A critical review of risk-sensitive foraging

Houston, Alasdair I.

Wiley Blackwell
2023

Houston, A I & Rosenström, T 2023, 'A critical review of risk-sensitive foraging', Biological Reviews. https://doi.org/10.1111/brv.13031

http://hdl.handle.net/10138/568123
10.1111/brv.13031

BIOLOGICAL
REVIEWS

Cambridge
Philosophical Society

Biol. Rev. (2023), pp. 000–000.
doi: 10.1111/brv.13031

A critical review of risk-sensitive foraging

Alasdair I. Houston[1,*] and Tom H. Rosenström[2]

[1]*School of Biological Sciences, University of Bristol, 24 Tyndall Avenue, Bristol, BS8 1TQ, UK*
[2]*Department of Psychology and Logopedics, Faculty of Medicine, University of Helsinki, PL 21 (Haartmaninkatu 3), 00014, Helsinki, Finland*

ABSTRACT

Foraging is risk sensitive if choices depend on the variability of returns from the options as well as their mean return. Risk-sensitive foraging is important in behavioural ecology, psychology and neurophysiology. It has been explained both in terms of mechanisms and in terms of evolutionary advantage. We provide a critical review, evaluating both mechanistic and evolutionary accounts. Some derivations of risk sensitivity from mechanistic models based on psychophysics are not convincing because they depend on an inappropriate use of Jensen's inequality. Attempts have been made to link risk sensitivity to the ecology of a species, but again these are not convincing. The field of risk-sensitive foraging has provided a focus for theoretical and empirical work and has yielded important insights, but we lack a simple and empirically defendable general account of it in either mechanistic or evolutionary terms. However, empirical analysis of choice sequences under theoretically motivated experimental designs and environmental settings appears a promising avenue for mapping the scope and relative merits of existing theories. Simply put, the devil is in the sequence.

Key words: energy budget, reproductive value, risk averse, risk prone, starvation, Weber's law.

CONTENTS

- I. Introduction . . . 2
- II. Measuring risk sensitivity . . . 4
- III. A brief data overview . . . 4
- IV. Risk sensitivity can be rational and optimal . . . 5
- V. Functional models . . . 6
  - (1) Energy budget rule (EBR) . . . 6
  - (2) Energy budget and variability in delays . . . 7
  - (3) Over-extensions and simplifications . . . 7
  - (4) Background mortality . . . 7
  - (5) Reproduction . . . 8
  - (6) Variable environments do not (automatically) favour risk-sensitive foraging . . . 8
- VI. Causal models . . . 8
  - (1) Neurocognitive models . . . 8
  - (2) Side-effect models . . . 9
    - (*a*) Scalar utility theory . . . 9
    - (*b*) Learning . . . 11
    - (*c*) Weber and non-linear perceived stimulus intensity . . . 12
  - (3) Sequences and causation . . . 12
- VII. Generality . . . 12
  - (1) Risk-sensitive plants . . . 13
  - (2) Different reward dimensions and environmental context . . . 13
- VIII. Testing general principles . . . 14
- IX. Conclusions . . . 14
- X. Acknowledgements . . . 15

---

[*] Author for correspondence (E-mail: A.I.Houston@bristol.ac.uk).

XI. References 15
XII. Supporting information 18

I. INTRODUCTION

Studies of risk-sensitive foraging involve giving a subject a choice between options that differ in terms of mean and variability of reward. For example, one option might always deliver one unit of food and the other might unpredictably deliver either two units or nothing, each with a probability of 0.5. Non-human animals have to learn the properties of the options. Assuming they have learnt, risk sensitivity can be investigated. If the animal prefers the first option, it is said to be risk averse for amount, while if it prefers the second option, it is said to be risk prone. [Cocker & Winstanley (2015, p. 262) use a much stronger definition: risk aversion is being 'more conservative as potential gains increase'.] No preference means the animal is risk neutral. In this paper, risk is usually variability in amount received but we sometimes consider variability in time until reward is obtained.

An agent shows risk-sensitive foraging (RSF) if its choices depend on the variability of the options as well as their mean. The key terms 'mean', 'variance' and 'variability' together with our abbreviations are defined in Table 1. Behaviour is not risk sensitive if it can be explained in terms of the mean rate of gain (Possingham, Houston & McNamara, 1990; Kacelnik & Bateson, 1996). Optimal foraging theory assumes that natural selection has resulted in animals that forage so as to maximise fitness, which is a function of some currency such as energy gained. Before 1980, optimal foraging models often assumed that the foraging choices of an animal should maximise expected net energy or, in some contexts, expected food rewards (Pyke, Pulliam & Charnov, 1977). The work of Caraco (1981) and Real (1980) drew attention to the importance of variation about the mean. If the value of energy in terms of its contribution to fitness is not a linear function of energy, then effects of increases and decreases in energy are asymmetric (i.e. variance about the mean can add or reduce expected value). To take account of this, optimal foraging theory has modelled the effects of variability on choice. From its origins in behavioural ecology, RSF is now analysed in terms of neurophysiology, and its implications for drug addiction, gambling and obesity are considered (Bickel, Giordano & Badger, 2004; Addicott *et al.*, 2015; Voon *et al.*, 2015; Cocker & Winstanley, 2015; Mobbs *et al.*, 2018; Stokes *et al.*, 2019). In this critical review, we discuss the current state of ideas in the field.

Table 1. Abbreviations and definitions.

Abbreviation	Definition
CE	Certainty equivalent
EBR	Energy budget rule
RSF	Risk-sensitive foraging
RV	Reproductive value
SPE	Scaled prediction error
SUT	Scalar utility theory

Concept	
Value, utility	A state (e.g. current energy) or an outcome (e.g. gain in energy) x has a value $V(x)$ to an animal. In evolutionary theories, $V(x)$ is usually reproductive value. In economics, it is usually the utility of an asset to an individual. These may, but typically do not, coincide.
Mean	The outcome (e.g. energy) if a variable option is chosen is a random variable X whereas x is a specific outcome. Expected energy from a choice option X across repeated sampling from its distribution P_X is $E[X] = \int x dP_X$, and the expected value is $E[V(X)]$.
Variance	Variance of reward values, $\mathrm{Var}[X] = E[(X - E[X])^2]$ (standard deviation squared; a symbol such as σ^2 may be used to denote a specific value for the general operator, Var).
Variability	Variance and other types (moments) of variability, such as skewness and kurtosis.

Broadly speaking, there are two approaches to modelling risk-sensitive behaviour. One involves explaining why natural selection could favour risk-sensitive behaviour by showing that it maximises the agent's reproductive value. This approach provides an ultimate (or functional) account of RSF. The alternative gives a proximate (or mechanistic) explanation based on how the agent makes decisions (Kacelnik & Bateson, 1996; Bateson & Kacelnik, 1998; Kacelnik & El Mouden, 2013). We make this distinction by using V for reproductive value and M for decision strength in some proximal mechanism.

Importantly, accepting a gamble is not the same as being risk prone, and is not directly pertinent to risk-sensitive behaviour. For example, Marshall-Pescini *et al.* (2016) gave dogs and wolves the choice between an option resulting in a pellet of dry food or one resulting in either their preferred food or a stone. The fact that wolves prefer the second option does not tell us about their preference for fixed *versus* variable amounts of food and so does not mean that they are risk prone (for other examples that also use different types of food, see Rosati & Hare, 2011, 2013). By contrast, risk sensitivity is probed by experiments involving variability in the *same dimension*. We usually take the dimension to be energy, often determined by amount of a food type or concentration of sugar in a liquid. For example, consider a foraging experiment where the animal has three options. The fixed (no-variance) option always yields a reward of a given unchanging amount. The moderate-variance option yields the same expected value as the fixed option but always a few units less than the common mean with probability 0.5 or a few units more with probability 0.5. The high-variance option behaves similarly but with several units deviations from the common mean. If the reward x is a given type of food and the animal needs x_s units of food to survive overnight and x_r units to both survive and reproduce, then the value of reward $V(x)$ for the animal might have a shape like the one shown in Fig. 1A. If the common mean of the foraging options is below x_s, the animal starves unless it chooses a variable option and has some luck: evolution favours risk-prone behaviour. If the common mean is above x_r, the animal does not need more food than that and can only lose by choosing the options other than the fixed one: evolution then favours risk-averse behaviour. However, between x_s and x_r, both risk aversion and proneness could be optimal, depending on whether variability serves to provide access to reproduction and/or to risk survival. We return to this example in Section V.5.

Maximising expected value has different risk-preference implications compared to maximising expected reward despite

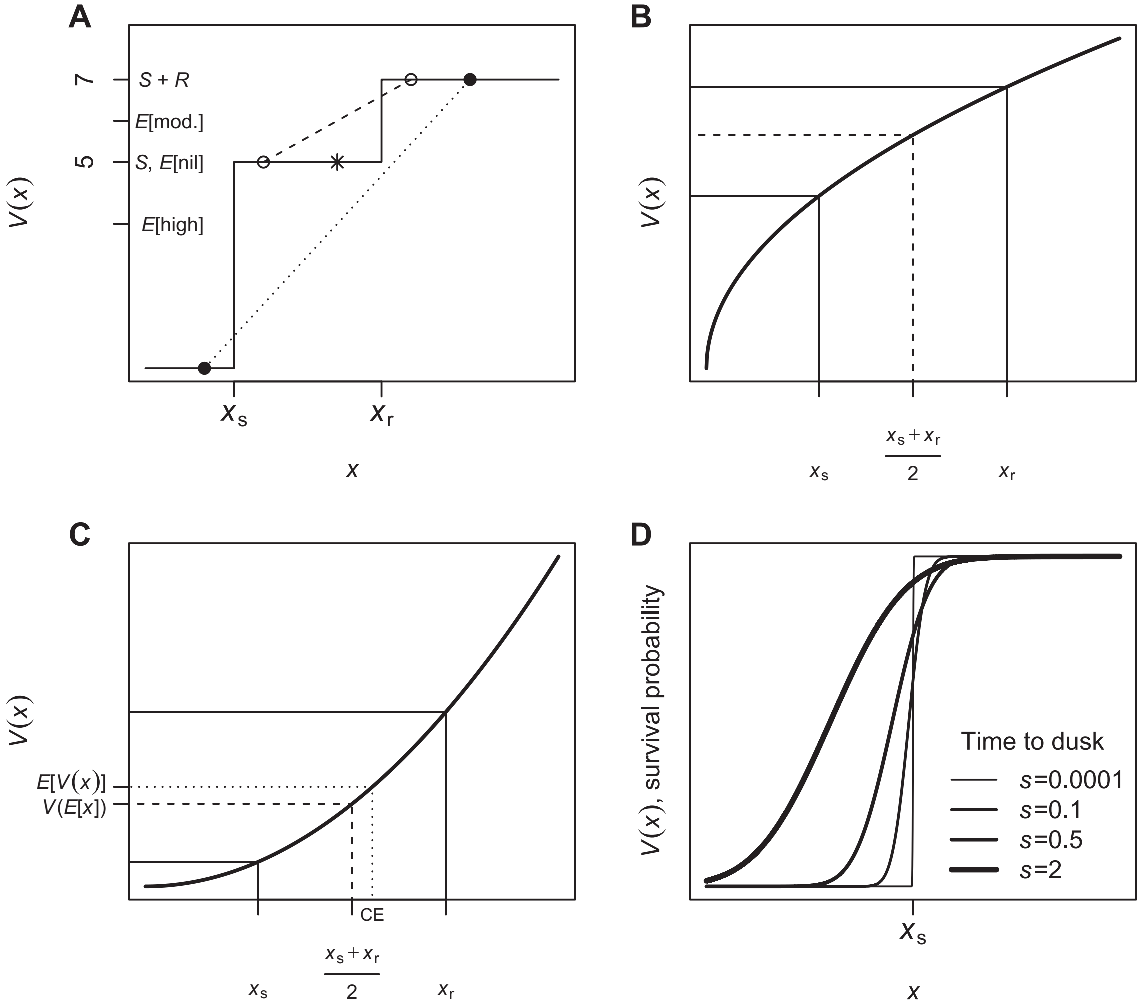

Fig. 1. Value- or utility-based risk sensitivity illustrated. (A) An animal that might reproduce today or later, if it survives overnight, has reproductive value S if it exceeds the survival threshold, x_s, that is greater than that of immediate reproduction given survival, R [here in the ratio 5:2, i.e. $V(x_s) = 5$ and $V(x_r) = 7$]. The expected values (E) of three competing foraging options providing different variability in energy but a common mean depend on which parts of the animal's value function (solid line) the variability provides access to. In the illustrated case, the moderate-variability option (open circles realised with 0.5 probability each, resulting in expected value E[mod]) provides the greatest expected utility because it accesses survival and sometimes reproduction, whereas the nil-variability option (E[nil], star with probability 1) accesses survival only, and the high-variability option (filled circles realised with 0.5 probability each, resulting in expected value E[high]) risks survival, which is more costly than losing access to reproduction. (B) A concave value function weights more heavily the lower end of any reward intervals, implying that $E[V(x)] \leq V(E[x])$ (Jensen's inequality) and that fixed expected reward (risk aversion) provides greater value than variable rewards of the same mean reward. (C) A convex value function weights more heavily the upper end of any reward interval, implying conclusions opposite to concave functions (risk proneness). The certainty equivalent reward, $\mathrm{CE} = V^{-1}(E[V(x)])$, is above the average reward $E[x]$. (D) When the animal can continue foraging before the survival threshold x_s takes effect (e.g. there is time left until dusk), the energetic states below the threshold have a non-zero value depending on the time left to reach the threshold (s). Hence, the energy budget rule (EBR) gives rise to smooth value functions (see online Supporting Information, Appendix S1 for details).

the rewards monotonically mapping to values. A function $V(x)$ is concave when $V(\lambda a + (1-\lambda)b) \geq \lambda V(a) + (1-\lambda)V(b)$ for any values a and b and for any λ between 0 and 1 (inclusive). That is, a concave function lies above a straight line joining any two of its values. Conversely, a convex function lies below such straight lines. In the case of our example shown in Fig. 1A, V is neither concave nor convex, which is why we can observe phenomena like preference for an intermediate-variance option (Hurly, 2003; Lim, Wittek & Parkinson, 2015). For strictly concave value functions and strictly value-based risk sensitivity, a general mathematical result known as Jensen's inequality always implies risk aversion (see Fig. 1B). Conversely, convex value functions imply risk proneness (Fig. 1C). In foraging theory, Jensen's inequality can be succinctly described by the notion that a decelerating value of a reward currency (i.e. diminishing returns) implies risk-averse behaviour whereas an accelerating function implies risk-prone behaviour.

