

On the Origin of Risk Sensitivity: the Energy Budget Rule Revisited

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Abstract

Highlights:

1. *Derived a gradual version of the energy budget rule.*
2. *Critically review the energy budget rule and scalar utility theory.*
3. *It explains experiment results better than the budget rule.*

The risk-sensitive foraging theory formulated in terms of the (daily) energy budget rule has been influential in behavioural ecology as well as other disciplines. Predicting risk-aversion on positive budgets and risk-proneness on negative budgets, however, the budget rule has recently been challenged both empirically and theoretically. In this paper, we critically review these empirical and theoretical challenges as well as the formal derivation of the budget rule and propose a ‘gradual’ view of the budget rule, which is normatively derived from a gradual nature of risk sensitivity and encompasses the conventional budget rule as a special case. The gradual view shows that the conventional budget rule holds when the expected reserve is close enough to a threshold for overnight survival, selection pressure being significant. The gradual view also reveals that the conventional budget rule does not need to hold when the expected reserve is not close enough to the threshold, selection pressure being insignificant. The proposed gradual view better fits the empirical findings including those that used to challenge the conventional budget rule.

Keywords: budget rule, risk-sensitive foraging

1. Introduction

1.1. The Energy Budget Rule

Life is full of risky decisions, from the humdrum to matters of life or death. Understanding the drivers and the underlying processes of risky decisions is important in many disciplines including behavioural ecology. [1] revolutionized foraging research by introducing risk sensitivity and the risk-sensitive foraging theory formulated in terms of the energy budget rule [1, 2] has been influential not only in behavioural ecology [3], but also other disciplines such as psychology, economy, and anthropology [4, 5, 6, 7].

The budget rule predicts that, given foraging options of a constant and a variable options of the equal mean, an animal should choose the constant option if the expected energy budget is higher than the threshold required for overnight survival (i.e. the daily energy requirement) and the variable one if the expected budget is lower than the threshold; i.e. risk-aversion on positive energy budgets and risk-proneness on negative budgets [2]. The budget rule is logically appealing; assuming that animals will behave to maximise the probability of avoiding the starvation, it has been formally derived [2]. The budget rule has been empirically supported as well [1, 8].

1.2. Challenges against the Budget Rule

In spite of the early successes and the significant influences, the budget rule has recently been challenged, both empirically and theoretically. [3, 9] reviewed the published empirical studies related to the budget rule and concluded that experimental support is weak. One caveat to this conclusion is that experiments yielding negative results against the budget rule tend to involve larger species than those yielding positive results. The z -score model which the budget rule is formally derived from assumes a small bird foraging in order to meet daily energetic requirement in winter [2], which is less critical for large species [8]. Thus, any application of the budget rule to large species is less suitable since the short-term energetic requirement does not impose a significant threat to survival unlike small species [8].

While in risk sensitivity thinking, more realistic models have been developed [10]. However, one of the main drawbacks with these models is that their predictions are less testable due to the increased complexity [3]. [3] asserts that risk sensitivity does not have adaptive value by itself and it is a side-effect caused by psychophysical features of animal information processing systems; based on Weber's law that relates the perceived difference between stimuli to the mean value of the stimuli, Scalar Utility Theory is proposed [3, 9]. However, Scalar Utility Theory predicts preference of only risk-aversion (when variability is in amount) whereas there are empirical findings that report preference of risk-proneness, which cannot be ignored. More importantly, the mechanistic (proximate) explanation based on the psychophysical features does not need to deny the functional (ultimate) explanations since they are complementary rather than competing alternatives. Based on a meta-analysis of the same studies listed in [9] as well as more recent ones, for instance, [11] draws a conclusion different from that of [3, 9]. While applying Weber's law as well, [11] presents regression-based results that accommodate both risk-aversion and risk-proneness to be compatible with the budget rule, which integrates the functional and mechanic explanations; the direction of preference is determined by functional considerations (the budget rule) and the strength of preference by perceptual considerations (Weber's law). Rather than exclusively deducing either risk sensitivity or risk-indifference per study, [11] examines the 'degree' of risk sensitivity from a perceptual perspective and shows that there is a gradient of responses to risk.

In this paper, we present a gradual view of risk sensitivity from a normative perspective and provide a gradual version of the budget rule, which not only explains the empirically observed gradual nature of risk sensitivity, but also can explain observations counted against the budget rule.

2. Critical Review of the Derivation of the Budget Rule

We review the formal derivation of the budget rule from the z -score model [2, 12] and point out what it overlooks. The z -score model assumes a small bird foraging in winter to survive a night during which it cannot forage. We adopt notations similar to those of [12]. The bird's energy reserve x at dusk is assumed to be normally distributed with mean μ and variance σ^2 . It is also assumed that the bird has behavioural control over μ and σ , having to meet a fixed daily energetic requirement R to survive the night. Note that fitness is proportional to short-term survivorship which is represented by a step function in the z -score model, yielding the expected fitness to be proportional to the survival probability f . The model seeks to maximise the survival probability

$$f = \Pr(\text{surviving the night}) \quad (1)$$

$$= \Pr(x > R) \quad (2)$$

$$= 1 - \Phi(z) \quad (3)$$

where $z = \frac{R-\mu}{\sigma}$ is a z -score and $\Phi(\cdot)$ is the cumulative distribution function of the standard normal distribution $\mathcal{N}_{0,1}(\cdot)$ with zero mean and unit variance. To maximise f for a given μ , one needs to check its first derivative

