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Risk-sensitive foraging: changes in choice due to reward quality and delay

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Past risk-sensitive foraging studies commonly manipulated delay to reward and reward magnitude, but recent risk-sensitive foraging research revealed that changes in reward quality resulted in changes in a forager's preference for a variable or fixed return. However, no studies have investigated the effects of changes in reward quality and delay to reward on risk sensitivity. Therefore, the current experiment was designed to explore rats' preference for a variable or fixed option when delay to reward and reward quality were manipulated. Using a within-subjects, ABACADA design, rats ($N = 10$) choose between a variable and constant option that delivered six food pellets but the amount of sugar (i.e. reward quality) and delay to reward differed per condition. In each baseline condition, pellets were 100% sugar and delivered after a 2 s mean delay. Subjects displayed a significant preference for the variable option in all baseline conditions. In condition B, pellets were 20% sugar, delivered after a 2 s mean delay, and rats were risk indifferent. In condition C, rats displayed a significant preference for the variable option when delay was 10 s and reward quality was 100%. Finally, in condition D, subjects showed the strongest variable option responses among all treatments when both reward quality and delay to reward were manipulated (i.e. 20% sugar pellets and 10 s mean delay). Preference was assessed relative to the daily energy budget rule, the scalar utility theory and the sequential choice model. The sequential choice model provided the most comprehensive and accurate prediction of subjects' preferences.

The literature on foraging behaviour is replete with studies where a forager makes choices between an option that yields a fixed or constant return and one that is variable or risky in return, commonly referred to as risk-sensitive foraging (Bateson, 2002; Kacelnik & Batson, 1996; Kacelnik & El Mouden, 2013). Typical experiments of risk-sensitive foraging have involved the manipulation of delay to reward or reward magnitude. For example, a procedure where reward amount was manipulated might provide the forager with the choice between one option that delivers a variable amount of reward and another option that returns a fixed reward that yields the mean of the variable option (e.g. Barnard & Brown, 1985; Clements, 1990). Similarly, a procedure where delay to reward was manipulated might provide a forager with a choice between two options that deliver the same amount of food but one after a variable delay to reward and the other following a fixed delay to reward that is equivalent to the mean delay in the variable option (e.g. Bateson & Kacelnik, 1995b; Bateson & Kacelnik, 1998; Kacelnik & Batson, 1996; Kacelnik & Bateson, 1997).

Although variation in reward magnitude and delay to reward are clearly factors that influence preference, animals' decisions are subject to far more complexity when foraging in a natural environment. For example, patches might contain the same amount of prey and the same delay to prey items but differ in the effort required to obtain prey (e.g. Kirshenbaum, Szalda-Petree, & Haddad, 2000; Kirshenbaum, Szalda-Petree, & Haddad, 2003). As such, shifts in preference could result from changes in factors other than amount and delay. Along this line, recent publications have indicated that a forager's experience with different reward qualities in a risk-sensitive foraging procedure causes changes in preference (e.g. Bacon, Hurly, & Healy, 2010; Craft, Church, Rohrback, & Bennet, 2011; Gilby & Wrangham, 2007). However, studies designed to investigate the effects of reward quality on risk-sensitive foraging are limited in number, are not understood in relation to other factors commonly manipulated in risk-sensitive foraging studies (e.g. delay to reward) and have not been thoroughly evaluated by theoretical models commonly used to describe and explain choice in a risk-sensitive foraging situation.

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In light of the aforementioned findings and gaps in the literature, the purpose of the current experiment was three-fold. The first goal of the current experiment was to examine a forager's preference in situations where reward quality and delay to reward were manipulated in order to further investigate the effects of reward quality in relation to factors commonly manipulated in risk-sensitive foraging studies. Second, past studies where reward quality was manipulated relied primarily on the daily energy budget rule to explain shifts in preference. However, it is possible that other models might provide a more accurate prediction or a better explanation of shifts in choice resulting from changes in reward quality. By manipulating both reward quality and delay to reward, a comparison can be made between theoretical models of risk-sensitive foraging while also controlling for any time cost involved in handling or consuming a reward that yields a different rate of gain. That is, manipulations of reward quality provide a unique opportunity to vary the rate of gain that a forager experiences while controlling any added time costs inherent when manipulating reward amount (Caraco, 1981; Harder & Real, 1987). Therefore, the second goal of the current experiment was to evaluate the accuracy of theoretical models in predicting changes in choice that result from reward quality and delay to reward manipulations. Finally, while certain risk-sensitive foraging models have been used to describe choice in a variety of species (e.g. daily energy budget rule), such studies are limited to work with small mammalian and avian species with a high metabolism whereas tests of other models (e.g. sequential choice model) remain unique to one species. Therefore, the final goal of this experiment was to generalize existing models to risk-sensitive foraging and assess risk-sensitive foraging in a relatively larger mammalian species (i.e. rats).

