Tracking a continually changing environment

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# Introduction

In many foraging environments the properties of the available food resources change. In order to adjust to and exploit changing resources, an animal can potentially learn and remember those properties. An animal can never learn everything about its environment; any learned information will always be incomplete, no matter how much effort is spent in obtaining it. One might then ask - when does the benefit of the learned information outweigh the cost of gaining it? The value of information lies in whether it can tell a forager something that changes its behaviour (Stephens, 2007). When a forager’s behaviour allows it to experience environmental change, and so gain information about the current state of the world, this might be termed ‘tracking.’ The information gained can then be translated into appropriate actions (Dunlap and Stephens 2012).

It can easily be seen that the value of seeking information depends on temporal parameters. When an environment changes rapidly any information that is gained by tracking it becomes outdated very soon. When an environment changes so slowly that there is no consequence in the animal’s lifetime, any effort spent in tracking would not yield usable information. Furthermore, the benefit of tracking lies in allowing a forager to choose the best of the options available in an environment - for example, the option that results in the highest caloric gain. For certain combinations of environmental rates of change and differences in the quality of the available options, environmental tracking is both possible and beneficial, in the sense of resulting in a higher energetic net yield. Under some other circumstances it may be preferable to adopt a ‘one size fits all’ or averaging approach, where a forager applies one behavioural response that does best on average over all the possible environmental states (Stephens and Dunlap 2008). One might then ask: what sort of environmental change is tracking, rather than applying an averaging response, beneficial?

An early attempt to model such a situation was done by Stephens (1987), attempting to answer the question of whether, and to what extent, a forager should modify its behaviour in response to a change in its environment. In this simple model the environment has a ‘variable’ option and a stable ‘alternative’ option. The latter has a single value, , and the former can vary between a good state, , and a bad state, , such that > > . The forager can recognise the type of resource (variable vs alternative) upon encounter, but must consume a resource to know its sub-type (good vs bad). The mechanism through which tracking happens is sampling, i.e., visiting the variable option when the last experience of it was the bad state, so as to detect what state it is in at the present time. The probability that the variable option stays the same from one encounter to the next is *q*. A forager can make two kinds of errors, (i.e., choices for the less rewarding option) in this environment: an overrun error if the forager visits the alternative option when the variable is in its good state, and a sampling error if the forager visits the variable when it is in its bad state. The relative cost of these two errors is the ratio .

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Thus the optimal sampling period, i.e., tracking, could be solved for in terms of these two variables. This simple model had several predictions. First, tracking behaviour should decrease with a decrease in . This is because sampling errors become more costly and overrun errors become less costly: increases. When , tracking behaviour should stop completely. Second, and conversely, tracking behaviour should increase with , as overrun errors become more costly, and decreases. Third, tracking behaviour should decrease as *q* decreases, as the states of the variable option become more stable.

These predictions were partially held up by some experimental studies. Hummingbirds were found to decrease their sampling rates as the probability of change of the varying option decreased, as predicted, but did not avoid the variable option when the value increased (Tamm 1987). Similarly, the behaviour of pigeons qualitatively conformed to the predictions of the model, but quantitatively best explained by a model of choice where reward rate is maximized on a moment-to-moment basis based on scalar expectancy (Shettleworth et al. 1988). These experiments manipulated but not *q*. When *q* was manipulated in an experiment with blue jays, presented with either a high and a low rate of change, both sampling and learning rates - i.e., tracking - were found to increase at faster rates of environmental change (Dunlap and Stephens 2012). Similarly, bumblebees sampled the variable resource more frequently when the probability of change was high, as predicted, but did not consistently choose the more rewarding option except when the probability of change was low and the potential reward was very high (Dunlap, Papaj, and Dornhaus 2017)

The merit of the Stephens model is that it outlines the minimum theoretical basis of the issue of environment tracking in order to generate quantitative predictions in a real environment. In a real-world context, however, it is instructive to consider the limitations of the model. A very important assumption of the model is that the forager not only knows the values of the parameters *q* and , but also knows the structure of the environment: that the variable option switches between a good and a bad state. A real foraging animal can only have a distribution of values as an estimate for the parameters, and can never know the whole structure of its environment. Indeed, since *q* is the probability of change at *every* encounter with the variable option, knowing the current state of the variable option does not say anything about what its state will be at the next encounter.

Another caveat that affects the predictions of the model is that sampling, by definition, should never occur when the forager is exploiting the variable option. When the state of variable option is known, the state of the environment is known, so a subsequent visit to the stable alternative option will not yield any further information. Thus, the model’s predictions only apply to what a forager does when it is at the alternative option. Thus, basic assumption of the model, namely that (a) the forager never visits the stable option when exploiting the variable one in its good state, and (b) that the forager immediately switches to the stable option when the variable option switches to its bad state are not met in any of the systems that have been studied. This is a serious issue because it means that while the conceptual contributions and rationale of the model are still valuable, its quantitative predictions are not valid because its assumptions are not fulfilled. These different kinds of foraging errors are discussed in a study by Kacelnik, Krebs and Ens (1987), which offers a series of models for a similar situation but in which the strategies are based on the observation that assumptions of the Stephens model are not met in real datasets.

