interest in integrating psychological (e.g., SSMs) and neurobiological approaches to simple decisions (e.g., Smith and Ratcliff, 2004; Gold and Shadlen, 2007; Bogacz, 2007; Soltani and Wang, 2008; Kable and Glimcher, 2009) and this resulted in three broad model categories: perceptual, motor and value-based decision processes. In perceptual models a decision is an action that follows a simple

⁵In anthropomorphic language, the subject is making a proper choice by asking “which of these options is the better one”, rather than thinking “should I respond to this stimulus now?” for each stimulus independently.

⁶Technically, the SCM is an accumulator model.

sensory stimulus presentation: for instance, in a random-dot motion direction discrimination task, a monkey is required to make a saccade in the perceived direction of ambiguous movement; in motor tasks, the focus is on the initiation of a movement: in a hypothetical motor task a saccade to an unambiguous target that appears at an unpredictable time and place in a computer screen is reinforced.

In both perceptual and motor models, the use of simple tasks makes the integration between behavioural and neuronal data possible and informative. Neural correlates for behavioural models (for which SSMs are only one example) start to be integrated, so that behavioural and neural firing data are related to parameters and outcomes of specific models (Kable and Glimcher, 2009; Ratcliff and Frank, 2012; Wang, 2008). For instance, Smith and Ratcliff (Smith and Ratcliff, 2004) gathered evidence relating eye movement decisions and corresponding neural firing. The emerging picture reveals a striking consistence between neuronal firing data and SSMs, at least in non-human primates. More recently, Churchland, Kiani, and Shadlen (Churchland, Kiani, and Shadlen, 2008) reported that a bounded accumulation model could be extended to decisions with more than two alternatives. Their model accounted quantitatively for the speed and accuracy of monkeys in a four-alternative perceptual task. Additionally, this accumulation of evidence was consistent with the firing patterns of neurons in the lateral intraparietal area (or LIP).

Value-based decisions (the core focus of the emerging field of Neuroeconomics), unlike perceptual or motor decisions, involve accessing the subjective value of a given option respective to one or several others (for comprehensive reviews see Rangel, Camerer, and Montague, 2008; Sugrue, Corrado, and Newsome, 2005). Under these situations, the additional complexity inherent to the options' differential value might lead researchers to consider more complex decision models, but the sequential sampling

approach has been successfully applied to binary and trinary value-based decisions with human participants (Krajbich, Armel, and Rangel, 2010; Krajbich and Rangel, 2011).

All these models, including value-based ones, are applied mostly to binary simultaneous choices (viz. Churchland, Kiani, and Shadlen, 2008; Krajbich and Rangel, 2011), without reference to their significance in terms of biological functionality. Such choices are likely to be ecologically infrequent, something that seems particularly important for value-based processes. If, as postulated by the SCM, the mechanism(s) driving simultaneous choices (especially choice related to consummatory/foraging behaviour) are those evolved to solve more common sequential encounters, such paradigms might not be ideal/suitable to reveal either how value is assigned or how it is used. One functionally-inspired question is why responses to singly presented food opportunities are not immediate but delayed in an orderly fashion. It makes sense to assume that when better alternatives can be expected to be present in the environment, animals will take longer to accept singly presented (especially poorer) options, reflecting a tendency to skip opportunities to keep searching (for better alternatives).

Thus, our reasoning is twofold:

- 1) We assume that the mechanism(s) used in simultaneous choices (especially choice related to foraging behaviour), evolved to deal with more common sequential choice situations.

- 2) By taking into account the animals' ecology, choice between simultaneous options should be predictable from latencies to respond to each option on its own.

Using empirical data from birds pecking at coloured keys for food rewards, the key objective of the present report is to stress the importance of no-choice behaviour in subsequent choice, by showing that the SCM can accurately predict simultaneous choices from latencies recorded during sequential (or no-choice) behaviour.

2. Methods

2.1. Subjects

Twelve adult wild-caught European starlings (*Sturnus vulgaris*) participated in the current experiment. Animals were captured and held in captivity under Natural England license 20104653.

All subjects were naïve to experimentation. Prior to testing, birds were housed communally in a large outdoor aviary (3m high x 3.2m wide x 4m long) where they received *ad libitum* food (a mixture of turkey crumbs and mealworms (*Tenebrio sp.*) and had continuous access to fresh drinking and bathing water.

During the course of the experiment, starlings were moved in pairs to indoor cages, which were visually, but not acoustically isolated. Indoor temperatures ranged from 16 to 18°C and lights followed a 12:12 dark schedule with daylight at 07h00, and gradual transitions at dawn and dusk. Starlings were rewarded with precision pellets throughout the experimental session and provided with four hours (13h00-17h00) of free access to a mixture of turkey crumbs and Orlux© Remiline universal granules, 10 mealworms, and social interaction with the respective pair. This regime maintains starlings at approximately 90% of their free feeding weight (Bateson, 1993). Birds had continuous access to drinking water and received bathing trays every day. On completion the birds were reintroduced into communal aviaries and eventually released into the wild. The experiment followed animal welfare regulations of Oxford University. Maintenance and experimental protocols adhered to the Guidelines for the Use of Animals in Research from the Association for the Study of Animal Behaviour/Animal Behavior Society (Guidelines for the treatment of animals in behavioural research and teaching, 2006).

2.2. Apparatus⁷

Each indoor cage [1350 mm x 784 mm x 800 mm (l x w x h)] was composed of two units, vertically mounted (800 mm each). Each unit included two experimental areas separated by a common middle section. Each experimental area had a panel attached 100 mm above the floor. The panel was 400 mm tall with three sections: a middle sub panel, facing the cage (115 mm wide), and two side subpanels (same length) attached to the cage at a 120 degree angle from the centre subpanel. The middle subpanel had one response key in the centre (110 mm from the bottom), and the food hopper (25 mm from the bottom), that was connected to the pellet dispenser (Campden Instruments) containing 20 mg precision dustless pellets. Each side subpanel had one response key in the centre (110 mm from the bottom). Every key was composed by 16 LED lights matrix that could display 16 different symbols in seven possible colours. Trials were governed by custom software running on the Microsoft® Windows® operating system and attached to an Animal Behaviour Environment Test System (Campden Instruments®) via WhiskerServer (Cardinal and Aitken, 2010).

2.3. Pre-training

Following magazine training, in the first phase of pre-training, the birds were trained to peck a flashing white centre key (700ms ON, 300ms OFF). A single peck to this key delivered four precision pellets, extinguished the keylight, and initiated a 120-s inter-trial-interval (ITI). Failing to peck the key within 30-s from the onset of flashing resulted in the same events as a peck. Training thus combined autoshaping with an operant response. Once birds were reliably pecking the centre key, the lateral keys were introduced. Trials again began with the flashing of a white centre key. A peck to this key

⁷ See Figs. 1 and 2, *Chapter 1*.

turned its light off and started flashing a white lateral key. A peck to the flashing lateral key turned it off and produced two food pellets followed by a 90-s ITI. During this phase, failing to peck the centre key within 30 s from trial onset resulted in a 10-s period with the light switched off, followed by the ITI. Failing to peck the flashing side key during the same time period was followed by food 75% of the time. This program was maintained 5 hours per day until the birds reliably pecked the centre and side keys on at least 80% of the trials.

Next, birds received preliminary, response-initiated *fixed interval* (FI) training. In this phase two pecks to the side key were required to deliver food. The first peck turned the symbol steadily on and began a delay, the duration of which was progressively increased from 1 to 20 s. The first peck after the delay elapsed extinguished the keylight, delivered two food pellets and initiated a 45-s ITI. Once birds were reliably obtaining food on FI 20-s trials, the experimental sessions began.

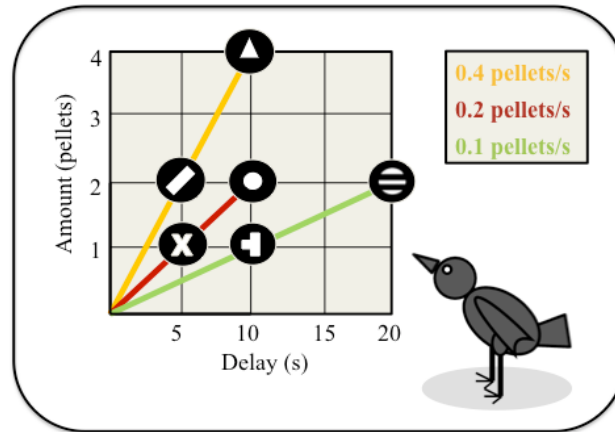
For experimental sessions a different set of symbols-colours were used for each bird.

2.4. General Procedure

Starlings were trained in an environment consisting of six different options⁸ composed by a different amount/delay to food combination [A: 2 pellets in 5 seconds, B: 4 pellets in 10 seconds, C: 1 pellet in 5 seconds, D: 2 pellets in 10 seconds, E: 1 pellet in 10 seconds, and F: 2 pellets in 20 seconds], hence each option signalled one out of three possible rates of reinforcement [0.4, 0.2, and 0.1 pellets per second, Fig. 1]⁹.

⁸For details, see *Chapter 4*, Supplementary Figure 1.

⁹In foraging theory this ratio is called profitability, and identifies reward per unit of time exclusively assigned to such prey. Intake rate instead includes the ITI and latency to respond (Kacelnik and Todd, 1992; Cassini, Kacelnik, and Segura, 1990). The ratio of amount to delay is appropriate for psychological studies of choice because the ITI is less clearly associated to each individual source of reward (Bateson and Kacelnik, 1996).



Adapted from Shapiro, Siller, & Kacelnik (2008), *J. Exp. Psych.: ABP*

Figure 1. Experimental environment. Schematic representation of the options' used (amount of food in represented on the *y*-axis, delay to a food reward on the *x*-axis).

Each training session was composed of 252 trials [240 single-option trials, 40 per option, 20 in each possible location, and 12 peak trials, 2 per option, one in each possible location; see details below].

Birds were moved to a testing phase after completing 15 days with more than 75% completion of daily trials or after 20 days of 60% of daily completion, whichever came first. In testing, no-choice trials were interspersed with binary-choice trials between all possible combinations of different options. Testing sessions were also 252 trials long [120 single-option trials, 20 per option, 10 in each possible location, 120 binary-choice trials, 8 per pairing, 4 in each possible location, and 12 peak trials, 2 per option, 1 in each possible location]. Testing ended after 2 blocks of 3 consecutive days with no trend in preferences (and $SD < .15$) or after 15 days, whichever came first.

2.4.1. Trial types

Single-option trials began with the flashing illumination of the centre attention key. A peck to this flashing key turned the key off and began flashing (700 ms ON, 300 ms OFF) one of the two side keys (randomly assigned). A peck to the illuminated flashing

side key turned the key steadily on and initiated its programmed delay. Once this interval elapsed, the first peck to the key turned the keylight off and delivered the pre-defined number of pellets of reward at a rate of 200 ms per pellet, after which a 45 s intertrial interval (ITI) was initiated. Not pecking the keys at any stage (flashing or steady keys) meant not moving forward to the next trial.

Probe trials were as single-option trials, but once pecked, a given option remained on for three times its typical delay. At the conclusion of this interval, the light extinguished without reward or requiring a peck, followed by the ITI (Catania, 1970; Roberts, 1981).

Choice trials offered individuals simultaneous choices between combinations of pairs of training stimuli, chosen among 15 possible binary-combinations of the 6 options. Trials again began with a flashing centre attention key. A peck to this key turned it off and began flashing the two side keys (each one displaying a different symbol). The location of presentation was also randomized. A peck to one of the flashing keys turned the selected key on and initiated its programmed contingencies, and turned the unselected key off. Thus the bird committed itself to a given option with a single peck. Absence of pecking produced the same consequences as in single-option trials.

2.5. Data analysis

Proportional (i.e., choice preference) and latency data were normalized for statistical analysis using arcsine square-root and natural log transformations (Grafen and Hails, 2002). An alpha level of 0.05 was adopted for all statistical comparisons. Only the last 6 training (i.e., for peak trials) and the last 6 testing days (i.e., for preferences and latencies) were considered in the analysis.

Three birds were excluded from all analyses after repeatedly failing to reach the experimental criteria¹⁰.

2.6. Simulations

2.6.1. Monte Carlo implementation of the SCM

Algorithmic models such as the SCM can be tested by their qualitative predictions (for instance by checking whether mean latencies in choice trials differ from latency in choice trials as generally predicted by the model) or by molecular predictions, namely predicting choices by implementing the algorithm. The latter involves elements of randomness and requires using a Monte Carlo simulation. Here we generated predictions using latencies from single-option trials during the last 6-day block of testing. The simulation included 100,000 runs of 720 trials each (48 choice predictions per binary-choice type - the equivalent to 6 days of testing). For every choice trial, the simulation drew two latencies (i.e., one for each option) from the latencies recorded during single-option trials, and the prediction was that the option yielding the shorter latency would be chosen in that particular choice trial.

2.6.2. Time-constrained SCM

Following the analysis introduced by Vasconcelos and colleagues¹¹ (Vasconcelos et al., 2010) we predicted individual choices using a hyperbolically weighted moving average of 32 previous single-option latencies. The weighted moving average was calculated as follows:

¹⁰See section 2.4. for details.

¹¹See *Chapter 2*.

$$\frac{\sum_{i=1}^n l_{-i} \cdot i^{-1}}{\sum_{i=1}^n i^{-1}}, \text{ Equation 1}$$

where $n = 32$, i corresponds to the i^{th} place preceding the current choice and l =latency. Notice that such a weighting assigns a weight of 1 to the predictive power of the last observed latencies, $\frac{1}{2}$ to the penultimate latency, $\frac{1}{3}$ to the one before that, and so on. Thus, memory discounting is very sharp at first and flatter earlier on, so that distant latencies reflect properties of the overall environment.

3.Results

3.1. Representation of delays to food

Figure 2 shows the response rate in peak trials (averaged across individuals) during the last 6-day block of training. Visual inspection of the data shows that the animals discriminated between the different options prior to testing: maximum response rates were on or near the programmed reward time associated with each option (vertical dashed lines signal due reinforcement time, omitted in peak trials).

A repeated measures ANOVA with option as fixed factor, subject as random factor and peak time (1-s bin with maximum response) as dependent variable supported this visual description, showing a significant effect of the delay (i.e., 5, 10 or 20 s) associated with each option [$F(1, 8)=84.359$, $p<.001$]. Post-hoc contrasts also showed significant differences between options signalling different delays to food [i.e., A vs. B, A vs. D, A vs. E, A vs. F, B vs. C, B vs. F, C vs. D, C vs. E, C vs. F, D vs. F, E vs. F; highest $p=.012$].

Peak times for options signalling the same delay to reward were not statistically different (i.e., A vs. C, B vs. D, B vs. E, D vs. E; smallest $p = .135$)¹².

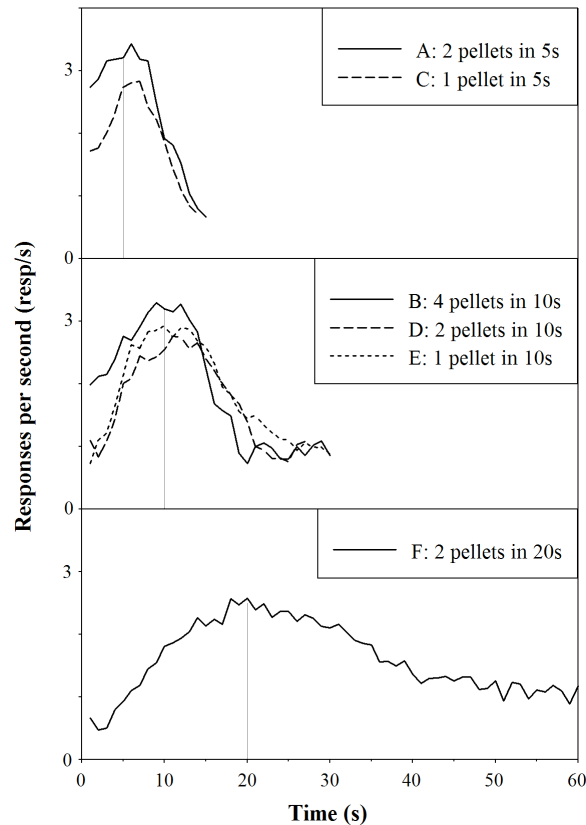


Figure 2. Response rate in peak trials. Pecks per second during peak trials, averaged across subjects, during the last 6-day block of training. Horizontal lines indicate 0 pecks per second, vertical dashed lines signal usual time of reinforcement availability (absent in peak trials). Inset legends show the amount/delay combination for each option.

3.2. Response latencies

Figure 3 shows median latencies during the last 6-day block of testing sessions, in both no-choice (*dark bars*) and choice trials (*white bars*) for each option (averaged across subjects, $\pm$ SEM). As assumed by the SCM, response latencies were inversely related to

¹²These results contrast with findings that showed that reward value (and magnitude) affect temporal discriminations in pigeons (see Galtress and Kirkpatrick, 2009; Galtress and Kirkpatrick, 2010).

the quality of the options, the higher the options' rate, the shorter the latency associated with it. A repeated-measures ANOVA with trial type and option as fixed factors and latency as dependent variable confirmed this prediction, showing a significant effect of option [$F(5,40)=48.375$, $p<.001$], with no significant effect of trial type [$F(1,5)=2.013$, $p=.194$], but a significant interaction between trial type and option [$F(5,40)=3.03$, $p=.021$]. Planned paired sample t -tests also showed significant differences in latency between all options [highest $p=.01$] except in A vs. B [$p=.377$] and C vs. F [$p=.086$]. In the A vs. B comparison, the lack of difference might be explained by a floor effect, as the two options had the highest rate of reward (i.e., 0.4 pellets per second) and caused extremely low latencies. The reason for a lack of difference in the C vs. F latency comparison is not obvious, C being richer (0.2 pellets per second) than F (0.1 pellets per second).

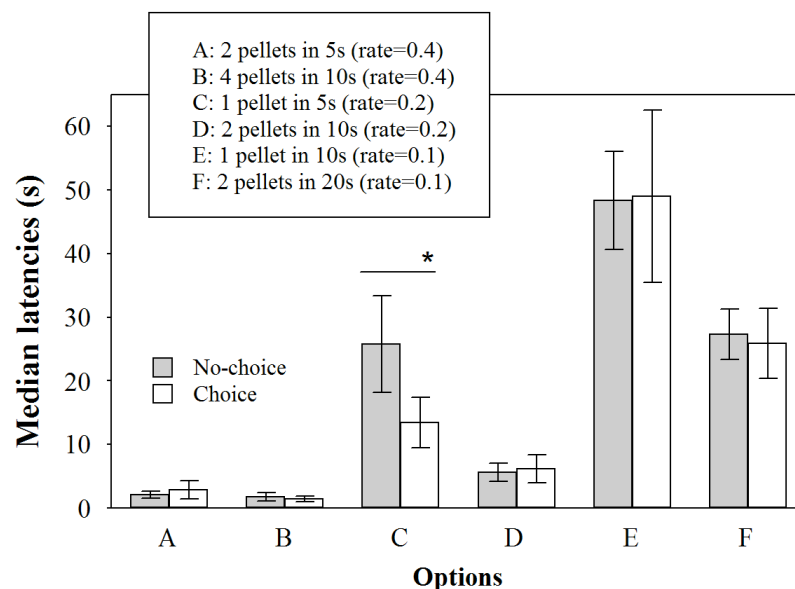


Figure 3. Latency data in no-choice trials. Median latencies in seconds, averaged across subjects ($\pm$ SEM), during the last 6-day block of testing sessions for no-choice (dark bars) and choice trials (white bars). Inset legend shows the amount/delay combination (rate) for each option. (*) $p<0.05$.

To investigate further the interaction between trial type and option, we conducted paired samples *t*-tests that revealed no significant differences [all $t(8) \geq -.682$ and ≤ 1.36 , smallest $p=.211$] between latencies in no-choice trials (*dark bars*) and latencies in choice situations (*white bars*), except for option C, where the significant effect was in the direction of a shortening in choice trials [$t(8)=2.904$, $p=.02$]. We also calculated individual cumulative frequencies scores¹³ for both choice and no-choice latencies. Figure 4 shows cumulative frequency scores (averaged across subjects $\pm$ SEM) for choice and no-choices latencies, respectively. The data used in the calculations was the individual data presented (on average) above (see Figure 3). Data points above the main diagonal indicate that latencies for a particular option were shorter during choices when compared to no-choice situations, data points below the main diagonal show that latencies for a given option were longer on choices, when compared to no-choice trials. As shown in Figure 4 most data points fell close to the main diagonal (i.e., indicating no detectable differences between choice and no-choice response latencies), with one clear exception. As shown in the previous analysis (see Fig. 3) latencies to respond to option C were shorter in choices than in no-choice trials, the direction predicted by the SCM. Paired-sample *t*-tests confirmed this result [$t(8)=-2.593$, $p=.032$]. All the remaining comparisons yielded non-significant results.

