Natural selection and context-dependent values

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SUMMARY

A simple model in which an animal makes a choice between two simultaneously available foraging options is used to show that we cannot expect natural selection to assign an absolute value (based on fitness) to each option. The example shows that the value of an option depends on its context; in particular, it depends on the option with which it is paired. This dependence results in a pattern of choice that violates a stochastic form of transitivity.

1. INTRODUCTION

There is widespread belief that evolution by natural selection results in animals choosing between options in such a way as to maximize fitness. It is tempting, but incorrect, to go from this view of natural selection to the conclusion that natural selection assigns an absolute value (based on fitness) to each option that an animal can perform. As McNamara & Houston (1986) emphasize, the value of an action depends on the actions that are subsequently performed. It follows that the value of an action cannot be considered without specifying future behaviour.

To illustrate the implications of the dependence of value on future actions, I present an analysis of the behaviour of a forager that can choose between simultaneously available food items. The model is based on the procedure used by Shafir (1994) to investigate the behaviour of honey bees (*Apis mellifera*). Shafir found that the bees' choices were not always transitive. (Roughly speaking, choice is transitive if a is preferred to b and b is preferred to c then a is preferred to c . A precise definition in the context of stochastic choice is given below.) Shafir takes the bees' intransitive choices to be support for a decision procedure in which an option is evaluated by comparing it to another option rather than by assigning an option an absolute value. Shafir refers to this as a 'comparative' evaluation. I show that violations of transitivity are, under some circumstances, a possible consequence of adaptive decisions. The basis of the result is that the contribution that an action makes to an animal's reproductive success depends on the context in which it occurs. In essence, comparative evaluations are likely to evolve. For simplicity, I assume that fitness is maximized by maximizing energetic gain, but the fundamental conclusion about context dependence is not restricted to this situation.

2. SIMULTANEOUS CHOICE WITH NO ERRORS

I consider a forager that is confronted at some time t with a choice between two options. Under option i ($i = 1, 2$) the forager obtains an amount of energy e_i but has to spend a handling time h_i before it can resume foraging. After the handling time is over, the animal can forage at rate γ until time T . If the animal is to maximize the energy that it has obtained by this time, then we can find the best choice by considering

$$H_i = e_i + \gamma(T - t - h_i), \quad (1)$$

where H_i is a measure of the pay-off that results from choosing option i . The optimal action is the one with the highest value of H .

In the current context, the animal should choose option 1 rather than option 2 if and only if $H_1 > H_2$, i.e. if and only if

$$e_1 - \gamma h_1 > e_2 - \gamma h_2. \quad (2)$$

A striking consequence of inequality (2) is that whether option 1 or 2 is best depends on the rate γ . Assume that $e_1 > e_2$ and $h_1 > h_2$. Then there is a critical rate

$$\hat{\gamma} = \frac{e_1 - e_2}{h_1 - h_2},$$

such that option 1 should be chosen if $\gamma < \hat{\gamma}$, and option 2 should be chosen if $\gamma > \hat{\gamma}$.

Switches of this kind are well known in the context of central-place foraging (e.g. Orians & Pearson 1979), where they are usually presented as a response to changes in the round-trip travel time τ . When τ is short, it can be optimal to take a prey type with the smaller e and the smaller h , whereas when τ is long it can be optimal to take the item with the larger e and the larger h . A repetition of the central-place foraging

cycle of foraging and returning with a load generates a rate γ . Because increasing τ decreases γ , the switch seen in the central-place foraging model is clearly analogous to the case that I have presented.

Although the switch from specializing on one prey type to specializing on the other is well known, I think that its full implications have not been realized. By describing the switch in terms of its dependence on the rate that can be achieved after the choice, it becomes clear that the best thing to do when faced with a choice between options depends on the future. The complete switch in the example presented is a dramatic effect based on changing the future rate γ . It serves as an introduction to the less dramatic effects that may occur when the future rate is explicitly derived from repeated choices between the options under consideration.

