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Clarifying the relationship between prospect theory and risk-sensitive foraging theory

Running title: Prospect theory and risk-sensitive foraging theory

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ABSTRACT

When given a choice between options with uncertain outcomes, people tend to be loss averse, risk averse regarding potential gains and risk prone regarding potential losses. These features of human decision making are captured by prospect theory (PT)—a hugely influential descriptive model of choice, but one which lacks any unifying principle that might explain why such preferences exist. Recently there have been several attempts to connect PT with risk-sensitive foraging theory (RSFT), a normative framework developed by evolutionary biologists to explain how animals should choose optimally when faced with uncertain foraging options. Although this seems a promising direction, here we show that current approaches are overly simplistic and, despite their claims, they leave key features of PT unaccounted for. A common problem is the failure to appreciate the central concept of reproductive value in RSFT, which depends on the decision maker's current state and the particular situation it faces. Reproductive value provides a common currency in which decisions can be compared in a logical way. In contrast, existing models provide no rational justification for the reference state in PT. Evolutionary approaches to understanding PT preferences must confront this basic problem.

1. Introduction

Prospect theory (Kahneman & Tversky, 1979) and risk-sensitive foraging theory (McNamara & Houston, 1992; Real & Caraco, 1986; Stephens, 1981) are two influential accounts of decision making under risk, when the outcomes of decisions are variable. Prospect theory (PT) was developed in the social sciences as a descriptive explanation of observed choices in humans, to accommodate consistent deviations from the rationality-based predictions of expected utility theory (EUT). Risk-sensitive foraging theory (RSFT) was developed by evolutionary behavioural ecologists as a normative explanation of how animals should choose between stochastic foraging options so as to maximise reproductive success. Central to RSFT is the concept of *reproductive value*, which (for simple scenarios) can be defined as the expected future number of offspring produced by an individual over the remainder of its lifetime, as a function of its current state (Houston & McNamara, 1999). Since natural selection will tend to favour decisions that maximise reproductive value, this provides a common currency in which decisions can be compared (McNamara & Houston, 1986).

A shared feature of PT and RSFT is that they both address how risk preferences depend on the decision maker's state (e.g. wealth or energy reserves). Because of this similarity, several researchers (Aktipis & Kurzban, 2004; Caraco & Lima, 1987; McDermott et al., 2008; Mishra, in press; Mishra & Fiddick, 2012; Mishra et al., 2012) have suggested that RSFT may offer an evolutionary explanation for some of the choice patterns described by PT. For example, McDermott et al. (2008) explicitly identified the reference state in PT with the amount of energy required to survive the night in RSFT, and used this to argue that PT preferences are in fact rational. Here we highlight a number of problems with this approach

and show that it fails to account for the key features of PT. Because the relationship between state and reproductive value depends critically on the biological details of the situation under consideration (McNamara & Houston, 1992), the patterns of choice predicted by RSFT do not, in general, match those described by PT. We closely examine the similarities and differences between PT and RSFT and discuss the extent to which the choices they predict are rational.

2. Prospect theory

The essential features of PT are captured by the value function in Fig. 1, which shows the subjective value a decision maker assigns to gains and losses of varying magnitudes. The form of this function was chosen to reflect three key findings from empirical studies of human decision making that were not readily accounted for by EUT:

Reference point. The origin in Fig. 1 marks a ‘reference point’ from which all gains and losses are assessed. Typically (though not always) this represents the decision maker’s current state, and reflects the view that changes in state matter more to the decision maker than the final state (i.e. the state at which it ends up after making a decision). As Kahneman (2003a, p. 704) puts it, ‘the carriers of utility are gains and losses—changes of wealth rather than states of wealth’. This represents a form of path dependence, in that the response to a given state differs depending on the route taken (gain or loss) to reach that state.

Reflection effect. The value function is concave (i.e. decreasing in slope) for gains and convex (i.e. increasing in slope) for losses. This curvature implies (by Jensen’s inequality; see

Box 1) that decision makers should be risk averse when choosing between alternative gains but risk prone when choosing between alternative losses, as found in some empirical studies (Kühberger, 1998; Levin et al., 1998; McNeil et al., 1982; Tversky & Kahneman, 1981). For example, Tversky & Kahneman (1981) found that most people preferred a certain gain of \$240 over a one-in-four chance of gaining \$1000 (and gaining \$0 otherwise), but preferred a one-in-four chance of losing \$1000 (and losing \$0 otherwise) over a certain loss of \$750.

Loss aversion. The value function is sharply ‘kinked’ about the origin (i.e. the slope changes abruptly, such that the function is not differentiable at this point) and is steeper for losses than gains, so that a loss of a given magnitude has a stronger effect on value than a gain of the same magnitude. This reflects the finding in some studies that people care more about losses than gains of equivalent magnitude (Kahneman & Tversky, 1984; Kahneman et al., 1991; Tversky & Kahneman, 1991, 1992). For example, Tversky & Kahneman (1992) found that participants would only accept an even chance of winning or losing money when the amount to be won was at least twice the amount to be lost. The general notion of loss aversion was famously captured by two professional tennis players, Jimmy Connors (“I hate to lose more than I love to win”; Aktipis & Kurzban, 2004, p. 142) and Andre Agassi (“A win doesn’t feel as good as a loss feels bad”; Agassi, 2009, p. 167).