¹³This measure is obtained by calculating the total area under each individual's cumulative distribution of latencies, for both no-choice and choice trials. Higher scores correspond to shorter response latencies (i.e., in these cases most latency values are within the first time-bins of their corresponding cumulative distribution).

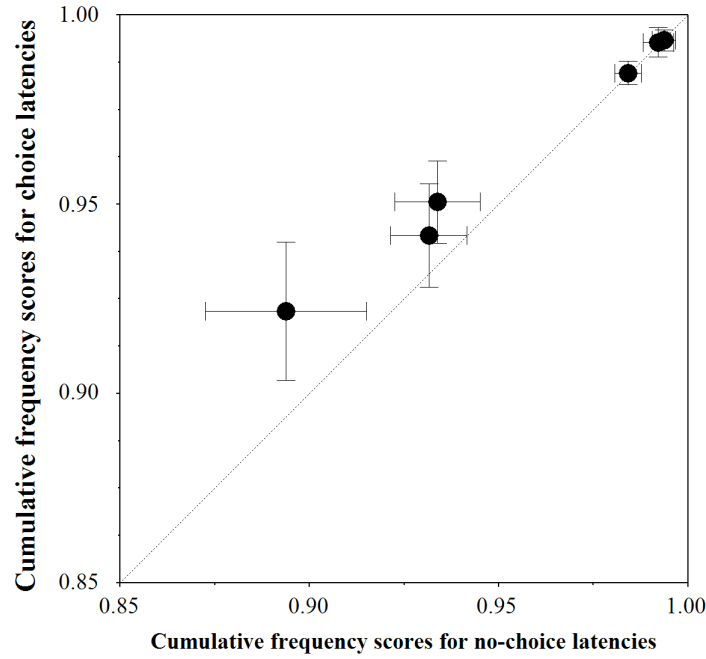


Figure 4. Normalized cumulative frequency scores for choice and no-choice latencies. Each dot represents the score for choosing a particular option in a no-choice situation and over the different binary-choice combinations where that option was included (averaged across individual subjects, $\pm$ SEM), during the last 6-day block of testing sessions. Points above the diagonal lines indicate that choice latencies were shorter than corresponding no-choice latencies. Both axes are clipped at 0.85 to facilitate visualization.

3.3. Preferences

Figure 5 shows the proportion of choices in every binary-choice pairing, averaged across subjects (*black dots*; $\pm$ SEM), during the experimental test sessions. Paired-samples *t*-tests showed that in all instances, choice proportions were significantly different from chance level [all $t_s(10) \geq -8.124$ and ≤ 24.733 , highest $p=.035$] except in the pairing C vs. F [$p=.369$]. These results might be generally interpreted as follows: 1) if the options' rate was the same (i.e., Fig. 5: left panel, $\text{Rate}_{[\text{first}]} = \text{Rate}_{[\text{last}]}$), animals chose the option associated with the highest amount of reward most of the times; 2) if the rate of one option was higher than the rate of the alternative (i.e., Fig. 5: middle panel, $\text{Rate}_{[\text{first}]} = 2\text{Rate}_{[\text{last}]}$; right panel, $\text{Rate}_{[\text{first}]} = 4\text{Rate}_{[\text{last}]}$), animals chose preferentially the option yielding a highest rate of reward (the exception was then the indifference between option C and F).

3.4. SCM predictions

Figure 5 also shows the predicted proportion of choices, averaged across subjects, in every binary-choice pairing, according to the Monte Carlo implementation of the SCM (*White dots*; $\pm$ SEM). As shown in the figure, this implementation of the model consistently under-predicted preference in all pairings, even though the predictions followed quite closely the observed preference [$r=.955$, $n=15$, $p<.001$]. Also in Figure 5, are the predictions averaged across subjects, of the time-constrained SCM (*grey dots*; $\pm$ SEM). This version of the model yielded a good agreement with trends in the observed data, but generally, with more extreme predictions than the ones observed. As observed for the Monte Carlo implementation of the model, the predicted outcome followed quite closely the observed performance [$r=.950$, $n=15$, $p<.001$]. The close relation between both predictions [$r=.945$, $n=15$, $p<.001$] shows that in a steady-state environment¹⁴ both methods have nearly equivalent performances, and the use of a localized temporal window to predict behaviour does not improve considerably the predicting capabilities of the model.

¹⁴Note that testing normally ended after 2 blocks of 3 consecutive days with no trend in preferences (and $SD<.15$), or after 15 days, whichever came first. The data reported here are precisely from the last 6-day block of testing, where the majority of birds were showing stable preferences.

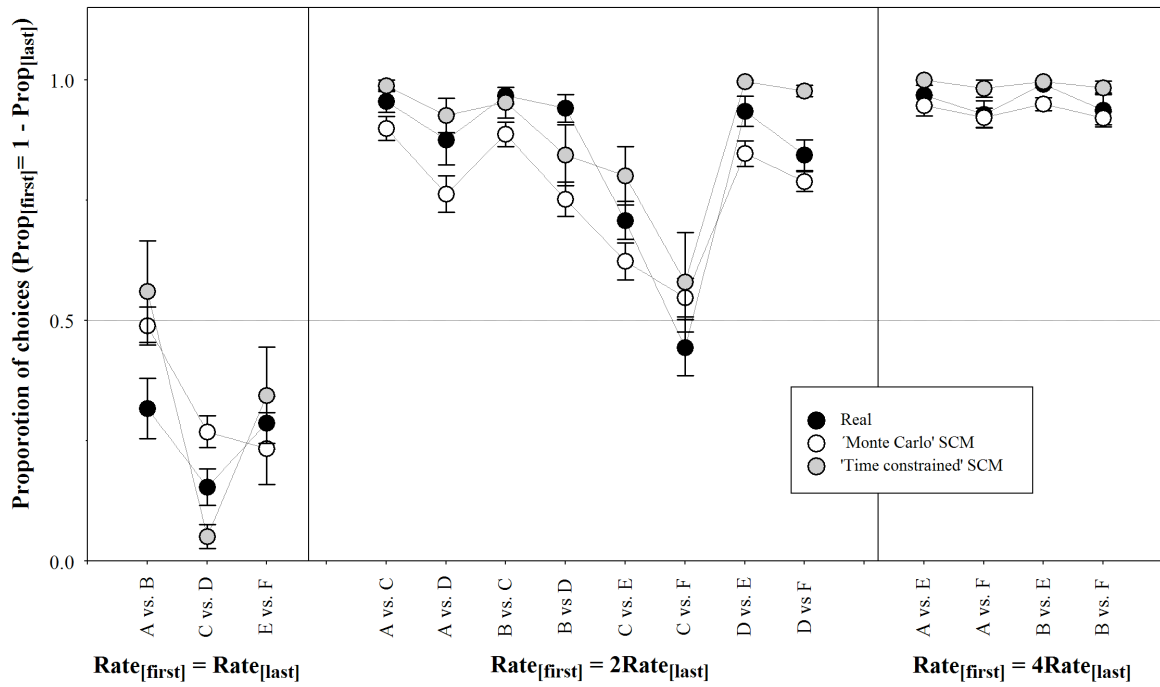


Figure 5. Observed and predicted preference. Black dots show the observed proportion of choices during the experimental test sessions, white dots show the predicted proportion according to the Monte Carlo implementation of the SCM and grey dots show the predictions of the time-constrained (32 trials) implementation of the SCM, in all choice pairings. All data is averaged across subjects ($\pm$ SEM). Left panel shows combinations of options with equal rate, middle (and right) panels show pairs where one option had twice (or four times) the rate of the alternative, respectively.

4. Discussion

In this study starlings faced sequential and simultaneous encounters (choices between two simultaneously presented options) with 6 different (and bi-dimensional) options (see Fig. 1). Unlike previous tests (Shapiro, Siller, and Kacelnik, 2008) that used the same parameters but in multiple (and successive) conditions (with only 2 options in each), here, the animals could face all six options either alone, or in 15 different pairings. This considerable increase to the background of alternatives was an additional challenge to the SCM¹⁵. Regardless of this complexity increment, the model successfully tracked the birds' preferences both globally (i.e., in the Monte Carlo implementation of the SCM) and in a 'time constrained' version of the model in which predictions were based on latencies

¹⁵ Other studies (see *Chapters 2 and 4*) also included experiments with multiple alternatives, but all options differed in a single dimension (delay to food). In the present study, options differed in two dimensions (i.e., the combination of amount/delay to a food reward).

weighted by their recency. Our results do not support the prediction that shorter response times should be observed during choice, the SCM's most counter-intuitive prediction, but neither did we find the opposite, as predicted by models postulating a time cost for deliberation time.

Our experimental procedure was close to that used by Shapiro and colleagues (2008)¹⁶, but the importance of the apparently subtle differences can be highlighted by remembering the significance of background information for the SCM. Shapiro et al. (2008) trained their animals with a single pair of options in each experimental condition (of a total 15 conditions¹⁷), while we increased the realism by training them with all options interspersed in the same context. Thus, in Shapiro et al.'s protocol a particular option was either better, worse or equivalent as the only possible alternative. In such environment a comparative rule between options is sufficient, while in the present study either multiple such comparisons must be remembered, or some computation of background mean quality needs to be computed. The latter is representative of the problem envisaged in Charnov's optimal diet model (Charnov, 1976a), where each prey type is included or not in the diet according to its profitability relative to the mean environmental average, including both prey types and encounter rates (in this case the reciprocal of ITI). Charnov's model does not propose a strategy for binary choices, only for sequential ones, but both Shapiro and collaborators and us presently do use forced choices among pairs of options, because our goal is to explore choice mechanisms¹⁸. These procedural differences may be responsible for differences in the results of the two studies. In both, three choice pairs were between options that were equalised in profitability (amount/delay). In the earlier one, the birds were either indifferent (i.e., two options both offering either 0.4 or 0.1

¹⁶See Fig. 1, above.

¹⁷The authors referred to these conditions as *successive treatments*.

¹⁸See Freidin and Kacelnik (2009) for a recent implementation of Charnov's (1976a) diet choice paradigm.

pellets per second) or preferred the alternative with larger reward and longer delay (i.e., two options offering 0.2 pellets per second). Here, these bias for larger-later over smaller-sooner was present in all three pairings. Notice that a preference for Larger-Later over Smaller-Sooner is the opposite of the often-repeated claim in the discounting-impulsivity literature¹⁹ (Stephens and Anderson, 2001; Fehr, 2002; Kagel, Green, and Caraco, 1986; Rachlin and Green, 1972; Henly et al., 2008; Mazur and Logue, 1978; Ainslie, 1974; Killeen, 1968). In fact, that widespread claim is unjustified empirically, as it is often based on studies where profitability is not equated (Kacelnik, 2003; Fawcett, McNamara, and Houston, 2012; see also Pavlic and Passino, 2010). The functional interpretation for a Larger-Later preference can be found in the importance of the ITI (Bateson and Kacelnik, 1996; Mazur, Snyderman, and Coe, 1985; Mazur, 2001). If the value of an option is computed including times other than the delay in the denominator for each option [in this case computing $\text{Amount}/(\text{Delay} + \text{ITI})$], then the resulting index gives a more accurate measure of rate. If $\text{Amount}/\text{Delay}$ is equated between options, this index invariably is larger for the Larger-Later option. Thus, by increasing the ecological realism of the environment we seem to have created conditions where this important correction to the impulsivity literature is evidenced.

Finally, then, consistently with the view that sequential, single opportunity encounters might be responsible for the evolution of choice mechanisms – we confirmed that latency to respond in single-option situations is a powerful predictor of choice in binary encounters, and we failed to find any evidence for a time cost for choices. Both observations reaffirm the validity of the SCM, but the model falls short of accounting for all results because while we did not identify a deliberation time cost neither did we find a shortening of response times during choices, as the model predicts.

¹⁹Also referred to as impatient behaviour, failure to delay gratification and lack of self-control.

The significance of sequential encounters and of lost opportunity as viable working hypotheses were already present in the early days of optimal foraging theory (OFT) through Charnov's Diet Choice model (Charnov, 1976a) and Marginal Value Theorem (Charnov, 1976b), both of which inspired empirical tests (Krebs et al., 1977; Cowie, 1977) that are now considered classical, but later research has been dominated by simultaneous choice paradigms (in both behavioural ecology, psychology and neuroscience). Re-focusing on single options and their interaction with the background context may offer a chance of linking functional ideas to precise mechanistic modelling, as we have attempted here²⁰.

²⁰See also *Chapters 2 to 4* and Stephens (2008).

5. References

- Ainslie, G.W. 1974. Impulse control in pigeons. *Journal of the Experimental Analysis of Behavior*, 21: 485.
- Bateson, M. 1993. Currencies for decision-making: the foraging starling as a model animal. Unpublished D. Phil dissertation. University of Oxford, Oxford, 143 p.
- Bateson, M. and Kacelnik, A. 1996. Rate currencies and the foraging starling: the fallacy of the averages revisited. *Behavioral Ecology*, 7: 341-352.
- Bogacz, R. 2007. Optimal decision-making theories: linking neurobiology with behaviour. *Trends in Cognitive Sciences*, 11: 118-125.
- Bogacz, R., Brown, E., Moehlis, J., Holmes, P. and Cohen, J.D. 2006. The physics of optimal decision making: A formal analysis of models of performance in two-alternative forced-choice tasks. *Psychological review*, 113: 700-765.
- Cardinal, R.N. and Aitken, M.R.F. 2010. Whisker: A client—server high-performance multimedia research control system. *Behavior research methods*, 42: 1059-1071.
- Cassini, M.H., Kacelnik, A. and Segura, E.T. 1990. The tale of the screaming hairy armadillo, the guinea pig and the marginal value theorem. *Animal Behaviour*, 39: 1030-1050.
- Catania, A.C. 1970. Reinforcement schedules and psychophysical judgments: A study of some temporal properties of behavior. *The Theory of Reinforcement Schedules*: 1-42.
- Charnov, E.L. 1976a. Optimal Foraging: Attack Strategy of a Mantid. *American Naturalist*, 110: 141-151.
- Charnov, E.L. 1976b. Optimal foraging, the marginal value theorem. *Theoretical population biology*, 9: 129-136.

- Churchland, A.K., Kiani, R. and Shadlen, M.N. 2008. Decision-making with multiple alternatives. *Nat Neurosci*, 11: 693-702.
- Cowie, R.J. 1977. Optimal foraging in great tits (*Parus major*). *Nature*, 268: 137-139.
- Fawcett, T.W., McNamara, J.M. and Houston, A.I. 2012. When is it adaptive to be patient? A general framework for evaluating delayed rewards. *Behavioural Processes*, 89: 128-136.
- Fehr, E. 2002. Behavioural science - The economics of impatience. *Nature*, 415: 269-+.
- Freidin, E., Aw, J. and Kacelnik, A. 2009. Sequential and simultaneous choices: Testing the diet selection and sequential choice models. *Behavioural Processes*, 80: 218-223.
- Galtress, T. and Kirkpatrick, K. 2009. Reward value effects on timing in the peak procedure. *Learning and Motivation*, 40: 109-131.
- Galtress, T. and Kirkpatrick, K. 2010. Reward magnitude effects on temporal discrimination. *Learning and Motivation*, 41: 108-124.
- Gold, J.I. and Shadlen, M.N. 2007. The Neural Basis of Decision Making. *Annual Review of Neuroscience*, 30: 535-574.
- Grafen, A. and Hails, R. 2002. *Modern statistics for the life sciences*. Oxford University Press, Oxford, 351 pp.
- Guidelines for the treatment of animals in behavioural research and teaching. 2006. *Animal Behaviour*, 71: 245-253.
- Henly, S.E., Ostdiek, A., Blackwell, E., Knutie, S., Dunlap, A.S. and Stephens, D.W. 2008. The discounting-by-interruptions hypothesis: model and experiment. *Behavioral Ecology*, 19: 154-162.
- Hick, W.E. 1952. On the rate of gain of information. *Quart. Journal of experimental psychology*, 4: 1.

- Hyman, R. 1953. Stimulus information as a determinant of reaction time. *Journal of Experimental Psychology*, 45: 188–196.
- Kable, J.W. and Glimcher, P.W. 2009. The Neurobiology of Decision: Consensus and Controversy. *Neuron*, 63: 733-745.
- Kacelnik, A. 2003. The evolution of patience. In: G. Loewenstein (Editor), *Time and Decision: Economic and Psychological Perspectives on Intemporal Choice*, Russel Sage, New York.
- Kacelnik, A. and Todd, I.A. 1992. Psychological mechanisms and the marginal value theorem: effect of variability in travel time on patch exploitation. *Animal Behaviour*, 43: 313-322.
- Kacelnik, A., Vasconcelos, M., Monteiro, T. and Aw, J. 2011. Darwin's "tug-of-war" vs. starlings' "horse-racing": how adaptations for sequential encounters drive simultaneous choice. *Behavioral Ecology and Sociobiology*, 65: 547-558.
- Kagel, J.H., Green, L. and Caraco, T. 1986. When foragers discount the future: constraint or adaptation? *Animal Behaviour*, 34: 271-283.
- Killeen, P. 1968. On the measurement of reinforcement frequency in the study of preference. *Journal of the Experimental Analysis of Behavior*, 11: 263.
- Krajbich, I., Armel, C. and Rangel, A. 2010. Visual fixations and the computation and comparison of value in simple choice. *Nat Neurosci*, 13: 1292-1298.
- Krajbich, I. and Rangel, A. 2011. Multialternative drift-diffusion model predicts the relationship between visual fixations and choice in value-based decisions. *Proceedings of the National Academy of Sciences*, 108: 13852-13857.
- Krebs, J.R., Erichsen, J.T., Webber, M.I. and Charnov, E.L. 1977. Optimal prey selection in the great tit (*Parus major*). *Animal Behaviour*, 25: 30-38.

- Mazur, J.E. 2001. Hyperbolic value addition and general models of animal choice. *Psychological Review*; *Psychological Review*, 108: 96.
- Mazur, J.E. and Logue, A. 1978. Choice in a “self-control” paradigm: effects of a fading procedure. *Journal of the Experimental Analysis of Behavior*, 30: 11.
- Mazur, J.E., Snyderman, M. and Coe, D. 1985. Influences of Delay and Rate of Reinforcement on Discrete-Trial Choice. *Journal of Experimental Psychology: Animal Behavior Processes*: 565–575.
- Pavlic, T. and Passino, K. 2010. When rate maximization is impulsive. *Behavioral Ecology and Sociobiology*, 64: 1255-1265.
- Rachlin, H. and Green, L. 1972. Commitment, choice and self-control. *Journal of the Experimental Analysis of Behavior*, 17: 15.
- Rangel, A., Camerer, C. and Montague, P.R. 2008. A framework for studying the neurobiology of value-based decision making. *Nat Rev Neurosci*, 9: 545-556.
- Ratcliff, R. and Frank, M.J. 2012. Reinforcement-Based Decision Making in Corticostriatal Circuits: Mutual Constraints by Neurocomputational and Diffusion Models. *Neural Computation*, 24: 1186-1229.
- Ratcliff, R. and Rouder, J.N. 1998. Modeling Response Times for Two-Choice Decisions. *Psychological Science*, 9: 347-356.
- Ratcliff, R. and Smith, P.L. 2004. A comparison of sequential sampling models for two-choice reaction time. *Psychological Review*, 111: 333.
- Roberts, S. 1981. Isolation of an internal clock. *Journal of Experimental Psychology: Animal Behavior Processes*, 7: 242-268.
- Schwartz, L. 2004. *The paradox of choice: why more is less*. Harper Collins, New York.
- Shapiro, M.S., Siller, S. and Kacelnik, A. 2008. Simultaneous and sequential choice as a function of reward delay and magnitude: Normative, descriptive and process-based

- models tested in the European Starling (*Sturnus vulgaris*). Journal of Experimental Psychology: Animal Behavior Processes, 34: 75-93.
- Smith, P.L. and Ratcliff, R. 2004. Psychology and neurobiology of simple decisions. Trends in Neurosciences, 27: 161-168.
- Soltani, A. and Wang, X.-J. 2008. From biophysics to cognition: reward-dependent adaptive choice behavior. Current Opinion in Neurobiology, 18: 209-216.
- Stephens, D.W. 2008. Decision ecology: Foraging and the ecology of animal decision making. Cognitive Affective & Behavioral Neuroscience, 8: 475-484.
- Stephens, D.W. and Anderson, D. 2001. The adaptive value of preference for immediacy: when shortsighted rules have farsighted consequences. Behavioral Ecology, 12: 330-339.
- Sugrue, L.P., Corrado, G.S. and Newsome, W.T. 2005. Choosing the greater of two goods: neural currencies for valuation and decision making. Nat Rev Neurosci, 6: 363-375.
- Usher, M. and McClelland, J.L. 2001. The time course of perceptual choice: The leaky, competing accumulator model. Psychological review, 108: 550-592.
- Vasconcelos, M., Monteiro, T., Aw, J. and Kacelnik, A. 2010. Choice in multi-alternative environments: A trial-by-trial implementation of the Sequential Choice Model. Behavioural Processes, 84: 435-439.
- Wang, X.J. 2008. Decision Making in Recurrent Neuronal Circuits. Neuron, 60: 215-234.

