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Is optimism optimal? Functional causes of apparent behavioural biases

Alasdair I. Houston[a,*], Pete C. Trimmer[a], Tim W. Fawcett[a], Andrew D. Higginson[a], James A.R. Marshall[b], John M. McNamara[c]

[a] Modelling Animal Decisions (MAD) Group, School of Biological Sciences, University of Bristol, Woodland Road, Bristol BS8 1UG, UK
[b] Behavioural & Evolutionary Theory Lab, Department of Computer Science and Kroto Research Institute, University of Sheffield, Regent Court, 211 Portobello, Sheffield S1 4DP, UK
[c] Modelling Animal Decisions (MAD) Group, School of Mathematics, University of Bristol, University Walk, Bristol BS8 1TW, UK

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ABSTRACT

We review the use of the terms 'optimism' and 'pessimism' to characterize particular types of behaviour in non-human animals. Animals can certainly behave as though they are optimistic or pessimistic with respect to specific motivations, as documented by an extensive range of examples in the literature. However, in surveying such examples we find that these terms are often poorly defined and are liable to lead to confusion. Furthermore, when considering behaviour within the framework of optimal decision theory using appropriate currencies, it is often misleading to describe animals as optimistic or pessimistic. There are two common misunderstandings. First, some apparent cases of biased behaviour result from misidentifying the currencies and pay-offs the animals should be maximising. Second, actions that do not maximise short-term pay-offs have sometimes been described as optimistic or pessimistic when in fact they are optimal in the long term; we show how such situations can be understood from the perspective of bandit models. Rather than describing suboptimal, unrealistic behaviour, the terms optimism and pessimism are better restricted to informal usage. Our review highlights the importance of choosing the relevant currency when attempting to predict the action of natural selection.

> What passes for optimism is most often the effect of an intellectual error.
> Raymond Aron (1957)

1. Introduction

In popular usage, *optimism* refers to a tendency to view situations in a favourable light, whereas *pessimism* is a tendency to view situations in an unfavourable light. Psychologists are particularly interested in the factors that make some people optimistic and others pessimistic (Plomin et al., 1992), and the consequences this has for their health and wellbeing (Carver et al., 2010). These terms have been taken from a human context and used by biologists to describe various aspects of behaviour in other animals (e.g., Arendt and Wilson, 1997; Bateson et al., 2011; Forbes, 2005; Iwasa, 1991; Kacelnik et al., 1987; Mendl et al., 2010; Mock and Forbes, 1995; Roitberg, 1990). For example, female *Rhagoletis* flies that lay their eggs on fruit have been classed as 'optimistic' if they overestimate the average quality of fruit clusters and leave a given cluster earlier than would be optimal, and as 'pessimistic' if they underestimate the average quality and stay on the cluster longer than would be optimal (Roitberg, 1990). Another usage focuses on how animals trained on two differently reinforced stimuli respond to an ambiguous stimulus with intermediate characteristics (Mendl et al., 2010). Animals adopting a positive response (i.e., similar to their response to the stimulus predicting more positive reinforcement) are described as optimistic, while those responding negatively are described as pessimistic (Bateson et al., 2011; Brydges et al., 2011; Harding et al., 2004; Matheson et al., 2008).

Table 1 lists some published definitions of optimism. Most definitions refer to the expectation of the focal individual. Humans can report their own expectations; for non-human animals expectations can sometimes be inferred from behaviour. Note that, with the exception of McNamara et al. (2011), the published definitions say nothing about whether the positive outlook is well-founded (based on appropriate beliefs in one's own ability or the situation being faced) or unrealistic (based on inappropriate beliefs). From a biological point of view, it is useful to distinguish between these cases. There are many reasons why we would expect animals to behave differently when the conditions they face are known to be favourable (Houston and McNamara, 1999). In this paper we consider the more puzzling phenomenon of apparently unwarranted optimism, where behaviour appears to be suboptimal given the true state of the world.