Risk-sensitive Foraging Theory

Optimal foraging theory describes a forager as behaving in a way that maximizes caloric return while minimizing time spent foraging (Charnov, 1976; Pyke, Pulliam, & Charnov, 1977). According to optimal foraging theory, if two options yield the same mean return per unit time, the forager should not display a preference for one option over another; in other words, the forager should be indifferent. Despite this prediction, empirical findings have shown that animals display a preference in circumstances where two options yield the same mean return but one option does so with uncertainty (e.g. Caraco, 1981; Caraco, Martindale, & Whittam, 1980; Caraco et al., 1990). That is, foragers are sensitive to risk or variability and develop choice biases that are inconsistent with optimal foraging theory.

Risk-sensitive foraging theory was developed as an extension of optimal foraging theory in order to explain a forager's choice when risk or uncertainty was involved. According to risk-sensitive foraging theory, an animal that is risk sensitive develops a bias towards an option that delivers a fixed return (i.e. risk-averse choice bias) or variable return (i.e. risk-prone choice bias). Preference in this regard is argued to depend on specific adaptations that allow a forager to maximize return while minimizing time cost and as a result, increase fitness (Kacelnik & El Mouden, 2013). Within risk-sensitive foraging theory, numerous models have been proposed to describe and explain changes in preference where uncertainty was involved (Bateson, 2002; Kacelnik & Batson, 1996; Kacelnik & El Mouden, 2013).

The daily energy budget rule assumes that a forager's choice is based on a functional relationship between caloric return and fitness such that a forager must obtain a precise caloric rate of gain per unit time in order to maintain a necessary daily caloric energy requirement and thus, survive (Caraco, 1981; Caraco et al., 1980, 1990; Stephens, 1981). If the animal is above the caloric requirement or threshold, the forager is in a positive energy budget, and the daily energy budget rule predicts that the animal will display a risk-averse choice bias. However, if the forager has fallen below threshold or, in other words, is in a negative energy budget, the animal will display a risk-prone bias (for a thorough review, see Kacelnik & El Mouden, 2013). In addition to changes in choice occurring due to fluctuations in energy budget, researchers (e.g. Stephens & Charnov, 1982; Stephens & Paton, 1986) argued that a forager's past experience with a particular caloric return could determine choice. For example, a forager with a wealth of caloric reserves could have past experience with a particular return that delivered a minimal rate of gain (e.g. poor quality). Given this, the daily energy budget rule would predict the forager to be risk prone despite being in a positive energy budget. Although elegant, support for the daily energy budget rule has been minimal (Kacelnik & El Mouden, 2013) with the most promising results from situations where ambient temperature (e.g. Caraco et al., 1990), response effort (e.g. Kirshenbaum et al., 2000; Kirshenbaum et al., 2003) and reward quality (e.g. Bacon et al., 2010) was manipulated.

Because of mixed support for the daily energy budget rule, scalar utility theory was proposed. Rather than describe choice as being the result of a forager's energy budget, scalar utility theory is an information-processing model that predict choice in a risk-sensitive foraging procedure (reviewed in: Bateson & Kacelnik, 1995b, 1996, 1998; Church, Meck, & Gibbon, 1994; Gibbon, 1977; Gibbon, Church, Fairhurst, & Kacelnik, 1988; Kacelnik & El Mouden, 2013). As an animal experiences choice options, a memory record is created for each option consistent with Weber's law. That is, after repeated experiences with a fixed option, the option will be represented by a normal distribution with the mean of the distribution being the same as the actual mean of the option and a standard deviation that is proportional to the mean. Similarly, a memory record will be created for the variable option, but the distribution will be positively skewed because smaller or sooner rewards will have more condensed standard deviations than larger or longer rewards. Therefore, when encountering choice options, subjects retrieve a sample from the distribution of each option and choose based on a comparison between samples (Bateson & Kacelnik, 1995b).

According to scalar utility theory, in a risk-sensitive foraging procedure where amount is held constant but delay is variable, the variable delay will be preferred over a fixed delay and thus, subjects will display a risk-prone bias. However, in a risk-sensitive foraging procedure where amount is variable and delay is held constant, forager's will prefer the fixed amount and thus, display a risk-averse bias. Empirical support for scalar utility theory has been considerable (e.g. Bateson & Kacelnik, 1995a, 1995b; Kacelnik & Bateson, 1997).

The aforementioned models describe a forager's preference as developing from the choice between a variable and constant option that is presented simultaneously. Although, researchers (e.g. Aw, Monteiro, Vasconcelos, & Kacelnik, 2012; Shapiro, Siller, & Kacelnik, 2008) argue that this understanding of risk sensitivity could be an artefact of laboratory- or field-based experimental procedures as opposed to the distribution of patches as they might occur in nature. That is, in a natural situation, foragers seldom experience a choice between two options simultaneously and in turn, do not compare alternatives simultaneously. Rather, a forager encounters patches sequentially, and as a result, the animal is forced to engage the current patch or forfeit it in order to move on to another, potentially richer patch. In other words, a forager would maximize return and minimize time expended foraging by engaging rich patches more quickly than poor patches. This perspective has been labelled the sequential choice model (Shapiro et al., 2008).