Rational choice by starlings: Transitivity and regularity for delay and probability of reward

[Monteiro, T., Vasconcelos, M., Kacelnik. A. (submitted)]

1. Introduction.....	146
2. Results.....	150
3. Discussion.....	153
4. Methods.....	154
4.1. Preliminary training.....	155
4.2. Trial structure.....	155
4.3. Particulars of Experiment 1.....	156
4.4. Particulars of Experiment 2.....	157
4.5. Data analysis.....	157
4.6. Notation.....	158
5. Supplementary information.....	159
Supplementary Table 1.....	159
Supplementary Table 2.....	160
Supplementary Figure 1.....	161
6. Acknowledgments.....	162
7. References.....	163

1. Introduction

The study of economic rationality has prospered in several disciplines, including behavioural ecology, experimental psychology and economics. Study species range from slime molds to humans, including birds and insects (Latty and Beekman, 2011; Kahneman and Tversky, 2000; Bateson, Healy, and Hurly, 2002; Waite, 2001; Bateson, 2002; Shafir, 1994; Edwards and Pratt, 2009). This ubiquity reflects the importance of rationality principles for any self-consistent theory of decision-making. Unfortunately, theoretical interpretation of the significance of such research can be marred by semantic difficulties, because rationality has different meanings in economics, biology and psychology. To mitigate these difficulties one of us (Kacelnik, 2006) introduced the terms PP-rationality, B-rationality and E-rationality to refer to the different meanings in psychology-philosophy, biology and economics, respectively. These meanings refer to whether decisions are reached by reasoning (PP-rationality), to fitness maximization (B-rationality), or simply whether they are consistent within-subject (E-rationality). Here we disregard PP-rationality, focusing on the other two, with emphasis on E-rationality, because B- and E-rationality are more amenable to experimental testing in non-human subjects, and because the criteria for economic rationality are more fully specified and are shared across disciplines.

E-rationality implies the maximization of a stable utility function (itself defined as the maximand of e-rational agents' behaviour), and this requires compliance to some deducible principles of choice, of which the main are completeness, transitivity and regularity (Gravelle and Rees, 2004; Kacelnik, 2006; Rieskamp, Busemeyer, and Mellers, 2006). Completeness requires well-defined preferences across all members of choice sets. Transitivity implies non-circularity of preferences; given $A \succ B$ and $B \succ C$, then $C \succ A$ is a violation (the symbol $\succ$ is used to express 'is preferred to', and to discuss strength of

preference). Matters would be simple if decision-makers showed exclusive preferences between options (as might be expected from rigorous maximization of outcomes), but frequently they do not, and the existence of partial preferences leads to the formulation of elaborate principles concerning the strength of preferences. Luce's choice axiom (Luce, 1959) defines degrees of stochastically transitive behaviour: weak stochastic transitivity (i.e., $A \succ C$), moderate stochastic transitivity (i.e., $A \succ C$ being at least as strong as the weakest of $A \succ B$ and $B \succ C$), and strong stochastic transitivity (i.e., $A \succ C$ at least as strong as the strongest of $A \succ B$ and $B \succ C$). Regularity states that the overall proportion of choices for an option cannot increase when the choice set is enlarged (Luce and Suppes, 1965). Luce's principle of independence of irrelevant alternatives (IIA; Luce, 1959) further requires that the introduction of a new option into any choice set should not change relative preferences between pre-existing options.

Most experiments use sets of three options (Bateson, 2002; Bateson, Healy, and Hurly, 2002; Waite, 2001; Hurly and Oseen, 1999; Schuck-Paim and Kacelnik, 2002; Addessi et al., 2008), establishing transitivity with binary combinations within the set, and/or evaluating the effects of introducing a third option. Added (irrelevant) options (e.g., decoys) are often equal or inferior to the focal options, probably to increase the likelihood of exposing violations of regularity, as well as of IIA (Bateson, Healy, and Hurly, 2002; Latty and Beekman, 2011; Bateson, Healy, and Hurly, 2003; Shafir, Waite, and Smith, 2002; Schuck-Paim, Pompilio, and Kacelnik, 2004). Transitivity is the most scrutinized principle, and has been examined in a few non-human studies (Latty and Beekman, 2011; Schuck-Paim and Kacelnik, 2002; Addessi et al., 2008; Sumpter, Temple, and Foster, 1999), while tests of IIA are rarer (Bateson, 2002; Schuck-Paim and Kacelnik, 2007). Apparent irrationalities can result from unplanned state-dependence effects (Schuck-Paim, Pompilio, and Kacelnik, 2004; Pompilio, Kacelnik, and Behmer, 2006; Nevai, Waite, and

Passino, 2007; Waite, Nevai, and Passino, 2007; Pompilio and Kacelnik, 2005), but this does not pose theoretical challenges to optimality approaches and in any case cannot explain all observations (Hurly and Oseen, 1999). Violations of rationality that are not procedural artefacts tend to be attributed to mechanisms of choice (themselves deduced from the observed choices) or to the subjects inferring future opportunities from the options they face (Houston, McNamara, and Steer, 2007a), but this does not replace functional analysis. Prominent examples of mechanistic accounts are the inferred use of comparative, as opposed to absolute choice processes. They include algorithms where the decision maker counts the dimensions in which one option beats the alternative, rather than weighing the perceived differences in a common currency (Bateson, 2004; Latty and Beekman, 2011; Bateson, Healy, and Hurly, 2002; Shafir, 1994; Bateson, Healy, and Hurly, 2003), and irrational context-dependence (Waite, 2001; Morgan et al., 2012; Kahneman and Tversky, 2000; Waite, 2001; Bateson, 2002; Hurly and Oseen, 1999; Shafir, Waite, and Smith, 2002). However, if choice mechanisms caused widespread breaches of rationality in problems of ecological relevance, the adaptationist perspective in behavioural ecology and the normative logic of microeconomics would be severely threatened. To accommodate apparent irrationalities, evolutionary theoreticians argue that there are in fact no violations at the level of state-dependent choice strategies, but considering preferences out of context can generate intransitive (but state-dependent and artefactual) choices (Houston, McNamara, and Steer, 2007b). With this in mind the present study aims at testing qualitatively and quantitatively the principles of transitivity and IIA, while controlling for possible state-dependence artefacts.

We designed two experiments to assess transitivity across binary-choice sets (i.e., choices where two options are simultaneously available) as well as evaluating the effect of introducing a third option to the set (i.e., creating trinary choices where three different

options were simultaneously available). We used multiple options (Fig. 1, A), combined in binary and trinary sets according to the principle under test (Fig 1, B). In contrast with previous studies, here we added options that were inferior, intermediate, and superior to one or both options in the contrasting binary set. We chose two dimensions of reward, delay (Exp. 1) and probability (Exp. 2), each for different reasons. Delay to food is perhaps the only manipulation where it is possible to test whether animals have accurate representations of the properties of each option. Extensive previous work shows that animals learn accurately the time when rewards are due, hence it is possible to relate preferences to knowledge, unconfounding distortions in the agent's available information from its strategic preferences (this is crucial for mechanistic accounts of context-dependent effects (Pompilio and Kacelnik, 2005; Freidin and Kacelnik, 2011)). Probability of reward, in turn, has special interest because humans are notoriously unable to treat probability rationally, especially when communicated verbally rather than by experience. Irrationalities such as the Allais paradox, or over- and under-valuation of extreme probabilities are common, and this has generated an extensive and heated literature (Tversky and Kahneman, 1992; Brighton and Gigerenzer, 2008; Kahneman and Lovallo, 1993).

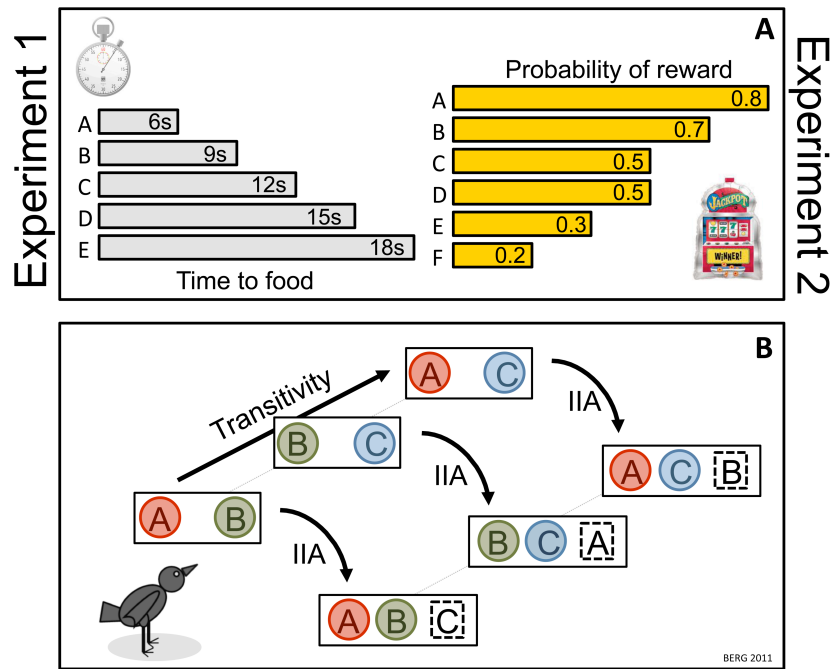


Figure 1. Experimental design. (A) Options used in Exp.1 (left) and Exp. 2 (right). (B) Example of trials used to test stochastic transitivity (left) and Independence of Irrelevant Alternatives (right). The black arrows show comparisons relevant to testing the principles identified next to each arrow.

2. Results

We define a transitivity set (TS) as a combination of all possible binary choices between three different options. Figure 2 shows the proportion of choices observed for the better option (shortest delay or highest probability) in all binary-choice combinations of TS s composed only of contiguous options for Experiments 1 and 2 (Fig. 2A and 2B, respectively; supplementary Tables 1 and 2 show all binary-choice combinations, pp. 161 and 162). To test for stochastic transitivity we compared preference for the best option in the extreme pair (red bars) of each TS with preference in the intermediate pairs (blue bars).

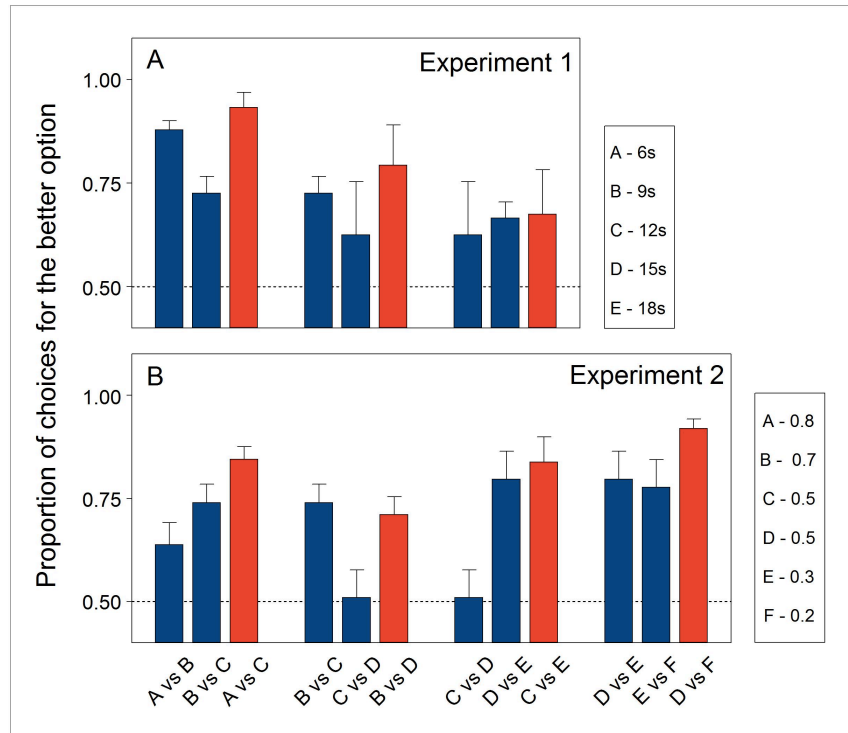


Figure 2. Stochastic transitivity. Proportion of choices (mean+ SEM) for the better option in each binary choice for transitivity sets (*TS*) composed of contiguous options in Exp. 1 (A) and Exp. 2 (B). Blue bars show preference between contiguous options and red bars between extreme options, for every set of three options.

An inspection of Figure 2 (and supplementary Tables 1 and 2, pp. 161 and 162, respectively) reveals that the requirement for Moderate Stochastic Transitivity was met for all *TS*s, with preference for each extreme pair being at least as strong as the weakest of those found in intermediate pairs. In fact, preference in the extreme pair was significantly stronger than the weakest preference found in the intermediate pairs in 7 out of 10 *TS*s in Experiment 1 [smallest significant $t(4)=2.953$, $p=.042$] and in 19 out of 20 *TS*s in Experiment 2 [smallest significant $t(9)=2.505$, $p=.034$]. With respect to Strong Stochastic Transitivity, in Experiment 1, 10 out of 10 comparisons were in the required direction (binomial $p=.002$), but these differences were not individually significant [all $t(4) \geq .057$ and ≤ 2.392 , n.s.]. In Experiment 2, 17 out of 20 comparisons were also in the required direction (there was one tie; binomial $p=.001$) and of those 8 were statistically significant while none was significant in the opposite direction, which is necessary to prove a

violation [all $t(9) \geq 2.462$, $p \leq .036$]. The results thus confirm statistically reliable Strong Stochastic Transitivity for both delay and probability of reward.

The IIA principle encompasses regularity, so we use it to examine both, enlarging choice sets with inferior, intermediate and superior alternatives. IIA requires demonstrating no change in relative proportion, namely the absence of an effect, and is thus statistically more demanding. We calculated the relative proportion of choices for the better of two options in trinary-choice trials as a function of the proportion of choices between the same two options when met in binary-choice trials (Figs. 3A and 3B for Exps. 1 and 2, respectively):

$$\text{RelPropA}_{[ABC]} = \frac{A_{[ABC]}}{A_{[ABC]} + B_{[ABC]}} \quad , \quad \text{Equation 1}$$

where $\text{RelPropA}_{[ABC]}$ is the relative proportion of choices for option A versus option B, and $A_{[ABC]}$ and $B_{[ABC]}$ are the number of choices for A and B in trinary [ABC] trials, respectively.

We display the effect of adding an option (e.g., C) to a binary choice (e.g., [AB]), plotting on the abscissa preference in binary choices (e.g., A over B in [AB]), and in the ordinate relative preference in trinary choices (e.g., preference for A over B in [ABC]). For IIA to hold, values should fall along the diagonal. With the exception of two outliers, this is the case regardless of the quality of the added third alternative (individual compliance to IIA is shown in Supplementary Figure 1, pp. 163).

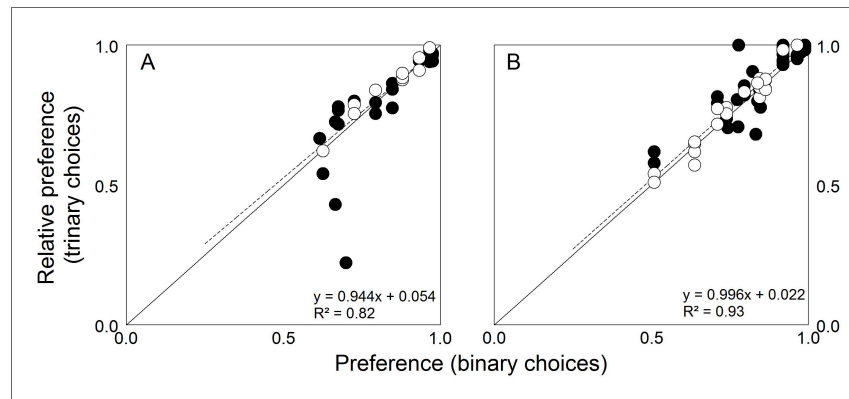


Figure 3. Independence of Irrelevant Alternatives. Relative proportion of choices (averaged across subjects) for the better of two options in trinary-choice trials plotted against preference for the better of those options in binary choices, for Exp. 1 (A) and Exp. 2 (B). Open circles identify sets where the third option is either poorer or equal to the target options, and filled circles sets where the third option was richer than the target pair. The IIA principle requires the points to lie along the diagonal. Weighted least squares linear regressions were conducted on average data. Equations and coefficients of determination are shown in the bottom right of each panel.

3. Discussion

Starlings' choices between multiple options differing in either delay to or probability of a food reward complied with the most demanding definitions of economic rationality, including strong stochastic transitivity and IIA, regardless of the added options' richness relative to the target option pair. Our results do not exclude the possible breach of rationality principles when alternatives differ in more than one dimension simultaneously. Such tests are complicated because the scaling of utility to physical dimensions probably differs and includes non-linearities when properties such as delay, probability, amount, energetic concentration of rewards, or perceived risk are traded against each other (Latty and Beekman, 2011; Bateson, Healy, and Hurly, 2002; Shafir, 1994; Bateson, Healy, and Hurly, 2003; Bateson, 2004). For these reasons, claims that violations of rationality are ubiquitous and that this questions the validity of the optimality approach and its adaptationist foundations are unfounded. Although restricted to uni-dimensional problems, our results do suggest that economic rationality is a fundamental property of uni-dimensional choices for at least some non-humans, as would be expected from an adaptive

(optimality) perspective when the confounding effects of the agent's state, or available information are suitably controlled.

4. Methods

Subjects were 20 adult wild-caught European starlings (*Sturnus vulgaris*) (Natural England licenses 20083718 and 20093673). Eight birds initiated Experiment 1 and 12 Experiment 2, of which 5 and 10 completed the experiment, respectively. Birds had experience pecking at keys but not with the contingencies and symbols used in this study. Prior to testing, birds were socially housed in outdoor aviaries with *ad libitum* food and water. For the experiment, subjects were housed in pairs in indoor cages [1350 mm x 784 mm x 800 mm (l x w x h)] and kept under a 12L:12D cycle with gradual transitions at dawn and dusk. They were confined individually to one section of their cage for tests, but after each session they had four hours of *ad lib* food and social interaction with the cage-partner. The experiments were run from April to June (Exp. 1) and from October to December, 2010 (Exp. 2). On completion the birds were reintroduced into communal aviaries and eventually released into the wild. We followed animal welfare regulations of Oxford University and maintenance and experimental protocols adhered to Guidelines for the Use of Animals in Research from the Association for the Study of Animal Behaviour/Animal Behavior Society (Guidelines for the treatment of animals in behavioural research and teaching, 2006). The experimental cages had two side areas that could be split with sliding panels from a shared middle section. Each side area had attached a working panel with three sections, each with a centrally placed response key. The central section also had a food hopper connected to a pellet dispenser (Campden Instruments®) containing 20 mg BioServ® precision dustless pellets. Contingencies were controlled by custom software running on the Microsoft® Windows® operating system and attached to

an Animal Behaviour Environment Test System (Campden Instruments®) via WhiskerServer (Cardinal and Aitken, 2010).

4.1 Preliminary training

After training to peck keys and obtain food, the birds received either response-initiated *fixed interval* (FI) training (Exp. 1) or probability training (Exp. 2). Trials started with an attention key lighting up. In Experiment 1, pecking the central attention key triggered a delay, and the first peck after the programmed delay caused the keylight to switch off and two food pellets to be delivered. In Experiment 2, a single peck to a flashing side key was followed by reinforcement with a programmed probability.