3. Risk-sensitive foraging theory

RSFT developed from the work of Caraco (1980) and Real (1980) to provide a general account of how animals should choose between stochastic foraging options so as to maximise their reproductive success (Houston & McNamara, 1999; McNamara & Houston, 1992; Real

& Caraco, 1986). The particular risk-sensitive foraging model that has been linked to PT is the daily energy budget rule (Stephens, 1981). This rule was developed to explain the behaviour of small birds foraging in winter, which need to obtain enough energy during the day to enable them to survive the night (when they cannot feed). Building on the work of Caraco (1980), Stephens (1981) analysed this problem by modelling a forager that has initial energy reserves x_0 and needs to get its reserves above some critical level, x_c , by dusk to avoid starving overnight. The forager has two foraging options that offer the same mean gain, g , but differ in variance. If the forager uses the same option throughout the foraging period, then the energy gained will have a normal distribution with a greater variance under the more variable option. Stephens showed that the probability of ending the day with reserves above x_c is maximised by choosing the high-variance option if $x_0 + gt < x_c$, where t is the time until nightfall, whereas the low-variance option is better if $x_0 + gt > x_c$. This result can be restated as: choose the more variable option if the daily energy budget is negative (i.e. if expected gains are insufficient to meet requirements) and the less variable option if the daily energy budget is positive.

Stephens's model was static, in that the forager could not change its behaviour during the foraging period; after making a one-off choice between the high- and low-variance options, it persisted with that option until nightfall. Houston & McNamara (1982) extended Stephens's analysis to allow the forager to make repeated (i.e. dynamic) choices between the two options and showed that the rule still holds. It also holds if starvation during the foraging period is possible (Houston & McNamara, 1985), except at low reserve levels. Empirical work by Caraco et al. (1980, 1990) supported the predictions of the daily energy budget rule, but subsequent tests have yielded mixed results (Kacelnik & El Mouden, 2013).

4. Connections between risk-sensitive foraging theory and prospect theory

Several researchers have noted a possible link between the patterns described by PT and the evolutionary predictions of RSFT (Aktipis & Kurzban, 2004; Caraco & Lima, 1987; McDermott et al., 2008; Mishra, in press; Mishra & Fiddick, 2012; Mishra et al., 2012). For example, Aktipis & Kurzban (2004) argued that the fact that the value function is concave for gains makes sense from an evolutionary perspective, because energetic gains will result in diminishing fitness returns—a given increase in energy matters much more to an animal that is close to starvation than to one that is well fed. They also argued that losses of energy have a bigger impact on fitness than equivalent gains, because losses can sometimes lead to death (and hence zero future reproductive success) whereas gains merely extend the lifespan. In a similar vein, Mishra (in press) asserted that ‘In fitness terms, marginal losses are much more significant than marginal gains of a similar magnitude; the prospect of not reproducing at all is substantially worse than increasing fitness slightly’. If such claims are valid, these factors could conceivably result in an optimal forager that is loss averse, risk averse when well fed and risk prone when close to starvation.

McDermott et al. (2008) took this approach further by explicitly identifying the reference state in PT with the critical level of energy x_c in Stephens’s (1981) daily energy budget rule. They presented a model to show that risk-prone behaviour is optimal in the ‘domain of losses’, where a forager expects an energetic shortfall compared to x_c , whereas risk-averse behaviour is optimal in the ‘domain of gains’, where it expects to exceed x_c . This strategy maximises the chance of surviving to the next day in an environment where the amount of food obtained before nightfall is drawn from a stable probability distribution (e.g.

a normal distribution). If McDermott et al.'s assumptions are valid, such risk proneness in losses and risk aversion in gains appears to provide an evolutionary justification for the reflection effect of PT.

While superficially appealing, on closer inspection these connections turn out to be problematic. There are two related issues: first, whether the function relating reproductive value to energetic gains is likely to have the form assumed by McDermott et al. (2008); and second, whether the reference state in PT corresponds to the critical level x_c in RSFT. We discuss both of these issues below.

5. What is the shape of the reproductive value function?

Following Stephens's (1981) daily energy budget model, McDermott et al. (2008) considered the goal of surviving a single day. They showed that under the assumptions of their model, the probability of survival—which they equated with fitness—is a symmetrical sigmoid function of the expected (i.e. mean) energy gain (Fig. 2). However, this particular function is only valid for a very restricted set of circumstances, namely: when the forager has no choice between foraging options; when there is no benefit of excess reserves above the critical threshold; and when there are no upper or lower boundaries on reserves. Below we examine each of these assumptions in turn.

No choice. In McDermott et al.'s model, the forager has no behavioural choices to make; the amount of food it gains before nightfall is a random draw from a stable probability distribution. This is equivalent to assuming that, after a one-off choice between alternative

options, the forager is constrained to follow some background strategy (McNamara & Houston, 1987). In contrast, Stephens (1981) assumed that, after choosing between a high-variance and a low-variance option, the forager would continue exploiting that food source for the rest of the day. This leads to a reproductive value function that is not symmetrical, but kinked at the critical value of reserves (Fig. 3, thick grey line). If, instead, the forager can switch dynamically between high- and low-variance options, reproductive value is greater than under either static option and the function is less kinked, but still asymmetric (Fig. 3, solid black line; Houston & McNamara, 1982).