$$\frac{\partial f}{\partial \sigma} = -\frac{\partial \Phi}{\partial \sigma} \quad (4)$$

$$= -\frac{d\Phi}{dz} \frac{\partial z}{\partial \sigma} \quad (5)$$

where $\frac{\partial z}{\partial \sigma} = \frac{\mu-R}{\sigma^2}$. Note that the sign of $\frac{\partial f}{\partial \sigma}$ is entirely determined by that of $\frac{\partial z}{\partial \sigma}$ in the sense that $\frac{d\Phi}{dz} > 0$ always holds; if z decreases, then survival probability f increases and vice versa. The analytical derivation of the budget rule then entirely focuses on the sign of $\frac{\partial z}{\partial \sigma}$ [12]. Given a constant mean and different variances, it yields the effect of σ on z as follows;

$$\frac{\partial z}{\partial \sigma} > 0 \quad \text{if } \mu > R, \quad (6)$$

$$\frac{\partial z}{\partial \sigma} < 0 \quad \text{if } \mu < R. \quad (7)$$

On positive budgets $\mu > R$, the standard deviation σ should be reduced to decrease z . On negative budgets $\mu < R$, σ should be increased to decrease z . This yields the extreme variance rule, predicting that the smallest variance possible is the optimal behaviour to be chosen on positive budgets and the largest variance possible on negative budgets [12]. The budget rule is a special case of the extreme variance rule with the smallest variance being zero, predicting the optimal risk sensitivity of risk-aversion on positive budgets and risk-proneness on negative budgets.

A caveat of this and its standard interpretation is an all-or-nothing view on animal decision-making, focusing mainly on the optimal behaviour. According to this all-or-nothing view, if an animal's response to variability does

not comply with the optimal risk sensitivity (in a statistically significant sense), it is counted against the budget rule [3, 9]. However, comparison of observed and predicted behaviours is not sufficient for testing a behavioural theory and one should not reject the theory without comparing the fitness of them [13]. Not all of the observations different from the prediction should be treated the same. If the difference in fitness between observed and predicted behaviours is insignificant, for instance, one should not use the observation to reject the theory. The degree of risk sensitivity under different experimental conditions is thus more informative than merely testing whether the response to risk complies with the prediction of the budget rule; according to the meta-analysis of the same empirical studies listed in [9], animals indeed show a gradient of responses to risk, the degree of risk sensitivity forming a continuum [11]. Thus, a more gradual view of the budget rule needs to be sought. Another caveat of the derivation is the z -score centric view. Since the z -score has an unlimited range of $-\infty < z < \infty$ whereas the survival probability has a limited range of $0 \leq f(z) \leq 1$ with an one-to-one correspondence between z and $f(z)$, a large change in z can yield little change in $f(z)$. If foraging options significantly differ in z , a z -score centric view can misleadingly imply a strong risk sensitivity whereas there is actually a weak risk sensitivity or a risk-indifference due to little difference in corresponding survival probability $f(z)$.

3. A Gradual View on Risk Sensitivity

There already exists a theoretical consideration on a gradual nature of risk sensitivity. [14] formulates decreasing risk-aversion of the z -score model based on the marginal rate of substitution [15],

$$\frac{\frac{\partial z}{\partial(\sigma^2)}}{\frac{\partial z}{\partial \mu}} = \frac{R - \mu}{2\sigma^2} = \frac{z}{2\sigma}. \quad (8)$$

A caveat of this analysis is that the gradual nature of risk sensitivity is considered only along an indifference curve of a constant z -score equivalent to a constant survival probability; the analysis varies mean μ and variance σ^2 such that a constant z -score is maintained. This is less compatible with the standard design of risk sensitivity experiments that offer a choice between a variable ($\sigma \neq 0$) and a constant ($\sigma = 0$) feeding options with an equal mean, yielding the options to differ in z -score.

The z -score model is considered to predict decreasing risk-aversion in the sense that preference switches from an option of higher variance to one of lower variance when the means of the feeding options increase [16]. A caveat is that the preference switching occurs only when the means of the feeding options increase from negative to positive budgets. Rather than decreasing risk-aversion, thus, it has more to do with switching from risk-proneness on negative budgets to risk-aversion on positive budgets. Decreasing risk-aversion should be considered only on positive budgets since the z -score model predicts risk-aversion only on positive budgets. If the means of the options increase within positive budgets, indeed, the z -score model predicts the consistent preference of lower variance rather than the preference

switching from higher variance to lower variance.

The Arrow-Pratt measure popular in economics [17]

$$\rho = -\frac{u''(x)}{u'(x)} \quad (9)$$

is often used as a risk-aversion measure where $u(x)$ is a utility (or fitness) function [18]. Decreasing risk-aversion is indicated by $\rho' = \frac{d\rho}{dx} < 0$. A caveat is that it is a local measure. It only informs of the response to risk at a single point along the fitness function whereas risk sensitivity deals with problems that requires more than information at a single point to predict preference, probability distributions spreading likelihood over many possible amounts [12]. Moreover, the Arrow-Pratt measure for the z -score model is not well defined since $u'(x) = u''(x) = 0$ due to the fitness function $u(x)$ being a step function (i.e. piece-wise constant).

These caveats of the existing measures call for a new measure of risk sensitivity, which should satisfy the following requirements:

1. It should reflect risk sensitivity in a choice between a variable and a constant feeding options with an equal mean.
2. It should take into consideration the whole distribution of reserve rather than a single value of it.