II. MEASURING RISK SENSITIVITY

The concept of the certainty equivalent (CE) reward provides a way of measuring risk sensitivity. We treat the value function V as a type of utility function for now, with Section IV discussing the relationships between value and utility. Given a variable option, its CE is the fixed option that is equivalent to the variable option in the sense that the animal is indifferent between the two options (e.g. Keeney & Raiffa, 1993, p. 143) (see also Fig. 1C). For the determination of CE, see e.g. Caraco, Martindale & Whittam (1980), Constantinople, Piet & Brody (2019) and Genest, Stauffer & Schultz (2016). It follows that the CE can be determined without a knowledge of the utility function. Thus, one can also determine the *risk premium*, $E[x]$ − CE, i.e. the difference between the expected reward $E[x]$ and the CE. A positive risk premium implies risk aversion, and willingness to pay for certainty relative to the actuarial value (i.e. relative to the mean). Hence, the insurance business is built on risk aversion. A negative risk premium implies risk proneness, and willingness to pay for gambling. In a way, then, the gambling business is built on risk proneness.

Successive empirical CEs can also be used to estimate complete utility functions using a fractile method (e.g. Machina, 1987; Genest *et al.*, 2016; Bujold, Ferrari-Toniolo & Schultz, 2021). In Section VI.2.*a*, we derive CEs as indifference points that are theoretically predicted rather than observed. Their intersection points with expected rewards correspond to the predicted transitions from risk aversion to risk proneness.

III. A BRIEF DATA OVERVIEW

Kacelnik & Bateson (1996) reviewed the data on RSF and found that there was an almost universal preference for variability in delays, whereas behaviour in response to variability in amount was largely risk averse or neutral. The existing reviews of the data (Kacelnik & Bateson, 1996; Shafir, 2000; Weber, Shafir & Blais, 2004) are out of date, and the more recent review by Kacelnik & El Mouden (2013) just considers experiments that test one model, the energy budget model (Section V). Thus, a sophisticated review of all the experiments on RSF is needed. Yet, we believe that the first task is to offer a theoretical review that clarifies the issues and will be helpful in setting the stage for a review of the data. Hence, we only offer here some highlights from the many qualitatively novel and relatively recent findings in the field.

Since the above data reviews, risk-prone behaviour for variability in amount has been observed in rhesus macaques (*Macaca mulatta*) (McCoy & Platt, 2005; Hayden & Platt, 2007; Xu & Kralik, 2014; Genest *et al.*, 2016; Farashahi *et al.*, 2018), great apes (Haun, Nawroth & Call, 2011), humans (Ludvig *et al.*, 2014; Rivière *et al.*, 2018), pigeons *Columba livia* (Ludvig *et al.*, 2014) and rats (Roitman & Roitman, 2010; Sugam, Saddoris & Carelli, 2014; Ishii *et al.*, 2015). Table 2 provides a list of studies that found risk proneness specifically when comparing a risky option providing one of two equiprobable amounts to a safe option that invariably provided an amount equal to the risky-option mean. We explain the theoretical importance of this specific case in Section VI.2.*a*. However, we are not convinced by the claim that chimpanzees (*Pan troglodytes*) hunting meat are risk prone (Gilby & Wrangham, 2007). Although hunting meat is a high-variance option, it has not been shown that

Table 2. Studies reporting risk-prone behaviour in experiments comparing a risky option with equiprobable large or small amounts to a safe option providing an amount equal to the risky option mean.

Reference	Species used as experimental subjects
Young (1981)	Pigeon *Columba livia*
Ludvig *et al.* (2014)	Pigeon
Sugam *et al.* (2014)	Rat
Ishii *et al.* (2015)	Rat
Ishii *et al.* (2018)	Rat
Roitman & Roitman (2010)	Rat
Lacombe *et al.* (2022)	Gorilla *Gorilla gorilla gorilla*
Lacombe *et al.* (2022)	Orangutan *Pongo abelii*
De Petrillo *et al.* (2015)	Tufted capuchin *Sapajus* spp.
Bujold *et al.* (2021)	Rhesus macaque *Macaca mulatta* (included based on their fractile method)
Genest *et al.* (2016)	Rhesus macaque (included based on their fractile method)
Hayden & Platt (2007)	Rhesus macaque
O'Neil & Schultz (2010)	Rhesus macaque
So & Stuphorn (2010)	Rhesus macaque
Xu & Kralik (2014)	Rhesus macaque
Ludvig *et al.* (2014)	Human *Homo sapiens*
Ratikainen *et al.* (2010)	Siberian jay *Perisoreus infaustus*

chimpanzees prefer a gamble for meat to obtaining the same mean amount of meat as a certainty (Sayers & Menzel, 2017).

Another important aspect of the data is that RSF within species is not fixed but depends on the details of the procedure [what Heilbronner & Hayden (2013) call contextual factors] such as the time between trials (Hayden & Platt, 2007) or reward size (Weber & Chapman, 2005; Fehr-Duda *et al.*, 2010) and the state of the subject. Metabolic state (hunger or thirst) influences risk sensitivity in mice (Leblond *et al.*, 2011) and humans (Symmonds *et al.*, 2010; Levy, Thavikulwat & Glimcher, 2013). Human financial-risk attitudes depend on emotional states (Conte, Levati & Nardi, 2018). Honeybee (*Apis mellifera*) workers are more risk averse than drones (Shafir, Menda & Smith, 2005). Ishii *et al.* (2018) found that both male and female rats were risk prone, but the preference was stronger in males. In the Siberian jay (*Perisoreus infaustus*) risk-sensitive behaviour depends on social status. Breeding birds preferred high variance but unrelated subordinate birds preferred low variance (Ratikainen, Wright & Kazem, 2010). The rhesus macaque has repeatedly shown risk-seeking behaviour in laboratory experiments but is risk averse when foraging in a large enclosure (Eisenreich, Hayden & Zimmermann, 2019). The way in which the variable option is presented influences risk sensitivity. Lacombe *et al.* (2022) distinguish between two procedures in which rewards are covered by cups. In one procedure (multiple cups) a reward is hidden under one of n cups, with each cup having a probability $1/n$ of covering the reward. In the other procedure (single cup) there is just one cup with a probability $1/n$ of covering the reward. These procedures are mathematically equivalent but Lacombe *et al.* (2022) found that gorillas (*Gorilla gorilla gorilla*) and orangutans (*Pongo abelii*) were risk-neutral in the single-cup procedure but risk prone in the multiple-cups procedure. Risk sensitivity also depends on whether animals work for tokens that can be exchanged for rewards at the end of a session rather than experiencing the usual procedure of obtaining rewards during the session (Lagorio & Hackenberg, 2012; Farashahi *et al.*, 2018).

People can learn about risk in two ways – through being told about it or as a result of experience. These ways may not be equivalent, i.e. there is a description–experience gap (Hertwig & Erev, 2009; Wulff, Mergenthaler-Canseco & Hertwig, 2018; Hertwig, Wulff & Mata, 2019; Garcia, Cerrotti & Palminteri, 2021). When options are described, rare outcomes tend to be overweighted, whereas learning from experience results in rare outcomes tending to be underweighted (Hertwig & Erev, 2009). The gap is not, however, confined to rare events; it has been found when people make decisions involving options with two equiprobable outcomes (Ludvig & Spetch, 2011; see also Heilbronner & Hayden, 2016). Some differences between risk preferences in humans and other animals might therefore be the result of using data from humans who are given a description of the decision. Ludvig *et al.* (2014) found that when humans and pigeons learn from experience in the same procedure, they display similar risk sensitivity (see also Hayden & Platt, 2007). Shafir *et al.* (2008) found that both humans and honeybees changed from risk-prone to risk-averse behaviour when discrimination of reward values was experimentally reduced by using a very easy task and then a much harder task (see Section VI.2.*a* for further discussion on their interpretation).

Heilbronner & Hayden (2013) claim that the risk-prone behaviour of monkeys is a consequence of factors in the experimental procedure such as small rewards, short delays between trials and learning from experience. This view is not supported by Xu & Kralik (2014), who found that monkeys show risk-prone behaviour in various procedures. It might be thought that the description–experience gap is confined to humans, who have unique capabilities for understanding description, but it is possible to design animal procedures in which the stimuli provide information about their associated outcomes. For example, Heilbronner & Hayden (2016) ran a study comparing options learned from experience with ones explicitly cued with visual stimuli to indicate the probability of getting nothing or a large reward. Rhesus monkeys were more risk-prone when faced with experienced rather than described (cued) options.

In addition to reviewing theory in connection to data, we also discuss how certain types of theoretically relevant data are currently underrepresented in the field. For example, the effects of recent outcomes on choice have been reported (Marshall & Kirkpatrick, 2013). We outline below and in the online Supporting Information (Appendix S2) some novel predictions and discuss how more data on sequences of choice would be useful.

IV. RISK SENSITIVITY CAN BE RATIONAL AND OPTIMAL

Barrett & Fiddick (2000, p. 251) claim that in contrast to expected-utility theory, RSF theory 'does not assume that animals are trying to maximise expected utility'. Brennan & Lo (2012) include examples of RSF (Young, 1981; Harder & Real, 1987) in their list of 'anomalous', 'clearly suboptimal' behaviour, and De Agrò *et al.* (2021) identify RSF as an irrational departure from optimality. Other papers that view RSF as suboptimal or irrational include Shafir, Bechar & Weber (2003) and De Petrillo *et al.* (2015). This misrepresents the nature of RSF. As we now explain, RSF may maximise expected utility as a consequence of natural selection.

Kacelnik (2006) defines three versions of rationality. For our current concerns, the two relevant ones are rationality as used in economics (E-rationality) and in behavioural ecology and evolutionary biology (B-rationality). E-rationality is based on the maximisation of utility, but utility is a description for the subjective value of outcomes rather than a given thing. This distinguishes it from B-rationality, in which the maximised quantity has a clear biological meaning, '… a substantive, externally defined variable, namely reproductive value' (Kacelnik & El Mouden, 2013, p. 1118). Reproductive value

(RV) is an 'externally defined' quantity in the sense that organisms reproducing more than others will eventually become the norm in the population, and this need have nothing to do with their subjective valuation of outcomes. There is an asymmetry between E-rationality and B-rationality: an explanation in terms of RV means we have an explanation in terms of utility but an explanation in terms of utility does not mean we have an explanation in terms of RV. Thus, behaviour can be E-rational but not optimal in terms of evolution.

When utility is equal to RV, optimal behaviour is both E- and B-rational. Many theoretical analyses have concentrated on explaining why natural selection could favour risk-sensitive behaviour. This involves presenting a model that derives the utility function for an animal that is maximising its fitness. In other words, theory shows that a utility function makes evolutionary sense.

Mayack & Naug (2011) construct an 'empirical utility function' for the honeybee by measuring the proportion of bees surviving after 6 or 24 h of starvation as a function of food consumed before starvation. As Kacelnik & El Mouden (2013) point out, RV is not just a matter of survival. In social insects, individual mortality and colony growth need to be considered (Houston, Schmid-Hempel & Kacelnik, 1988), so Mayack & Naug (2011) have not measured RV. Furthermore, if we focus on energy reserves, and assume that RV is proportional to the probability of avoiding starvation, then survival time in the absence of food does not measure RV. Even if this time is proportional to energy reserves, the relationship between RV and energy depends on the environment (McNamara & Houston, 1986, 1990; Houston & McNamara, 1993, 1999; Higginson, McNamara & Houston, 2014).