No benefit of excess reserves above the critical threshold. Like Stephens (1981), McDermott et al. assumed that the reproductive value at dusk is a step function for which there are no additional benefits of having excess reserves above the critical level x_c . All the forager has to do is survive the night; any decisions made after that point are deemed irrelevant to future reproductive success. But unless there is sure to be plentiful food the next day, reserves at dawn will influence survival that day (e.g. Houston & McNamara, 1993; McNamara & Houston, 1986). To derive the appropriate reproductive value function for this situation, we can use the computational technique of dynamic programming to identify the foraging strategy that maximises survival over a period of several days (Clark & Mangel, 2000; Houston & McNamara, 1999; McNamara & Houston, 1986). The resulting function (Fig. 4, dashed black line) deviates from the symmetrical sigmoid form assumed by McDermott et al., and reveals the importance of having excess reserves above the critical level required to survive the night.

No upper or lower boundaries on reserves. McDermott et al. assumed that the amount of energy gained or lost during the day has no upper or lower limits. But high reserve levels,

although beneficial for overnight survival, may be constrained by physiological limits or entail fitness costs, such as an increased risk of predation (Houston et al., 1997; Witter & Cuthill, 1993). Incorporating an upper limit alters the shape of the reproductive value function (Fig. 4, solid black line). Moreover, in focusing on whether or not the forager has sufficient reserves to survive overnight, McDermott et al. ignored the possibility of starvation during the day. A lower lethal limit changes the shape of the reproductive value function at low reserves (Houston & McNamara, 1999).

The above modifications, which incorporate more biological realism, show that reproductive value will not in general have the symmetrical sigmoid relationship with energy suggested by McDermott et al. (2008). Other complexities, such as fluctuating environmental conditions (Higginson et al., 2012) or the ability to reproduce at high reserves (McNamara et al., 1991), will change the relationship further. Clearly, then, the curvature of the reproductive value function (i.e. where it is convex and where it is concave), and hence the predicted pattern of risk sensitivity, depends critically on the biology of the animal in question and the situation it is facing (McNamara & Houston, 1992; McNamara et al., 1991). To derive the appropriate form of this function, it is necessary to specify how foraging decisions affect the animal's future survival and reproduction (Houston & McNamara, 1999).

One clear advantage of this approach is that it reveals how the value of the animal's life affects its willingness to take risks. Aktipis & Kurzban (2004), McDermott et al. (2008) and Mishra (in press) all claimed that animals should be loss averse because energetic losses can lead to death and are therefore more important for fitness than energy gains, but this claim is unjustified because they did not consider how the value of the animal's life depends on its future expectations. This is something that is explicitly taken into account when deriving the

relationship between reproductive value and energy reserves (Houston & McNamara, 1999). Certain forms of this relationship could, in principle, imply loss aversion. McDermott et al.'s survival function does not do so, however, because it is symmetric about the critical level of energy (see Fig. 2) and therefore predicts equal sensitivity to gains and losses at this point. At the same critical level, Stephens's (1981) model predicts differential sensitivity to gains and losses due to a kink in the function (Fig. 3, thick grey line), but the pattern is opposite to that described by prospect theory (cf. Fig. 1): the loss of a fixed amount of reserves implies a *smaller* change in reproductive value than a gain of the same amount. So a simple application of the daily energy budget rule cannot account for this key feature of PT. The same is true for dynamic choices (Fig. 3, solid black line).

6. Where is the reference point?

In their model, McDermott et al. (2008) explicitly identified the critical level of energy x_c with the reference state in PT. Anything less than this critical level, representing energetic shortfall, was interpreted as a 'loss' and, as identified by Stephens (1981), should favour risk-prone behaviour. Anything above the critical level was interpreted as a 'gain' and should favour risk-averse behaviour. According to McDermott et al., this switch in risk sensitivity above and below x_c is consistent with the reflection effect of PT.

However, the gains and losses in PT represent *changes* in state, rather than final outcomes such as exceeding or falling short of a critical energy level at nightfall (Kahneman & Tversky, 1979, p. 277). Kahneman (2003a) illustrated the importance of changes rather than end states by comparing the attitudes of two people, one whose wealth has decreased

from 4 million to 3 million and the other whose wealth has increased from 1 million to 1.1 million. The second person typically feels happier with their financial report, which is something that McDermott et al.'s model, by focusing on end states, cannot explain. Stephens's (1981) daily energy budget rule is clearly not reference-dependent in the sense used by the architects of PT (Tversky & Kahneman, 1991).

In principle, an optimal individual would be risk averse for gains and risk prone for losses if it sat exactly at the inflection point of McDermott et al.'s (2008) survival function, representing the situation where it expects to gain exactly the right amount of energy to be at the critical level x_c when night falls. But any gain or loss of reserves would change its position on this curve, leading to a different predicted pattern of risk sensitivity. This illustrates a major challenge facing attempts to connect PT with RSFT: for a sigmoidal reproductive value function to predict risk aversion in gains and risk sensitivity in losses consistently, its inflection point needs to track the current level of reserves. None of the existing approaches successfully address this issue. Aktipis & Kurzban (2004) suggested that 'the differently shaped curves for organisms in different states can be profitably thought of as the *same* prospect theory curve with reference points above (in the case of a sated individual) and below (in the case of a hungry individual) the origin' (p. 146), but they gave no clear indication as to what the reference point represents, nor how this state-dependent view can accommodate the reflection effect of PT.