4.2. Trial structure

Both experiments included training and testing phases. There were three types of trial: single-option, choice and peak trials. Single-option trials began with a flashing attention key (location randomly assigned). Pecking at the flashing key turned it off, and caused one of the three available keys (randomly assigned) to begin flashing (700 ms ON, 300 ms OFF). A peck to the illuminated flashing key either turned the key steadily on and initiated a delay to food (Exp. 1) or turned the key off and delivered food with a certain probability (Exp. 2). Choice trials offered simultaneous choices between two or three options. All combinations of two and three different options were used. Trials began with a flashing attention key at a random location. A peck to it turned it off and began the flashing of two (binary choices) or three (trinary choices) randomly located keys (each displaying a different symbol). A peck to one of the flashing keys initiated its programmed contingency, and turned the unselected key(s) off. Peak trials were similar to single-option trials and were used to determine the animals' knowledge of the delay to reward associated

with each option in Experiment 1¹. In these trials, the chosen option remained on for three times its typical delay and then extinguished without reward. Successive trials were separated by a 45-s (Exp. 1) or 30-s (Exp. 2) inter-trial-interval.

4.3. Particulars of Experiment 1

There were five different options that differed in delay to food reward (6, 9, 12, 15 or 18 s), each signalled by a different colour/symbol combination². The experiment lasted for 35 days. After seven days of no-choice training [150 daily single-option trials, 30 per option], the birds were randomly assigned to two groups and experienced 7 days of choice-training wherein a number of choice trials with binary or trinary presentations of the five options were interspersed among single-option trials [90 single-option trials, 18 per option, and 60 choice trials, 6 per pair or trio combination, daily]. One group faced first all possible binary combinations of the different options (10 binary choices), while the other group faced all possible trinary combinations (10 trinary choices). After the first choice-training period, no-choice training resumed for 7 days before the choice-training contingencies were reversed between groups and the procedure repeated. Finally, birds were tested for 7 days, with both binary and trinary-choice trials interspersed between no-choice trials [75 single-option trials, 15 per option, 60 binary-choice trials and 60 trinary-choice trials]. In summary, one group received the sequence Training → Binary → Training → Trinary → Training → **Binary+Trinary**, while the other the sequence Training → Trinary → Training → Binary → Training → **Binary+Trinary**. If a bird failed to peck any of the flashing keys for 120 s after onset, the key was turned off and the ITI started, followed appropriately by the next trial.

¹See Fig. 7, *Chapter 4*.

²See Supplementary Figure 1, *Chapter 4*.

4.4. Particulars of Experiment 2

Birds learned about six different options³ signalling different probabilities of food reward (viz., 0.8, 0.7, 0.5, 0.5, 0.3 and 0.2). They first encountered single-option trials for 12 days [414 single-option trials daily, 69 per option]. Afterwards, birds were tested for 30 days with single-option trials interspersed with choice trials of all possible binary (15), and trinary (20) combinations of different options [216 single-option trials, 36 per option, 90 binary-choice trials, 6 per pair, and 120 trinary-choice trials, 6 per trio]. The attention key was removed during the last 7 days of the experiment to eliminate possible influence of the location of the attention key on the subsequent choice. Trials proceeded as in Experiment 1, but the program did not advance to the next trial unless the animal responded.

4.5. Data Analysis

All proportion data were successfully normalized using an arcsine square-root transformation (Grafen and Hails, 2002). An alpha level of 0.05 was adopted for all statistical comparisons. For Experiment 1, only the test sessions (i.e., last 7 days) were considered in the analysis. For Experiment 2, the last 3 days of testing were used. In both experiments, we set an experimental criterion of 80% completion of all daily trials, for a session to be included in the analysis. Five birds were excluded from all analyses after repeatedly failing to reach the experimental criterion (4 birds, 3 from Exp. 1 and 1 from Exp. 2) or due to showing a strong side preference (one bird from Exp. 2).

Testing for stochastic transitivity requires comparisons of strength of preferences in binary choices. Given inter-individual variation, within each transitivity set we identified the pair with higher statistical significance (smaller p value) as the stronger preference, and

³For details, see *Chapter 4*, Supplementary Figure 1.

used it to test strong stochastic transitivity, while the other pair was used to test moderate stochastic transitivity.

Relative preferences are meaningless if neither option is chosen at least once. This occurred 3 times out of 150 possible ones in Experiment 1 (distributed between 2 subjects) and 24 times out of 600 in Experiment 2 (one subject missed 5, one 4, three 3, two 2 and two 1). These cases were omitted.

Weighted least squares linear regressions were calculated both for the average and individual data. Number of choices between every two options in each trinary-choice combination was used as weighing factor.

4.6. Notation.

To facilitate description and visualization of the data, in the figures and parts of the text option values are replaced by letters, from A to E in Experiment 1 (i.e., $A > B > C > D > E$) and from A to F in Experiment 2 (i.e., $A > B > C = D > E > F$), where A is the most profitable option.

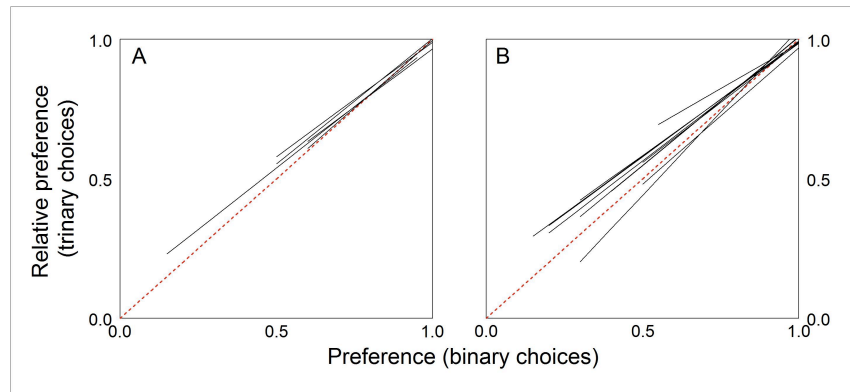
5. Supplementary information

Supplementary Table 1. Stochastic transitivity in Experiment 1. Proportion of choices (mean+s.e.m.) for intermediate (Inter. 1 and Inter. 2) and extreme pairs (Extr.) in each *Transitivity Set (TS)*, for Experiment 1. Paired sample *t*-tests were conducted between the proportion of choices for the extreme pair and the intermediate pairs with weaker and stronger preference for Moderate (MST) and Strong Stochastic Transitivity (SST), respectively [see Data Analysis section for details]. The values for *TS*s composed of contiguous options are depicted in bold.

Experiment 1								
Preference				MST		SST		
<i>TS</i>		Inter. 1	Inter. 2	Extr.	t(4)	<i>p</i>	t(4)	<i>p</i>
ABC	mean	0.88	0.73	0.93	4.520	.011	1.515	.204
	s.e.m.	0.02	0.04	0.04				
ABD	mean	0.88	0.79	0.97	4.088	.015	2.392	.075
	s.e.m.	0.02	0.10	0.02				
ABE	mean	0.88	0.85	0.97	3.783	.019	1.587	.188
	s.e.m.	0.02	0.09	0.01				
ACD	mean	0.93	0.63	0.97	2.953	.042	.872	.433
	s.e.m.	0.04	0.13	0.02				
ACE	mean	0.93	0.67	0.97	3.750	.020	.597	.583
	s.e.m.	0.04	0.11	0.01				
ADE	mean	0.97	0.67	0.97	15.235	.000	.043	.968
	s.e.m.	0.02	0.04	0.01				
BCD	mean	0.73	0.63	0.79	2.768	.050	.956	.393
	s.e.m.	0.04	0.13	0.10				
BCE	mean	0.73	0.67	0.85	3.344	.029	1.617	.181
	s.e.m.	0.04	0.11	0.09				
BDE	mean	0.79	0.67	0.85	1.952	.123	1.772	.151
	s.e.m.	0.10	0.04	0.09				
CDE	mean	0.63	0.67	0.67	1.169	.307	.057	.958
	s.e.m.	0.13	0.04	0.11				

Supplementary Table 2. Stochastic transitivity in Experiment 2. Proportion of choices (mean+s.e.m.) for intermediate (Inter. 1 and Inter. 2) and extreme pairs (Extr.) in each *Transitivity Set (TS)* for Experiment 2. Paired sample *t*-tests were conducted between the proportion of choices for the extreme pair and the intermediate pairs with weaker and stronger preference for Moderate (MST) and Strong Stochastic Transitivity (SST), respectively [see Data Analysis section for details]. The values for *TS*s composed of contiguous options are depicted in bold.

Experiment 2								
Preference					MST		SST	
TS		Inter. 1	Inter. 2	Extr.	t(9)	p	t(9)	p
ABC	mean	0.64	0.74	0.84	4.963	.001	1.269	.236
	s.e.m.	0.05	0.04	0.03				
ABD	mean	0.64	0.71	0.86	4.695	.001	2.462	.036
	s.e.m.	0.05	0.04	0.05				
ABE	mean	0.64	0.92	0.96	7.588	.000	1.825	.101
	s.e.m.	0.05	0.04	0.02				
ACD	mean	0.84	0.51	0.86	8.119	.000	.962	.361
	s.e.m.	0.03	0.07	0.05				
ACE	mean	0.84	0.84	0.96	5.536	.000	3.906	.004
	s.e.m.	0.03	0.06	0.02				
ADE	mean	0.86	0.80	0.96	4.211	.002	2.492	.034
	s.e.m.	0.05	0.07	0.02				
BCD	mean	0.74	0.51	0.71	2.505	.034	.731	.483
	s.e.m.	0.04	0.07	0.04				
BCE	mean	0.74	0.84	0.92	3.817	.004	1.459	.178
	s.e.m.	0.04	0.06	0.04				
BDE	mean	0.71	0.80	0.92	4.554	.001	1.675	.128
	s.e.m.	0.04	0.07	0.04				
CDE	mean	0.51	0.80	0.84	4.072	.003	.732	.483
	s.e.m.	0.07	0.07	0.06				
ABF	mean	0.64	0.99	0.98	9.125	.000	1.010	.339
	s.e.m.	0.05	0.01	0.01				
ACF	mean	0.84	0.92	0.98	8.636	.000	6.614	.000
	s.e.m.	0.03	0.03	0.01				
ADF	mean	0.86	0.92	0.98	7.464	.000	3.332	.009
	s.e.m.	0.05	0.02	0.01				
AEF	mean	0.96	0.78	0.98	2.967	.016	.123	.905
	s.e.m.	0.02	0.07	0.01				
BCF	mean	0.74	0.92	0.99	10.186	.000	7.073	.000
	s.e.m.	0.04	0.03	0.01				
BDF	mean	0.71	0.92	0.99	12.540	.000	8.870	.000
	s.e.m.	0.04	0.02	0.01				
BEF	mean	0.92	0.78	0.99	3.592	.006	3.339	.009
	s.e.m.	0.04	0.07	0.01				
CDF	mean	0.51	0.92	0.92	3.112	.012	.011	.991
	s.e.m.	0.07	0.02	0.03				
CEF	mean	0.84	0.78	0.92	3.207	.011	.924	.379
	s.e.m.	0.06	0.07	0.03				
DEF	mean	0.80	0.78	0.92	1.474	.175	.878	.403
	s.e.m.	0.07	0.07	0.02				



Supplementary Figure 1. Individual least squares linear (wls) regressions. The principle of Independence of Irrelevant alternatives (IIA) requires regressions to fall along the diagonal. Each solid line shows the individual wls regressions for Experiment 1 (A, $n=5$) and Experiment 2 (B, $n=10$). Number of choices between every two options in each ternary-choice combination was used as weighing factor. Exp. 1: Average slope= 0.88 (range: 0.82 to 0.97) and average intercept=0.11 (range: 0.02 to 0.17). Exp. 2: average slope= 0.88 (range: 0.64 to 1.19) and average intercept=0.11 (range: -0.16 to 0.34).

6. Acknowledgments

This research was supported by Grant BB/G007144/1 from the UK Biotechnology and Biological Sciences Research Council to AK. TM was supported by a doctoral grant from the Portuguese Foundation for Science and Technology and a Pembroke College Graduate Scholarship. MV was funded by the abovementioned BBSRC grant followed by post-doctoral grant SFRH/BPD/79311/2011 from the Portuguese Foundation for Science and Technology. TM, MV and AK jointly designed the experiments, TM collected the data, TM and MV processed and analysed the data, TM, MV and AK jointly wrote the paper.

We thank Alan Grafen and Justine Aw for their comments on earlier versions of this manuscript, and Simon and Jan Parry for trapping our participants.

7. References

- Addessi, E., Mancini, A., Crescimbene, L., Padoa-Schioppa, C. and Visalberghi, E. 2008. Preference Transitivity and Symbolic Representation in Capuchin Monkeys (*Cebus apella*). Plos One, 3: e2414.
- Bateson, M. 2002. Context-dependent foraging choices in risk-sensitive starlings. Animal Behaviour, 64: 251-260.
- . 2004. Mechanisms of decision-making and the interpretation of choice tests. Animal Welfare, 13: S115-S120.
- Bateson, M., Healy, S.D. and Hurly, T.A. 2002. Irrational choices in hummingbird foraging behaviour. Animal Behaviour, 63: 587-596.
- Bateson, M., Healy, S.D. and Hurly, T.A. 2003. Context-dependent foraging decisions in rufous hummingbirds. Proceedings of the Royal Society of London Series B-Biological Sciences, 270: 1271-1276.
- Brighton, H. and Gigerenzer, G. 2008. Probabilistic minds and cognitive mechanisms: Harmony or dissonance? In: N. Chater and M. Oaksford (Editors), The Probabilistic Mind: Prospects for Bayesian Cognitive Science, Oxford University Press, Oxford.
- Cardinal, R.N. and Aitken, M.R.F. 2010. Whisker: A client—server high-performance multimedia research control system. Behavior research methods, 42: 1059-1071.
- Edwards, S.C. and Pratt, S.C. 2009. Rationality in collective decision-making by ant colonies. Proceedings of the Royal Society B: Biological Sciences, 276: 3655-3661.
- Freidin, E. and Kacelnik, A. 2011. Rational Choice, Context Dependence, and the Value of Information in European Starlings (*Sturnus vulgaris*). Science, 334: 1000-1002.

- Grafen, A. and Hails, R. 2002. *Modern statistics for the life sciences*. Oxford University Press, Oxford, 351 pp.
- Gravelle, H. and Rees, R. 2004. *Microeconomics*. FT/Prentice Hall, Harlow, 738 pp.
- Guidelines for the treatment of animals in behavioural research and teaching. 2006. *Animal Behaviour*, 71: 245-253.
- Houston, A.I., McNamara, J.M. and Steer, M.D. 2007a. Violations of transitivity under fitness maximization. *Biology Letters*, 3: 365-367.
- . 2007b. Do we expect natural selection to produce rational behaviour? *Philosophical Transactions of the Royal Society B-Biological Sciences*, 362: 1531-1543.
- Hurly, T.A. and Oseen, M.D. 1999. Context-dependent, risk-sensitive foraging preferences in wild rufous hummingbirds. *Animal Behaviour*, 58: 59-66.
- Kacelnik, A. 2006. Meanings of rationality. In: S. Hurley, & Nudds, M. (Editor), *Rational Animals?*, Oxford University Press, Oxford, New York.
- Kacelnik, A., Schuck-Paim, C., Pompilio, L. 2006. Inconsistency in animal and human choice. In: C. Engel and L. Daston (Editors), *Is there value in inconsistency?*, Nomos Verlagsgesellschaft.
- Kahneman, D. and Lovallo, D. 1993. Timid choices and bold forecasts: a cognitive perspective on risk taking. *Management Science*, 39: 17-31.
- Kahneman, D. and Tversky, A. 2000. *Choices, values, and frames*. Cambridge University Press, Russell Sage Foundation, Cambridge, New York, 840 pp.
- Latty, T. and Beekman, M. 2011. Irrational decision-making in an amoeboid organism: transitivity and context-dependent preferences. *Proceedings of the Royal Society B: Biological Sciences*, 278: 307-312.
- Luce, R.D. 1959. *Individual choice behaviour: A theoretical analysis*. Wiley, New York.

- Luce, R.D. and Suppes, P. 1965. Preference, utility, and subjective probability. In: R.D. Luce, R. Bush and E. Galanter (Editors), *Handbook of mathematical psychology*, John Wiley, New York.
- Morgan, K.V., Hurly, T.A., Bateson, M., Asher, L. and Healy, S.D. 2012. Context-dependent decisions among options varying in a single dimension. *Behavioural Processes*, 89: 115-120.
- Nevai, A.L., Waite, T.A. and Passino, K.M. 2007. State-dependent choice and ecological rationality. *Journal of Theoretical Biology*, 247: 471-479.
- Pompilio, L. and Kacelnik, A. 2005. State-dependent learning and suboptimal choice: when starlings prefer long over short delays to food. *Animal Behaviour*, 70: 571-578.
- Pompilio, L., Kacelnik, A. and Behmer, S.T. 2006. State-dependent learned valuation drives choice in an invertebrate. *Science*, 311: 1613-1615.
- Rieskamp, J., Busemeyer, J.R. and Mellers, B.A. 2006. Extending the bounds of rationality: evidence and theories of preferential choice. *Journal of Economic Literature*, 44: 631-661.
- Schuck-Paim, C. and Kacelnik, A. 2002. Rationality in risk-sensitive foraging choices by starlings. *Animal Behaviour*, 64: 869-879.
- . 2007. Choice processes in multialternative decision making. *Behavioral Ecology*, 18: 541-550.
- Schuck-Paim, C., Pompilio, L. and Kacelnik, A. 2004. State-Dependent Decisions Cause Apparent Violations of Rationality in Animal Choice. *PLoS Biology*, 2: e402.
- Shafir, S. 1994. Intransitivity of preferences in honey-bees – support for comparative-evaluation of foraging options. *Animal Behaviour*, 48: 55-67.

- Shafir, S., Waite, T.A. and Smith, B.H. 2002. Context-dependent violations of rational choice in honeybees (*Apis mellifera*) and gray jays (*Perisoreus canadensis*). *Behavioral Ecology and Sociobiology*, 51: 180-187.
- Sumpter, C.E., Temple, W. and Foster, T. 1999. The transitivity of choices between different response requirements. *Journal of the Experimental Analysis of Behavior*, 72.
- Tversky, A. and Kahneman, D. 1992. Advances in prospect theory: Cumulative representation of uncertainty. *Journal of Risk and Uncertainty*, 5: 297-323.
- Waite, T.A. 2001. Background context and decision making in hoarding gray jays. *Behavioral Ecology*, 12: 318-324.
- . 2001. Intransitive preferences in hoarding gray jays (*Perisoreus canadensis*). *Behavioral Ecology and Sociobiology*, 50: 116-121.
- Waite, T.A., Nevai, A.L. and Passino, K.M. 2007. State subsidies induce gray jays to accept greater danger: an ecologically rational response? *Behavioral Ecology and Sociobiology*, 61: 1261-1266.

CHAPTER 7.

Concluding remarks

[Unpublished manuscript]

This thesis investigates how animals choose between different sources of food in order to understand the decision mechanisms driving strategic behaviour in foraging situations. In John Emlen's (1966) seminal paper¹, he clearly stressed the importance of foraging in the life of all animals:

“The efficient exploitation of available food is a vital requirement of all animals. The study of feeding and food preference, therefore, should be of vital importance to the field of ecology.”

(pp. 611)

To study foraging behaviour, particularly feeding preferences, I conducted several laboratory experiments with wild-caught European starlings (*Sturnus vulgaris*). Central to all the work reported here is the behavioural laboratory, unavoidably artificial and seldom precisely mimicking natural foraging situations, but regardless of, and precisely because of its artificiality, the main available tool to treat behavioural problems experimentally.

Under the controlled environment of the laboratory precise manipulations of critical features of the environment were possible while keeping the remaining features properly controlled for. For instance, the foraging laboratory makes it possible to control for the number of options available in each environment (i.e., from 2 to 6 options); what properties were associated with each particular option (e.g., amount of food, time to food, probability of yielding a food reward, rate of reinforcement); how many options would the animals encounter simultaneously, and in what proportion, respective to single-option encounters.

In line with previous work from the Behavioural Ecology Research Group (*BERG*), I chose the Sequential Choice Model (SCM; Shapiro, Siller, and Kacelnik, 2008; reviewed in Kacelnik et al., 2011 – see *Appendix 1*) as a starting point to generate hypotheses, and

¹In conjunction with MacArthur and Pianka's (1966) paper, published in the same issue of the *American Naturalist*, both papers are considered to be the classic foundations of modern quantitative behavioural ecology, especially regarding foraging.

aimed at testing its applicability to different choice situations, always with the end goal of making a significant contribution to the broad theory of decision-making, in both human and non-human animals.