In a related issue, Mishra (2014) criticises the use of utility functions because they merely describe the data. But once a utility function has been fitted, it can be used to make predictions about choices in new contexts – see Shapiro, Couvillon & Bitterman (2001) for honeybees and Genest *et al.* (2016) for monkeys. These studies do not attempt to link their utility functions to RV, and hence do not provide a functional account; in fact, Shapiro *et al.* (2001) present a mechanistic account of learning about stochastic rewards. Our review discusses both functional (ultimate, evolutionary) and causal (proximate, mechanistic) accounts of risk-sensitive behaviour and utility functions. We begin with functional models.

V. FUNCTIONAL MODELS

Although RV depends on survival and reproduction, several models focus on surviving a period such as winter when for some species reproduction is not possible. Perhaps the most influential approach investigates survival as a function of energy budget.

(1) Energy budget rule (EBR)

The EBR, also commonly known as the daily energy budget (DEB) rule, was developed to provide a functional explanation of the foraging behaviour of small birds in winter. These birds need to obtain enough energy during the day to enable them to survive the following night (when they cannot feed). The model assumes that a forager with initial energy reserves x_0 needs to get its reserves above a critical level x_s during a time foraging s if it is to survive the night (Stephens, 1981). It has two foraging options that have the same mean gain but differ in variance. If the forager uses the same option throughout the foraging period (i.e. adopts a non-sequential choice policy), then the energy gained will have a normal distribution with a greater variance under the more variable option. The probability of ending the day with reserves above x_s is greater if the forager chooses the high-variance option when $x_0 + gs < x_s$ and the low-variance option when $x_0 + gs > x_s$, where g is the common mean rate of gain (Stephens, 1981). This result can be restated as: be risk prone if the daily energy budget is negative (below the survival threshold) and be risk averse if the daily energy budget is positive (above the survival threshold).

It is important to realise that the model is static as opposed to dynamic, i.e. the forager cannot change its behaviour during the foraging period. For reviews of dynamic models of RSF in which a forager can base its decisions on its energy reserves and time, see McNamara & Houston (1992) or Houston & McNamara (1999). When the forager can make repeated choices between the two options, the EBR still holds in the sense that the variable option is favoured when the current expected reward at dusk is below the critical threshold and *vice versa* (Houston & McNamara, 1982). We can describe the model in terms of the relationship between energy at dusk and survival: a critical level of energy x_s is required for overnight survival, so the reproductive value of energy is 0 when energy is below this level, and otherwise some constant V_s. Thus, value is not a linear function of energy (*cf.* Figure 1A without the second threshold for x_r). The EBR thus assumes step utility functions – a limit for a sequence of increasingly steep sigmoids. Sigmoid utility functions have been reported from monkey and human experiments, although the form has been attributed to neuronal threshold and saturation effects rather than an energy budget (Genest *et al.*, 2016). For repeated foraging decisions during a day, or other energy-accumulation period, it is possible for each energetic state to change at each time point preceding dusk and thus the EBR leads to sigmoid functions (see Appendix S1 for details). That is, the value function of the energy-budget model is sigmoid when time until dusk remains ($s > 0$ in Fig. 1D) and a step function only at dusk (when $s = 0$). Thus, besides neural thresholds, the observed sigmoid-like utility function for sucrose liquid in monkeys (Genest *et al.*, 2016) could result from an energetic threshold.

The continuity of the energy-budget-implied utility functions has not always been appreciated in the theoretical literature either. For example, Lim *et al.* (2015) argued that the Pratt–Arrow index ρ [for a twice differentiable utility function u the index is $\rho(x) = -\frac{u''(x)}{u'(x)}$] is not well defined in the energy-budget model because of the step value function at dusk (*cf.* Figure 1D thin line with $V = u$) and the ensuing zero or undefined first derivative. This claim is incorrect, however, because the relevant utility is that at the time the decision is made (see Pratt, 1964 p. 123), when $s > 0$ in our Fig. 1D rather than for s approaching zero.

We believe the EBR can be more appropriately criticised on empirical grounds than theoretically. If the animal is near the survival threshold, then the EBR leads to strong predictions about how decisions should depend on the previous choice and its outcome (see Appendix S2). If rats choose an option with two possible outcomes, they are very likely to choose it again if they get the good outcome (Stopper & Floresco, 2011; Stopper, Green & Floresco, 2014), a pattern called 'win–stay'. Leaving the variable option after the bad outcome is called 'lose–shift'. Win–stay lose–shift (WSLS) has been observed in monkeys (McCoy & Platt, 2005) and it is prevalent in humans too (Hayden & Platt, 2009; Steywers, Lee & Wagenmakers, 2009). Rosati & Hare (2013) report it in bonobos (*Pan paniscus*) but not in chimpanzees, but unlike the procedures we have focused on, the variable option gave outcomes that differed in food type rather than amount. Although the extent to which WSLS is adopted depends on the details of the foraging environment (Marshall & Kirkpatrick, 2013), its existence is not predicted by a sequential version of the EBR; indeed the rule never predicts switching from the variable option after a loss (see Appendix S2). Moving from predictions about sequences to the broad pattern of choice, Kacelnik & El Mouden (2013) (their fig. 3) report that only 10 studies out of 35 found the predicted switch in sensitivity to variability in amount with manipulation of the energy budget. Of course, 'predicted switch' here refers to the experimentalists' predictions, which may sometimes fail to capture the complex natural environment that the animal expects and is evolved to (McNamara, 1996).

(2) Energy budget and variability in delays

Craft *et al.* (2011, p. 44) claim that '… the DEB rule [i.e. EBR] makes no prediction when delay is manipulated'. [See also Craft (2016, p. 43): 'The daily energy budget rule makes no predictions based on changes in delay to reward'.] This is not correct; McNamara & Houston (1987*a*) look at variation in both energy and time in the context of a fixed time available for foraging. When the reward at the end of the foraging period is a step function, such as might reflect overnight survival, McNamara & Houston (1987*a*) show that the optimal response to variability in delay depends on reserves and the time left for foraging.

(3) Over-extensions and simplifications

Prospect theory (Kahneman & Tversky, 1979) offers an explanation of human decisions based on losses or gains as measured from a reference point. A key feature is that the function that measures the cost of deviating from the reference point is different for losses and gains. This very influential theory accounts for many surprising features of human behaviour. McDermott, Fowler & Smirnov (2008) argue that the EBR provides an evolutionary justification of prospect theory (see also De Petrillo *et al.*, 2020). This argument is wrong: the EBR is rational but prospect theory is not (Houston *et al.*, 2014). It is possible, however, that the patterns of behaviour associated with prospect theory can emerge from a model of optimal behaviour in a changing environment (Mallpress *et al.*, 2015).

'Satisficing' (Simon, 1956) claims that instead of optimising, decision-makers satisfice, i.e. do well enough to meet some basic requirement. The importance of the concept for the study of animal foraging has been debated (Ward, 1992; Nonacs, 1993) but it is frequently used in the study of human behaviour (Gigerenzer & Goldstein, 1996; Lieder & Griffiths, 2020). Mishra (2014) views risk-sensitive behaviour as a form of satisficing. Gonzales, Mishra & Camp (2017, p. 462) make a stronger claim: 'Unlike other decision-making theories which focus on maximisation …, risk-sensitivity theory is focused on satisficing. Decision-makers are considered to be primarily focused on meeting their needs, not maximising utility independent of context (Mishra, 2014)'. Contrary to this view, much of RSF theory assumes that animals are maximising RV. In some models (Stephens, 1981), RV is a step function of energy at the final time (dusk on a focal day or the last of a series of days), which means that the animal is satisfied with any energy level above a survival threshold. However, this RV becomes a curve with decreasing slope as number of days to go increases (see fig. 2 in McNamara, Houston & Krebs, 1990). The intuitive explanation is that when it is necessary to avoid starvation over a series of days, it is better not to start the next day with very low reserves. Similar smoothing effects occur within a day (*cf.* Figure 1D and Appendix S1).

The reason for risk-prone behaviour in the EBR is clear: the animal needs a certain amount of energy to survive the night. This need is the result of a low level of energy reserves. As is noted by McNamara & Houston (1992) and Houston & McNamara (1999), it does not follow that whenever reserves are low it is optimal to be risk prone as is sometimes suggested. For example, Mishra (2014) argues that decision-makers should be risk prone when they are at a distance from a desired end-state. This would then lead to a theoretical extension such that 'risk-sensitivity theory is therefore broadly relevant to understanding decision-making both for wants (i.e. non-essential motivations; for example, consumer purchases) and canonical needs (essential motivations; for example, survival)' (Mishra 2014, p. 288). We return to this claim in Section VIII.

(4) Background mortality

In some models of RSF based on survival, starvation is the only source of mortality (Stephens, 1981; Houston & McNamara, 1982; Caraco & Chasin, 1984). This ignores predation and disease, which may always be a possibility. We refer to such factors as background mortality. In models based on avoiding starvation, if background mortality is the same for all choice options then it has no effect: the optimal policy is the same as the policy when there is no background mortality (McNamara, Merad & Houston, 1991). If background mortality differs across options, then we need to consider the trade-off between energy and mortality (Houston & McNamara, 1999; Brown & Kotler, 2004). If in addition to starvation at a lower energetic boundary there is an upper energetic boundary at which reproduction occurs, background mortality has an effect on RSF even if it is the same for all options (McNamara *et al.*, 1991).

Background mortality can favour risk-prone behaviour even when the mean rate of gain is positive (McNamara *et al.*, 1991). Intuitively, taking risk today to achieve an important goal such as reproduction becomes more acceptable when there may not be tomorrow for reaching the same goal. Thus, both a low resource state and background mortality can increase risk taking. Evolutionary psychologists have argued that mortality cues appear to propel individuals toward diverging [evolved] life-history strategies as a function of childhood socioeconomic status (Griskevicius *et al.*, 2011; Stearns & Rodrigues, 2020). But could the same evolved, but *state-dependent*, strategies result in largely the same behaviour? A recent meta-analysis indicates that harshness and unpredictability in early life did slightly correlate with self-reported risk taking, but not with risk preference measured by hypothetical choice tasks or laboratory behaviour tasks (Wu *et al.*, 2020). If self-reports reflect past states more than present behaviour in laboratory tasks (a reasonable assumption), this finding appears to be more in line with state-dependent behaviour than with following a life-history strategy determined in youth.

(5) Reproduction

Hurly (2003) uses the twin threshold model to explain the experimental finding that rufous hummingbirds (*Selasphorus rufus*) prefer an intermediate variance option (Hurly & Oseen, 1999). When there are two thresholds, one for survival and another for reproduction (or for two other outcomes of value), and several foraging options with differing reward variance, then the probability of reaching these thresholds depends on the (common) mean and the variance of the reward distributions (Fig. 1A and Appendix S3). The twin thresholds model illustrates the flexibility of even minimal optimal foraging models – flexibility that is often reduced in experimental treatments by selective over-simplification (McNamara, 1996). Naturally, RSF models like the twin threshold model can be applied to novel situations with a little extra effort: in Appendix S4 we show how to derive RSF model predictions for skewed reward distributions (Caraco & Chasin, 1984; *cf*. Genest *et al.*, 2016).

(6) Variable environments do not (automatically) favour risk-sensitive foraging

The idea of ecological rationality or ecological intelligence is that the decision-making abilities of a species will be shaped by its environment (Rosati, 2017; De Petrillo & Rosati, 2019; Henke-von der Malsburg, Kappeler & Fichtel, 2020). Several papers discuss ecological rationality in the context of how RSF might be linked to foraging ecology. For example, Heilbronner *et al.* (2008) investigate the way in which chimpanzees and bonobos choose between foraging options that have the same mean but differ in variance. The study found that chimpanzees preferred the variable option. Heilbronner *et al.* (2008, pp. 246–247) state that because chimpanzees probably face uncertain food sources in the wild, they should be more risk prone than bonobos. Marshall-Pescini *et al.* (2016) make the same sort of argument in the context of dogs and wolves. Starting from the observation that dogs scavenge whereas wolves hunt, they suggest that dogs have a more stable foraging environment than wolves and hence wolves should have a stronger preference for variability. We are not convinced by this line of reasoning. What we might expect is that in an environment with variability we will see the evolution of ways to cope with it, for example, by reducing energy expenditure (Caraco, 1981) or hoarding resources. This might not be associated with a preference for variability unless such a preference is advantageous. The study of lemurs (*Lemur catta*, *Eulemur mongoz*, *Varecia rubra*) by MacLean, Mandalaywala & Brannon (2012) is relevant here. Because lemurs come from Madagascar, an island with a demanding and unpredictable environment, MacLean *et al.* (2012) argue that they will have been selected to avoid risks and hence will be risk averse. In line with this, lemurs prefer the constant option to a variable option with the same mean, and some of them continued to prefer the constant option when the mean of the variable option was twice that of the constant one.

VI. CAUSAL MODELS

(1) Neurocognitive models

Different types of neurocognitive models pertain to RSF. In one group of models, memories of time delays to reward are represented as an accumulator of neural firing, leading to random (inverse-Gaussian distributed) samples of the retrieved memorised delay (Ratcliff, 1978; Simen *et al.*, 2011; Zwicker & Rivest, 2022). When such samples are compared across different choice options, e.g. to choose the one with the least delay to reward, the ensuing risk preference predictions appear highly similar to another model derived from behavioural data (Rosenström, Wiesner & Houston, 2016). We discuss models of that type in Section VI.2.*a*.