3. SIMULTANEOUS CHOICE WITH ERROR

In the previous section, the rate γ could be manipulated independently of the animal's choice between two options. I now describe an approach in which the animal makes repeated choices between items. The basic idea is to assume that the animal is selected to maximize its energetic gain, but the decision process is subject to errors. I assume that errors that are costly in terms of energetic gain are less likely than errors that are cheap.

I consider a simultaneous choice procedure in which an animal can choose at time t between the two options introduced above, i.e. option i has energetic content e_i and handling time h_i . After the animal has finished handling the selected option, a time τ elapses before the choice between the two options is again possible. The analysis of simultaneous choice given above will now be applied to this situation, with the rate γ after a choice being derived from repeated opportunities for choice. In addition, I will follow McNamara & Houston (1987) in assuming that choice is subject to error, with the probability of error decreasing as its cost increases. Building on the work of Yellott (1977), McNamara & Houston show that if the probability p_i of choosing option i is given by

$$p_i = \frac{\exp(\beta H_i)}{\sum_j \exp(\beta H_j)}, \quad (3)$$

where H_i is the pay-off if option i is chosen (see equation (1)) and β is a positive constant, then the model satisfies both the choice axiom of Luce (1959) and a weaker condition introduced by Yellott. The parameter β controls the weight that is given to the pay-off for choosing an action. As β decreases, the probability of a suboptimal action being chosen increases. When there are only two options it follows that

$$p_1 = \frac{\exp(\beta(H_1 - H_2))}{1 + \exp(\beta(H_1 - H_2))} \quad (4)$$

and

$$p_2 = 1 - p_1. \quad (5)$$

Equation (4) shows that the probability of choosing an option depends on the difference in the two H s; this difference is a measure of the cost of choosing one action as opposed to another (cf. McNamara & Houston 1986, 1987).

If the animal chooses option i with probability p_i ($i = 1, 2$), then the resulting rate is

$$\begin{aligned} \gamma &= \frac{p_1 e_1 + p_2 e_2}{p_1 h_1 + p_2 h_2 + \tau} \\ &= \frac{p_1 e_1 + (1 - p_1) e_2}{p_1 h_1 + (1 - p_1) h_2 + \tau}. \end{aligned} \quad (6)$$

From equations (1) and (4),

$$p_1 = \frac{\exp(\beta(e_1 - e_2 - \gamma(h_1 - h_2)))}{1 + \exp(\beta(e_1 - e_2 - \gamma(h_1 - h_2)))}. \quad (7)$$

We now have an equation for γ in terms of p_1 and an equation for p_1 in terms of γ . It is straightforward to solve these simultaneous equations, and hence to find p_1 .

We are now in a position to investigate whether stochastic transitivity holds in the model with simultaneous choice with errors. Let $a, b, c, \dots$ be possible options. To make the context of choice explicit, let $p(a, b)$ be the probability of choosing a when faced with a choice of a and b . Choice satisfies strong stochastic transitivity (SST) if

$$\begin{aligned} p(a, b) \geq 0.5 \quad \text{and} \quad p(b, c) \geq 0.5 \\ \text{imply} \quad p(a, c) \geq \max[p(a, b), p(b, c)]. \end{aligned} \quad (8)$$

Tversky & Russo (1969) show that SST is equivalent to substitutability. Choice satisfied substitutability if

$$p(a, c) > p(b, c) \quad \text{implies} \quad p(a, b) > 0.5 \quad (9)$$

and

$$p(a, c) = p(b, c) \quad \text{implies} \quad p(a, b) = 0.5. \quad (10)$$

I follow Houston (1991) in using condition (10) as a test for SST. The condition states that if a and b are equivalent in terms of their probability of being chosen when paired with c , then they should be equally attractive when paired with each other. Rather than carrying out the test with two equivalent options, table 1 gives details of a test that is based on five equivalent options. These are denoted as option i ($i = 1, \dots, 5$). The standard option (corresponding to option c in the above description) has an energy content of four units and a handling time of two units. For a given value of β , the first two columns give the energy content and handling time of a set of options that are equivalent, in that each one has a probability of 0.2 of being chosen when the other option is the standard option. For example, when $\beta = 0.5$, the probability of choosing option 1 ($e = 2, h = 3.569$) when faced with it and the standard option ($e = 4, h = 2$) is 0.2, and the probability of choosing option 2 ($e = 4, h = 7.630$) when faced with it and the standard option is also 0.2.