3.1. Measure of Risk Sensitivity

We propose a measure of risk sensitivity from a normative perspective

$$S = \frac{U(\mu, \sigma) - U(\mu, 0)}{\Delta U_{\max}} \quad (10)$$

where U is the expected fitness of a feeding option with mean μ and variance σ^2 , and ΔU_{\max} is the maximum possible difference in V . It satisfies the aforementioned two requirements. It uses expected fitness $U(\mu, \sigma) = \int \mathcal{N}(\mu, \sigma)u(x)dx$ where $u(x)$ is a fitness function of energy reserve x at dusk and \mathcal{N} is a normal distribution of x , which takes the whole distribution into consideration. It uses the difference in expected fitness between a variable and a constant feedings options $U(\mu, \sigma) - U(\mu, 0) \neq 0$. The reason why animals should show risk sensitivity in a normative sense is a consequence in expected fitness, which is well reflected in the proposed measure S of risk sensitivity; the more difference in expected fitness, the more sensitivity of risk should animals show. Note that the proposed measure S is invariant under an affine transformation of U due to the division by ΔU_{\max} and the subtraction $U(\mu, \sigma) - U(\mu, 0)$. With $W = aU + b$ where $a \neq 0$ and b being a scaling and an offset parameters respectively, we have $S = \frac{U(\mu, \sigma) - U(\mu, 0)}{\Delta U_{\max}} = \frac{W(\mu, \sigma) - W(\mu, 0)}{\Delta W_{\max}}$. The affine-invariance is important; for instance, the animal's internal representation may not use expected fitness U directly, but its affine transformation W . One of the reasons why the Arrow-Pratt measure involves the division by $u'(x)$ is to maintain the affine-invariance.

Since the expected fitness in the z -score model is proportional to the survival probability f and $\Delta f_{\max} = 1$, we have $S = \frac{f(\mu, \sigma) - f(\mu, 0)}{\Delta f_{\max}} = f(\mu, \sigma) - f(\mu, 0)$. The difference in survival probability $\Delta f(\mu, \sigma) = f(\mu, \sigma) - f(\mu, 0)$

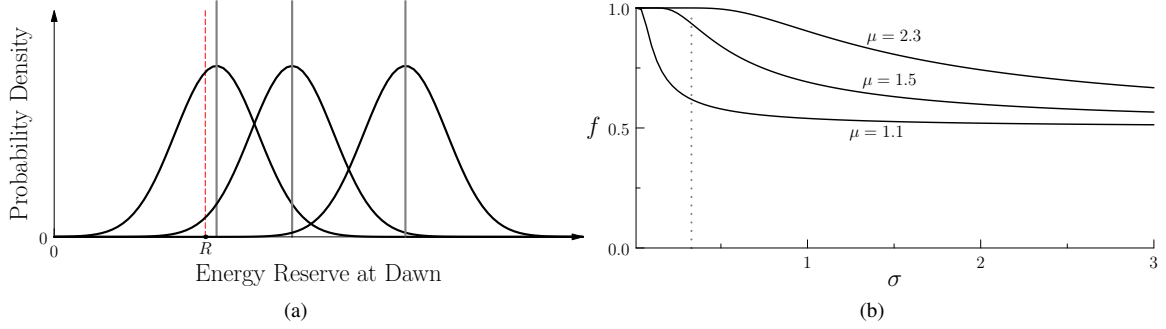


Figure 1: Gradual nature of risk sensitivity. (a) Three pairs of distributions for a variable ($\sigma \neq 0$) and a constant ($\sigma = 0$) foraging options are shown, each pair having an equal mean. The overnight survival threshold R is indicated by a dashed line. For a given variance σ^2 , difference in survival probability between a variable and a constant options changes, depending on the mean μ of each reserve distribution. Note that the survival probability is equal to the area under the distribution graph beyond R . As the mean of a distribution increases, the difference in survival probability between a pair of the options decreases from $\frac{1}{2}$ to 0. In other words, strength of selection for risk-aversion gradually decreases and can diminish as mean increases; i.e. decreasing and diminishing risk aversion. For instance, the distribution for the variable option that is the furthest away from the threshold has the survival probability close to 1 while the probability for the constant option is 1 and so the difference is close to 0; i.e. weak selection for risk-aversion. The further away from the threshold, the weaker selection for risk sensitivity. (b) The survival probability f as a function of standard deviation σ of the reserve distribution with mean $\mu = 1.1, 1.5$, and 2.3 and threshold $R = 1$ as those in (a). As μ increases for a given σ , f increases and approaches to 1, the optimal probability obtained at $\sigma = 0$; for example, $\sigma = 0.33$ used for the three distributions in (a) is indicated by a dotted line. The higher μ , the wider range of σ yielding f close to 1.

between a variable and a constant foraging options with an equal mean μ thus serves as a measure of risk sensitivity that an animal should show due to a consequence in expected fitness. The sign of Δf can discriminate between risk-aversion and risk-proneness; $\Delta f < 0$ implies selection for risk-aversion and $\Delta f > 0$, risk-proneness. The magnitude of Δf indicates strength of selection for risk sensitivity; the larger $|\Delta f|$, the stronger selection for risk sensitivity.