Another line of research argues that neurons in the basal ganglia and cortex perform reinforcement learning of not only reward value of choice options but also of reward variability, i.e. risk (Mikhael & Bogacz, 2016). This could offer a mechanistic basis for adaptive RSF. By contrast, Moeller *et al.* (2021) have presented a model where risk preferences arise as side-effects of dopaminergic reward prediction errors whose main purpose is to guide learning of reward value, and in the scaled prediction error (SPE) model of Möller, Manohar & Bogacz (2022) the function of the learned risk estimate is to scale the aforementioned reward prediction errors to enhance their effect on learning [see Hirschbichler, Rothwell & Manohar (2022) for some experimental support]. Future research could further explore interconnections between these dopaminergic computational models, their relationships with adaptive and non-adaptive RSF models and the extent to which they improve understanding of the ecological data on RSF. One crucial theoretical issue may be that these dopaminergic models assume a standard decision rule (known as softmax) in which costly deviations from optimality are rare [Sutton & Barto (2018), see also McNamara & Houston (1987*b*) and McNamara *et al.* (1997)], whereas ideally such assumptions should be supplemented with a theoretical rationale.

In Appendix S7, we compare qualitative predictions of the scaled prediction error learning rule to another simple learning rule when choice randomness is not added (Möller *et al.*, 2022). We show how such learning rules themselves may lead to apparent risk aversion, risk proneness, and non-optimality depending on the reward sequences. Although our analysis suggests that the additional parameters of the SPE rule are not without consequences, and the jury seems still to be out regarding in what sense the SPE rule is 'more robust than learning from unscaled prediction errors' (Möller *et al.*, 2022, p. 2), it also underscores the study of choice sequences as a promising avenue for mapping the scope and relative merits of existing theories.

(2) Side-effect models

It has been suggested that risk sensitivity is a side-effect of either the general properties of mechanisms for learning or a particular mechanism for assessing rewards (Kacelnik & Bateson, 1996, 1997; March, 1996; McNamara, 1996; Niv *et al.*, 2002; Buchkremer & Reinhold, 2010; Kacelnik & El Mouden, 2013). If this claim is true, then attempts to view risk-sensitive behaviour as an adaptation to uncertainty are misguided. We now discuss some specific side-effect models. The arguments are sometimes associated with the view that animals are risk averse or risk neutral for amounts, but as we point out in Section III, this view is an oversimplification – animals of several species are sometimes risk prone for amounts.

(a) *Scalar utility theory*

Scalar utility theory (SUT) developed from successful accounts of responses to delays (Gibbon, 1977; Gibbon *et al.*, 1988). Kacelnik & Brito e Abreu (1998) present SUT from the starting point of Weber's law, which states that the just noticeable difference between a test stimulus and a standard stimulus is proportional to the value of the latter. In practice, the model is based on the idea that there are systematic errors in the representation of outcomes in memory such that the standard deviation of the error is proportional to the magnitude (Kacelnik & Brito e Abreu, 1998; Rosenström *et al.*, 2016). That is, a reward of learned size μ is returned to memory as having a size X, where X is one realisation of a random variable with distribution $\mathcal{N}(\mu, \gamma\mu)$, where $\mathcal{N}$ stands for normal distribution, μ for its mean and $\gamma\mu$ its standard deviation. Hence, memory accuracy has a 'scalar' property, its variance scaling in proportion γ to magnitude μ. The parameter γ is fixed over reward amount but may depend on species, context, and reward type. When risk is involved, e.g. a reward μ_1 is given with probability p and a reward μ_2 with probability $(1-p)$, memories are drawn from a mixture of scalar representations. That is, X is distributed as $p\mathcal{N}(\mu_1, \gamma\mu_1) + (1-p)\mathcal{N}(\mu_2, \gamma\mu_2)$. The idea readily generalises to more than two possible outcomes (Rosenström *et al.*, 2016). The parameter μ can represent either mean memory of reward amount or delay to reward (Kacelnik & Brito e Abreu, 1998). Animals are assumed to prefer larger amounts and smaller delays to reward.

It is optimal to choose the optimal action and no other action, which means that optimality models predict all-or-nothing or exclusive choice (Stephens & Krebs, 1986). This issue has been frequently discussed in the context of choosing between different types of prey. Types differ in energy content and time required to 'handle' them [see Stephens & Krebs (1986) for details]. If rate of gain is to be maximised, then a given type is either always accepted or always rejected. In experiments, however, partial preferences are seen (Stephens & Krebs, 1986). Various explanations for this have been considered (McNamara & Houston, 1987*b*).

In contrast to optimality models, SUT is inherently stochastic (random) – it predicts partial preferences even when options are deterministic (Shapiro, Siller & Kacelnik, 2008; Shapiro, Schuck-Paim & Kacelnik, 2012). Kacelnik & Brito e Abreu (1998; their tab. 1) showed that the partial preferences predicted by SUT for variance in amount matched data from starlings (*Sturnus vulgaris*) for two parameter values. It is not clear that such agreement is general; for example, SUT does not predict the strong preference for variable delay (Kacelnik & Brito e Abreu, 1998; their tab. 1) and more generally does not predict the near-exclusive preferences sometimes found in pigeons (Mazur, 2010). SUT can predict preference for variable delay over a fixed delay when both have the same mean delay and reward (Gibbon *et al.*, 1988; Kacelnik & Brito e Abreu, 1998), but Mazur (2010) contrasted fixed *versus* fixed delays and mixed *versus* mixed delays of *different* mean delay. Mixed delays were variable delays with half the mean delay with probability 0.5 and 1.5 times the mean delay with probability 0.5. We mapped Mazur's (2010) experimental parameters to SUT predictions (Fig. 2). SUT was able to accommodate near-exclusive preferences for fixed delays when γ was given a low value but no

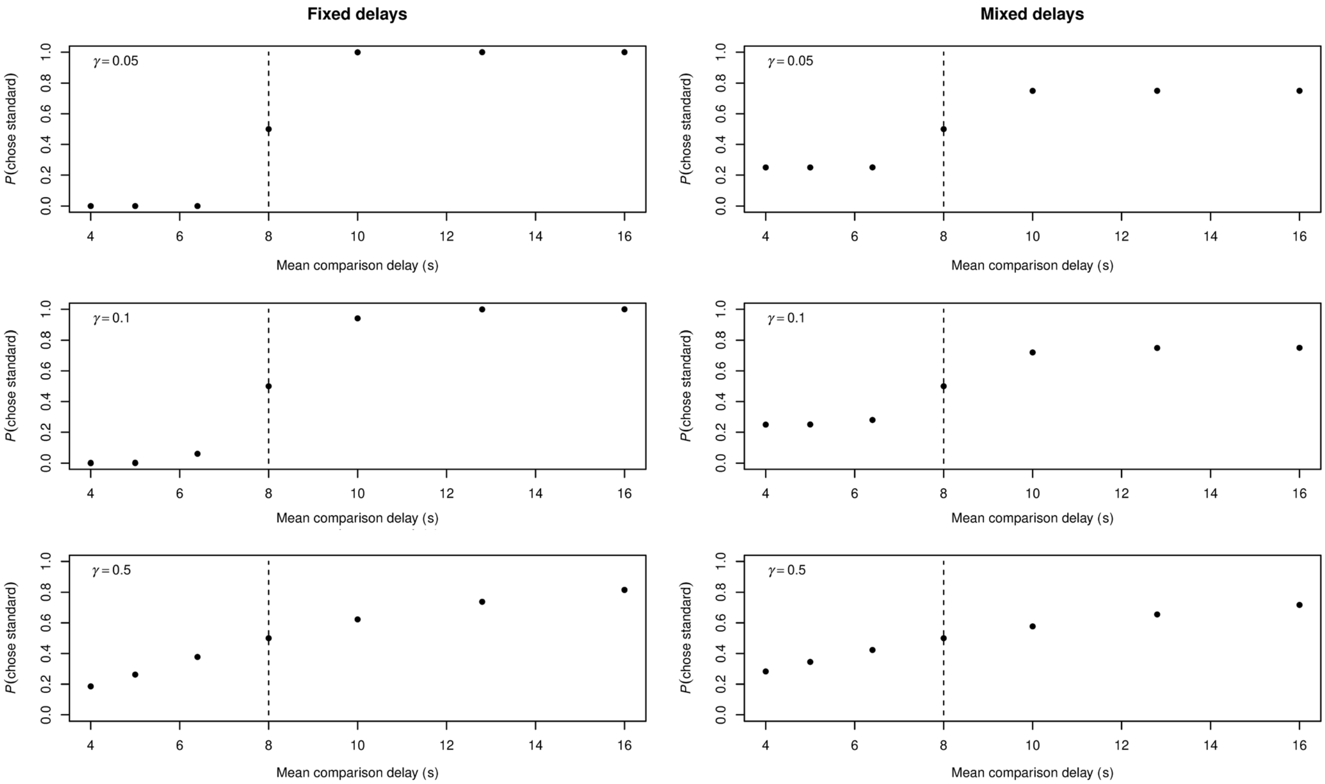

Fig. 2. Scalar utility theory (SUT) predictions for fixed and mixed delays in Mazur's (2010) experiment. Left column: pigeons chose between a fixed standard reward option with an 8 s delay (dashed line) and a fixed comparison option with the delay given by the *x*-axis. The pigeon's observed behaviour resembled the upper-left panel where SUT's memory error (scalar parameter γ) is very small. Right column: a standard option now provided the reward in 4 s with probability 0.5 and 12 s with probability 0.5. The pigeons compared it to a comparison option with mean reward given by the *x*-axis and actual values by 0.5 and 1.5 times the mean with probability 0.5 each. The behaviour of the pigeons again resembled the upper-left panel but no panel in the right-hand [model-derived] column produces it. The reason is that with high memory error, choices approach random choices and with low memory error the animal happens to sample 25% of the time a memory value close to 0.5 times the high mean for the higher mean-delay option together with 1.5 times the low mean for the lower mean-delay option. With these experimental parameters the memorised delay in SUT is then greater for the option with lower mean delay in 25% of trials. Thus, SUT predicts 25% preference for the worse [longer-delay] option when, in fact, the real pigeons rarely chose it.

value yielded such preferences for mixed delays. The reason is that jointly the mixture-distribution and scalar-error assumptions attribute more randomness to behaviour than Mazur (2010) observed in the pigeons (see legend to Fig. 2). Furthermore, previous work shows how SUT qualitatively reproduces the 'certainty effect' of Shafir *et al.* (2008) but quantitatively fails to reproduce the extent of risk aversion they predicted and found in humans [compare fig. 2D of Rosenström *et al.* (2016) to fig. 1b and tab. 2 in Shafir *et al.* (2008)]. This is noteworthy because Shafir *et al.* (2008) informally derived their predictions from a SUT-like idea.

Bateson & Kacelnik (1995) show that when the variable option involves two equiprobable outcomes, SUT predicts risk-prone behaviour for delays and risk-averse behaviour for amounts. Subsequent accounts do not always make it clear that the result depends on equiprobable outcomes. For example, Kacelnik & El Mouden (2013 p. 1127) state: 'Thus, when universal principles of psychophysics, which are not specific to foraging, are applied to foraging, they predict risk aversion for reward sizes and risk proneness for delays to reward' (see also Marsh & Kacelnik, 2002; Shapiro *et al.*, 2012). In fact, this simple pattern of risk sensitivity does not hold in general (Rosenström *et al.*, 2016). In particular, SUT can predict risk-averse behaviour when an animal is faced with variable delays. This finding depends on the SUT scalar parameter but applies to experimentally feasible values. An example is given in Fig. 3.