7. Is prospect theory rational?

RSFT, like EUT, offers a rational account of behaviour (Table 1), although the two theories invoke different concepts of rationality. EUT assumes that agents seek to maximise utility (i.e. the satisfaction they derive from decision outcomes) and in this sense are *economically* rational (Bateson, 2010; Houston et al., 2007; Kacelnik, 2006). Utility is not directly measurable and is instead inferred, post facto, from observed choices (for a discussion of the problems this approach entails, see Kacelnik, 2006 and Houston et al., 2007). In contrast, RSFT is founded on the concept of *biological* rationality, according to which individuals have evolved to maximise their inclusive fitness (Bateson, 2010; Houston et al., 2007; Kacelnik, 2006). Differently from utility, fitness can be measured independently of the decisions made, in the currency of reproductive value (Houston et al., 2007). In Stephens's (1981) daily energy budget model, overnight survival is the key determinant of reproductive value; the optimal strategy thus maximises the chance that energy reserves at nightfall exceed the critical level x_c . Comparing final energy reserves to x_c is logical, because the forager dies (and hence has zero future reproductive success) if reserves at nightfall are below x_c and survives if they are above x_c .

Unlike EUT and RSFT, PT does not offer a rational account of behaviour (Table 1). The value function in PT is inferred from empirically observed choices, redefining the utility function of EUT relative to a reference state in a way that can accommodate deviations from economically rational behaviour. Despite their claims, current attempts to explain this value function from an evolutionary perspective fail to offer a rational justification for the reference state. The effects generated by the reference state are not logical in any of the models proposed; indeed, they appear to be irrational (Kahneman, 2003a,b). An economically rational decision maker should be concerned with final outcomes, rather than gains and losses from an earlier state.

8. Concluding remarks

RSFT provides a predictive framework for when individuals should switch between risk-prone and risk-averse behaviour (Houston & McNamara, 1999; McNamara & Houston, 1992). This framework may yet prove to offer useful insights into the evolutionary origins of PT preferences (Caraco & Lima, 1987) and we encourage further research along these lines. For example, a central feature of RSFT is the dependence of risk attitudes on the decision maker's current state. Recent evidence suggests that economic decisions in humans vary with metabolic state (Symmonds et al., 2010) and financial need (Mishra et al., 2012), but in general such state-dependence is underexplored in the PT literature. However, we are unconvinced by recent attempts to marry RSFT with PT (Aktipis & Kurzban, 2004; McDermott et al., 2008; Mishra in press), which are based on an overly simplistic view of how decisions affect reproductive value and fail to account for the key features of PT. Fresh approaches are needed to understand the evolutionary basis of decision making under risk.

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Box 1. Jensen’s inequality and risk sensitivity. Given a particular utility function, the decision maker’s attitude towards risk (*sensu* variability in outcomes) can be inferred from noting the curvature of the function—specifically whether it is convex, concave or linear. This rests on a mathematical proof first given by Danish mathematician Johan Jensen (Jensen, 1906) and has since become known as Jensen’s inequality. To understand the basic concept in graphical terms, consider a decision maker choosing between two options of equal expected monetary value, z . The *fixed* option always provides exactly z units of money, whereas the *variable* option provides $z - \varepsilon$ units on half of occasions and $z + \varepsilon$ units on the other half of occasions. Which option should the decision maker choose to maximise their expected utility? If the relationship between utility (U) and monetary gains is concave (Fig. A, solid line), the decision maker prefers the fixed option and hence is risk averse. This is because the known utility under the fixed option (dashed black line and black arrowhead) exceeds the expected utility under the variable option (dotted grey lines and grey arrowhead), i.e. $U(z) > \frac{1}{2}U(z - \varepsilon) + \frac{1}{2}U(z + \varepsilon)$. If, on the other hand, the relationship is convex (Fig. B), the decision maker prefers the variable option and hence is risk prone, because $U(z) < \frac{1}{2}U(z - \varepsilon) + \frac{1}{2}U(z + \varepsilon)$. If the relationship is linear, the decision maker should be indifferent between the two options (i.e. risk neutral), because $U(z) = \frac{1}{2}U(z - \varepsilon) + \frac{1}{2}U(z + \varepsilon)$. See also Frankenhuis & del Giudice (2012) and Kacelnik & El Mouden (2013).

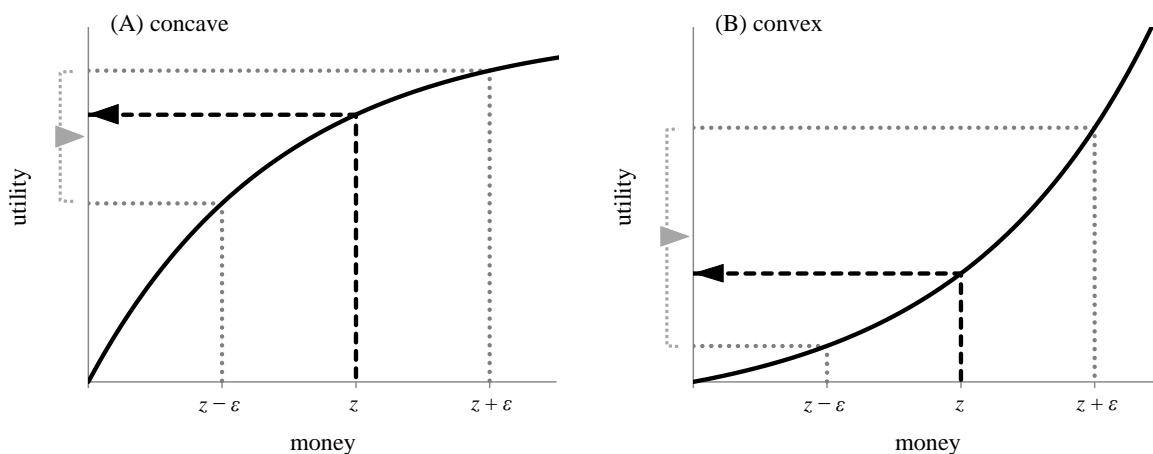


Fig. 1. The value function of prospect theory. Panel (a) shows the perceived value of gains and losses, with the origin marking a reference point from which these gains and losses are measured; panel (b) shows how the slope of this value function changes with the amount gained or lost. Note that the value function is convex (i.e. has a positive change in slope) for losses, implying risk proneness, whereas it is concave (i.e. has a negative change in slope) for gains, implying risk aversion (see Box 1). The steeper slope for losses (associated in this case with a ‘kink’ at the origin, which is indicated by the downward spike in panel (b)) implies loss aversion. Adapted with permission from Kahneman & Tversky (1979).