3.2. Derivation of Gradual Nature of Risk Sensitivity

For a given σ , we have

$$\frac{\partial f}{\partial \mu} = -\frac{d\Phi}{dz} \frac{\partial z}{\partial \mu} \quad (11)$$

$$= \frac{1}{\sqrt{2\pi}} \exp\left(-\frac{(R-\mu)^2}{2\sigma^2}\right) \frac{1}{\sigma} \quad (12)$$

which is a normal distribution and thus $\frac{\partial f}{\partial \mu} > 0$. On positive budgets $\mu > R$, we have $\Delta f(\mu, \sigma) = f(\mu, \sigma) - f(\mu, 0) = f(\mu, \sigma) - 1 < 0$ and so $|\Delta f(\mu, \sigma)| = -(f(\mu, \sigma) - 1)$, yielding $\frac{\partial |\Delta f|}{\partial \mu} = -\frac{\partial f}{\partial \mu} < 0$. In other words, $|\Delta f|$ decreases as μ increases on positive budgets for a given σ . Moreover, we have $f \rightarrow 1$ as μ increases for a given σ , yielding $|\Delta f| \rightarrow 0$. On positive budgets, thus, the strength of selection for risk-aversion monotonically decreases and can diminish as reserve mean increases for a given variance. This gradual and diminishing nature of risk sensitivity can be intuitively understood as well; see Figure 1. On negative budgets, by a similar argument, the strength of selection for risk-proneness monotonically decreases and can diminish as mean decreases for a given variance; see Figure 2. In other words, degree of the optimal risk sensitivity predicted by the conventional budget rule gradually changes. Being purely based on an adaptive rationale, this ‘gradual’ view of the z -score model (or the gradual budget rule hereafter)

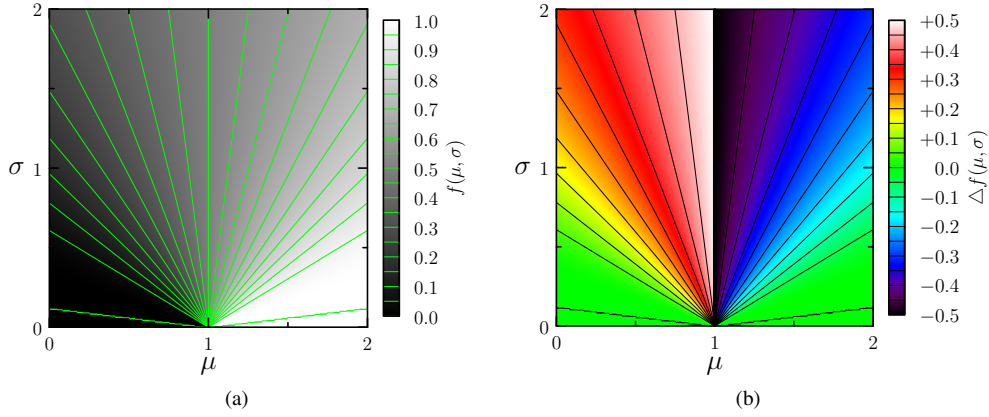


Figure 2: (a) The values of the survival probability $f(\mu, \sigma)$ with the threshold $R = 1$ are plotted as gray-level intensities on the $\mu - \sigma$ plane. Contours corresponding to $f = 0.05, 0.1, \dots, 0.9, 0.95$ are also plotted. (b) The probability residuals $\Delta f(\mu, \sigma) = f(\mu, \sigma) - f(\mu, 0)$ are plotted in colour. Showing the difference in survival probabilities between variable and constant foraging options, the residual indicates levels of selection pressure for risk sensitivity. Contours at $\Delta f = -0.5, -0.45, \dots, 0.45, 0.5$. The more $|\Delta f|$ with $\Delta f > 0$, the more selection pressure for risk-proneness (red-white); the more $|\Delta f|$ with $\Delta f < 0$, the more selection pressure for risk-aversion (blue-black); $\Delta f \approx 0$, weak selection pressure for risk sensitivity (green).

predicts that the conventional budget rule holds if difference in expected fitness (or survival probability) between the feeding options is significant (e.g. when reserve mean is close to starvation threshold for a given deviation) and may not do so otherwise, risk sensitivity gradually weakening. The gradual budget rule not only encompasses the conventional budget rule as a special case of it, but also may explain empirical results that are often counted against the conventional budget rule and the adaptive rationale of risk sensitivity behind it.

3.3. Weak Selection Pressure vs. Weak Risk Sensitivity

The empirical findings that report risk-indifference or weak risk sensitivity used to be counted against the conventional budget rule [3, 9]. According to the gradual budget rule, however, if difference in expected fitness between the feeding options is insignificant, risk-indifference is feasible in the sense that there is weak selection for the optimal risk sensitivity predicted by the conventional budget rule and, thus, weak selection against risk-indifference. Note that weak selection for the optimal risk sensitivity does not imply strong selection for risk-indifference, the latter of which would predict only risk-indifference. Instead, it implies weak selection against suboptimal risk sensitivity as well as risk-indifference in the sense that there is little difference in expected fitness between these and the optimal risk sensitivity. In other words, any of risk-aversion and risk-proneness as well as risk-indifference is feasible under the condition of weak selection, which may explain empirically observed risk-indifference and suboptimal risk sensitivity such as risk-proneness on positive budgets and risk-aversion on negative budgets. Thus, one should not simply conclude that any observation apparently contradicting the optimal risk sensitivity challenges the conventional budget rule and the adaptive rationale of risk sensitivity behind it. Instead, one should take into consideration the expected fitness of the observation and that of the optimal risk sensitivity.