As stated in the *General Introduction*², most chapters involved the empirical study of simple decision-making situations, while testing the applicability of the SCM to different scenarios. Using several variations of the same basic operant protocol, I tested whether:

(1) Latencies to accept a given option were relative to the background of opportunities, or on the contrary, they were invariable and/or dependent only on the absolute properties of the option concerned. This issue is of interest as it enriches the reaction time literature with a directly strategic perspective.

(2) Shorter latencies in no-choice situations correlated with a stronger preference in simultaneous choices. This is interesting because a vast majority of studies of choice are framed as if simultaneous choices were a natural and crucial category for which decision mechanisms are adapted, perhaps reifying putative processes that may not, in fact, exist at all.

(3) Latencies for each option, in choice situations, were shorter when compared to no-choice situations. The significance here is that virtually all models of choice lead one to expect a time cost of the cognitive operations necessary to take the best alternative, and here the suggestion was exactly the opposite.

(4) Strength of preference in simultaneous encounters with opportunities could be predicted with quantitative detail from latencies in no-choice situations – this is a quantitative, stronger, version of (2) and (3).

²See General Introduction, section 4. Organisation of the thesis.

Overall the results were mixed, offering empirical support for some aspects of the SCM but not others. In particular, I found consistent evidence for (1) and (2), no clear support for (3), but no evidence for the opposite effect either (i.e., latencies in choice situations were generally not longer than latencies in no-choice trials, as would follow from a time-to-decide deliberation cost), and different degrees of accuracy regarding the quantitative power of the model (4).

Stearns and Schmid-Hempel (1987) made an important remark concerning the problem, common in optimality analysis, of what to do when some predictions are rejected while others are confirmed (as happened here, with the SCM):

“(...) Strictly speaking, the hypothesis should be discarded. However, some failures are inevitable when a simple model is applied to a complex situation. (...) It is ‘normal’ procedure in science not to reject theories simply because they sometimes fail, either because alternatives are not available, or because the theory makes other correct predictions considered valuable.”
(pp. 121)

One crucial concern regarding the ecological relevance of laboratory findings is that in nature the number of opportunities is large and poorly defined, while in the lab it is most often simply reduced to only two options (or schedules of reinforcement). To mitigate this difficulty, in *Chapter 2* (Vasconcelos et al., 2010), I presented the first empirical test of the SCM in an environment composed of multiple alternatives. Following the experiments reported by Shapiro et al. (2008) and Freidin et al. (2009), in this paper I tested the SCM in an environment composed of four alternatives³. This study also enabled a new test of the model – labelled as a molecular implementation⁴. Overall, the model did a good job in predicting each individual choice on a trial-by-trial basis. However, the nearly exclusive

³In Shapiro et al.'s (2008) study they dealt with 6 different options, but in every experimental condition the animals faced only two different options, either alone or together in a choice trial.

⁴Molecular here refers to trial-by-trial analysis, as oppose to ‘molar’ a term used for tests on the aggregate of many responses.

preferences for the better options did not allow a strong test of the claim that latencies to accept a particular option, in a choice situation, should be shorter than latencies to accept that same option in sequential encounters, particularly so for the worse options. In summary, and following the premises enumerated above, I found empirical support for all of the SCM's assumptions except (3) (see above), due to near exclusive preferences. Moreover, in this experiment, there was a 20-s time limit after which the trials were terminated, and for data analysis these events were coded with 20-s latencies. It is possible that the conservative nature of this criterion was in fact too conservative and dwarfed the signal in the data, yielding a false negative. This cannot be sorted with the present data.

In *Chapter 3* (Aw et al., 2012), I presented two experiments in which starlings faced choices between a fixed option and a variable (or risky) one. Across experiments, this risky option was associated with two equiprobable values (see *Chapter 3* for details), rather than a fixed delay to or amount of food (contingent across conditions to the fixed options). I explored whether choosing imposes an evaluation cost or, as argued by the SCM (previously tested only in the absence of risk, or variance within a particular option), no time-consuming evaluation takes place. The birds first encountered the options during forced (or no-choice) trials, and then in simultaneous choices in one of two treatments (either delay or amount to food), composed of 5 conditions each. This design allowed me to test the predictive power of the SCM in a probabilistic environment – according to the SCM, animals do not have dedicated cognitive mechanisms for simultaneous choices, but instead they process each stimulus independently, and a choice is the result of acting on the fastest of the competing alternatives. One of the SCM's main assumptions, that latencies during sequential encounters reflect the value of those options relative to the background of alternatives (see (1), above), was clearly observed, both for delay and amount of reward. The data collected also showed that latencies in forced trials could be used as a proxy to

predict subsequent choice – a corollary of the SCM (see (4), above). Overall, these results confirmed the SCM's assumptions and predictions, but with one substantial deviation. As with the experiment reported in *Chapter 2*, I did not observe a significant shortening of latencies in choice respect to forced trials – the most counterintuitive feature of the model (see (3), above), but neither did I see a time cost of evaluating the alternatives. In this experiment, subjects had to respond within 20 seconds since the option was presented, after which the trials were terminated and coded with 20-s latencies. Consequently, latencies that would have been larger than 20 seconds were never observed (but they were in Shapiro et al., 2008, where the latency shift predicted by the model was detected). As I stated above, it thus appeared possible that this procedural difference caused the difference between their positive and my negative result.

Chapter 4 had a dual purpose: in two different experiments I aimed at tracking the effect of learning about the properties of each available option on choice behaviour, and extending the analyses of decision making to simultaneous choice opportunities involving three (not only two) simultaneously available options. In both experiments, I observed that latencies to respond to individually presented options were relative to the background of alternatives presented in the environment (see (1), above), and that these latencies could be used, with different degrees of accuracy, to predict choice between two and three simultaneous options (see (4), above) both retrospectively and prospectively. I also increased the response time-window from 20 (as in previous experiments) to 120 seconds. However, I did not observe a latency shortening during choices (see (3), above) in this case either, suggesting that the imposition of response time limits is not a sufficient explanation for the missing latency shortening.

In *Chapter 5*, I implemented a more complex environment to test the SCM, composed of 6 distinct bi-dimensional options. Most previous studies (see *Chapters 2, 3*

and 4), also included experiments with multiple alternatives, but all options differed only in a single dimension (delay to food). In one study (Shapiro, Siller, and Kacelnik, 2008), bi-dimensional differences between options were also considered, but in successive treatments, where the environment was composed of only two options at any particular time, so that in comparing a present option against the background the subjects only had to consider one other (ghost) option. The main purpose here was twofold: to test the ecological validity of the SCM, by using a more complex environment in which the background to each decision was a mixture of many possible alternatives. The SCM successfully tracked the birds' preferences both globally and when temporal constraints⁵ were introduced (see (4) above). To further investigate the potential shortening of responses times during simultaneous choice (see (3) above), the animals had no time limit to emit a response, with no responses meaning not moving forward to next trial. Despite this fact, no clear evidence for shortening of response-times during choices was found, but as previously observed, the lengthening that would have been consistent with deliberative models of decision was also absent. Furthermore, besides adding to the collection of data evaluating the assumptions and predictions of the SCM (see (1) to (4), above), *Chapter 5* served to revisit the theory, highlighting the importance of considering evolutionary and natural history constraints on decision-making, drawing attention to the importance of no-choice situations to the study of decision-making processes.

Considering the results of all these different experiments (*Chapters 2 to 5*) it is possible to attempt defining some overarching conclusions. The SCM was applied using different approaches, each designed to assess different aspects of the mechanism proposed. These included trial-by-trial performance (see *Chapters 2 and 3*), sensitivity to local fluctuations in preference (see *Chapters 2 and 5*), and by emulation of empirical tests via

⁵We introduced a “*discounting memory rule*” To the SCM: individual choices were predicted using a hyperbolically weighted moving average of 32 previous single-option latencies for each option, respectively. See also *Chapter 2*.

Monte Carlo simulations (see *Chapters 4 and 5*). All these techniques were used as an alternative to applying the model analytically, following the mathematical formalisation described in *Appendix 1* (Kacelnik et al., 2011). The main reason for this was to avoid making detailed assumptions about empirical latency distributions or applying curve-fitting techniques to the empirical data. The drawback might have been, in some occasions, a poorer fit of the model, but on the positive side we avoided using free parameters that would have made the model more flexible and precise, at the cost of weaker biological or behavioural justification. Goldstein and Gigerenzer (2011), while commenting on the potential applicability of their recognition heuristic research approach, emphasised a very important and pertinent point regarding simple models:

“The beauty of simple models lies in their transparency. One can measure how often and in what situations models predict behavior and when they fail. The benefits are in their robustness: the ability of a strategy to work well in new situations. A complex model with many adjustable parameters is more prone to overfitting than a simple model (...)”

(pp. 394)

Gigerenzer and the ABC group (Gigerenzer, Todd, and ABC Research Group, 1999; Gigerenzer and Selten, 2002; Gigerenzer, Hertwig, and Pachur, 2011) have been working mostly with humans, arguing that decision-makers use *fast and frugal* heuristics to make most of their day-to-day choices. They use terms like *adaptive toolbox* and *bounded rationality*, as alternative strategies/logic to the optimality approach. In contrast, in *Chapter 6*, I report a thorough study of principles of economic rationality as applied to non-human choice. I explicitly applied axiomatic principles from microeconomics to birds making decisions along either of two dimensions, reward probability or delay to reward, and relate this to the optimality approach used in behavioural ecology. I tested two principles of rationality (i.e., transitivity and independence of irrelevant alternatives – see

Chapter 6 for details) with European starlings, training them either with 5 options differing in food delay or with 6 options differing in reward probability, before letting them choose repeatedly one option out of several sets made of either two or three different options. Strikingly, although I observed partial preferences and thus payoffs were not fully maximised, the birds' behaviour satisfied the most stringent tests for rational choice as understood in the economic literature, showing strong stochastic transitivity and full compliance with the independence principle (see *Chapter 6* for details).

More generally, throughout chapters and following their presentation order (i.e., 2 to 6), there was a broadening of the theoretical implications addressed: in *Chapter 2* there was only a slight methodological modification and the implementation of a new modelling technique, respective to previous experiments. In *Chapter 3*, things became more akin to the real world. Some options, rather than being fixed, were now probabilistic (real life scenarios are by nature stochastic, at least in some respects). In such situations, animals should act as statisticians, collecting and storing information as they forage and using this information to make foraging decisions (Pyke, 1984, pp. 527). The use of a risky choice paradigm also allowed me to examine the relative performance between the SCM and alternative predictors of choice, by comparing the results obtained with other models, such as the Expectation of the Ratios (EoR; cf. Bateson and Kacelnik, 1996) and Scalar Utility Theory (SUT; Reboresda and Kacelnik, 1991). In *Chapter 4*, I address the importance of *when* animals learn that choices exist in their environment, and whether 'learning to choose' has a long-lasting effect. In other words, if an animal learns about all opportunities by always meeting them simultaneously as opposed to meet them sequentially, does it learn something different, so that this affects the parameters of choice behaviour in later tests? This was important in order to establish if results in previous chapters (and related studies) were narrowly dependent on training protocols. Instead of receiving training with options

met in sequential (no-choice) trials (or with no-choices and choices intermixed), the animals were exposed only to choice situations from the outset of the experiment, and only afterwards no-choice trials were introduced. Secondly, I introduced, also for the first time (but in a separate experiment), choices between three options, as a way to increase the contrast between models predicting a deliberation time (i.e., choosing among more options should take longer) and the SCM, where decisions should have taken even less time the greater the number of options present. The goal of *Chapter 5* was to theoretically reconcile and integrate decision-making research from 3 different fields: behavioural ecology, mathematical psychology and neuroscience. This was achieved by showing the parallels and commonalities of Sequential Sampling Models (SSM) used in all these fields, while ultimately stressing the importance of no-choice protocols for the study of animal decision-making. Finally, in *Chapter 6* I discussed and tested experimentally whether the rationality/optimality approach used by theoretical economists and behavioural ecologists is sustainable given many recent claims that both human and non-human decision makers systematically breach rationality principles (Kahneman and Tversky, 2000; Latty and Beekman, 2011; Bateson, Healy, and Hurly, 2003; but see also Schuck-Paim, Pompilio, and Kacelnik, 2004 for an alternative view). My view is that most reports of apparent violations of logical decision principles in non-human studies result from failing to follow preconditions for their validity, such as constancy of the agent's state and lack of satiety effects from the commodity (Freidin and Kacelnik, 2011; Kacelnik, 2006; Houston, McNamara, and Steer, 2007a; Houston, McNamara, and Steer, 2007b; Pompilio and Kacelnik, 2005; Pompilio, Kacelnik, and Behmer, 2006; Waite, Nevai, and Passino, 2007). Variations in preference following variations in subjects' energetic reserves, or when the testing conditions allow subjects to infer differences in their circumstances, are perfectly consistent with normative, rationality-based theories (An organism caught in one such

irrationality could say, paraphrasing Keynes⁶: “When my circumstances change I change my preferences. What do you do, sir?”). The matter is of great significance because if it were convincingly shown that when necessary conditions such as the agent’s circumstances (including information state) are controlled, logical principles do not apply to decision processes, the foundation of the whole field of normative modelling in behavioural biology would be questionable. In an extensive series of tests I reported that the behaviour of captive starlings actually does fit the demands of established economic rationality principles (Luce, 1959; Gravelle and Rees, 2004). The results are relevant to decision making across multiple taxa, including humans, and highlight the value of integrating decision research across economics, psychology and biology. My discussion endorsed the rational choice and optimality approaches used in behavioural ecology, while accepting that irrationality and suboptimal choice are observed in many experimental protocols, but arguing that such observations should be used to dig deeper on the artefactual nature of experimental protocols, asking under which ecological conditions would observed decision processes be rational, rather than to dismiss optimality and its expression in consistent behaviour.

As a final note I would like to point out that every chapter, although independent (but nevertheless complementary) could, potentially, lead to different lines of research, either independently or in conjunction with other(s) and that the SCM should be extended and/or modified so that some of the difficulties found could be addressed and explored in more detail.

Overall, I collected a series of empirical observations that failed to show clear evidence for shortening of response times during simultaneous choices relative to response

⁶John Maynard Keynes wrote: When the facts change, I change my mind. What do you do, sir? Reply to a criticism during the Great Depression of having changed his position on monetary policy, as quoted in *Lost Prophets: An Insider's History of the Modern Economists* (1994) by Alfred L. Malabre, pp. 220 (http://en.wikiquote.org/wiki/John_Maynard_Keynes).

times to the same alternative when encountered sequentially (and in isolation). Accepting the null hypothesis that choice and single-option decisions do not differ in the time it takes to act should worry proponents of all models of choice. I cannot specify what kind of future model could solve this puzzle, but I do feel that this may be an important challenge for decision theory in coming years. For instance, it would be highly desirable to find suitable theoretical explanations (or a new and more sophisticated modelling approach) for the fact that latencies can be used as proxy for subsequent choice behaviour (as they reflect parallel and presumably independent accumulation processes), while no shortening (as predicted by the SCM) or lengthening in response times (i.e., latencies) during simultaneous choices is clearly found.

Inspiration may originate on very different systems. For instance, similar modelling approaches were implemented to collective decision-making of social insects: Robinson and collaborators (Robinson et al., 2011) showed that the rock ants' decisions while house-hunting could be explained by a simple threshold rule where individuals' choice was achieved without the need of an explicit comparison between different options (i.e., prospective new nests), and Seeley and colleagues (Seeley et al., 2012) showed that a cross-inhibition of accumulating evidence was sufficient to overcome deadlock problems when a swarm of bees chooses its new nesting site. Perhaps some of the mechanisms uncovered in insect colonies can serve as models for new models of how vertebrate brains work.

In summary, on the balance of probability, and taking into account my results and those from other experiments, I believe that the notion that the main comparison used by my model animals in foraging choices is between each option and the remembered background, but that the simplest idea, that action results from parallel processing of each

option with cross-censoring is insufficient, as while no deliberation time could ever be documented, it is also not safe to conclude that simultaneous choices lead to shorter latencies than sequential ones.

More importantly and in retrospect, I believe that regardless of the shortfalls of the Sequential Choice Model applicability (i.e., consistent under prediction of the observed preference) and lack of data favouring its most counterintuitive outcome (i.e., shorter latencies in simultaneous choice), I found sound evidence, across several different laboratory situations, for the use of latency measures (or response times) as an index of value of different options and in different contexts. This novel finding, might pave the way to new experiments and models hopefully broadening our understanding of decision processes, particularly in non-human animals. To be continued...

References

- Aw, J., Monteiro, T., Vasconcelos, M. and Kacelnik, A. 2012. Cognitive mechanisms of risky choice: Is there an evaluation cost? *Behavioural Processes*, 89: 95-103.
- Bateson, M., Healy, S.D. and Hurly, T.A. 2003. Context-dependent foraging decisions in rufous hummingbirds. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 270: 1271-1276.
- Bateson, M. and Kacelnik, A. 1996. Rate currencies and the foraging starling: the fallacy of the averages revisited. *Behav. Ecol.*, 7: 341-352.
- Emlen, J.M. 1966. The role of time and energy in food preference. *American Naturalist*: 611-617.
- Freidin, E., Aw, J. and Kacelnik, A. 2009. Sequential and simultaneous choices: Testing the diet selection and sequential choice models. *Behavioural Processes*, 80: 218-223.
- Freidin, E. and Kacelnik, A. 2011. Rational Choice, Context Dependence, and the Value of Information in European Starlings (*Sturnus vulgaris*). *Science*, 334: 1000-1002.
- Gigerenzer, G., Hertwig, R. and Pachur, T. 2011. *Heuristics: The Foundations of Adaptive Behavior*. Oxford University Press.
- Gigerenzer, G. and Selten, R. 2002. *Bounded rationality: The adaptive toolbox*. the MIT Press.
- Gigerenzer, G., Todd, P.M. and ABC Research Group. 1999. *Simple heuristics that make us smart*. Oxford University Press, New York.
- Goldstein, D.G. and Gigerenzer, G. 2011. The beauty of simple models: Themes in recognition heuristic research. *Judgment and decision making*, 6: 392-395.
- Gravelle, H. and Rees, R. 2004. *Microeconomics*. FT/Prentice Hall, Harlow, 738 pp.

- Houston, A.I., McNamara, J.M. and Steer, M.D. 2007. Violations of transitivity under fitness maximization. *Biology Letters*, 3: 365-367.
- . 2007. Do we expect natural selection to produce rational behaviour? *Philosophical Transactions of the Royal Society B-Biological Sciences*, 362: 1531-1543.
- Kacelnik, A., Schuck-Paim, C., Pompilio, L. 2006. Inconsistency in animal and human choice. In: C. Engel and L. Daston (Editors), *Is there value in inconsistency?*, Nomos Verlagsgesellschaft.
- Kacelnik, A., Vasconcelos, M., Monteiro, T. and Aw, J. 2011. Darwin's "tug-of-war" vs. starlings' "horse-racing": how adaptations for sequential encounters drive simultaneous choice. *Behavioral Ecology and Sociobiology*, 65: 547-558.
- Kahneman, D. and Tversky, A. 2000. *Choices, values, and frames*. Cambridge University Press, Russell Sage Foundation, Cambridge, New York, 840 pp.
- Latty, T. and Beekman, M. 2011. Irrational decision-making in an amoeboid organism: transitivity and context-dependent preferences. *Proceedings of the Royal Society B: Biological Sciences*, 278: 307-312.
- Luce, R.D. 1959. *Individual choice behaviour: A theoretical analysis*. Wiley, New York.
- MacArthur, R.H. and Pianka, E.R. 1966. On Optimal Use of a Patchy Environment. *The American Naturalist*, 100: 603-609.
- Pompilio, L. and Kacelnik, A. 2005. State-dependent learning and suboptimal choice: when starlings prefer long over short delays to food. *Animal Behaviour*, 70: 571-578.
- Pompilio, L., Kacelnik, A. and Behmer, S.T. 2006. State-dependent learned valuation drives choice in an invertebrate. *Science*, 311: 1613-1615.
- Pyke, G.H. 1984. Optimal Foraging Theory: A Critical Review. *Annual Review of Ecology and Systematics*, 15: 523-575.