Fig. 2. The survival function used by McDermott et al. (2008). The animal gains an amount of energy drawn from a stable probability distribution with mean μ and will only survive to the next day if it reaches a critical level of energy x_c (τ in the notation used by McDermott et al.) by nightfall. Panel (a) shows how the mean amount gained (μ , horizontal axis) affects the probability of overnight survival (vertical axis), which is assumed to be equivalent to fitness; panel (b) shows how the slope of this survival function changes with μ . Note that the function is symmetric about x_c and so does not predict loss aversion. Adapted with permission from McDermott et al. (2008).

Fig. 3. The reproductive value function when the forager can choose between high- and low-variance options. Panel (a) shows the relationship between reproductive value and energy reserves; panel (b) shows how the slope of this function changes with energy reserves (a positive change in slope implies risk proneness, whereas a negative change implies risk aversion; see Box 1). If the forager makes a one-off choice and then persists with the chosen option for the rest of the day (static model; thick grey line), it should choose the high-variance option (dashed black line) at low reserves and the low-variance option (dotted black

line) at high reserves. However, it can increase its reproductive value by switching dynamically between the two options (solid black line). The sudden change in slope just before $x = 500$ indicates a ‘kink’ in the reproductive value function as the forager switches from the high-variance option to the low-variance option; but note that this is an abrupt *increase* in slope rather than the abrupt *decrease* shown in the prospect theory curve (Fig. 1). Parameter values: $x_c = 500$; mean net energy gain per time step = 0 (both options), variance = 3.125 (high-variance option) or 1.25 (low-variance option); 60 time steps remaining until nightfall.

Fig. 4. The reproductive value function when the forager has to survive more than one day. Panel (a) shows the relationship between reproductive value and energy reserves; panel (b) shows how the slope of this function changes with energy reserves (a positive change in slope implies risk proneness, whereas a negative change implies risk aversion). Black lines illustrate the case where excess reserves (beyond those needed to survive the night) increase the chances of surviving the following day, with either no limit (dashed black line) or an upper limit of $x = 550$ (solid black line) on the amount of reserves the forager can carry. The appropriate function for reproductive value is found by maximising survival over several days, using dynamic programming (Clark & Mangel, 2000; Houston & McNamara, 1999; McNamara & Houston, 1986). The equivalent function for surviving a single day is shown for comparison (dotted grey line). In all cases we assume dynamic choices (see Fig. 3). Parameter values: $x_c = 500$; mean net energy gain per time step = 0 (both options), variance = 3.125 (high-variance option) or 1.25 (low-variance option); 60 time steps remaining until nightfall.

Table 1. Comparison of the key features of three influential theories of decision making.

Theory	Normative or descriptive?	Rational?	Basis of utility function
Expected utility theory (EUT)	Normative	Yes (economically*)	Inferred from choices
Prospect theory (PT)	Descriptive	No—violates economic rationality	Inferred from choices
Risk-sensitive foraging theory (RSFT)	Normative	Yes (biologically*)	Independently measurable in terms of reproductive value