3.3.1. Risk-proneness on Positive Budgets and Risk-aversion on Negative Budgets

Other than the argument of weak selection, can we provide additional explanations why risk sensitivity (especially, suboptimal risk sensitivity such as risk-proneness on positive budgets and risk-aversion on negative budgets) rather than risk-indifference can be empirically observed in a statistically significant sense? Any model is an approximation or simplification of the reality, leaving out many features. The z -score model that the budget rule is formally derived from incorporates the survival, but leaves out other functional and mechanical features such as reproduction and perception. Under the condition of weak selection for the optimal risk sensitivity (e.g. reserve mean is distant enough from the survival threshold for a given deviation), any of risk-proneness, risk-aversion and risk-indifference is feasible from the gradual view of the z -score model. However, only one of them may be feasible from the perspective of a feature that the z -score model leaves out, say, reproduction; e.g. only risk-proneness may yield expected fitness substantially higher than that of any other alternatives in terms of reproduction. We elaborate this aspect.

Being built upon the z -score model, the twin threshold model seeks to maximise the combined probability g of surviving the night and succeeding in reproduction [19]

$$g(\mu, \sigma) = w \Pr(\text{surviving the night}) + (1 - w) \Pr(\text{succeeding in reproduction}) \quad (13)$$

$$= w \Pr(x > R) + (1 - w) \Pr(x > Q) \quad (14)$$

$$= w \left(1 - \Phi \left(\frac{R - \mu}{\sigma} \right) \right) + (1 - w) \left(1 - \Phi \left(\frac{Q - \mu}{\sigma} \right) \right) \quad (15)$$

where Q is reproduction threshold, $R < Q$ and $w \in [0, 1]$. Whereas the original twin threshold model uses combination weights w and 1, we use the convex combination of the two probabilities with w and $1 - w$ to ensure that the combination $g(\mu, \sigma)$ remains to be a probability. With starvation threshold R and reproduction threshold Q , their associated residual or difference in probability $\Delta g(\mu, \sigma) = g(\mu, \sigma) - g(\mu, 0)$ is qualitatively different from the residual $\Delta f(\mu, \sigma)$ associated with a single threshold R ; see Figure 3. As empirically observed from some species, the twin threshold model predicts risk-proneness on positive budgets (i.e. $\Delta g > 0$ being significant) in a range of parameters (μ, σ) where reserve mean μ is close to but lower than reproduction threshold Q . This makes sense since risk-proneness offers a possibility of reproduction whereas risk-aversion does not. In the same range of parameters, the gradual budget rule can yield weak selection for the optimal risk sensitivity predicted by the conventional budget rule (i.e. Δf being insignificant) and so predicts that all of risk-proneness, risk-aversion and risk-indifference are feasible, there being little difference in expected fitness between them. Near at $(\mu, \sigma) = (2.9, 1.0)$, for instance, we have $\Delta g \approx 0.25$ whereas $\Delta f \approx 0.0$ in Figure 3. Rather than conflicted predictions, the inclusion of reproduction feature refines the predictions based on only survival feature in the sense that the latter predicts all of risk-proneness, risk-aversion and risk-indifference being feasible and the first predicts only one of them (i.e. risk-proneness) being feasible. Note that they make similar predictions when both of the models are under conditions of strong selection. As reserve mean μ is lowered and becomes close to starvation threshold R on positive budgets for a given deviation

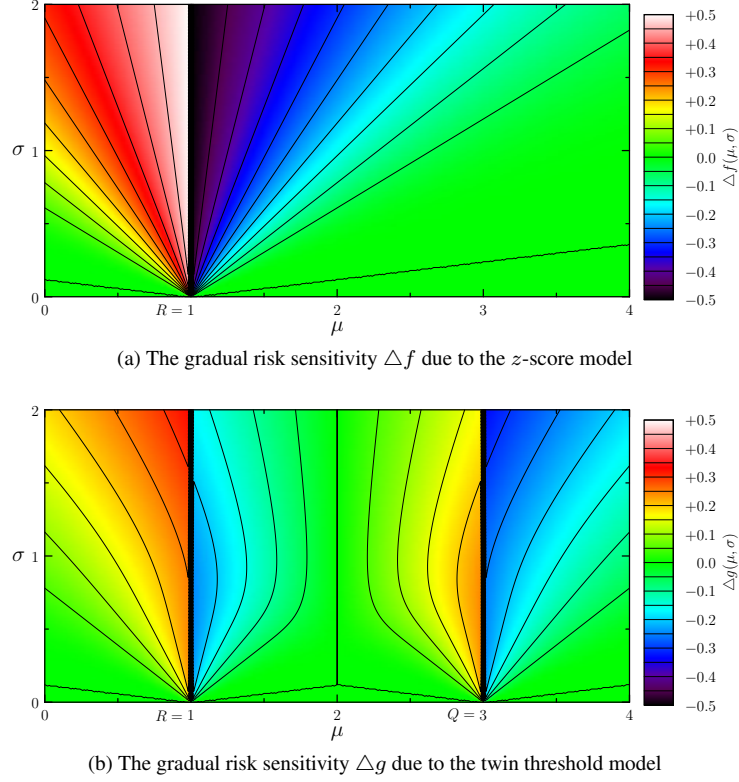


Figure 3: The budget rule still holds when the reserve mean μ is near the starvation threshold $R = 1$, less so when the reserve mean μ approaches reproduction threshold $Q = 3$. Note that $w = \frac{1}{2}$.

σ^2 , the selection for risk-proneness to succeed in reproduction weakens whereas the selection for risk-aversion to survive the night strengthens and, thus, the twin threshold model predicts risk-aversion as the gradual budget rule does. Near at $(\mu, \sigma) = (1.1, 1.0)$, for instance, we have $\Delta g \approx -0.25$ and $\Delta f \approx -0.4$ in Figure 3, both yielding strong selection for risk aversion.