- Reboreda, J.C. and Kacelnik, A. 1991. Risk sensitivity in starlings: variability in food amount and food delay. *Behavioral Ecology*, 2: 301-308.
- Robinson, E.J.H., Franks, N.R., Ellis, S., Okuda, S. and Marshall, J.A.R. 2011. A Simple Threshold Rule Is Sufficient to Explain Sophisticated Collective Decision-Making. *PLoS ONE*, 6: e19981.
- Schuck-Paim, C., Pompilio, L. and Kacelnik, A. 2004. State-Dependent Decisions Cause Apparent Violations of Rationality in Animal Choice. *PLoS Biology*, 2: e402.
- Seeley, T.D., Visscher, P.K., Schlegel, T., Hogan, P.M., Franks, N.R. and Marshall, J.A.R. 2012. Stop Signals Provide Cross Inhibition in Collective Decision-Making by Honeybee Swarms. *Science*, 335: 108-111.
- Shapiro, M.S., Siller, S. and Kacelnik, A. 2008. Simultaneous and sequential choice as a function of reward delay and magnitude: Normative, descriptive and process-based models tested in the European Starling (*Sturnus vulgaris*). *Journal of Experimental Psychology: Animal Behavior Processes*, 34: 75-93.
- Stearns, S.C. and Schmid-Hempel, P. 1987. Evolutionary insights should not be wasted. *Oikos*: 118-125.
- Vasconcelos, M., Monteiro, T., Aw, J. and Kacelnik, A. 2010. Choice in multi-alternative environments: A trial-by-trial implementation of the Sequential Choice Model. *Behavioural Processes*, 84: 435-439.
- Waite, T.A., Nevai, A.L. and Passino, K.M. 2007. State subsidies induce gray jays to accept greater danger: an ecologically rational response? *Behavioral Ecology and Sociobiology*, 61: 1261-1266.

Appendix 1.

Darwin's 'Tug-of-war' vs. Starlings' Horse-Racing: how adaptations for sequential encounters drive simultaneous choice

[Kacelnik, A., Vasconcelos, M., Monteiro, T. and Aw, J. 2011. Darwin's "tug-of-war" vs. starlings' "horse-racing": how adaptations for sequential encounters drive simultaneous choice. *Behavioral Ecology and Sociobiology*, 65: 547-558.¹]

¹doi: 10.1007/s00265-010-1101-2

Darwin's "tug-of-war" vs. starlings' "horse-racing": how adaptations for sequential encounters drive simultaneous choice

Alex Kacelnik · Marco Vasconcelos · Tiago Monteiro · Justine Aw

Received: 24 February 2010 / Revised: 28 October 2010 / Accepted: 29 October 2010
© Springer-Verlag 2010

Abstract Charles Darwin aided his private decision making by an explicit deliberation, famously deciding whether or not to marry by creating a list of points in a table with two columns: "Marry" and "Not Marry". One hundred seventy-two years after Darwin's wedding, we reconsider whether this process of choice, under which individuals assign values to their options and compare their relative merits at the time of choosing (the tug-of-war model), applies to our experimental animal, the European Starling, *Sturnus vulgaris*. We contrast this with the sequential choice model that postulates that decision-makers make no comparison between options at the time of choice. According to the latter, behaviour in simultaneous choices reflects adaptations to contexts with sequential encounters, in which the choice is whether to take an opportunity or let it pass. We postulate that, in sequential encounters, the decision-maker assigns (by learning) a subjective value to each option, reflecting its payoff relative to background opportunities. This value is expressed as latency and/or probability to accept each opportunity as opposed to keep searching. In simultaneous encounters, choice occurs through each option being processed independently, by a race between the mechanisms that generate option-specific latencies. We describe these alternative models and review data supporting the predictions of the sequential choice model.

Keywords Choice · Latency · Sequential choice model · Tug-of-war model · *Sturnus vulgaris*

Introduction

When Charles Darwin set out to decide whether or not to marry his cousin, Emma Wedgewood, he found himself facing a difficult decision. To help himself decide about the advantages of marrying (apparently regardless of the identity of the partner), he wrote his two possible actions ("Marry" and "Not Marry") at the top of a split page and proceeded to list the pros and cons of each of these options under each heading. At the bottom of the page, he seems to have weighted the relative strength of each argument, writing "Marry. Marry. Marry. Q.E.D.", and a few months later, he did indeed marry (Darwin 1838). This method offers a starting point for the theoretical analysis of decision processes. In modern terminology, these columns might have been labelled "go" and "no go". Half a century earlier, Benjamin Franklin (1772) had described his own preferred method to deal with hard decisions in a letter to Joseph Priestley. Franklin explained that, when faced with complex decisions including a number of opposing factors, he would write the pros on one column and the cons in another, then proceed to simplify the dilemma by crossing out elements of equivalent weight on each column, until only a few pros or cons remained, thus determining the right course of action. He called his method "Moral, or Prudential Algebra". It is tempting to assume that something similar to these procedures might be embodied in the cognitive mechanisms underlying choice in humans and other species, but, as we will discuss here, this assumption deserves close scrutiny. An implicit property of any such process would be that choosing involves a number of

Communicated by Guest Editor A. Houston

This contribution is part of the Special Issue "Mathematical Models in Ecology and Evolution: Darwin 200" (see Marshall et al. 2010).

A. Kacelnik (✉) · M. Vasconcelos · T. Monteiro · J. Aw
Department of Zoology, University of Oxford,
South Parks Road,
Oxford OX1 3PS, UK
e-mail: alex.kacelnik@zoo.ox.ac.uk

Published online: 01 December 2010

cognitive operations and should thus take time: acting in the presence of a single alternative should be faster than acting when a choice between two or more is required. We contest this intuition both theoretically and empirically.

Motivated by a number of empirical observations (reviewed later), we propose instead that, when two options are simultaneously available, animals do not explicitly deliberate between two options, but instead rely on the same process as when facing independent, sequential opportunities. When an animal faces a single foraging opportunity, it can choose whether to chase it or skip it. Many factors can exert influence, including the payoff of the present option relative to other opportunities available in the environment. Let us assume the animal decides to chase the prey. Action, of course, is not synchronous with perception, and the time between perception and action is of interest here. We argue that the duration of this latency to act reflects a tendency to skip the prey in favour of continuing to forage. Latency is not the minimum processing time in the neural path between perception and action (the reaction time), but the sum of the minimal processing time and a motivational component that expresses (or, in behavioural terms, is) the willingness to chase that prey type. Across sequential encounters with various prey types, the animal builds up a library of subjective values, each corresponding to a prey type and generating a probability density function of latencies to chase that prey type in different encounters. The functional expectation, from an optimal foraging perspective, is that the central tendency and spread of the resulting latency distribution will be a decreasing function of the expected fitness gain from that prey type relative to the lost opportunity in the whole environment. For simplicity, we are treating the environment and the resulting library of prey types used by the decision-maker as static. This is valid for the laboratory tests we discuss presently, but, in natural situations, an additional complication may arise from how the organism tracks the temporal variations in its field of opportunities.

The core question for this article is what happens when two prey types are met simultaneously. This, we surmise, is easily and frequently arranged in the laboratory, but probably rare in natural hunting situations. Quantitative estimates of the relative frequency of simultaneous versus sequential encounters are hard to achieve because, to some extent, there will always be some minor difference in the moment of perception and proximity of stimuli relevant to each item. Indeed, categorising an encounter as simultaneous may be a matter of setting a threshold for the temporal/spatial proximity between multiple stimuli. We assume, however, that encountering multiple stimuli in sufficient proximity to qualify as simultaneous is sufficiently rare not to lead to the development of special neuro-behavioural adaptations to deal with them optimally, so that

simultaneous choices are dealt with using the same mechanisms evolved for efficient handling of sequential encounters. When multiple stimuli overlap, these mechanisms operate in parallel: each option sets in motion a process that would normally generate a latency and then action, but the option that generates the shorter latency “censors” the alternative(s) so that one of them is expressed behaviourally and one latency is measured. In other words, we postulate that each simultaneous choice is treated as independent, non-interfering sequential opportunities. Crucially, there is no comparative evaluation of the merits of each available option at the time of choice. Most alternative models of choice, however, assume some sort of comparison at the time of choice.

At the heart of conventional models of decision processes lies the assumption that there is a trade-off between the accuracy of choice and cost of evaluation and that this implies longer time costs in simultaneous than sequential encounters. This is a natural assumption whether the agent has incomplete knowledge of the alternatives’ parameters or is fully acquainted with them. When knowledge is incomplete (for instance, when facing stochastic options of unknown probabilities), it may be adaptive to allocate a number of initial responses to gain knowledge and optimise the balance between exploration and exploitation, so that a short-term exploratory cost is paid to decrease the long-term cost of errors (Krebs and Kacelnik 1978). The optimal amount of behaviour allocated to exploration increases with the number of alternatives, since exploration gives no gains when the agent only faces one option.

If the agent deals instead with fully known sources of reward, the same logic applies to the handling of previously encoded information: facing two or more options can be expected to call for some evaluation of previous experience and the entailed processing of information to cause greater latency to act (the time cost of the evaluation) than when no choice is faced. Delay to act under this scenario implies a time cost and should be minimal when only one option is present, as there is no point in paying any evaluation cost if there is nothing to choose.

This intuitive logic also applies to mechanistic (rather than functional) models of choice: the chain from perception of potential targets to action might be thought to be longer when facing more than one option, since competition for control of the behavioural final common path must involve more cognitive operations for greater number of options. When only one option is present, action may not involve any competition and should thus be faster.

Triggered by some recent findings in the decision behaviour of starlings (*Sturnus vulgaris*), we examine the two previously mentioned alternative views of choice

processes. We start with an informal description of the models, then discuss them from a functional perspective and offer some formalisation. Finally, we move on to contrast their predictions against empirical results. Although we present two basic approaches, we are aware that they are not the only possibilities, but hope that they are sufficiently broad to illustrate the main issues to which other theoretical constructs could be related. We call them, for reasons that will become clear, the tug-of-war model (ToW) and the sequential choice model (SCM). A detailed review of a set of models dealing with forced choices between two alternatives has been presented by Bogacz et al. (2006). These authors focused on an experimental paradigm (the two-alternative forced choice) in which a complex ambiguous stimulus is presented and subjects choose between two responses (left or right), only one of which is correct. We deal, instead, with subjects facing either one or two foraging alternatives that differ in their attractiveness and examine behaviour when either a single alternative is present or both are presented simultaneously. Our primary emphasis here is not on optimality in the process by which the subject judges the correctness of two contrasting hypotheses, but on narrowing down the plausible processes by which subjects may use stored information to reach action.

Models of choice mechanisms

We assume that, as an animal experiences a source of reward in a given context, it develops a certain valuation of it. This valuation is sensitive to absolute properties of each source (particularly the ratio of amount of reward to the delay between action and outcome; e.g. Bateson and

Kacelnik 1996; Shapiro et al. 2008), to the state of the subject during learning about it (sources encountered under greater need are valued more highly as they yield greater effective utility; e.g. Marsh et al. 2004; Pompilio et al. 2006; Vasconcelos and Urcuioli 2008) and to the available alternatives in the same context (a source is more highly valued the lower the average gains in the environment where it is typically found; e.g. Fantino and Abarca 1985; Pompilio and Kacelnik 2010). From a functional point of view, this scenario relates to the sequential choice situations that dominate optimal foraging theory models, such as Charnov (1976a, b) and see also, Houston (2010). Rather than assuming that the dominant selective pressure that modelled present-day mechanisms of choice was the balance between accuracy of choice between simultaneous opportunities and time costs to evaluate each choice, we assume that the prevalent conflict was between taking a given opportunity and letting it pass to pursue what the background environment had to offer. Hence, our explicit reference to sequential choices.

To model how valuation is transduced into action in such choice situations, both models assume that when a decision-maker encounters a stimulus associated with a source of reward a set of neurons (not necessarily contiguous) starts discharging at a given (stochastic) rate R_i , where i indicates the option (see Fig. 1, top panel). The rate of discharge is assumed to be positively related to the subjective value of the option encountered, and, as explained earlier, this value is a function of learning. The output R_i of this assemblage is then integrated to produce a quantity S_i that expresses the instantaneous tendency of the subject to respond to the option. When, after responding, the stimulus disappears, the value of S_i is reset to zero. We

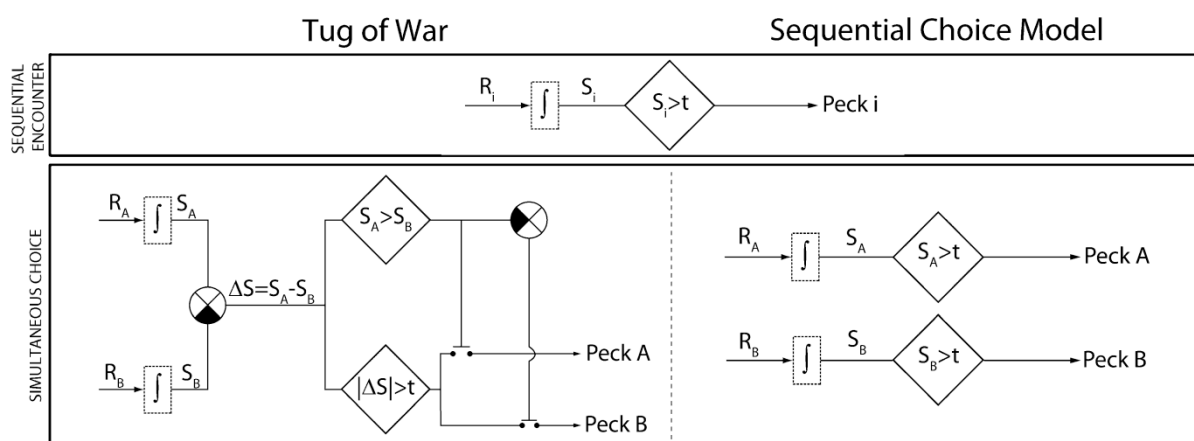


Fig. 1 Top panel: Block diagram of a sequential choice. R rate of neuronal discharge, S integrated signal, t threshold. Bottom left panel: Block diagram of a simultaneous choice according to the ToW model. R rate, S integrated signal, t threshold, and $\otimes$ and $\oplus$ = sum, where

black indicates negative input. Bottom right panel: Block diagram of a simultaneous choice according to the SCM. R rate, S integrated signal, t threshold

refer to the time elapsed between the onset of the stimulus and action as the “latency” to respond. For a given option, this latency varies from sequential encounter to sequential encounter due to the stochasticity in the neurons’ discharge rate. Consequently, across encounters, an observer can build up a specific distribution of latencies to accept each of the options available in the environment. The two models we contrast differ, however, in the way tendencies to act compete for behavioural expression when more than one option is simultaneously available; although in both of them, preference is constructed at the time of choice (e.g. Slovic 1995).

Tug-of-war

In this model (see Fig. 1, bottom left panel), when the stimuli relevant to two or more potential targets are simultaneously present, a computation of their relative instantaneous tendency to generate action occurs. In the figure, this is implemented as the difference between the S_i values, but we have no empirical access to the quantitative values of R_i or S_i , and the precise comparison operation is not crucial for our argument. What is important, however, is that at this stage, the subject computes an index of the relative attractiveness between the options and somehow ranks them. In the figure’s example, when the difference in attractiveness exceeds a given threshold, the animal takes action, with the selected target depending on which of the values is larger (i.e. on the sign of the difference). The left panel of Fig. 2 illustrates the same idea in a different format. Here, the value of the difference between S_A and S_B is seen in an imaginary trial progressing irregularly (due to the stochasticity of R_A and R_B) until it reaches a threshold, when action occurs. The probability distributions shown upwards and downwards of the threshold lines indicate the

latencies to act that an observer would see across trials when either option is chosen.

Because the signals from each candidate option compete, they can be seen as tugging the input to the behavioural final common path in opposite directions. At the extreme, if for the sake of illustration, we assume that two equally valuable targets are present and that the process has no noise, their difference might never reach the action threshold and the decision-maker would be caught in the dilemma of Buridan’s Ass, who died when facing two piles of hay because it could not choose between them (Zupko 2006). On a more plausible case, it is to be expected that action towards each candidate would take longer in the presence of competitors than when the same option is encountered alone. In the context of Fig. 1 (bottom left panel), if, say, $S_B=0$, then the difference will be just S_A , which will find it easier to pass the threshold for action than when S_B detracts from the overall sum (i.e. $S_B > 0$). Thus, the probability distributions to be observed when only one option is present would be shifted to the left respect to those shown.

Different versions of this model could include the evaluation before the integration steps, the use of a proportional ratio [say $S_A/(S_A+S_B)$] rather than a difference for the comparison and the use of different thresholds for each action. None of these variations are of importance for our present purposes, as will become clear below. The core of this model is that any process where there is a competitive evaluation between attractors is likely to have a time cost because of the computation of an index of attractiveness and a consequent ranking before action takes place.

The intuitively expected increase in choice time with number of options has empirical support in humans, where it is encapsulated in Hick-Hyman Law (Hick 1952; Hyman 1953), an empirical regularity that is popular in human–

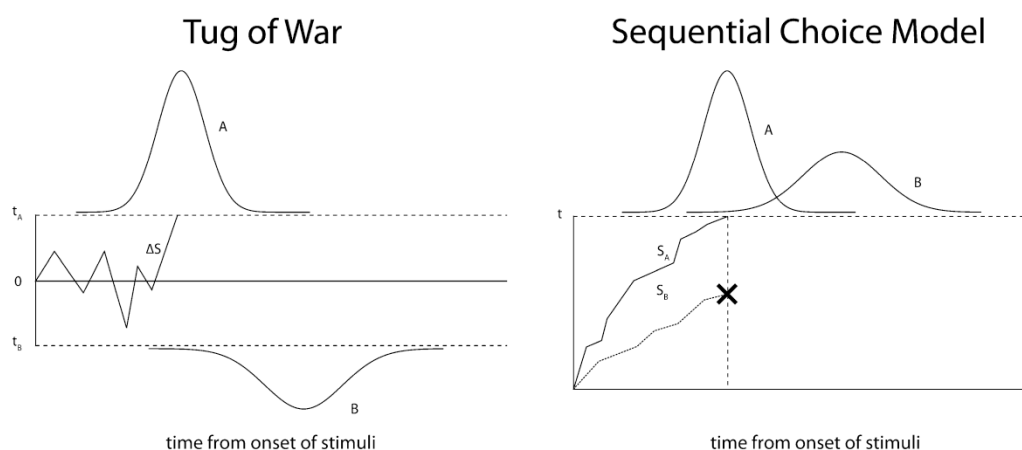


Fig. 2 Left panel: progression of ΔS (see Fig. 1) in an imaginary trial. Right panel: progression of S_A and S_B in an imaginary trial. When one signal reaches the threshold, the other is censored. A and B represent frequency distributions of latencies observed when each option is chosen

computer interaction studies. Hick-Hyman's law says that the time T required to make a choice among n items is described by $T = b \cdot \log_2(n+1)$, where b is a fitted parameter and n the number of alternatives in the set. Thus, time to choose should increase sub-linearly with the number of options. The view that adding options makes choice more demanding and time-consuming is widely accepted and frequently described as the "Paradox of Choice" (Schwartz 2004).

Sequential choice model

This model differs from the previous one in that it does not include a comparative evaluation between the tendencies to respond to each action, but cross-censorship occurs at the final stage (see Fig. 1, bottom right panel). Here, the values S_i are compared with a threshold for action independently, so that, when one of them reaches the threshold, the agent responds, the stimuli for all options go away and all S_i are reset to zero. This simple process has an interesting consequence for the empirical observations of latency to act. When two options are present, each act of choice produces a latency observation for the candidate that has reached the threshold earlier, but no information about the aborted process regarding other options. Observed latencies thus show the result of cross-censorship between the underlying distributions of latencies for each candidate option. By "underlying" here we mean the distribution of latencies to act that is observed when that option is encountered multiple times without competition. The result of this cross-censorship is that the latencies to act recorded during simultaneous choice situations should be shorter than those for encounters with single options because censorship is bound to suppress the underlying distributions asymmetrically, censoring longer-than-average samples more severely than shorter-than-average samples. This is shown in the right panel of Fig. 2. Here, we see how, in a given trial, both tendencies to act race towards the threshold. The winning tendency is expressed as latency, while the losing one remains unobserved. Due to stochasticity, it is to be expected that each option will have a higher chance of winning in trials when its rate R_i has been faster than average, so that more latencies will be recorded from the left than from the right tail of each underlying distribution.