In this study, we attempted an empirical investigation of the tracking behaviour of the nectar-feeding bat *Glossophaga mutica* (Calahorra-Oliart, Ospina-Garcés, and León-Paniagua 2021) inspired by the rationale of diverse optimality models of sampling behaviour. The natural foraging environment of these animals consists of mainly of flowers that contain varying levels of nectar. From the point of view of an individual bat that encounters a flower, the nectar levels change up continuously according to the flower’s nectar secretion rate and down abruptly, decreasing according to the activity of competitors present in the environment. Because of this, bats must constantly compare flowers in different states: full, partially full, or empty.

In our experiments we placed captive bats in an environment containing two artificial ‘flowers’: a flower that always yielded the same volume of reward - the fixed option - and a flower whose reward volume changed as a sinusoidal function of time, taking values both above and below that of the fixed option. We termed the latter a ‘fluctuating’ option instead of a ‘variable’ option, to differentiate it from an option that could only be in two states, good and bad. While previous empirical tests of tracking models manipulated either the rate of environmental change (*q*) or the relative cost of the two kinds of errors (), we varied the equivalents of both parameters systematically.

The average relative cost of sampling two options, which we term contrast, was determined by the volume of the fixed option. An additional factor is that behaviour may not be driven directly by the absolute real values, but by how they are perceived, and it may be useful to take into account how perception works. In many foraging situations, animals discriminate between relevant variables such as reward magnitudes and time costs according to Weber’s Law, that states that the just-noticeable difference to a stimulus is proportional to the magnitude of the stimulus (Fechner 1860; see Kacelnik and Brito e Abreu 1998 for its application to foraging). In our first experiment the fixed option yielded a reward at the arithmetic mean of the maximum and minimum volumes of the fluctuating option. In the second, the fixed output was smaller than the arithmetic mean. By fixing it at the geometric mean of the variable extremes, we aimed at making the fixed volume equally discriminable from the minimum and maximum values of the fluctuating option, that is, we fixed it at the variable option’s ‘subjective’ mean.

The environmental rate of change in our experiment was determined by the period of the sine function governing the fluctuating output: the smaller the period, the faster the change. In both experiments the bats experienced the same four periods. It is important to note that in this study the rate of environmental change does not correspond to Stephens’ *q*, as the fluctuating option changes not probabilistically, but systematically. From the point of view of the bats however, the reward on an encounter with the fluctuating option changes from the last encounter only when it is discriminably different. The lower the period, the more likely it is that the the fluctuating output is different for a given encounter rate, and so is logically related to the parameter *q*.

In such an environment, a perfectly omniscient, rate maximising animal would allocate its behaviour entirely to whichever option was yielding a higher reward at any point in time. While the original mathematical model and previous studies put tracking in terms of sampling as a mechanism, we redefined tracking behaviour in our experiment as an outcome, along the lines of Dunlap, Papaj, and Dornhaus (2017): allocating choice behaviour by matching the option yielding the larger reward at time of each choice **(see Figure whatever - I will insert an explanatory figure later in the Methods where it is appropriate)**. A closer match between an animal’s choice behaviour and the state of the environment meant that the animal was tracking more efficiently: a perfectly tracking bat would always choose the fluctuating output when it was larger than the fixed and choose the fixed when it was larger than the fluctuating.

We predicted that tracking would be better when a) the period of the sine function was larger, i.e., the environment was changing more slowly and b) when the contrast between the fixed and fluctuating options was higher. The latter condition was satisfied, not when the fixed output was at the arithmetic mean, but when it was at the subjective mean. In the latter case, because of Weber’s Law one may expect for the subjective mean to be equally discriminable from the best and worst fluctuating outputs. In contrast, when the fixed option was placed at the arithmetic mean it could be expected to be less discriminable from the highest fluctuating output than from the lowest, thus making the fixed option to be perceived as being better than the average of the variable one.

We also investigated how much the bats had learned about the structure of their environment. We did not expect the bats to learn how the environment was programmed, i.e., that fluctuating output varied sinusoidally. Instead, we thought it was possible for the bats to detect an increasing or decreasing trend in the fluctuating output and for this to influence their choice behaviour. If a bat could extrapolate so as to expect a visit to follow the trend of recent ones, it may be able to anticipate the benefit of visits with some sensitivity to the trend of change, rather than just its mean recently experienced value. Thus we compared the choice for fluctuating volumes when these volumes were part of a downward trend, to the same volumes when they were part of an upward trend.

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