If substitutability is to hold then when a forager is faced with these two options, or with any two options from the set of equivalent options, the probability of choosing either option should be 0.5 (see condition (10)). To test this, I present the model with two options

Table 1. *A test of the substitutability condition (condition (10)).*

(For each value of β , the table gives a set of five options denoted as option i ($i = 1, \dots, 5$). All members of the set are equivalent, in that they each have the same probability ($p = 0.2$) of being chosen when the other option has an energy of four units and a handling time of two units. Travel time $\tau = 5$. The column headed $p(1, i)$ gives the probability of choosing option 1 when it is paired against option i . See text for further details.)

option	$\beta = 0.5$			$\beta = 1$		
	e	h	$p(1, i)$	e	h	$p(1, i)$
1	2	3.569	0.50	2	0.846	0.50
2	4	7.630	0.40	4	4.606	0.38
3	6	11.692	0.34	6	8.365	0.32
4	8	15.757	0.31	8	12.125	0.29
5	10	19.816	0.29	10	15.880	0.27

from the set of equivalent options. One option is option 1, and the other is option i . The entry on row i gives the probability $p(1, i)$ that option 1 is chosen. For example, when $\beta = 0.5$ the second value of $p(1, i)$ is $p(1, 2)$, which is the probability of choosing option 1 ($e = 2$, $h = 3.569$) when faced with a choice between this option and option 2 ($e = 4$, $h = 7.630$). It can be seen that $p(1, 2) = 0.4$, i.e. substitutability does not hold. The table also shows that substitutability fails to hold in all the other non-trivial cases considered. It follows from the equivalence of substitutability and strong stochastic transitivity (Tversky & Russo 1969) that strong stochastic transitivity does not necessarily hold in this model.

4. DISCUSSION

I have shown that a simple model of simultaneous choice between foraging options that is subject to errors can result in violations of strong stochastic transitivity. I have also found violations when options are encountered successively. The reason for this result is that the probability of choosing an option depends on the achieved rate of gain, γ , which in turn depends on the probability of choosing the option. An option does not have a fixed value, its value depends on the context of choice which determines γ .

It is important to note that although the violations depend on errors in decision making, errors alone are not sufficient to produce violations. We can see this by taking γ to be fixed. Equivalent options have equal H s in the context of choice against a standard option. When γ is fixed, they also have equal H s in the context of choice against each other. The importance of errors is that it makes the rate γ depend on both options available, and hence the H s depend on context.

The context of choice involves the two options presented at time t being available until some time T ,

when the amount of energy obtained is assessed. I have made the assumption that the animal is maximizing the energy obtained by T , which gives results that are independent of t and T . This independence will not necessarily hold if some function of the energy obtained by T is maximized (cf. McNamara & Houston 1987).

Shafir (1994) suggests that the comparative evaluation of options is suboptimal in that it can produce intransitive choice, whereas an independent evaluation of options will produce transitive choice. Shafir goes on to argue that the former choice mechanism may only produce intransitive choices under rare conditions, so that selection against it is weak. I have argued that natural selection on decision making is likely to result in comparative or context-dependent assessment of options. The reason for this is that an option does not make a fixed contribution to fitness; the contribution depends on subsequent actions, and hence on the context of choice.

Although the result provides a possible explanation of the findings of Shafir (1994), my main purpose is not to fit the data of Shafir, but to show that adaptive choice can result in context-dependent values for options. I believe that this is a general conclusion which may be relevant to many aspects of human decision making. For example, the framing effects described by Tversky & Kahneman (1981), in which decisions depend on how problems are described, might be understandable as a consequence of context-dependent values.

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