Notice that this prediction has the opposite sign of that of the ToW model: rather than predicting a time cost of evaluation, here, we predict a shortening of the delay to act when two stimuli are present, with respect to when an option is encountered alone. When two candidate options that differ in attractiveness are met, the more attractive option will rarely be censored, and thus, in most choice trials, its latency will be expressed and that of the alternative will not. This means that the latency distribution

for the less preferred option will be more severely censored than that of the preferred option. In fact, the few values we do observe for the less preferred option will only be those that out-compete the latencies of the preferred option and thus must have been sampled from the left tail of its underlying latency distribution. This leads to another prediction: that the shortening of latencies to act in choice with respect to sequential encounters should be more extreme for the option that is chosen less frequently.

In summary, by assuming that only the decision mechanisms involved in sequential encounters have been pruned by natural selection (i.e. there are no special adaptations for simultaneous choices) and that these are co-opted whenever two or more options are presented simultaneously, we progress toward a model that challenges the conventional expectation of a time cost for choosing. Importantly, the model makes several experimentally testable predictions. In essence, the SCM implies that (a) the valuation process involves learning and reflects the attractiveness of the present option relative to the background of opportunities, (b) cross-censorship between the processes generating latencies to act leads to observing shorter latencies during simultaneous choices than sequential encounters, particularly for the less preferred option and (c) one should be able to predict partial preferences between options, when faced simultaneously, from behaviour (i.e. latencies) during sequential encounters.

The predictions of the SCM can be made more mathematically explicit, without loss of generality. Suppose that sequential encounters with options A and B generate the distributions of latencies f_A and f_B , respectively, with cumulative distributions Φ_A and Φ_B . When these two options are met simultaneously, the probability of choosing A is simply the probability P_A of a sample from f_A being shorter than one from f_B and is given by

$$P_A = p(l_A < l_B) = \int_0^\infty f_A(x) \cdot [1 - \Phi_B(x)] dx \quad (1)$$

where l_A and l_B are random samples from the respective distributions and x is a particular latency value.

Equation 1 can be used to predict the distribution of latencies for each option in choice trials. For A, this is given by the conditional probability that $l_A = x$ given that $l_A < l_B$ in that trial, for all x . Formally, we seek $F(R|S)$, where R means " $x < l_A \leq x + dx$ " and S means $l_A < l_B$. Generally,

$$F(R|S) = \frac{F_1(R, S)}{F_2(S)} \quad (2)$$

where $F_1(R, S)$ gives the probability of joint occurrence of R and S , and $F_2(S)$ gives the probability of S independently of R . We can express F_1 as:

$$F_1(R, S) = f_A(x) \cdot P[l_B > x] = f_A(x)[1 - \Phi_B(x)] \quad (3)$$

Since $F_2(S)$ is given by Eq. 1, we can write Eq. 2 as

$$F(R \setminus S) = \frac{f_A(x) \cdot [1 - \Phi_B]}{\int_0^\infty f_A(x) \cdot P[1 - \Phi_B(x)] dx} \quad (4)$$

Eq. 4 predicts the distribution of latencies in choice trials using the distributions of latencies in sequential encounters (i.e. latencies observed when only one option is present). Mean latencies during choice are obtained by integration of this function.

Tug-of-war versus sequential choice: empirical tests of the two models

Latencies as an expression of a valuation process

Thus far, all explicit tests of the SCM have been performed with European starlings working for food reinforcement in operant chambers. Previous research (e.g. Bateson and Kacelnik 1995; Reboreda and Kacelnik 1991) had already suggested that latencies in no-choice trials offer an orderly view of preferences in choice trials, particularly when options are risky. More recent studies have probed the relationship between latencies and preferences more directly. Shapiro et al. (2008) trained starlings in multiple environments, each defined by two possible options. Each option was signalled by a different symbol in a response key and offered a particular combination of amount and delay to food (henceforth, we use the terms rate or profitability to refer to the ratio between amount and delay). Notice that throughout we use “delay” to refer to the time elapsed between an animal’s action and the consequences. In computations of actual rates of return, the time between each outcome and the forthcoming choice opportunity (including such time components as inter-trial intervals, search, travel times and handling times) should be included. We assume that these times form part of the valuation of each option (the sparser the encounter of opportunities the higher the valuation of all options in such a context), but since they affect all options in the same direction, the learning mechanism by which stimuli are attributed responsibility for specific outcomes downgrade their influence. Consequently, times other than delays between actions and outcomes play a small role in the choices we discuss (for an explicit discussion of this point see Kacelnik 2003).

The main assumptions and predictions of the SCM can be tested independently. In terms of assumptions, the SCM crucially depends on the dependence between latency to respond to an opportunity when encountered on its own and the benefit that would result from taking that opportunity given the background alternatives. This is shown in top

panel of Fig. 3. The top panel of the figure shows the median latencies to accept each option in sequential encounters (i.e. when only one option was present) as a function of the option’s rate and the rate of the alternative option in that environment, as observed by Shapiro et al. (2008). The figure shows that the average of individual’s median latencies to respond depends both on the rate of the option present in any particular sequential encounter and on the rate of the alternative in that particular treatment, even though this alternative is not present at the time. As predicted, latencies to accept each option decrease as a function of an option’s profitability and increase as a function of the profitability of the background alternative. Since Shapiro et al. tested this effect within individuals, it is clear that this is a learning-dependent effect. Thus, the main assumption of the SCM is fulfilled.

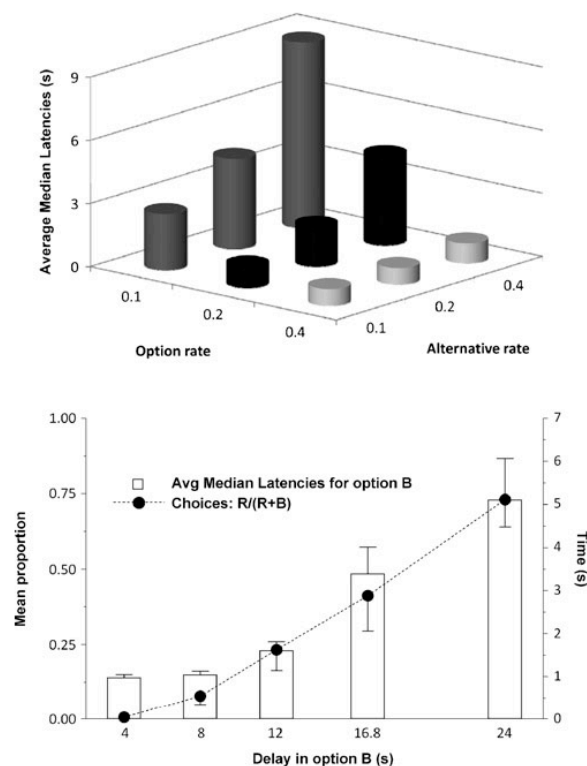


Fig. 3 *Top panel:* Median latencies, averaged across subjects, to accept each option during sequential (single-option) encounters as a function of the option’s rate (amount/delay) and the rate of the alternative option that can potentially be encountered in that environment. Statistical analyses confirmed a significant effect of the option’s rate, the rate of the alternative and their interaction (adapted from Shapiro et al. 2008). *Bottom panel:* dots represent the average proportion of choices (SEM) of R (the “reject” key) in trials offering a choice between B (the leaner of the reinforced alternatives) and R; bars show median latencies (+SEM) in sequential encounters with option B, averaged across subjects (adapted from Freidin et al. 2009)

From a functional perspective, we have argued that the latency variation reflects a tendency to skip opportunities in favour of the background. This is supported by Freidin et al. (2009). Here, starlings were again trained with two options that led to food, A and B, each signalling a different delay to reinforcement. Option A always signalled a delay of 1 s while option B signalled a delay of 4, 8, 12, 16.8 or 24 s, depending on condition. However, in this study, birds also encountered a third option (R) that was never reinforced but gave the subjects the chance to terminate the current trial and advance to the next one after the usual inter-trial-interval. As expected, during sequential encounters, latencies to accept the best option (A) were very short (average of individual's median latencies <1.0 s) with little variation across conditions, but latencies to accept B were not only longer than those for A in every condition, but also increased significantly as B's rate decreased (Fig. 3, bottom panel). This study also supports the functional rationale of the SCM, as R allowed the birds to actively reject options in favour of continuing to forage for alternatives. When A and R were presented together, birds chose R (i.e. rejected A) on less than 1% of the trials, independently of the profitability of B in that treatment. But, the pattern in B vs. R trials was quite different: birds increasingly rejected B as its signalled delay increased, up to a rejection level of 73%. This trend follows the predictions of Chamov's (1976a) diet choice model. What is crucial for our present discussion, however, is that longer delays to food were associated with both longer latencies to accept the option and an increasing probability of rejecting it when given the opportunity.

These results suggest a strong correlation between latencies to accept an option and willingness to reject it ($r=0.99$ in this particular study), supporting the logic of the SCM and the assumption that latencies observed during sequential encounters are an index of the option's attractiveness relative to the background opportunities.

While these observations are a crucial necessity for the SCM, they are also compatible with the alternative that we called the tug-of-war model. However, the two models make different predictions which we will proceed to examine.

Latency predictions: shortening of latencies during simultaneous choices

As previously mentioned, the SCM makes the rather counterintuitive prediction that latencies observed during simultaneous choices should be shorter than latencies observed during sequential encounters and that this effect should be stronger for the least preferred option. In contrast, the ToW model predicts that latencies in simultaneous encounters should be longer than in sequential ones, due to the time taken to evaluate their relative worth. Latencies observed by Shapiro et al. (2008) support the shortening

predicted by SCM. To compare latency distributions during sequential and simultaneous encounters, the authors summarised these distributions as cumulative frequency scores. They divided latencies into 70 bins and calculated the proportion of all latencies accounted for by each bin. The cumulative score was then given by the total area under the cumulative distribution plot. High scores capture shorter latencies to respond because, in such cases, most latencies must occur in earlier bins (the maximum possible score of 70 occurs when all latencies occur in the first bin). Figure 4 plots the differences between the cumulative scores of the latency distributions observed during sequential and simultaneous encounters. Negative values indicate earlier latency

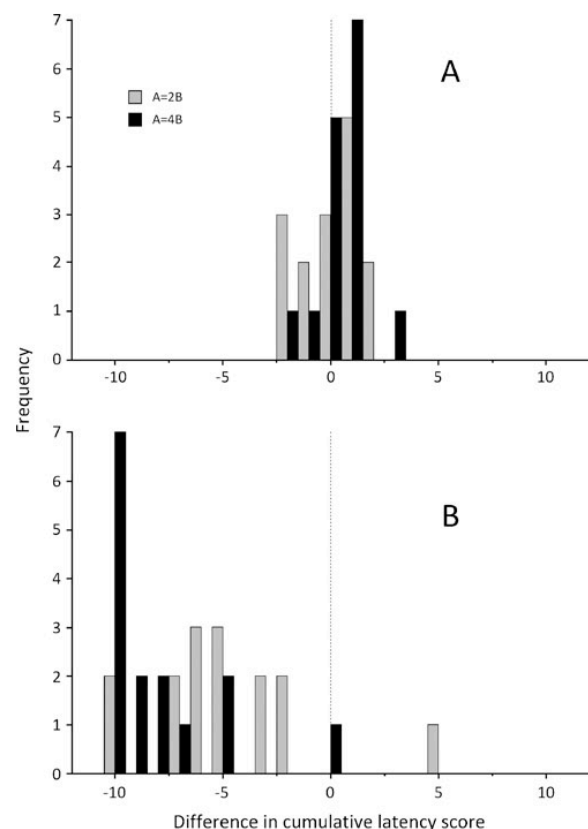


Fig. 4 Differences between latency distribution scores observed during sequential and simultaneous encounters (modified from Shapiro et al., 2008). To summarise shifts in the distributions of latencies, these authors generated cumulative frequency scores using the areas under the cumulative distributions, so that higher scores indicate shorter latency distributions. The category axis displays the difference between these scores, with negative values corresponding to shorter latencies in choice than in single-option trials. The vertical axis gives frequency as number of individuals. Latencies to options A and B are shown in the top and bottom panel, respectively. Grey and black bars identify treatments in which option A's profitability was twice or four times that of option B, respectively. Vertical, dashed lines indicate no differences in cumulative scores between choice and single-option trials

distributions during simultaneous encounters relative to the latency distribution during sequential encounters. The figure neatly contrasts the predictions of the two models: the ToW model predicts bars to be to the right of the origin while the SCM predicts them to be to the left. For the richer option (A; upper panel), there were no substantial differences between the frequency distributions for latencies expressed in simultaneous and sequential encounters, regardless of whether A's rate was two or four times that of B (grey and black bars, respectively). However, for the less preferred option (B; lower panel), latencies during simultaneous encounters were significantly shorter than latencies observed during sequential encounters with B, both whether the rate of A was two or four times the rate of B (grey and black bars, respectively).

Thus, the expected shift towards shorter latencies in simultaneous relative to sequential encounters is supported by the data, and, as expected, this shift is stronger for the least preferred (most censored) option. This prediction is hard to test in experiments when the preference for one of the options nears exclusivity, as in those cases the distribution of the preferred option is hardly censored at all and the sample sizes for choice latencies of the least preferred option can be too small to assess. There is also an expected floor effect, as latencies are likely to be composed of two elements (a minimum reaction time and a facultative and potentially variable "strategic" latency related to the value of each option relative to its context). When this value is very high, the strategic component is close to zero, and all we see in either choice or single-option trials is the reaction time so that the shift simply cannot occur.

Predicting simultaneous choice from sequential encounters

A further, exclusive, prediction of SCM is that we should be able to predict choices made when facing more than one alternative simultaneously from the latencies expressed during sequential encounters with those same alternatives. Several studies suggest that such predictions are not only possible but also surprisingly accurate (Shapiro et al. 2008; Freidin et al. 2009; Aw 2008; Vasconcelos et al. 2010).

Shapiro et al. (2008) tested this prediction in the study discussed above. To this effect, they trained starlings in several environments, each composed of two options, A and B, where A signalled a rate of reinforcement that was equal, two times greater or four times greater than B. They calculated the preference for A predicted by the model using latencies observed during sequential encounters with A and with B and compared those predictions with observed levels of preference in simultaneous choice trials. To avoid making assumptions regarding the shape of the latency distributions, the authors calculated the proportion of consecutive pairs of sequential encounters (one with A

and the other with B) in which the latency for A was shorter than the latency for B and used that proportion as their overall prediction of preference strength for A. The top panel of Fig. 5 shows the results of this analysis. The slope of the resulting regression was close to one and the intercept close to zero, with R^2 ranging from 0.93 to 0.94

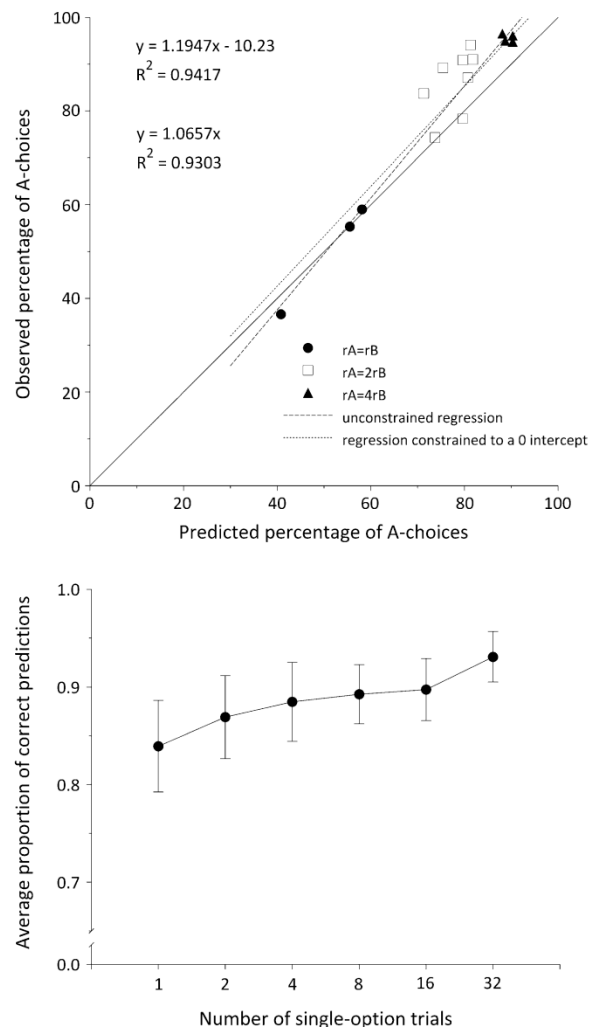


Fig. 5 *Top panel:* scatter plot of the obtained (ordinate) versus predicted (abscissa) proportion of choices for the option with a higher rate according to the SCM. Each rate is represented by a different symbol. Two linear regression lines are included, using the across-subject proportions as data, as well as their parameters and regression coefficients (generated by the average obtained results; from Shapiro et al., 2008). *Bottom panel:* proportion of choices ($\pm$ SEM) accurately predicted by SCM, averaged across subjects and binary-choice pairs, as a function of the number of preceding sequential encounters used to predict each individual choice. The weighted moving average was

calculated as follows:
$$\frac{\sum_{i=1}^n l_{-1} \cdot i^{-1}}{\sum_{i=1}^n i^{-1}}$$
 where $n=1, 2, 4, 8, 16$ or 32 and

l =latency (from Vasconcelos et al. 2010)

depending on whether or not they imposed a y -intercept of zero. This implies a very high level of accuracy in the predictions.

While the previous analysis shows that it is possible to predict the overall preference strength in simultaneous choices from latencies expressed during sequential encounters, these predictions of overall preference strength may fail to capture local fluctuations in motivation or preference. It is to be expected that latencies registered in sequential encounters may lead to closer predictions in choice trials that are temporally close than in choice trials that are temporally distant from the sequential trials in which latencies are measured. Furthermore, while Shapiro et al. (2008) tested the predicted versus observed proportion of choices of A distributed across their data set, it should be possible to make a specific prediction for each choice based on the latencies of sequential encounters that occur in temporal vicinity.

The performance of the model in terms of global and local predictions, although presumably correlated, can in fact be dissociated. Obviously, any model capable of predicting each individual choice is necessarily also efficient over aggregates of choices, but the reverse is not necessarily true. A model that performs well over aggregates of choices can fail to predict each particular choice (e.g. Prokasy and Gorezano 1979). Suppose that an animal encounters options A and B simultaneously ten times and chooses A in the first five encounters and B in the last five. A model could predict a choice of B in first five and of A in the last five. Overall, the model's predictions would match the animal's preferences (the model would predict that A would be chosen 50% of the time and the animal would have chosen A in exactly that proportion). However, for each particular simultaneous encounter, there would be a complete mismatch between prediction and observed behaviour (every time the model predicted choice of A, the animal chose B and vice versa). Such an extreme situation is admittedly unlikely, but the point remains that global (or "molar", as they are sometimes called) predictions are not identical to local (or "molecular") predictions, and models that can be tested at both levels should be examined at both.

Vasconcelos et al. (2010) set out to test the predictions of the SCM at global and local levels, training starlings with four different options, each signalling a different delay to food reward (3, 6, 12 or 24 s). Starlings encountered these options either alone (sequential encounters) or in pairs during simultaneous presentations of two of the four options, which could generate any of six possible pairs (simultaneous choices). This was, by design, a stricter test of the model than those tried by Shapiro et al. (2008) and Freidin et al. (2009): starlings were trained not with two but with four options in the same context and faced not only

one type of simultaneous binary choice but six possible choice pairings. Again, instead of fitting theoretical functions to the distributions of latencies, Vasconcelos et al. (2010) used the empirical latencies recorded during sequential encounters to generate the local predictions. To make predictions, the authors used an algorithm, developed by Aw (2008), whereby, for each particular simultaneous encounter they took, the latencies from the most recent sequential encounters involving those options and predicted that the option with the shortest latency would be chosen. Using this rather simple procedure, the authors accurately predicted 84% of all individual choices.

If the success of such a local approach is due to the sensitivity of their algorithm to local fluctuations in preference, it could be argued that such fluctuations could be better captured by some weighted average of latencies in the temporal vicinity of the choice. To test this possibility, Vasconcelos et al. (2010) generated predictions using a weighted average of recent sequential encounters, including 2, 4, 8, 16 or 32 sequential encounters per option. They used a hyperbolically decaying moving average to account for recency, with each latency's weight inversely proportional to its distance (in number of trials) from the simultaneous choice that was being predicted. Of course, this may not be the optimal decay parameter for the temporal aggregation of latencies, but despite this shortcoming, the results were surprising: the ability of the model to accurately predict each choice increased monotonically as the number of sequential encounters considered per option increased (Fig. 5, bottom panel). When the most recent 32 sequential encounters per option were considered, the model was able to accurately predict 93% of all choices.