*See text for the distinction between economic and biological rationality

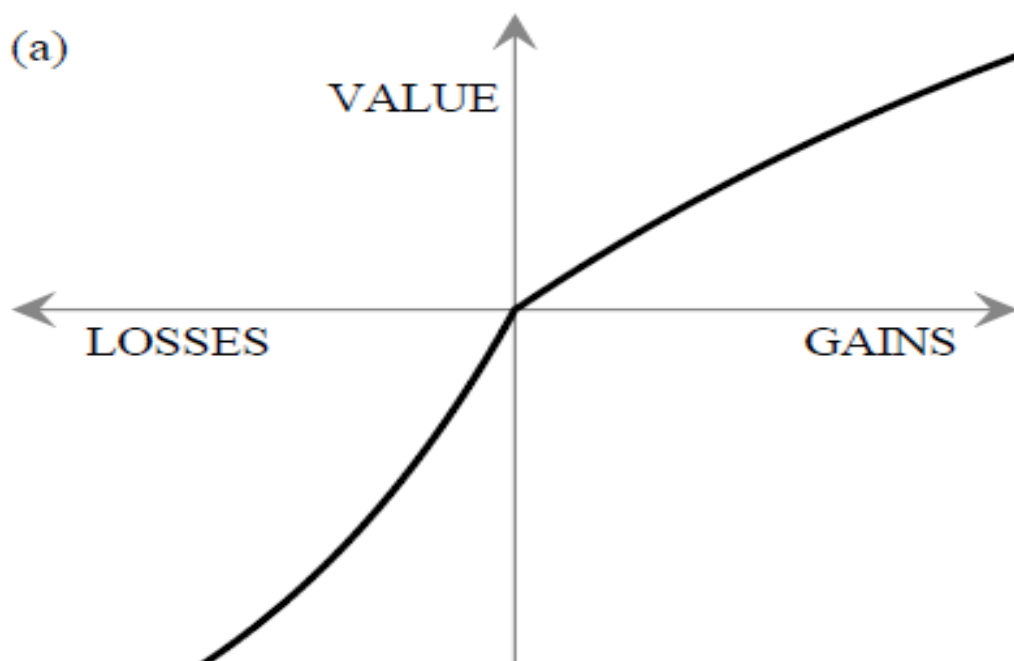
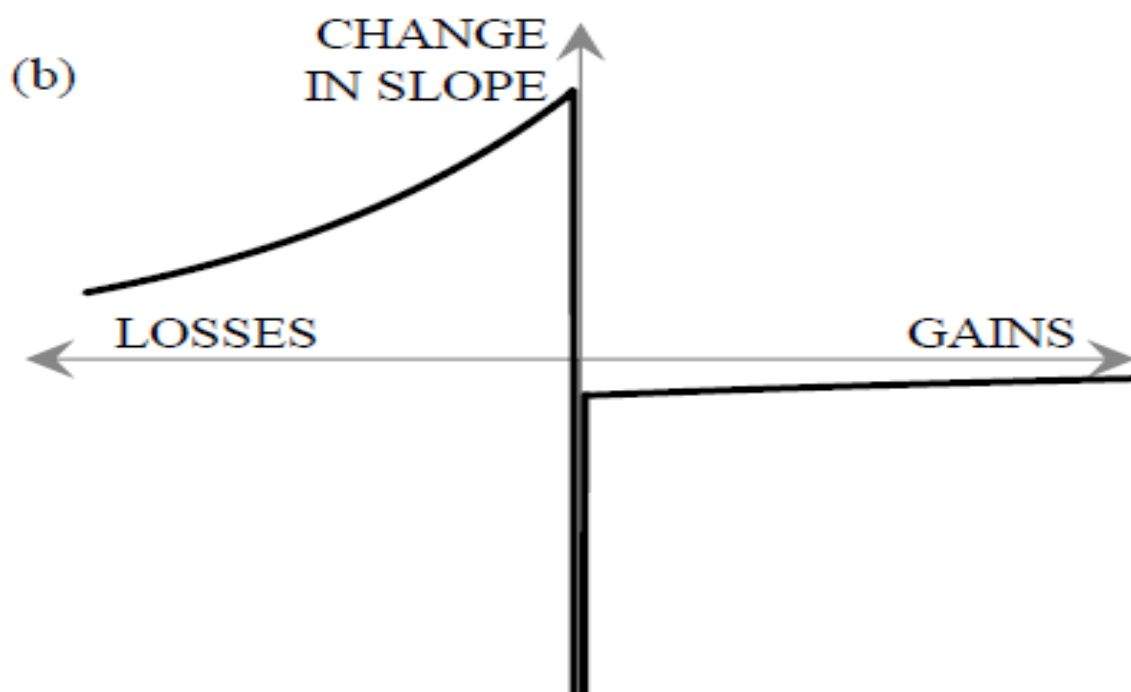