One problem with the view of Kacelnik and colleagues is that, as pointed out above, animals are sometimes risk prone for amounts. While SUT predicts risk-prone behaviour for desirable outcomes under some circumstances, unfortunately for the claim that risk sensitivity is a side-effect of SUT, SUT always predicts risk-aversion when means are equal and the risky option has two equiprobable outcomes (Rosenström *et al.*, 2016). Risk-prone behaviour in this condition has been found in many studies and for many species (Table 2). More generally, SUT predicts risk-averse behaviour when choosing between two symmetric stochastic options with different

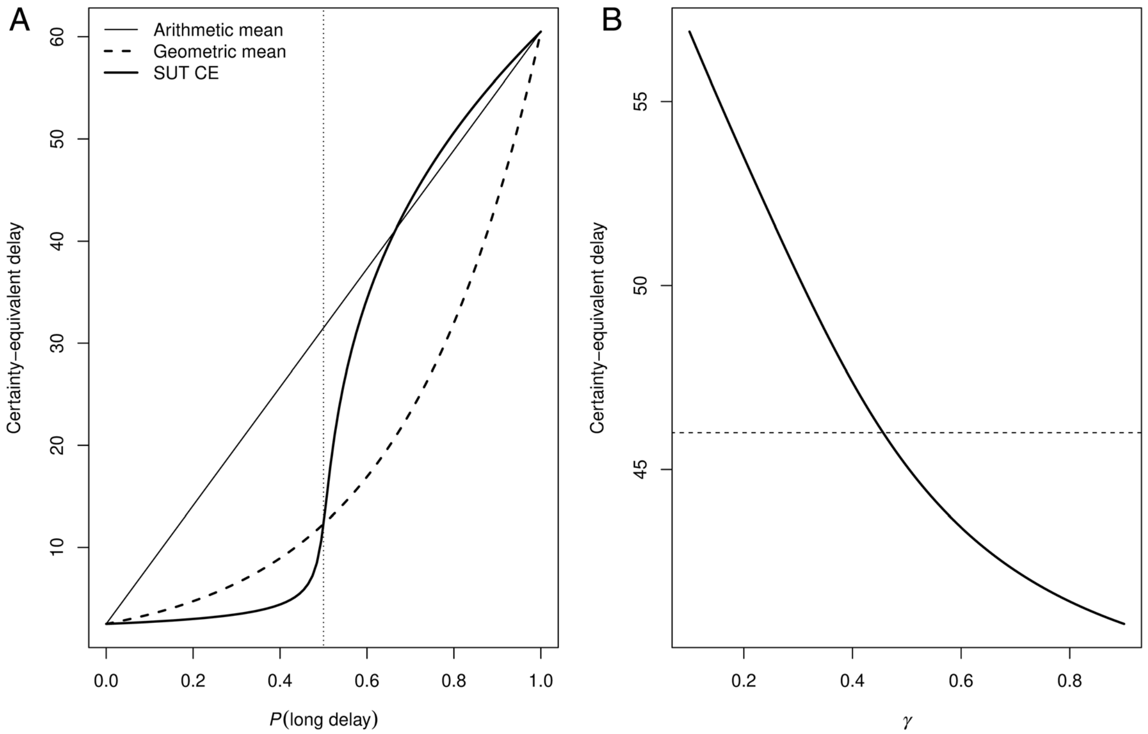

Fig. 3. Scalar utility theory (SUT) can predict risk-prone and risk-averse preferences. Bateson & Kacelnik (1995) tested preferences of pigeons for a certain reward option of 5 units of food with 20 s fixed delay *versus* a variable option with 5 units of food with 2.5 s delay (short delay) with probability 0.5 or 5 units with 60.5 s delay (long delay) with probability 0.5. The birds chose the variable option more often despite it involving a longer mean delay compared to the fixed option (31.5 s *versus* 20 s). This risk proneness aligned with predictions of SUT (A). In fact, SUT predicts the certainty equivalent (CE) of this variable delay option (point of indifference) to be only 12.3 s (at the intersection of the dotted and thick solid line), which coincides exactly with the geometric mean of the variable outcomes. However, predictions of SUT have no simple relation with geometric nor arithmetic means when considering arbitrary probability P for the longer delay (x-axis; the shorter delay then has probability $1 - P$). That is, the SUT CE intersects both the arithmetic and geometric mean reference for risk proneness *versus* aversion. This SUT prediction is for the scalar value $\gamma = 0.4$ that Kacelnik & Brito a Abreu (1998) estimated for starlings. They noted considerable variation in the literature ($0.16 \leq \gamma \leq 0.6$). (B) SUT CE as a function of memory error γ, when P(long delay) = 0.75 (solid line), and the arithmetic mean (dashed line), showing how risk aversion changes to risk proneness with increasing memory errors. The derivations are based on simple single-parameter optimisation routines.

variance (see Appendix S5), whereas Genest *et al.* (2016) reported a switch from risk proneness to risk aversion as they increased the (common) expected value of the choice options.

(*b*) *Learning*

In experiments on RSF, non-human animals have to learn about the options. It is known that learning can result in risk-sensitive behaviour (Regelmann, 1986; March, 1996; Niv *et al.*, 2002; Buchkremer & Reinhold, 2010). Our focus in this section is the following argument that predicts risk aversion from general properties of learning (Kacelnik & Bateson, 1996, 1997; Bateson & Kacelnik, 1998; Kacelnik & El Mouden, 2013): 'Given the concave relation between reinforcement effects and reward size and the convex relation between reinforcement effects and delay, Jensen's inequality implies that variance in amount should have a negative impact on reinforcement and variance in delay a positive one. … Thus similarly to SUT, associative learning processes predict risk aversion for food amounts and risk proneness for food delays'. (Kacelnik & El Mouden, 2013, p. 1128; see also their fig. 7).

We refer to this as Kacelnik's argument from associative learning. It can be traced to the analysis of preference for variable delays by Reboreda & Kacelnik (1991), which does not use Jensen's inequality, but does involve explicit averaging. Subsequent presentations of the delay case all use Jensen's inequality (Kacelnik & Bateson, 1996, p. 425; Kacelnik & Bateson, 1997, p. 307; Bateson & Kacelnik, 1998, p. 327). As Houston & McNamara (1999) point out, the use of Jensen's inequality in this argument is problematic. Jensen's inequality is a mathematical result about the properties of functions. A learning mechanism does not have to obey Jensen's inequality (Houston & McNamara, 1999, p. 112) so Kacelnik's argument may not hold in general.

As an example, consider an experiment in which the variable option has two equiprobable outcomes, 0 and 2. If preference strength M is a strictly increasing and decelerating function of outcome reward, Jensen's inequality tells us that the average preference over the variable outcome is less than the preference evaluated at the average outcome. The implication is that a decision-maker should prefer a fixed intermediate outcome over the variable option. There is, however, no clear justification for the assumption that the decision-maker represents the variable option by taking the average of the preference value associated with each outcome (see Section VI.2.*c*). As an example, consider again an experiment in which the variable option has two equiprobable outcomes, 0 and 2. Assume a very long sequence of trials, with an equal number of the two outcomes, so that the average = 1. The average is independent of the sequence of outcomes. By contrast, it is likely that an animal's memory M will involve giving more weight to recent outcomes and hence will depend on the sequence. In particular, if the sequence is all the zeros then all the twos, the ensuing M at the end will be close to 2. If the sequence is all the twos then all the zeros, M will be close to 0 instead. We analyse a similar example in Appendix S6 and show that a simple learning rule (Sutton & Barto, 2018, p. 32) tracks locally average reward or preference, and can lead to risk-prone or risk-averse preferences depending on the situation.

Experiments on animal preferences frequently ensure that the animal experiences all the choice options, and our above arguments pertain to these situations. In nature animals are free to explore or exploit the available choice options as they desire and therefore may never learn the properties of an option that initially appears suboptimal – 'the hot stove effect' (Denrell & March, 2001; but see Biele, Erev & Ert, 2009) or 'learned helplessness' (Trimmer *et al.*, 2015; Maier & Seligman, 2016) may ensue. The hot stove effect refers to a proverbial cat who sat on a hot stove and will therefore never approach a nice warm one either. In general, it is important to pay attention to the relationship of choice and information accumulation when investigating sequences of choices.

Kacelnik's argument from associative learning starts with a non-linear function (concave or convex) of reward or delay and assumes that the animal averages over the values of this function. Because the animal's mechanism does not necessarily average, Kacelnik's argument is not valid in general. It remains possible, however, that the actual mechanism may produce risk sensitivity even without a non-linear function. Niv *et al.* (2002) and Buchkremer & Reinhold (2010) do not use a non-linear function of reward (see Niv *et al.*, 2002, p. 953) and obtain risk sensitivity as a side-effect of selection for maximising rate of gain.

(*c*) *Weber and non-linear perceived stimulus intensity*

SUT can be based on Weber's law (see Section VI.2.*b* and Kacelnik & Brito e Abreu, 1998) but it does not involve a non-linear relation between stimulus and perceived value. By contrast, many papers (e.g. Hamm & Shettleworth, 1987; Waddington & Gottlieb, 1990; Perez & Waddington, 1996; Shafir, 2000; Shafir *et al.*, 2003; Weber *et al.*, 2004) offer an explanation for RSF based on psychophysics (how the world is perceived). The argument runs as follows. The psychophysics of stimulus perception (Weber's law) means perceived stimulus intensity is a decelerating function of the objective stimulus magnitude. By Jensen's inequality, the average perceived intensity of a variable option is less than the intensity of a constant option when the means are equal, and therefore the non-linearity of perceived intensity leads to risk aversion. We believe that this argument involves a use of Jensen's inequality that can be challenged.

The Weber approach to risk sensitivity suggests that animals guide their behaviour by taking an average of perceived rewards (a decelerating function of actual reward) across the rewards received from given option. Such an assumption is vastly different from how Jensen's inequality applies in the context of maximising RV. Arguments based on RV assume that nature is counting (averaging) individuals who survive and reproduce, thereby making no additional assumptions to those found in the standard theory of evolution. If we wish to apply Jensen's inequality to a particular mechanism that animals use, we have to justify the assumption that the mechanism performs averaging. The assumption that animals compute averages of their perceptions is a crucial aspect of the argument that non-linear perceived stimulus intensity predicts risk aversion.

(3) Sequences and causation

Temporal ordering of events is frequently considered to shed light on causal mechanisms (Hill, 1965). Although commonplace in behavioural sciences, exchanging between time- and group-averages is generally valid only under conditions that are likely to be rare (Molenaar & Campbell, 2009). We advise both theorists and empirical researchers to be explicit about the time dimension. For example, outlining time-dependent theoretical predictions of EBR that do not depend on learning (see Appendix S2) when the model was introduced might have made it less tempting for empirical studies to routinely average multiple choices by the same subject. Instead, showing how different subjects' behaviour over time fits to different models of decision-making (e.g. Steywers *et al.*, 2009) may be necessary to reveal behavioural effects that become diluted when aggregating over time and experimental group. The full behavioural sequences contain information that can increase both statistical and theoretical power and their use and reporting is increasingly supported by the availability of computing resources and the publishing of supplementary material.

VII. GENERALITY

Although it has been suggested that risk sensitivity may not be unitary (Kacelnik & Bateson, 1996; Bateson & Kacelnik, 1998), there has been interest in finding general principles that might link risk sensitivity in humans and other animals. We refer to such general accounts as monolithic theories. SUT is an example of a monolithic theory. Marsh & Kacelnik (2002) claim that it explains not only the risk-sensitive response to amount and delay but also data from humans associated with prospect theory. We tentatively suggest that risk sensitivity to amount and delay may be distinct phenomena. They have different patterns of optimal behaviour (McNamara & Houston, 1987*a*) and, more compellingly, the preference for variability in delay seems stronger and more consistent than risk aversion for amount. Furthermore, the results of Marsh & Kacelnik (2002) can be explained without viewing them as analogous to results on gains and losses that are explained by prospect theory (Houston & Wiesner, 2020).

Kacelnik's argument from associative learning (Section VI.2.*b*) and the approach based on perceived stimulus intensity (Section VI.2.*c*) are also examples of monolithic theories. Both predict risk-averse behaviour if amounts are variable, but animals are sometimes risk prone for amounts (see Table 2). Shafir (2000) and Weber *et al.* (2004) stress that risk sensitivity is strongly influenced by the coefficient of variation (CV). The CV-model (Shafir, 2000) has been proposed as a general account of risk (Weber *et al.*, 2004) but it is a descriptive model (Shafir, 2000, p. 668) in which risk aversion or risk proneness is predicted by the EBR, whereas the strength of preference is determined by the coefficient of variation.

Heilbronner (2017) reviews risk-sensitive behaviour in species used in neurobiological experiments (macaques, rats, and mice), compares it to behaviour of humans and concludes that there are conserved circuits and shared features. By contrast, De Petrillo & Rosati (2021) compare humans with other primates and find both similarities and differences. Sometimes the allure of a monolithic theoretical account leads to surprising views on the generality of adaptive responses to risk. RSF in plants might represent such a case, as we next review.

(1) Risk-sensitive plants

Dener, Kacelnik & Shemesh (2016) investigate the response of pea *Pisum sativum* plants to variability in growing conditions indexed by nutrient availability. The experiment involves splitting the root system of a plant into two components so that each one can experience a different pattern of nutrient concentration. A plant growing more roots to a pot with variable rather than constant nutrient availability was considered a risk-prone pea plant. That is, the measure of preference was relative root mass in the constant *versus* variable option for growth. Dener *et al.* (2016) found risk-prone behaviour when mean nutrient concentrations were low and risk-averse behaviour when they were high. Dener *et al.* (2016) argue that the pattern follows from the EBR. This has attracted interest because it raises the possibility that an adaptive response to risk might not require a brain (Schmid, 2016).