In summary, the SCM's predictions appear to be fulfilled. Both Shapiro et al. (2008) and Vasconcelos et al. (2010) clearly show that latencies expressed during sequential encounters can be used to predict simultaneous choices. Most importantly, the model is able to generate both global and local predictions with considerable accuracy. The alternative model that we discussed, which involves a comparative evaluation at the time of simultaneous encounters does not, in its present form, predict choices from behaviour in sequential encounters.

Concluding remarks

We have contrasted the predictions and assumptions of two models of the mechanisms of foraging choices using starlings as model organism. The main distinction between the two models is the putative temporal cost of the cognitive operations leading to a choice. We found empirically that, when an action is pursued after being met in the presence of a simultaneous alternative, the time it takes starlings to respond is shorter than when the same

action is performed in response to the same option presented alone.

On these and other collateral pieces of evidence, we favour a model of choice in which choices between simultaneously present opportunities result from each alternative being processed independently at the time of choice. Since foraging opportunities encountered individually are taken after a delay that is variable and inversely related to the context-dependent profitability of each option, the choice process resembles a horse race rather than a tug-of-war.

Although we framed our paper in a concrete, empirically based setting, we are aware of raising broader issues in the sphere of quantitative approaches to behavioural research. These issues include (1) the extent to which it is possible to produce mathematical expressions that, with few parameters and acceptable generality, model cognitive mechanisms of choice; (2) the relation between functional (optimality) considerations and mechanistic modelling approaches; (3) the criteria that are appropriate to prefer one model or class of models over another and (4) the role of parsimony in this last respect. We use these concluding remarks to explore some of the ways we feel our research relates to these questions.

The problem of models' uniqueness is central to all of this. Because information-processing mechanisms are invisible, they must be inferred from behaviour (in humans, introspection contributes, albeit in a potentially misleading way, at least to the formulation of hypotheses). This implies that, for any given behavioural data set, there may be an infinite number of models capable of simulating the qualitative properties of the data, but it does not deny the possibility of rejecting classes of models. For the experimental protocols used here, we can discard models that lead to a time cost of choice. We cannot, however, discard all models that use some form of evaluation at the time of choice, but differ from our preferred proposal of independent, parallel processing. As an example, imagine a model like our ToW (Fig. 1, bottom left) but in which the instantaneous attractiveness (S_i) of the options are summed at the time of choice instead of their difference being computed. This model would have both an evaluation component and show a shortened time to action in choices than in sequential encounters because the simultaneously present options would act synergistically, rather than competitively, shortening the time required in reaching the threshold for action.

Our leaning towards the parallel processing model instead of synergistic evaluation reflects a preference for parsimony, in two respects. The first is a preference for simpler processes. According to the SCM, there is no dedicated mechanism evolved to optimise the control of simultaneous choices. The same system that drives action in

sequential encounters results in choices when options happen to be met simultaneously. Heyes (1998) forcefully made the point that parsimony may be unjustified if it is only based on a given interpretation being simpler for us to deal with, rather than being simpler for the brain to implement. We agree with her point and feel that our preference for SCM is based on the latter, rather than the former. A related second argument can be derived from evolutionary considerations. It is reasonable to assume, but not empirically tested as yet, that, in nature, foraging animals encounter feeding opportunities sequentially more often than simultaneously (Stephens and Krebs 1986). This may be particularly so for secondary consumers whose preys are likely to be more sparsely occurring and mobile. If two kinds of prey are encountered during search, each with an independent probability distribution of intervals, simultaneous encounters will involve the product of these probabilities. Admittedly, prey encounters may not be totally independent, since prey of different species may aggregate, but only very extreme and implausible aggregation parameters would make simultaneous choice as frequent as sequential encounters. As a result, natural selection has greater opportunity to optimise mechanisms that regulate behaviour in sequential than in simultaneous encounters. If mechanisms that are suitable for sequential encounters are capable of satisfactory performance and good account of data in choice situations, it seems inappropriate to postulate the existence of dedicated mechanisms for choice.

Admittedly, animals face behavioural decisions other than prey choice, and some have proposed that such decisions may often involve simultaneous choice. If this were indeed the case, then it would be possible for the mechanisms pruned by natural selection to deal efficiently with such simultaneous choice situations to be co-opted to deal with simultaneously available prey. Sexual selection offers here a paradigmatic example. It has been suggested, for example, that simultaneous choice is involved in female choice when males display in a common area, a lek (e.g. Bradbury and Gibson 1983) and when females use acoustical cues to choose (e.g. Catchpole et al. 1984; Ryan and Wilczynski 1988). But, even these claims are, at least for the time being, controversial as females probably approach displaying males sequentially (e.g. Ryan, 1985; Gibson 1990). In most other female choice situations, it is seems uncontroversial that females evaluate males sequentially (e.g. Janetos 1980; Wittenberger 1983; Parker 1983; Real 1990, 1991; Bakker and Milinski, 1991; Gibson and Langen 1996).

At the risk of belabouring the point, a further methodological consideration is worth mentioning. We instrumentalised the contrast between sequential and simultaneous encounters using trials where only one or two options were

available. The fact that we can predict choices in two-option trials from behaviour in single-option trials makes it worth discussing whether this is simply a correlation or implies a causal link. We favour the latter because there is a substantial asymmetry: while it is possible to predict choices in two-option trials from latencies in single-option trials, the reverse is not possible. The data from single-option trials contain more information than those from choice trials.

One caveat relates to the broader application of our results and ideas. No set of experimental results can be used to completely exclude a model or class of models in situations or species different from those on which the ideas are tested. We have used a number of laboratory choice paradigms on a single species, and in all cases, we found that assuming independent, parallel processing of each input accommodates the results better than assuming a competitive interaction between them. At this stage, there is no way of telling whether some yet-unexplored experimental protocol or physical configuration might eventually prove the presence of an evaluation mechanism at the time of choice, that starlings' choices in other dimensions or after further training might lead to different conclusions, or that other species might use different choice processes. The confidence in our hypothesis grows inductively: the greater and more diverse the number of protocols in which the parallel approach is a winner the greater our confidence in its correctness and its broader implications.

While fitting empirical results is a positive metric, other factors come into the picture. Different models differ in the conceptual bridges they establish with other fields. For instance, a strong tradition in animal decision-making research relates to the logic of optimal foraging theory, where decision rules (sometimes called rules of thumb or heuristics) are assumed to have evolved as a consequence of their efficiency to achieve maximal rates of return. The two most influential optimal foraging models are those proposed by Charnov to analyse rate-maximising diet choice (1976a) and rate-maximising patch exploitation (the marginal value theorem, 1976b). These models, and many later developments, incorporate the economic principle of contrasting the value of a given option against that of the background environment. This comparison may explain the presence of substantial latencies to respond in single-option trials. The latency to respond may reflect the searching effort for alternatives. Hence, when an option is the worse in its environment, an animal facing it might spend some time searching for alternatives. This was corroborated by a design in which a "reject" action was included (Freidin et al. 2009). The animals used the rejection key only when facing the worst option in the environment. This result was consistent with the predictions of the diet choice model and was predicted by the latencies

to respond in encounters with the same option when the rejection key was not present, suggesting that the SCM efficiently implements the rate-maximising diet choice model.

Our continuing aim is to further explore the performance of this model across a larger number of experimental protocols and animal species, but present empirical results give us reasons for optimism for the predictive power of the SCM.

Author note This work was supported by Biotechnology and Biological Sciences Research Council Grant BB/G007144/1 to AK. MV, TM, and JA were supported by an Intra-European Marie Curie Fellowship, a doctoral grant from the Portuguese Foundation for Science and Technology, and a Biotechnology and Biological Sciences Research Council Fellowship, respectively. We are grateful to Miguel Rodríguez-Gironés for discussions and advice.

Conflict of Interest The authors declare that they have no conflict of interest.

References

- Aw J (2008) Decisions under uncertainty: common processes in birds, fish and humans. University of Oxford, Dissertation
- Bakker TCM, Milinski M (1991) Sequential female choice and the previous male effect in sticklebacks. *Behav Ecol* 29:205–210
- Bateson M, Kacelnik A (1995) Preferences for fixed and variable food sources: variability in amount and delay. *J Exp Anal Behav* 63 (3):313–329
- Bateson M, Kacelnik A (1996) Rate currencies and the foraging starling: the fallacy of the averages revisited. *Behav Ecol* 7 (3):341–352
- Bogacz R, Brown E, Moehlis J, Holmes P, Cohen JD (2006) The physics of optimal decision making: a formal analysis of models of performance in two-alternative forced-choice tasks. *Psychol Rev* 113(4):700–165
- Bradbury JW, Gibson RM (1983) Leks and mate choice. In: Bateson P (ed) *Mate choice*. Cambridge University Press, Cambridge, pp 109–138
- Catchpole CK, Dittami J, Leisler B (1984) Differential responses to male song repertoires in female songbirds implanted with oestradiol. *Nature* 312:563–564
- Charnov EL (1976a) Optimal foraging: attack strategy of a mantid. *Am Nat* 110:145–156
- Charnov EL (1976b) Optimal foraging: the marginal value theorem. *Theor Pop Biol* 9:129–136
- Darwin CR (1838) 'This is the question Marry Not Marry' [Memorandum on marriage]. CUL-DAR210.8.2 (Darwin Online, <http://darwin-online.org.uk/>)
- Fantino E, Abarca N (1985) Choice, optimal foraging, and the delay-reduction hypothesis. *Behav Brain Sci* 8:315–329
- Franklin B (1772) Letter to Joseph Priestley. Printed 1987 in Writings, pp. 877–878. New York: The Library of America.
- Freidin E, Aw J, Kacelnik A (2009) Sequential and simultaneous choices: testing the diet selection and sequential choice models. *Behav Process* 80:218–223
- Gibson RM (1990) Relationship between blood parasites, mating success and phenotypic cues in male sage grouse *Centrocercus urophasianus*. *Am Zool* 30:271–278

- Gibson RM, Langen TA (1996) How do animals choose their mates? *Trends Ecol Evol* 11:468–470
- Heyes C (1998) Theory of mind in nonhuman primates. *Behav Brain Sci* 21:101–148
- Hick WE (1952) On the rate of gain of information. *Quart J Exp Psychol* 4:11–26
- Houston A (2010) Central-place foraging by humans: transport and processing. *Behav Ecol Sociobiol*. doi:10.1007/s00265-010-1119-5
- Hyman R (1953) Stimulus information as a determinant of reaction time. *J Exp Psychol* 45:188–196
- Janetos AC (1980) Strategies of female mate choice: a theoretical analysis. *Behav Ecol Sociobiol* 7:107–112
- Kacelnik A (2003) The evolution of patience. In: Loewenstein G, Read D, Baumeister R (eds) *Time and decision: economic and psychological perspectives on intertemporal choice*. New York, Russell Sage, pp 115–138
- Krebs JR, Kacelnik TP (1978) Tests of optimal sampling by foraging great tits. *Nature* 275:27–31
- Marsh B, Schuck-Paim C, Kacelnik A (2004) Energetic state during learning affects foraging choices in starlings. *Behav Ecol* 15 (3):396–399
- Marshall J, McNamara J, Houston A (2010) The state of Darwinian theory. *Behav Ecol Sociobiol*. doi:10.1007/s00265-010-1121-y
- Parker GA (1983) Mate quality and mating decisions. In: Bateson P (ed) *Mate choice*. Cambridge University Press, Cambridge, pp 141–166
- Pompilio L, Kacelnik A (2010) Context-dependent utility overrides absolute memory as a determinant of choice. *PNAS* 107(1):508–512
- Pompilio L, Kacelnik A, Behmer ST (2006) State-dependent learned valuation drives choice in an invertebrate. *Science* 311:1613–1615
- Prokasy WF, Gorezano I (1979) The effect of US omission in classical aversive and appetitive conditioning of rabbits. *Anim Learn Behav* 7(1):80–88
- Real L (1990) Search theory and mate choice. I. Models of single-sex discrimination. *Am Nat* 136:376–405
- Real L (1991) Search theory and mate choice. II. Mutual interaction, assortative mating, and equilibrium variation in male and female fitness. *Am Nat* 138:901–917
- Reboreda JC, Kacelnik A (1991) Risk sensitivity in starlings: variability in food amount and food delay. *Behav Ecol* 2 (4):301–308
- Ryan MJ (1985) *The Túngara frog, a study in sexual selection and communication*. University of Chicago Press, Chicago
- Ryan MJ, Wilczynski W (1988) Coevolution of sender and receiver: effect on local mate preference in cricket frogs. *Science* 240:1786–1788
- Schwartz L (2004) *The paradox of choice: why more is less*. Harper Collins, New York
- Shapiro MS, Siller S, Kacelnik A (2008) Simultaneous and sequential choice as a function of reward delay and magnitude: normative, descriptive and process-based models tested in European starling (*Sturnus vulgaris*). *J Exp Psych Anim Behav Proc* 34:75–93
- Slovic P (1995) The construction of preference. *Am Psychol* 50:364–371
- Stephens DW, Krebs JR (1986) *Foraging theory*. Princeton University Press, Princeton
- Vasconcelos M, Urciuoli P (2008) Deprivation level and choice in pigeons: a test of within-trial contrast. *Learn Behav* 36:12–18
- Vasconcelos M, Monteiro T, Aw J, Kacelnik A (2010) Choice in multi-alternative environments: a trial-by-trial implementation of the sequential choice model. *Behav Process* 84:435–439
- Wittenberger JF (1983) Tactics of mate choice. In: Bateson P (ed) *Mate choice*. Cambridge University Press, Cambridge, pp 435–447
- Zupko J (2006) J Buridan. *Stanford Encyclopedia of Philosophy*. <http://plato.stanford.edu/entries/buridan/>. Accessed 18 February 2010.

On the flexibility of lizards' cognition: a comment on Leal and Powell (2011)

[Vasconcelos, M., Monteiro, T. and Kacelnik, A. 2011. On the flexibility of lizards' cognition: a comment on Leal & Powell (2011). *Biology Letters*, 8: 42-43.¹]

¹doi: 10.1098/rsbl.2011.0848

Comment

On the flexibility of lizards' cognition: a comment on Leal & Powell (2011)

Leal & Powell [1] (L&P) report experiments on the tropical lizard *Anolis evermanni* which, in their view, 'show that *A. evermanni* exhibits behavioural flexibility across multiple cognitive tasks, including solving a novel motor task using multiple strategies and reversal learning, plus rapid associative learning'. Given the standards that the authors themselves establish ('a robust demonstration of behavioural flexibility should show that individuals are capable of solving multiple cognitive tasks'), their findings and conclusions deserve careful scrutiny, especially because the issue of interpretive parsimony is at the heart of progress in comparative cognition [2].

L&P exposed six lizards to an apparatus with two wells, of which a randomly chosen one contained food. The baited well was partly covered by a blue disc that was progressively moved until it fully blocked food access. Four subjects became proficient at removing the disc on an average of 28 trials after full obstruction ('motor task', L&P's table 1). The movements differed among individuals, including using the snout as a lever, and lifting the disc with the mouth. Once they learned to systematically remove the blue disc, a second (yellow) disc was added, occluding the empty well. All four lizards continued to remove the blue disc ('discrimination, first experiment', L&P's table 1; one lizard tackled the alternative once). After six such trials, the yellow disc was replaced by another coloured with yellow and blue concentric rings. The lizards continued to respond to the blue disc ('discrimination, second experiment', L&P's table 1). After six further trials, the bait was placed in the well under the concentric rings disc. The lizards continued to respond to the (now unrewarded) blue disc, two of them until losing interest through response extinction. The remaining two eventually explored the other well, and after about 58 trials ('choice reversal', L&P's table 1), switched to remove consistently the concentric rings disc.

We do not think this demonstrates problem-solving flexibility of individuals across multiple tasks, reversal learning or rapid associative learning. The animals learned a discrimination gradually during the pre-training and motor task phases: food was under the blue disc, not elsewhere. Since pre-training length is not reported, the time to acquisition is unknown. The next two phases (discrimination experiments 1 and 2) involved no new learning (they showed persistent

responses to the rewarded blue disc), hence they also do not yield estimates of rate of learning.

New learning took place for the two lizards that eventually switched to the concentric rings disc. L&P correctly describe this as choice reversal, rather than reversal learning, but they conclude elsewhere that they studied reversal learning. In reversal learning, contingencies of two stimuli are learnt and then reversed, repeatedly in the case of serial reversal learning. By contrast, the lizards had not previously demonstrably learned anything about the concentric rings disc (see [3,4] for demonstrations of reversal learning in ectothermic tetrapods).

Thus, rather than multiple problem-solving tasks, two lizards learned the same thing (a colour signal for food location) twice. Their speed of learning cannot be assessed because they learned during the pre-training period, for which quantitative measures are not given. The only measure given for speed of behavioural change is the number of trials to choice reversal, but these data cannot be compared with typical reversal learning studies.

What is the evidence of cognitive and behavioural flexibility? As L&P explained, individual flexibility across multiple tasks would be informative with respect to cognitive flexibility, but this was not investigated in their study. Inter-individual variation in the disc-removal techniques is interesting, but differences in the form of the final response nearly always emerge by chance during instrumental conditioning, and do not indicate cognitive flexibility [5,6]. In summary, we agree that it should be interesting to conduct a comparative analysis of cognitive flexibility as a function of diversity in species' ecology using multiple tasks, measuring speed of associative learning, and including reversal learning, but this is yet to be done. L&P's experiments do not 'strongly suggest a re-thinking of our understanding of the cognitive abilities of ectothermic tetrapods'. They certainly do not show that lizards possess cognitive abilities 'comparable with those of some endothermic species including species recognized as having highly flexible behaviours', since they offer no metric for such comparison. The study is valuable because it broadens the taxonomic range of experimental models [7], and because there are those who, ignoring the existing literature on learning across many different taxa (see [4,7] and references therein), continue to hold an unjustified scepticism about cognitive complexity outside birds and mammals.

This work was supported by BBSRC Grant BB/G007144/1 to A.K. T.M. was supported by the Portuguese Foundation for Science and Technology. M. Leal generously contributed additional details of their study.

Marco Vasconcelos, Tiago Monteiro and
Alex Kacelnik*

Department of Zoology, University of Oxford,
South Parks Road, Oxford OX1 3PS, UK

*alex.kacelnik@zoo.ox.ac.uk

The accompanying reply can be viewed at <http://dx.doi.org/10.1098/rsbl.2011.1031>.

1 Leal, M. & Powell, B. J. 2011 Behavioural flexibility and problem-solving in a tropical lizard. *Biol. Lett.* 7. (doi:10.1098/rsbl.2011.0480)

- 2 Shettleworth, S. J. 2010 Clever animals and killjoy explanations in comparative psychology. *Trends Cogn. Sci.* **14**, 477–481. (doi:10.1016/j.tics.2010.07.002)
- 3 Schmajuk, N. A., Segura, E. T. & Rebores, J. C. 1980 Appetitive conditioning and discriminatory learning in toads. *Behav. Neural Biol.* **28**, 392–397. (doi:10.1016/S0163-1047(80)91698-2)
- 4 Gaalema, D. E. 2011 Visual discrimination and reversal learning in rough-necked monitor lizards (*Varanus rudicollis*). *J. Comp. Psychol.* **125**, 246–249. (doi:10.1037/a0023148)
- 5 Guthrie, E. R. & Horton, G. P. 1946 *Cats in a puzzle box*. New York, NY: Holt, Rinehart & Winston.
- 6 Thorndike, E. L. 1911 *Animal intelligence*. New York, NY: Macmillan.
- 7 Shettleworth, S. J. 2009 The evolution of comparative cognition: is the snark still a boojum? *Behav. Process.* **80**, 210–217. (doi:10.1016/j.beproc.2008.09.001)

Word cloud design¹ for the cover of *Behavioural Processes*

[Comparative cognition: Function and mechanism in the lab and field. A tribute to the contributions of Alex Kacelnik².]

¹The cloud was created, in collaboration with the special issue's guest editors, using the online free tool *Wordle* (<http://www.wordle.net/>). It shows the most frequent words in the titles of Alex Kacelnik's publication list and

²Volume 89, Issue 2, Pages 75-196 (February 2012), ISSN 0376-6357.

Behavioural Processes



Special issue:

Comparative cognition: Function and mechanism in lab and field.

A tribute to the contributions of Alex Kacelnik.

Guest Editors: Sara Shettleworth and Marco Vasconcelos