Figure 1a**Figure 1b**

Figure 1

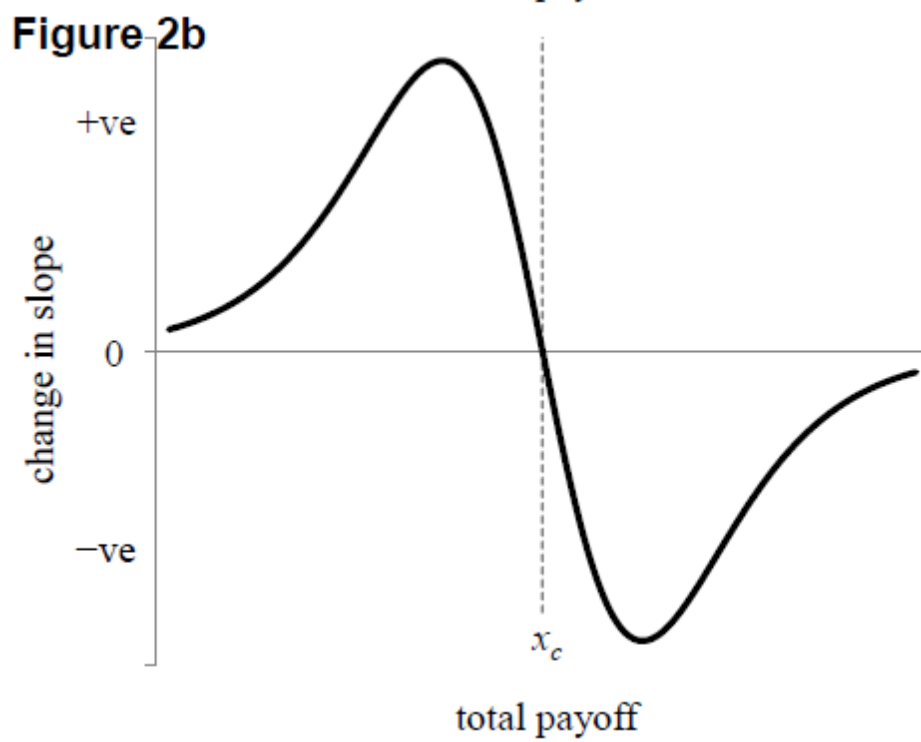
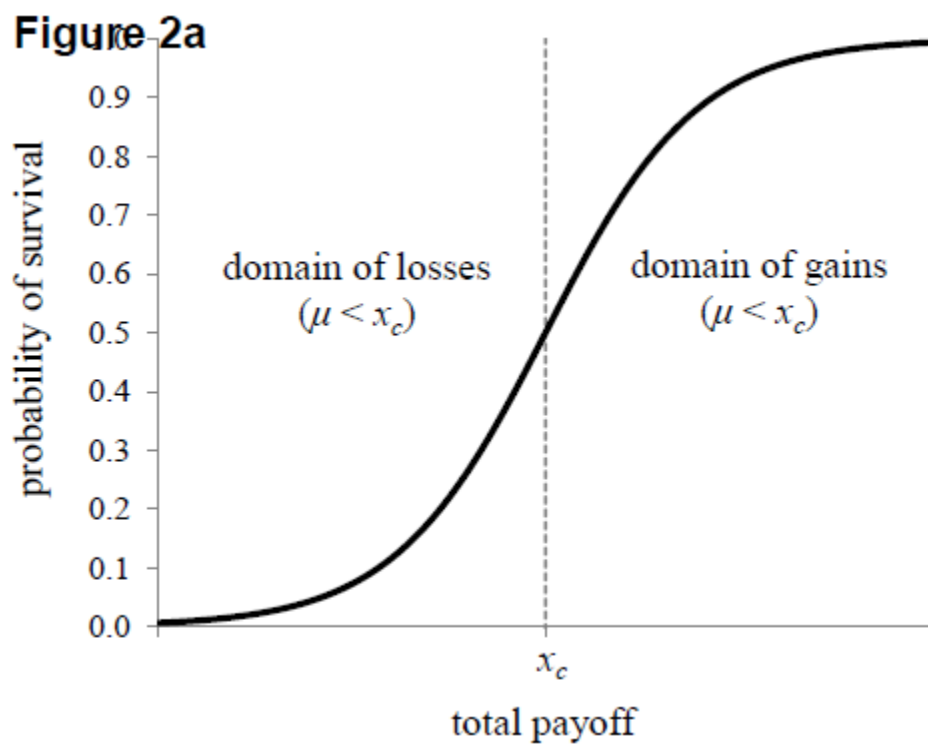