Another feature that the z -score model leaves out is possibility of starvation (to death) during foraging [9]. If it is taken into consideration (i.e. a forager has to stay above a lethal limit of reserves during foraging, which is lower than the overnight starvation threshold R), risk-aversion on negative budgets would be predicted when reserve mean is close to but higher than the lower lethal limit [9]. For species showing risk-aversion on negative budgets, one can apply a logic similar to the one used above for risk-proneness on positive budgets. When reserve mean is close to but higher than the lower lethal limit for a given variance, the possibility of starvation during foraging yields strong selection for risk-aversion and the gradual budget rule can yield weak selection for all of risk-aversion, risk-proneness and risk-indifference. As reserve mean increases and becomes close to the overnight starvation threshold R on negative budgets, the selection for risk-aversion to avoid starvation during foraging weakens whereas the selection for risk-proneness to survive the night strengthens, predicting risk-proneness.

In summary, additional features that the z -score model leaves out can refine predictions made by the gradual budget

rule under conditions of weak selection, which may explain risk-proneness on positive budgets and risk-aversion on negative budgets, contrary to the conventional budget rule.

4. Discussions

4.1. Partial Preference and Behavioural Landscapes

220 A related notion is the canonical cost of a suboptimal behaviour $c = U^* - U$ where U^* is the expected fitness for the optimal behaviour and U for a suboptimal behaviour [20]. A caveat of this metric is that it is not affine-invariant. For instance, the expected fitness scaled by $a \neq 0$ fails the invariance, i.e. $U^* - U \neq aU^* - aU$; rather than expected fitness itself (i.e. the expected number of offsprings surviving to adulthood), note that a scaled expected fitness is often used [21]. As a function of the canonical cost c , the probability of choosing a suboptimal behaviour
 225 can be derived, assuming that the perception of expected fitness U is subject to error [22]. When an animal makes a choice between two simultaneously available options, one has $\pi(c) = \frac{\exp(-\beta c)}{1 + \exp(-\beta c)}$ for the probability of a suboptimal option and $1 - \pi(c)$ for the optimal option where β is a positive free parameter [23]. It yields $\pi(c) \approx \frac{1}{2}$ when $c \approx 0$, predicting only risk-indifference when there is little difference in expected fitness between the optimal and a suboptimal behaviours in the context of risk sensitivity. Contrary to this prediction, however, risk-proneness and
 230 risk-aversion should be feasible as well as risk-indifference in the sense that selection against all of them is weak when $c \approx 0$.

A related metric is U/U^* where U is the expected fitness of an observed (suboptimal) behaviour and U^* is the expected fitness for the predicted (optimal) behaviour [13]; in our context of risk sensitivity, $U = U(\mu, \sigma)$ and $U^* = U(\mu, 0)$ on positive budgets and vice versa on negative budgets. A caveat of this metric is that it is not affine-
 235 invariant. For instance, the expected fitness offset by $b \neq 0$ fails the invariance, i.e. $U/U^* \neq (U + b) / (U^* + b)$. Another caveat is that it cannot capture the gradual nature of risk sensitivity on negative budgets since we have $U/U^* = U(\mu, 0)/U(\mu, \sigma) = 0$ regardless of $U^* = U(\mu, \sigma) \neq 0$. This contrasts the case on positive budgets where $U/U^* = U(\mu, \sigma)/U(\mu, 0) = U(\mu, \sigma)$ gradually increases to 1 as mean μ increases for a given variance σ^2 .

4.2. Scalar Utility Theory

240 Not viewing risk sensitivity as having adaptive value per se, [3] instead asserts that it is caused as a side-effect of perception and proposes SUT (Scalar Utility Theory) as an alternative to the conventional budget rule [24]. SUT consists of two parts, modelling the animal's knowledge of the food amounts and postulating a decision process. Among feeding options with the same mean but different variance, the memory representation of the option with smaller vari-
 245 ance has larger skew-sensitive measures (e.g. mode) as a consequence of Weber's law. If the animal's decision process uses mode or other skew-sensitive measures in comparing (the memory representations of) the feeding options, it is argued that the animal will prefer the constant option since it provides an 'apparently' larger amount of food than the variable option does, yielding risk-aversion; see Figure 4(a). Predicting only risk-aversion regardless of energy

budgets, however, this side-effect assertion of SUT suffers from numerous caveats from both empirical and theoretical perspectives.

250 4.2.1. *Weak empirical support*

As the empirical evidences supporting SUT, [3] refers to a set of 22 studies reviewed in [9], the majority of which report (consistent) risk-aversion as predicted by SUT. However, those studies do not manipulate the energy budgets of the subjects. Since the energy budgets are not manipulated, the conventional budget rule cannot be fully tested nor fairly compared using these studies. Risk-aversion reported from the studies without budget manipulation does not
255 exclusively support SUT in the sense that risk-aversion is also predicted by the conventional budget rule when the animals are on positive budgets. Even from a perspective of the conventional budget rule, it is already understood that risk-aversion occurs more often than risk-proneness because the positive budgets are commonly realised levels of energy budgets [25]. The 35 studies reviewed in [3] are better suited to fairly test both SUT and the conventional budget rule using the same data set since these studies manipulated energy budgets; additional benefits include higher
260 number of studies as well as an inclusion of more recent studies. Among the 35 studies, 8 studies report consistent risk-aversion (as predicted by SUT), 11 of ‘some amount’ (of risk-aversion), and 16 of ‘no’ (of risk-aversion). Only 8/35 support SUT, which is even lower than 10/35 of supporting the conventional budget rule. Empirical support of SUT is weaker than that of the conventional budget rule.