However, the analysis of Dener *et al.* (2016) rests on the assumption that the plant's fitness at final time T is a sigmoid function of soil nutrient concentration (see fig. 1 in Schmid, 2016) and that the EBR can be used to predict optimal behaviour. They estimated the fitness function by delivering various *constant* nutrient levels to different plants and then used it to make inferences about the fitness of a plant experiencing *variable* nutrient conditions. Above the inflection point, the function is concave and so Dener *et al.* (2016) predict risk aversion, whereas below it the function is convex and risk proneness is predicted. We do not believe these predictions to be valid. The argument of Dener *et al.* (2016) rests on an analogy between the growth of a plant and the foraging of an animal as characterised by the assumptions underlying the EBR. The animal makes a series of choices between options, with the consequences of choosing an option being independent of previous choices. Because the plant is growing and growth depends on previous decisions, the consequences of the current decision are likely to depend on what the plant has done in the past. The EBR involves the assumption that fitness depends on just the total amount of energy obtained. For a growing plant, this is unlikely to be the case. To highlight this, consider a plant that spends the first half of the time period in nutrient environment N_1 and the second half in N_2 and a plant that spends the first half of the time period in N_2 and the second half in N_1. We do not expect the two plants to be in the same state (and hence have the same fitness) at T. In the model that underpins the EBR, the order in which rewards are obtained does not matter. In the case of a growing organism, the order is important because they change the organism's morphology. This is not an issue in the model of growth analysed by Houston & McNamara (1990) because they assume that conditions do not change during a growing season. In their model, a parent decides whether to put their young into a habitat with a known growth rate or one in which the growth rate, although constant over the season, is not known in advance and is therefore treated as random. Although Dener *et al.* (2016) demonstrated that their plants are sensitive to nutrient variability over time and hence are risk sensitive, we do not consider them to have demonstrated optimal risk sensitivity in plants. The suggestion that pea plants make optimal decisions about risk (Karban & Orrock, 2018; Severino, 2021; Lee, Segundo-Ortin & Calvo, 2023) and hence are more rational than animals (Schmid, 2016) cannot be accepted.

(2) Different reward dimensions and environmental context

Although we have focused on risk-sensitive responses to energy, responses to other dimensions (e.g. water or money) have been investigated (Kagel *et al.*, 1986; Yamada *et al.*, 2013; Rosati & Hare, 2016). It can then be asked whether a particular pattern of risk sensitivity is typical of an animal when faced with any currency or whether it depends on the particular rewards (Rosati & Hare, 2016).

Sayers & Menzel (2017) find that the risk-sensitive behaviour of chimpanzees depends on the type of food reward, but unlike them we do not see this as problematic.

If the functional approach is correct, risk sensitivity is not a fixed trait; it is likely to depend not just on the type of reward but on its distribution (*cf.* Bujold *et al.*, 2021). In other words, RV is not a fixed property of the animal but something that depends on the animal and its environment (McNamara & Houston, 1989). This means that effects of social context on risk (e.g. Zoratto *et al.*, 2018) can be expected, but their exact form might not be easy to predict.

It is important to note that risk-sensitive behaviour can be produced by a variety of mechanisms. For example, consider the choice between a fixed and a variable option with the same mean. Risk-prone behaviour could be the result of basing the decision on a non-linear function of reward value (see Fig. 1C), or of choosing the option associated with the reward that is more variable and hence perhaps less monotonous. Roig *et al.* (2022) suggest that risk-prone behaviour in young children may be the result of a desire to explore. Possibly related to curiosity, monkeys prefer randomly varying (stochastic) rewards and starlings randomly varying delays to reward over orderly alternating outcomes with similar mean and variance properties (Hayden *et al.*, 2008; Bateson & Kacelnik, 1997).

VIII. TESTING GENERAL PRINCIPLES

There is a sense in which the functional approach provides a general account of risk-sensitive behaviour: risk-sensitive foraging arises because RV is not directly proportional to energy. The problem with this is that there is no simple and general shape of, nor explanation for, the non-linear relationship. The EBR is simple, but although it is sometimes treated as the only functional model, this is not the case – it is not general (Houston, 1991; McNamara & Houston, 1992; Kacelnik & Bateson, 1996). The twin threshold model predicts risk-prone behaviour on both a positive or negative energy budget, which means that it is not as straightforward to test as the EBR. Strong evidence for it would be finding a preference for the intermediate variance (Hurly, 2003) or finding two behavioural switches as conditions improve.

There are two opinions about the complexity of functional explanations of RSF. One is that state-dependent models are hard to parameterise and so it is difficult to generate testable predictions (Kacelnik & Bateson, 1996; Kacelnik & El Mouden, 2013). By contrast, Mishra (2014) reduces RSF to one simple principle: be risk prone when at a distance from a desired goal or outcome. This principle is 'easily operationalizable, testable, and falsifiable because of its simplicity … With a few simple parameters, it is possible to make precise predictions about expected behaviour regarding preferences for risk in a given context. Furthermore, because need is strictly defined as disparity between one's present and desired (or goal) states, but can manifest in multiple domains, there is freedom in how to manipulate and measure perceptions and objective manifestations of need'. (Mishra, 2014, p. 299).

We agree with Kacelnik & El Mouden (2013). Although the EBR tends to dominate discussions of optimal RSF, there are other models. Mishra (2014) discusses the twin threshold model but does not bring out the complexity of behaviour that is found between the thresholds. This behaviour is not given by something as simple as the EBR (Stephens, 1981). Mishra (2014) does not consider state-dependent models such as McNamara *et al.* (1991). In this model risk-prone behaviour is optimal once the forager is near to the level of reserves at which reproduction is possible, but how near depends on both the mean rate of gain and the level of background mortality.

Ideas from RSF models may be instructive in many contexts, including human behaviour and neuroscience (Bickel *et al.*, 2004; Mobbs *et al.*, 2018). Consider, for example, the twin threshold model in the context of behavioural disorders. The model might help explain why individuals begin gambling (to get something extra beyond a second threshold) and why they continue to gamble even after losing a significant amount (to have at least a chance of escaping ruin below a first threshold – 'chasing losses' is one of the criteria for gambling disorder).

IX. CONCLUSIONS

(1) When Kacelnik & Bateson (1996) reviewed data patterns of RSF, they found that animals were risk prone with respect to delays and risk averse or neutral with respect to amounts. Subsequent findings have complicated this picture in two ways. There are now many experiments in which animals are risk prone for amounts. There is also considerable evidence of variation in risk-sensitive behaviour within a species, e.g. in honeybees (Shafir *et al.*, 2005) and Siberian jays (Ratikainen *et al.*, 2010). As a consequence, it might not be possible to characterise a species as risk prone or risk averse.

(2) It has been claimed that SUT predicts risk aversion for nice things (e.g. amount of food) and risk proneness for nasty things (e.g. delay until food). Although this is true when the variable option involves two equiprobable outcomes, it is not true in general. We illustrate this by showing that SUT can predict aversion to variable delays (see Fig. 3).

(3) Although SUT has an advantage over many other theories in predicting a degree of randomness in choice and that preferences are thus partial rather than absolute, Fig. 2 shows that SUT does not predict the quantitative magnitude of partial preferences, implying too much randomness compared to data from pigeons (Mazur, 2010).

(4) Risk-sensitive behaviour could be a side-effect. SUT has received attention in this regard (Kacelnik & Bateson, 1996, 1997; Bateson & Kacelnik, 1998; Kacelnik & El Mouden, 2013), but another possibility is that RSF is a side-effect of selection for the maximisation of rate of gain (McNamara, 1996; Niv *et al.*, 2002; Buchkremer & Reinhold, 2010; Moeller *et al.*, 2021).

(5) The Energy Budget Rule (EBR) makes a clear prediction that foragers should be risk averse when their energy budget is positive and risk prone when it is negative. The data do not match this prediction (Kacelnik & El Mouden, 2013).

(6) Contrary to the impression given by Schmid (2016), peas have not been shown to be more rational than animals. Dener *et al.* (2016) are cautious in that they suggest the behaviour of peas might not have evolved as adaptive response to risk but claim that the results agree with predictions of RSF theory. We are not convinced, and believe that further theoretical work on the optimal response to risk in growing organisms is required.

(7) Monolithic theories have a strong appeal, but we are not convinced by any of the claims to have found one. Although the EBR is sometimes treated as monolithic (i.e. very general), it only applies in specific circumstances. There are many functional models of RSF and only some are easy to test. The attempt to derive risk sensitivity from mechanistic models based on non-linear perception involves a questionable use of Jensen's inequality. Thus, we conclude that we do not have a simple general account, either functional (e.g. EBR, Mishra's threshold principle) or mechanistic (e.g. SUT, non-linear perception), of RSF.

(8) To advance the field in its present state, instead of forcing the data to conform to monolithic theories, researchers could, for example, focus on theoretically motivated studies of sequences of rewards and choices to tease apart existing theories and to map their relative merits under important contexts and internal states. Our analysis here reveals a number of surprising theoretical implications about choice sequences and further similar predictions should be readily attainable. In studying choice sequences, however, it is critical to pay attention to the role of choice in information accumulation.

X. ACKNOWLEDGEMENTS

We thank Alex Kacelnik, John McNamara and two anonymous referees for comments on previous versions of this manuscript. T. H. R. was supported by the Academy of Finland (grant numbers 334057, 335901, and 358138).

XI. REFERENCES

References identified with an asterisk (*) are cited only within the online supporting information.

Addicott, M. A., Pearson, J. M., Kaiser, N., Platt, M. L. & McClernon, F. J. (2015). Suboptimal foraging behavior: a new perspective on gambling. *Behavioral Neuroscience* **129**, 656–665.

Barrett, H. C. & Fiddick, L. (2000). Evolution and risky decisions. *Trends in Cognitive Sciences* **4**, 251–252.

Bateson, M. & 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. & Kacelnik, A. (1997). Starlings' preferences for predictable and unpredictable delays to food. *Animal Behaviour* **53**, 1129–1142.

Bateson, M. & Kacelnik, A. (1998). Risk-sensitive foraging: decision making in variable environments. In *Cognitive Ecology: The Evolutionary Ecology of Information Processing and Decision Making*, pp. 297–341. The University of Chigago Press, Chigago.

Bickel, W. K., Giordano, L. A. & Badger, G. J. (2004). Risk-sensitive foraging theory elucidates risky choices made by heroin addicts. *Addiction* **99**, 855–861.

Biele, G., Erev, I. & Ert, E. (2009). Learning, risk attitude and hot stoves in restless bandit problems. *Journal of Mathematical Psychology* **53**, 155–167.

Brennan, T. J. & Lo, A. W. (2012). An evolutionary model of bounded rationality and intelligence. *PLoS One* **7**, e50310.

Brown, J. S. & Kotler, B. P. (2004). Hazardous duty pay and the foraging cost of predation. *Ecology Letters* **7**, 999–1014.

Buchkremer, E. M. & Reinhold, K. (2010). The emergence of variance-sensitivity with successful decision rules. *Behavioral Ecology* **21**, 576–583.

Bujold, P. M., Ferrari-Toniolo, S. & Schultz, W. (2021). Adaptation of utility functions to reward distribution in rhesus monkeys. *Cognition* **214**, 104764.

Caraco, T. (1981). Energy budgets, risk and foraging preferences in dark-eyed juncos (*Junco hyemalis*). *Behavioral Ecology and Sociobiology* **8**, 213–217.

Caraco, T. & Chasin, M. (1984). Foraging preferences: response to reward skew. *Animal Behaviour* **32**, 76–85.

Caraco, T., Martindale, S. & Whittam, T. S. (1980). An empirical demonstration of risk-sensitive foraging preferences. *Animal Behaviour* **28**, 820–830.

Cocker, P. J. & Winstanley, C. A. (2015). Irrational beliefs, biases and gambling: exploring the role of animal models in elucidating vulnerabilities for the development of pathological gambling. *Behavioural Brain Research* **279**, 259–273.

Constantinople, C. M., Piet, A. T. & Brody, C. D. (2019). An analysis of decision under risk in rats. *Current Biology* **29**, 2066–2074.e5.

Conte, A., Levati, M. V. & Nardi, C. (2018). Risk preferences and the role of emotions. *Economica* **85**, 305–328.

*Cover, T. A. & Thomas, J. A. (2006). *Elements of Information Theory*, Second Edition. John Willey & Sons, Inc., Hoboken.

Craft, B. B. (2016). Risk-sensitive foraging: changes in choice due to reward quality and delay. *Animal Behaviour* **111**, 41–47.

Craft, B. B., Church, A. C., Rohrbach, C. M. & Bennett, J. M. (2011). The effects of reward quality on risk-sensitivity in *Rattus norvegicus*. *Behavioural Processes* **88**, 44–46.

De Agrò, M., Grimwade, D., Bach, R. & Czaczkes, T. J. (2021). Irrational risk aversion in an ant. *Animal Cognition* **24**, 1237–1245.

De Petrillo, F., Paoletti, M., Bellagamba, F., Manzi, G., Paglieri, F. & Addessi, E. (2020). Contextual factors modulate risk preferences in adult humans. *Behavioural Processes* **176**, 104137.

De Petrillo, F. & Rosati, A. G. (2019). Ecological rationality: convergent decision-making in apes and capuchins. *Behavioural Processes* **164**, 201–213.

De Petrillo, F. & Rosati, A. G. (2021). Variation in primate decision-making under uncertainty and the roots of human economic behaviour. *Philosophical Transactions of the Royal Society B: Biological Sciences* **376**, 20190671.

De Petrillo, F., Ventricelli, M., Ponsi, G. & Addessi, E. (2015). Do tufted capuchin monkeys play the odds? Flexible risk preferences in *Sapajus* spp. *Animal Cognition* **18**, 119–130.

Dener, E., Kacelnik, A. & Shemesh, H. (2016). Pea plants show risk sensitivity. *Current Biology* **26**, 1763–1767.

Denrell, J. & March, J. G. (2001). Adaptation as information restriction: the hot stove effect. *Organization Science* **12**, 523–538.

Eisenreich, B. R., Hayden, B. Y. & Zimmermann, J. (2019). Macaques are risk-averse in a freely moving foraging task. *Scientific Reports* **9**, 15091.