Figure 2

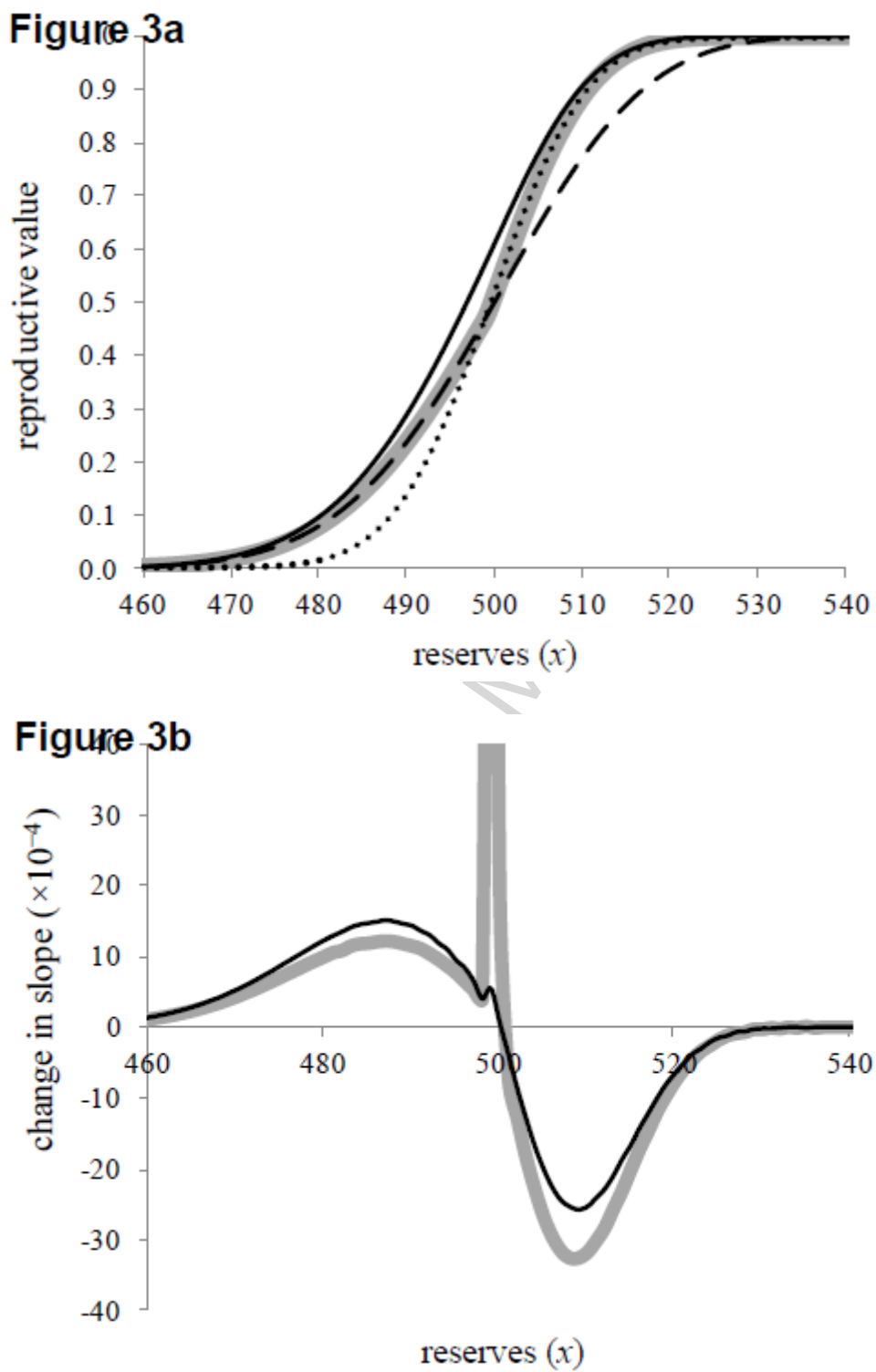


Figure 3

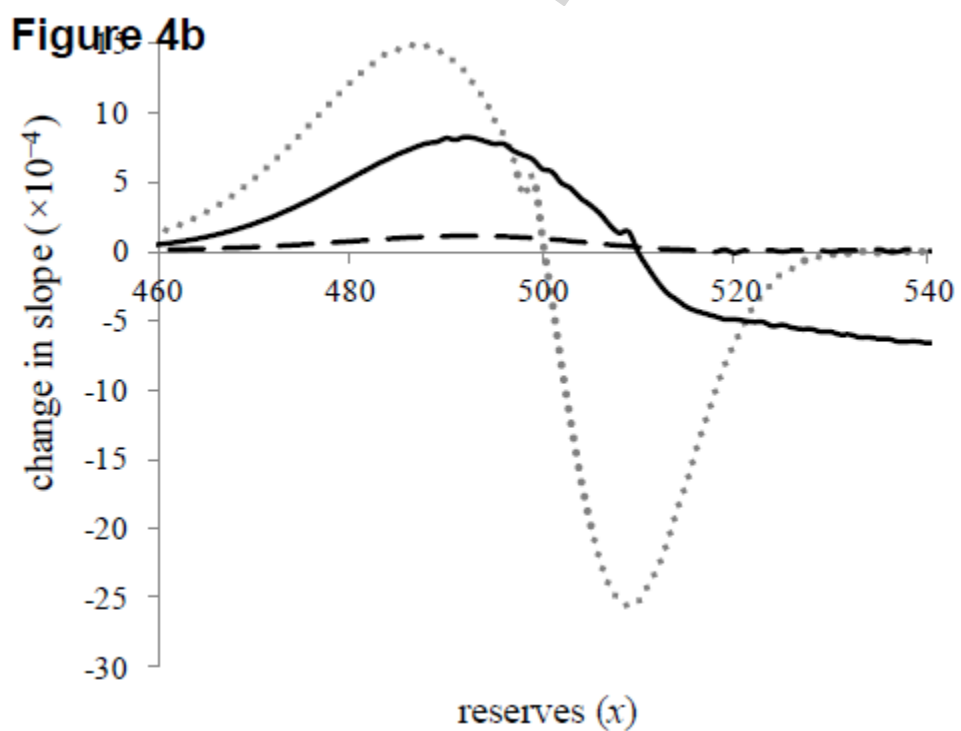
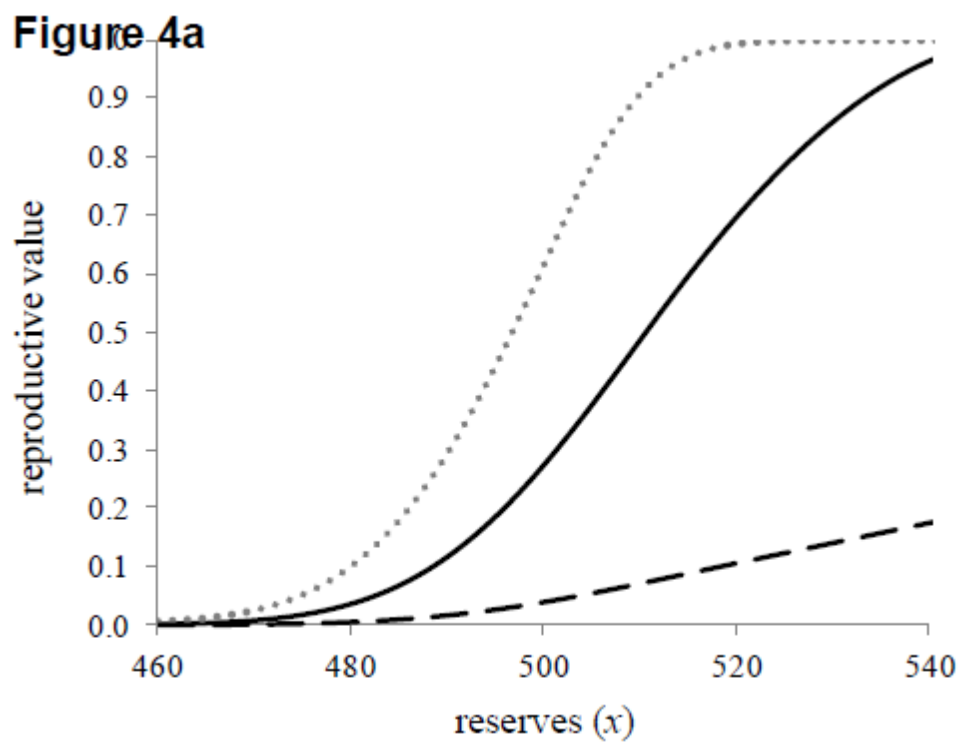


Figure 4