4.2.2. *Description but not explanation*

265 Animals are assumed to prefer larger amounts of food [3]. Depending on the statistics of the memory representation used for accessing food amounts, however, the hypothetical decision process would yield a different choice among feeding options of the same mean and different variances. If mean of the memory representation is assumed to be used, it yields no bias to variability of food amounts (i.e. risk-indifference) since the animal would ‘perceive’ the food amounts of the options to be the same. If maximum is used, it yields bias in favour of variability (i.e. risk-proneness) since the animal would ‘perceive’ the amount of the variable option to be greater; its positively skewed
270 memory representation leads to the maximum greater than that of the symmetric distribution of the constant option. If mode is used, it yields bias against variability (i.e. risk-aversion) since the animal would ‘perceive’ the amounts of the constant option to be greater. What is the rationale or justification of SUT’s assumption that the animal’s decision process would use mode (or any other skew-sensitive statistic) of the memory representations rather than an alternative
275 statistic such as mean or maximum? If mode is used in choice process, it would fit to the empirical data of animals’ bias against variability of food amounts whereas mean nor maximum would not [24]. This is hardly an ‘explanation’ of the empirically observed bias, but just a ‘description’ of it, merely fitting to the data. If the empirical data showed no bias related to variability, according to the logic of SUT, one would simply need to assume the decision process to use mean since it would better fit to the data than other statistics would. If the data showed bias in favour of variability,
280 one would just assume to use maximum or any other static that would yield the bias, according to the fitting-to-data

logic of SUT.

4.2.3. *Fitness consequence of erroneous preferences*

Another caveat of the usage of mode or any other skew-sensitive statistic is that it logically contradicts SUT's assumption of linear fitness. Unlike other relevant theories in biology, psychology and economics, SUT assumes fitness (or utility) as a 'linear' function of food amounts [24]. It is well known that, under the linear relations, only mean of food amounts has effect on mean of fitness (i.e. expected fitness), but variance or any other variability-sensitive statistic does not [27, 12]. In any theory that assumes a linear fitness function, thus, the animal's decision process should use and compare mean of food amounts, but not any skew-sensitive statistic such as mode. This is not a merely logical issue, but has a serious fitness consequence as well. If the decision process is based on a skew-sensitive statistic such as mode as assumed by SUT, it can yield an erroneous preference of an option whose expected fitness is lower than that of the alternative; see Figure 4 (b). There should be natural selection against the erroneous decision process.

Even if Weber's law (e.g. a Weberian memory representation of food amounts) is empirically supported [28],¹ thus, it does not support the remaining key component of SUT, the hypothetical decision process based on skew-sensitive statistics, which suffers from the numerous caveats.

Note that, contrary to SUT that predicts only risk-aversion, one can still accommodate both risk-aversion and risk-proneness to be compatible with the conventional budget rule while applying Weber's law [11].

4.3. *Comparison to hybrid explanations*

While revealing gradual nature of risk sensitivity from a meta-analysis based on regressions, [11] concludes that the direction of preference is determined by functional considerations (complying with the conventional budget rule) and the strength of preference by perceptual considerations (complying with Weber's law). When risk-aversion is predicted by the conventional budget rule, for instance, the regression coefficient is positive, indicating that an increase in relative variability yields stronger risk-aversion. According to Weber's law, relative variability or the coefficient of variation $CV = \frac{\sigma}{\mu}$ correlates with capability of perceptual discrimination between a variable and a constant feeding options. Thus, the stronger risk-aversion or the increasing preference of a constant option on positive budgets with increasing CV of the variable feeding option is explained by perceptual considerations in the sense that perceptual discrimination of a constant option (i.e. the optimal choice) from a variable one (i.e. the suboptimal choice) improves as difference in CV between the options increases [11]. On the other hand, the conventional budget rule is considered

¹Empirical supports of Weber's law has little to do with the support for SUT, contrary to Kacelnik's misleading assertion.

[3]; "Among sources of food with the same mean but different variance, the memory representation of the source with greater variance has smaller median. This could lead to preference for the least variable one (if the animal prefers larger outcomes) or the more variable one (if the animal prefers the smaller outcome). This immediately suggests a difference between preferences of variability in amount and variability in delay to food, because animals prefer smaller delays and larger amounts of food (Reboreda & Kacelnik 1991). 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. These predictions and many of the theory's assumptions are supported by a large number of experiments."