Farashahi, S., Azab, H., Hayden, B. & Soltani, A. (2018). On the flexibility of basic risk attitudes in monkeys. *The Journal of Neuroscience* **38**, 4383–4398.

*Fawcett, T. W., Fallenstein, B., Higginson, A. D., Houston, A. I., Mallpress, D. E. W., Trimmer, P. C. & McNamara, J. M. (2014). The evolution of decision rules in complex environments. *Trends in Cognitive Sciences* **18**, 153–161.

Fehr-Duda, H., Bruhin, A., Epper, T. & Schubert, R. (2010). Rationality on the rise: why relative risk aversion increases with stake size. *Journal of Risk and Uncertainty* **40**, 147–180.

Garcia, B., Cerrotti, F. & Palminteri, S. (2021). The description–experience gap: a challenge for the neuroeconomics of decision-making under uncertainty. *Philosophical Transactions of the Royal Society B: Biological Sciences* **376**, 20190665.

Genest, W., Stauffer, W. R. & Schultz, W. (2016). Utility functions predict variance and skewness risk preferences in monkeys. *Proceedings of the National Academy of Sciences of the United States of America* **113**, 8402–8407.

Gibbon, J. (1977). Scalar expectancy theory and Weber's law in animal timing. *Psychological Review* **84**, 279–325.

Gibbon, J., Church, R. M., Fairhurst, S. & Kacelnik, A. (1988). Scalar expectancy theory and choice between delayed rewards. *Psychological Review* **95**, 102–114.

Gigerenzer, G. & Goldstein, D. G. (1996). Reasoning the fast and frugal way: models of bounded rationality. *Psychological Review* **103**, 650–669.

Gilby, I. C. & Wrangham, R. W. (2007). Risk-prone hunting by chimpanzees (*Pan troglodytes schweinfurthii*) increases during periods of high diet quality. *Behavioral Ecology and Sociobiology* **61**, 1771–1779.

Gonzales, J., Mishra, S. & Camp, R. D. II (2017). For the win: risk-sensitive decision-making in teams. *Journal of Behavioral Decision Making* **30**, 462–472.

Griskevicius, V., Tybur, J. M., Delton, A. W. & Robertson, T. E. (2011). The influence of mortality and socioeconomic status on risk and delayed rewards: a life history theory approach. *Journal of Personality and Social Psychology* **100**, 1015–1026.

Hamm, S. L. & Shettleworth, S. J. (1987). Risk aversion in pigeons. *Journal of Experimental Psychology: Animal Behavior Processes* **13**, 376–383.

Harder, L. D. & Real, L. A. (1987). Why are bumblebees risk averse? *Ecology* **68**, 1104–1108.

Haun, D. B. M., Nawroth, C. & Call, J. (2011). Great apes' risk-taking strategies in a decision making task. *PLoS One* **6**, e28801.

Hayden, B. Y., Heilbronner, S. R., Nair, A. C. & Platt, M. L. (2008). Cognitive influences on risk-seeking by rhesus macaques. *Judgement and Decision Making* **3**, 389–395.

Hayden, B. Y. & Platt, M. L. (2007). Temporal discounting predicts risk sensitivity in rhesus macaques. *Current Biology* **17**, 49–53.

Hayden, B. Y. & Platt, M. L. (2009). Gambling for Gatorade: risk-sensitive decision making for fluid rewards in humans. *Animal Cognition* **12**, 201–207.

Heilbronner, S. R. (2017). Modeling risky decision-making in nonhuman animals: shared core features. *Current Opinion in Behavioral Sciences* **16**, 23–29.

Heilbronner, S. R. & Hayden, B. Y. (2013). Contextual factors explain risk-seeking preferences in rhesus monkeys. *Frontiers in Neuroscience* **7**, 7.

Heilbronner, S. R. & Hayden, B. Y. (2016). The description-experience gap in risky choice in nonhuman primates. *Psychonomic Bulletin & Review* **23**, 593–600.

Heilbronner, S. R., Rosati, A. G., Stevens, J. R., Hare, B. & Hauser, M. D. (2008). A fruit in the hand or two in the bush? Divergent risk preferences in chimpanzees and bonobos. *Biology Letters* **4**, 246–249.

Henke-von der Malsburg, J., Kappeler, P. M. & Fichtel, C. (2020). Linking ecology and cognition: does ecological specialisation predict cognitive test performance? *Behavioral Ecology and Sociobiology* **74**, 154.

Hertwig, R. & Erev, I. (2009). The description-experience gap in risky choice. *Trends in Cognitive Sciences* **13**, 517–523.

Hertwig, R., Wulff, D. U. & Mata, R. (2019). Three gaps and what they may mean for risk preference. *Philosophical Transactions of the Royal Society B: Biological Sciences* **374**, 20180140.

Higginson, A. D., McNamara, J. M. & Houston, A. I. (2014). The starvation–predation trade-off shapes the strategic use of protein for energy during fasting. *Journal of Theoretical Biology* **359**, 208–219.

Hill, A. B. (1965). The environment and disease: association or causation? *Proceedings of the Royal Society of Medicine* **58**, 295–300.

Hirschbichler, S. T., Rothwell, J. C. & Manohar, S. G. (2022). Dopamine increases risky choice while D2 blockade shortens decision time. *Experimental Brain Research* **240**, 3351–3360.

Houston, A., Schmid-Hempel, P. & Kacelnik, A. (1988). Foraging strategy, worker mortality, and the growth of the colony in social insects. *The American Naturalist* **131**, 107–114.

Houston, A. I. (1991). Risk-sensitive foraging theory and operant psychology. *Journal of the Experimental Analysis of Behavior* **56**, 585–589.

Houston, A. I., Fawcett, T. W., Mallpress, D. E. W. & McNamara, J. M. (2014). Clarifying the relationship between prospect theory and risk-sensitive foraging theory. *Evolution and Human Behavior* **35**, 502–507.

Houston, A. I. & McNamara, J. (1982). A sequential approach to risk-taking. *Animal Behaviour* **30**, 1260–1261.

Houston, A. I. & McNamara, J. M. (1990). The effect of environmental variability on growth. *Oikos* **59**, 15–20.

Houston, A. I. & McNamara, J. M. (1993). A theoretical investigation of the fat reserves and mortality levels of small birds in winter. *Ornis Scandinavica* **24**, 205–219.

Houston, A. I. & McNamara, J. M. (1999). *Models of Adaptive Behavior: An Approach Based on State*. Cambridge University Press, Cambridge.

Houston, A. I. & Wiesner, K. (2020). Gains v. losses, or context dependence generated by confusion? *Animal Cognition* **23**, 361–366.

Hurly, A. T. (2003). The twin threshold model: risk-intermediate foraging by rufous hummingbirds, *Selasphorus rufus*. *Animal Behaviour* **66**, 751–761.

Hurly, T. A. & Oseen, M. D. (1999). Context-dependent, risk-sensitive foraging preferences in wild rufous hummingbirds. *Animal Behaviour* **58**, 59–66.

Ishii, H., Ohara, S., Tobler, P. N., Tsutsui, K.-I. & Iijima, T. (2015). Dopaminergic and serotonergic modulation of anterior insular and orbitofrontal cortex function in risky decision making. *Neuroscience Research* **92**, 53–61.

Ishii, H., Onodera, M., Ohara, S., Tsutsui, K.-I. & Iijima, T. (2018). Sex differences in risk preference and c-Fos expression in paraventricular thalamic nucleus of rats during gambling task. *Frontiers in Behavioral Neuroscience* **12**, 68.

Kacelnik, A. (2006). Meanings of rationality. In *Rational Animals?* (eds S. Hurley and M. Nudds), pp. 87–106. Oxford University Press, Oxford.

Kacelnik, A. & Bateson, M. (1996). Risky theories—the effects of variance on foraging decisions. *American Zoologist* **36**, 402–434.

Kacelnik, A. & Bateson, M. (1997). Risk-sensitivity: crossroads for theories of decision-making. *Trends in Cognitive Sciences* **1**, 304–309.

Kacelnik, A. & Brito e Abreu, F. (1998). Risky choice and Weber's law. *Journal of Theoretical Biology* **194**, 289–298.

Kacelnik, A. & El Mouden, C. (2013). Triumphs and trials of the risk paradigm. *Animal Behaviour* **86**, 1117–1129.

Kagel, J. H., MacDonald, D. H., Battalio, R. C., White, S. & Green, L. (1986). Risk aversion in rats (*Rattus norvegicus*) under varying levels of resource availability. *Journal of Comparative Psychology* **100**, 95–100.

Kahneman, D. & Tversky, A. (1979). Prospect theory: an analysis of decision under risk. *Econometrica* **47**, 263–291.

Karban, R. & Orrock, J. L. (2018). A judgment and decision-making model for plant behavior. *Ecology* **99**, 1909–1919.

Keeney, R. L. & Raiffa, H. (1993). *Decisions with Multiple Objectives: Preferences and Value Tradeoffs*. Cambridge University Press, Cambridge.

*Klenke, A. (2008). *Probability Theory: A Comprehensive Course*. Springer-Verlag, London.

Lacombe, P., Brocard, S., Zuberbühler, K. & Dahl, C. D. (2022). Rationality and cognitive bias in captive gorillas' and orangutans' economic decision-making. *PLoS One* **17**, e0278150.

Lagorio, C. H. & Hackenberg, T. D. (2012). Risky choice in pigeons: preference for amount variability using a token-reinforcement system. *Journal of the Experimental Analysis of Behavior* **98**, 139–154.

Leblond, M., Fan, D., Brynildsen, J. K. & Yin, H. H. (2011). Motivational state and reward content determine choice behavior under risk in mice. *PLoS One* **6**, e25342.

Lee, J., Segundo-Ortin, M. & Calvo, P. (2023). Decision making in plants: a rooted perspective. *Plants* **9**, 1799.

Levy, D. J., Thavikulwat, A. C. & Glimcher, P. W. (2013). State dependent valuation: the effect of deprivation on risk preferences. *PLoS One* **8**, e53978.

Lieder, F. & Griffiths, T. L. (2020). Resource-rational analysis: understanding human cognition as the optimal use of limited computational resources. *Behavioral and Brain Sciences* **43**, 1–60.

Lim, I. S., Wittek, P. & Parkinson, J. (2015). On the origin of risk sensitivity: the energy budget rule revisited. *Animal Behaviour* **110**, 69–77.

Ludvig, E. A., Madan, C. R., Pisklak, J. M. & Spetch, M. L. (2014). Reward context determines risky choice in pigeons and humans. *Biology Letters* **10**, 20140451.

Ludvig, E. A. & Spetch, M. L. (2011). Of black swans and tossed coins: is the description-experience gap in risky choice limited to rare events? *PLoS One* **6**, e20262.

Machina, M. J. (1987). Choice under uncertainty: problems solved and unsolved. *Journal of Economic Perspectives* **1**, 121–154.

MacLean, E. L., Mandalaywala, T. M. & Brannon, E. M. (2012). Variance-sensitive choice in lemurs: constancy trumps quantity. *Animal Cognition* **15**, 15–25.

Maier, S. F. & Seligman, M. E. P. (2016). Learned helplessness at fifty: insights from neuroscience. *Psychological Review* **123**, 349–367.

Mallpress, D. E. W., Fawcett, T. W., Houston, A. I. & McNamara, J. M. (2015). Risk attitudes in a changing environment: an evolutionary model of the fourfold pattern of risk preferences. *Psychological Review* **122**, 364–375.

March, J. G. (1996). Learning to be risk averse. *Psychological Review* **103**, 309–319.

Marsh, B. & Kacelnik, A. (2002). Framing effects and risky decisions in starlings. *Proceedings of the National Academy of Sciences* **99**, 3352–3355.

Marshall, A. T. & Kirkpatrick, K. (2013). The effects of the previous outcome on probabilistic choice in rats. *Journal of Experimental Psychology: Animal Behavior Processes* **39**, 24–38.

Marshall-Pescini, S., Besserdich, I., Kratz, C. & Range, F. (2016). Exploring differences in dogs' and wolves' preference for risk in a foraging task. *Frontiers in Psychology* **7**, 1241.

Mayack, C. & Naug, D. (2011). A changing but not an absolute energy budget dictates risk-sensitive behaviour in the honeybee. *Animal Behaviour* **82**, 595–600.

Mazur, J. E. (2010). Distributed versus exclusive preference in discrete-trial choice. *Journal of Experimental Psychology: Animal Behavior Processes* **36**, 321–333.

McCoy, A. N. & Platt, M. L. (2005). Risk-sensitive neurons in macaque posterior cingulate cortex. *Nature Neuroscience* **8**, 1220–1227.

McDermott, R., Fowler, J. H. & Smirnov, O. (2008). On the evolutionary origin of prospect theory preferences. *The Journal of Politics* **70**, 335–350.

McNamara, J. M. (1996). Risk-prone behaviour under rules which have evolved in a changing environment. *American Zoologist* **36**, 484–495.

McNamara, J. M. & Houston, A. I. (1986). The common currency for behavioral decisions. *The American Naturalist* **127**, 358–378.