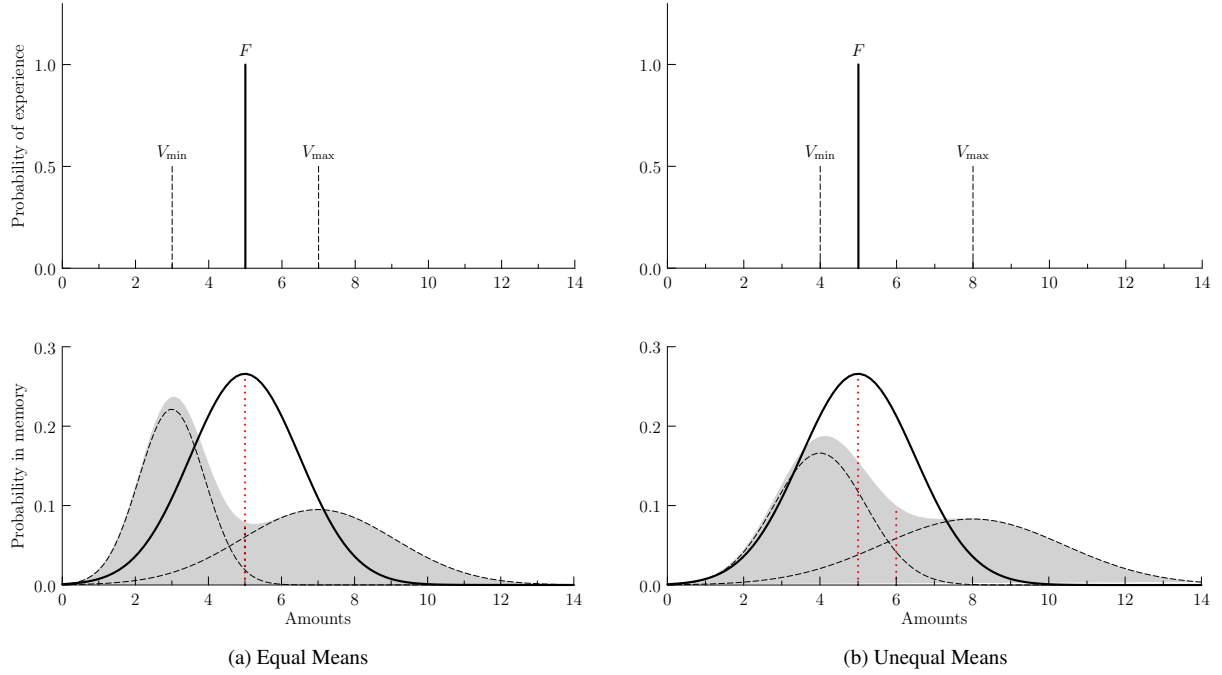


Figure 4: A graphic description of flaws of SUT (Scalar Utility Theory). The memory representation of the constant feeding option $F = 5$ is shown as a solid curve. The overall memory representation of the variable option is shown in shading while each of the small and large amounts is indicated by a dashed curve. All of the three (normal) distributions have the same coefficient of variation ($SD/mean$) = 0.3 which is empirically observed from starlings [24]. The mean of each representation is indicated by a dotted line. (a) A variable option V yields $V_{\min} = 3$ or $V_{\max} = 7$ with equal probability. The memory representations of the constant and variable options have the same mean = 5. The mode of the constant option is 5 and the mode of the variable one is 3; note that the mode of a continuous probability distribution is the value at which the distribution has its global maximum. According to SUT, the animal will prefer the constant option since its mode is larger than that of the variable option, perceiving the amount of the first to be greater than that of the latter and so yielding risk-aversion [24]. SUT typically presents the case of the same mean only, where both options yield the same expected fitness under the assumption of a linear fitness relation. [3, 24]. (b) A variable option V yields $V_{\min} = 4$ or $V_{\max} = 8$ with equal probability. The mode of the variable option is 4 while the mean is 6. According to SUT, the animal will still prefer the constant option since the mode of the constant one is larger than that of the variable one (i.e. $5 > 4$). However, the expected fitness of the constant option is lower than that of the variable option since the mean of the constant one is less than that of the variable one (i.e. $5 < 6$) and SUT assumes a linear fitness relation, the expected fitness depending only on mean of food amounts but no other statistic. The hypothetical decision process of SUT yields an erroneous preference of a lower expected fitness.

unable to predict this changing levels of risk sensitivity between experimental conditions [11, 29]. According to the
 310 gradual budget rule, however, even the strength of preference can be explained by functional considerations as well.
 For a given standard deviation $\sigma \neq 0$, as mean μ decreases on positive budgets, the difference in expected fitness
 between the feeding options increases (i.e. selection for risk-aversion strengthens) while difference in CV increases
 as well since $CV = \frac{\sigma}{\mu}$ negatively correlates with mean μ . A positive correlation between strength of risk-aversion and
 CV thus stems from functional considerations as well.

315 4.4. Empirical Tests of the Gradual Budget Rule

While the aforementioned meta-analysis supports the gradual budget rule, it is based on different groups of sub-
 jects under different energy budgets. To empirically test the gradual budget rule within the same individuals, one
 needs to involve a wide range of parameters. Instead of a single or a limited range of reserve mean on positive bud-

gets, for instance, a wider range should be tested out since the gradual budget rule not only predicts a richer set of risk sensitivity than the conventional budget rule does, but also complies with the latter, depending on reserve mean. For example, hummingbirds not only become more risk-averse on positive budgets as reserve mean gets closer to the survival threshold, but also show more risk-proneness on positive budgets when reserve mean gets further away from the threshold [19]. European starlings become more risk-averse on positive budgets as ambient temperature decreases, the latter of which is equivalent to raising the survival threshold, yielding reserve mean closer to it [30].

5. Conclusion

The gradual budget rule is proposed, which normatively reflects the gradual nature of risk sensitivity and encompasses the energy budget rule as a special case. The gradual budget rule predicts significant selection pressure for risk sensitivity complying with the energy budget rule in a limited range of parameters, but less significant in the remaining range, the latter of which can allow for behaviours not complying with the energy budget rule. This can explain some of empirical findings that used to be counted against the energy budget rule and even the adaptive value of risk sensitivity. We also critically reviewed the assertions of risk sensitivity being a side effect due to perceptual considerations and challenged them.

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