McNamara, J. M. & Houston, A. I. (1987*a*). A general framework for understanding the effects of variability and interruptions on foraging behaviour. *Acta Biotheoretica* **36**, 3–22.

McNamara, J. M. & Houston, A. I. (1987*b*). Partial preferences and foraging. *Animal Behaviour* **35**, 1084–1099.

McNamara, J. M. & Houston, A. I. (1989). State-dependent contests for food. *Journal of Theoretical Biology* **137**, 457–479.

McNamara, J. M. & Houston, A. I. (1990). The value of fat reserves and the tradeoff between starvation and predation. *Acta Biotheoretica* **38**, 37–61.

McNamara, J. M. & Houston, A. I. (1992). Risk-sensitive foraging: a review of the theory. *Bulletin of Mathematical Biology* **54**, 355–378.

McNamara, J. M., Houston, A. I. & Krebs, J. R. (1990). Why hoard? The economics of food storing in tits, *Parus* spp. *Behavioral Ecology* **1**, 12–23.

McNamara, J. M., Merad, S. & Houston, A. I. (1991). A model of risk-sensitive foraging for a reproducing animal. *Animal Behaviour* **41**, 787–792.

McNamara, J. M., Webb, J. N., Collins, E. J., Székely, T. & Houston, A. I. (1997). A general technique for computing evolutionarily stable strategies based on errors in decision-making. *Journal of Theoretical Biology* **189**, 211–225.

Mikhael, J. G. & Bogacz, R. (2016). Learning reward uncertainty in the basal ganglia. *PLoS Computational Biology* **12**, e1005062.

Mishra, S. (2014). Decision-making under risk: integrating perspectives from biology, economics, and psychology. *Personality and Social Psychology Review* **18**, 280–307.

Mobbs, D., Trimmer, P. C., Blumstein, D. T. & Dayan, P. (2018). Foraging for foundations in decision neuroscience: insights from ethology. *Nature Reviews Neuroscience* **19**, 419–427.

Moeller, M., Grohn, J., Manohar, S. & Bogacz, R. (2021). An association between prediction errors and risk-seeking: theory and behavioral evidence. *PLoS Computational Biology* **17**, e1009213.

Molenaar, P. C. M. & Campbell, C. G. (2009). The new person-specific paradigm in psychology. *Current Directions in Psychological Science* **18**, 112–117.

Möller, M., Manohar, S. & Bogacz, R. (2022). Uncertainty-guided learning with scaled prediction errors in the basal ganglia. *PLoS Computational Biology* **18**, e1009816.

Niv, Y., Joel, D., Meilijson, I. & Ruppin, E. (2002). Evolution of reinforcement learning in foraging bees: a simple explanation for risk averse behavior. *Neurocomputing* **44–46**, 951–956.

Nonacs, P. (1993). Is satisficing an alternative to optimal foraging theory? *Oikos* **67**, 371–375.

O'Neill, M. & Schultz, W. (2010). Coding of reward risk by orbitofrontal neurons is mostly distinct from coding of reward value. *Neuron* **68**, 789–800.

Perez, S. M. & Waddington, K. D. (1996). Carpenter Bee (*Xylocopa micans*) risk indifference and a review of nectarivore risk-sensitivity studies. *American Zoologist* **36**, 435–446.

Possingham, H. P., Houston, A. I. & McNamara, J. M. (1990). Risk-averse foraging in bees: a comment on the model of Harder and Real. *Ecology* **71**, 1622–1624.

Pratt, J. W. (1964). Risk aversion in the small and large. *Econometrica* **32**, 122–136.

Pyke, G. H., Pulliam, H. R. & Charnov, E. L. (1977). Optimal foraging: a selective review of theory and tests. *The Quarterly Review of Biology* **52**, 137–154.

Ratcliff, R. (1978). A theory of memory retrieval. *Psychological Review* **85**, 59–108.

Ratikainen, I. I., Wright, J. & Kazem, A. J. N. (2010). Social class influences degree of variance sensitivity in wild Siberian jays. *Behavioral Ecology* **21**, 1067–1072.

Real, L. A. (1980). Fitness, uncertainty, and the role of diversification in evolution and behavior. *The American Naturalist* **115**, 623–638.

Reboreda, J. C. & Kacelnik, A. (1991). Risk sensitivity in starlings: variability in food amount and food delay. *Behavioral Ecology* **2**, 301–308.

Regelmann, K. (1986). Learning to forage in a variable environment. *Journal of Theoretical Biology* **120**, 321–329.

Rivière, J., Stomp, M., Augustin, E., Lemasson, A. & Blois-Heulin, C. (2018). Decision-making under risk of gain in young children and mangabey monkeys. *Developmental Psychobiology* **60**, 176–186.

Roig, A., Meunier, H., Poulingue, E., Marty, A., Thouvarecq, R. & Rivière, J. (2022). Is economic risk proneness in young children (*Homo sapiens*) driven by exploratory behavior? A comparison with capuchin monkeys (*Sapajus apella*). *Journal of Comparative Psychology* **136**, 140–150.

Roitman, J. D. & Roitman, M. F. (2010). Risk-preference differentiates orbitofrontal cortex responses to freely chosen reward outcomes. *European Journal of Neuroscience* **31**, 1492–1500.

Rosati, A. G. (2017). Foraging cognition: reviving the ecological intelligence hypothesis. *Trends in Cognitive Sciences* **21**, 691–702.

Rosati, A. G. & Hare, B. (2011). Chimpanzees and bonobos distinguish between risk and ambiguity. *Biology Letters* **7**, 15–18.

Rosati, A. G. & Hare, B. (2013). Chimpanzees and bonobos exhibit emotional responses to decision outcomes. *PLoS One* **8**, e63058.

Rosati, A. G. & Hare, B. (2016). Reward currency modulates human risk preferences. *Evolution and Human Behavior* **37**, 159–168.

Rosenström, T., Wiesner, K. & Houston, A. I. (2016). Scalar utility theory and proportional processing: what does it actually imply? *Journal of Theoretical Biology* **404**, 222–235.

Sayers, K. & Menzel, C. R. (2017). Risk sensitivity, phylogenetic reconstruction, and four chimpanzees. *Behavioral Ecology and Sociobiology* **71**, 26.

Schmid, B. (2016). Decision-making: are plants more rational than animals? *Current Biology* **26**, R675–R678.

Severino, L. S. (2021). Plants make smart decisions in complex environments. *Plant Signaling & Behavior* **16**, 1970448.

Shafir, S. (2000). Risk-sensitive foraging: the effect of relative variability. *Oikos* **88**, 663–669.

Shafir, S., Bechar, A. & Weber, E. U. (2003). Cognition-mediated coevolution – context-dependent evaluations and sensitivity of pollinators to variability in nectar rewards. *Plant Systematics and Evolution* **238**, 195–209.

Shafir, S., Menda, G. & Smith, B. H. (2005). Caste-specific differences in risk sensitivity in honeybees, *Apis mellifera*. *Animal Behaviour* **69**, 859–868.

Shafir, S., Reich, T., Tsur, E., Erev, I. & Lotem, A. (2008). Perceptual accuracy and conflicting effects of certainty on risk-taking behaviour. *Nature* **453**, 917–920.

Shapiro, M. S., Couvillon, P. A. & Bitterman, M. E. (2001). Quantitative tests of an associative theory of risk-sensitivity in honeybees. *The Journal of Experimental Biology* **204**, 565–573.

Shapiro, M. S., Schuck-Paim, C. & 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. & 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.

Simen, P., Balci, F., de Souza, L., Cohen, J. D. & Holmes, P. (2011). A model of interval timing by neural integration. *The Journal of Neuroscience* **31**, 9238–9253.

Simon, H. A. (1956). Rational choice and the structure of the environment. *Psychological Review* **63**, 129–138.

So, N.-Y. & Stuphorn, V. (2010). Supplementary eye field encodes option and action value for saccades with variable reward. *Journal of Neurophysiology* **104**, 2634–2653.

Stearns, S. C. & Rodrigues, A. M. M. (2020). On the use of 'life history theory' in evolutionary psychology. *Evolution and Human Behavior* **41**, 474–485.

Stephens, D. W. (1981). The logic of risk-sensitive foraging preferences. *Animal Behaviour* **29**, 628–629.

Stephens, D. W. & Krebs, J. R. (1986). *Foraging Theory*. Princeton University Press, Princeton, NJ.

Steywers, M., Lee, M. & Wagenmakers, E.-J. (2009). A Bayesian analysis of human decision-making on bandit problems. *Journal of Mathematical Psychology* **53**, 168–179.

Stokes, L.-J. G., Davies, A., Lattimore, P., Winstanley, C. & Rogers, R. D. (2019). Exploring preferences for variable delays over fixed delays to high-value food rewards as a model of food-seeking behaviours in humans. *Philosophical Transactions of the Royal Society B: Biological Sciences* **374**, 20180141.

Stopper, C. M. & Floresco, S. B. (2011). Contributions of the nucleus accumbens and its subregions to different aspects of risk-based decision making. *Cognitive, Affective, & Behavioral Neuroscience* **11**, 97–112.

Stopper, C. M., Green, E. B. & Floresco, S. B. (2014). Selective involvement by the medial orbitofrontal cortex in biasing risky, but not impulsive, choice. *Cerebral Cortex* **24**, 154–162.

Sugam, J. A., Saddoris, M. P. & Carelli, R. M. (2014). Nucleus accumbens neurons track behavioral preferences and reward outcomes during risky decision making. *Biological Psychiatry* **75**, 807–816.

Sutton, R. S. & Barto, A. G. (2018). *Reinforcement Learning*, Second Edition. The MIT Press, Cambridge, MA.

Symmonds, M., Emmanuel, J. J., Drew, M. E., Batterham, R. L. & Dolan, R. J. (2010). Metabolic state alters economic decision making under risk in humans. *PLoS One* **5**, e11090.

Trimmer, P. C., Higginson, A. D., Fawcett, T. W., McNamara, J. M. & Houston, A. I. (2015). Adaptive learning can result in a failure to profit from good conditions: implications for understanding depression. *Evolution, Medicine, and Public Health* **2015**, 123–135.

Voon, V., Derbyshire, K., Rück, C., Irvine, M. A., Worbe, Y., Enander, J., Schreiber, L. R. N., Gillan, C., Fineberg, N. A., Sahakian, B. J., Robbins, T. W., Harrison, N. A., Wood, J., Daw, N. D., Dayan, P., *et al.* (2015). Disorders of compulsivity: a common bias towards learning habits. *Molecular Psychiatry* **20**, 345–352.

Waddington, K. D. & Gottlieb, N. (1990). Actual vs perceived profitability: a study of floral choice of honey bees. *Journal of Insect Behavior* **3**, 429–441.

Ward, D. (1992). The role of satisficing in foraging theory. *Oikos* **63**, 312–317.

Weber, B. J. & Chapman, G. B. (2005). Playing for peanuts: why is risk seeking more common for low-stakes gambles? *Organizational Behavior and Human Decision Processes* **97**, 31–46.

Weber, E. U., Shafir, S. & Blais, A. (2004). Predicting risk sensitivity in humans and lower animals: risk as variance or coefficient of variation. *Psychological Review* **111**, 430–445.

Wu, J., Guo, Z., Gao, X. & Kou, Y. (2020). The relations between early-life stress and risk, time, and prosocial preferences in adulthood: a meta-analytic review. *Evolution and Human Behavior* **41**, 557–572.

Wulff, D. U., Mergenthaler-Canseco, M. & Hertwig, R. (2018). A meta-analytic review of two modes of learning and the description-experience gap. *Psychological Bulletin* **144**, 140–176.

Xu, E. R. & Kralik, J. D. (2014). Risky business: rhesus monkeys exhibit persistent preferences for risky options. *Frontiers in Psychology* **5**, 258.

Yamada, H., Tymula, A., Louie, K. & Glimcher, P. W. (2013). Thirst-dependent risk preferences in monkeys identify a primitive form of wealth. *Proceedings of the National Academy of Sciences of the United States of America* **110**, 15788–15793.

Young, J. S. (1981). Discrete-trial choice in pigeons: effects of reinforcer magnitude. *Journal of the Experimental Analysis of Behavior* **35**, 23–29.

Zoratto, F., Oddi, G., Gori, E., Micucci, A., De Petrillo, F., Paglieri, F., Adriani, W., Laviola, G. & Addessi, E. (2018). Social modulation of risky decision-making in rats (*Rattus norvegicus*) and tufted capuchin monkeys (*Sapajus* spp.). *Behavioural Brain Research* **347**, 37–48.

Zwicker, J. & Rivest, F. (2022). Interval timing: modelling the break-run-break pattern using start/stop threshold-less drift–diffusion model. *Journal of Mathematical Psychology* **108**, 102663.

XII. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. A model behind the energy budget rule (EBR).
Appendix S2. The EBR and choice sequence.
Appendix S3. An analysis of the twin-threshold EBR model.
Appendix S4. A formal EBR model of variance and skewness risk near the survival threshold.
Appendix S5. Scalar utility theory (SUT) and symmetric stochastic options.
Appendix S6. Learning.
Appendix S7. Scaled prediction error (SPE) model of learning.

(*Received 28 February 2023; revised 31 October 2023; accepted 1 November 2023*)