Why might animals have unrealistic expectations? Inaccurate estimation of future outcomes may relate to (i) the probability that

* Corresponding author. Tel.: +44 117 9287481; fax: +44 117 3317985.
E-mail address: a.i.houston@bris.ac.uk (A.I. Houston).

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Table 1
Some general and technical definitions of optimism. We do not give definitions of pessimism, which here we regard as having the opposite meaning.

Definition	Source
General	
Hopefulness and confidence about the future or the successful outcome of something; a tendency to take a favourable or hopeful view.	OED Online (2010)
Psychological	
A generalized expectancy that good, as opposed to bad, outcomes will generally occur when confronted with problems across important life domains.	Scheier and Carver (1985)
A mood or attitude associated with an expectation about the social or material future—one which the evaluator regards as socially desirable, to his [or her] advantage, or for his [or her] pleasure.	Tiger (1979)
The inclination to expect favourable life outcomes.	Marshall et al. (1992)
Biological	
High expectation of positive events and/or low expectation of negative events.	Mendl et al. (2010)
Behaving in a way that gives too much weight (in terms of producing surviving offspring) to positive events.	McNamara et al. (2011)
Overestimation of the expected gains from future outcomes.	This paper

an outcome will occur, (ii) the magnitude of the pay-off from an outcome or (iii) a combination of these factors. McNamara et al. (2011) focus on biased estimation of probabilities, i.e., an individual is optimistic if it overestimates the probability with which good outcomes occur. Here we take a more general approach and define optimism as *overestimation of the expected gains from future outcomes*, a definition that also encompasses the overestimation of pay-off magnitudes. An individual is optimistic if it behaves in a way that would be optimal only if future gains were greater than they actually are. We consider pessimism to be the direct opposite of this, i.e., the underestimation of the expected gains from future outcomes, so we largely refrain from explicitly discussing pessimism in the following.

Descriptions of optimism can be either based around cognitive processes or the actions that result from such processes. The former approach addresses internal mechanisms while the latter adopts an external, behavioural view. Here we review the literature relating to external views, in an attempt to clarify and further the understanding of optimistic actions, without concern for the details of the internal workings by which approximations to optimal behavioural choices are generated. Note that this approach explains little or nothing about whether an individual may 'feel' optimistic or pessimistic, rather than simply acting in an optimal manner without such emotions. Our aim, instead, is to explain apparent behavioural biases from a functional viewpoint, and explore the ways in which the evolution of such biases could be favoured by natural selection.

For the purposes of this review, we will not consider the type of cognitive biases identified by Bateson et al. (2011), Brydges et al. (2011), Harding et al. (2004) and Matheson et al. (2008) in how animals respond to ambiguous stimuli. In our framework, optimistic biases are defined relative to optimal behaviour, but it is not clear how to define the optimal response in these kinds of experiments (McNamara et al., 2011). We focus instead on the fitness consequences of decisions, examining two broad classes of apparently optimistic behaviour. First, behaviour may appear to be optimistic in terms of the gains resulting directly from current actions. This may be because of an asymmetry in the immediate pay-offs associated with alternative actions, or because the pay-offs are uncertain. Second, if an individual's current decision influences its future state, this can sometimes generate a conflict between short-term and long-term pay-offs. Such conflicts exist at several temporal scales; for instance between the time to the next reward (short-term) and the rate of energy gain (long-term), or between the rate of energy gain (short-term) and the lifetime production of offspring (long-term). We argue that behaviour may appear to be optimistic when assessed in terms of a short-term currency such as immediate gain and yet be optimal with respect to the long-term currency of fitness. Finally, we discuss cases where apparently optimistic behaviour may arise from an asymmetry in the costs of deviating from the optimum.

2. Direct consequences of current actions

2.1. Asymmetry in immediate pay-offs

Animals must assess the extent to which cues are indicative of particular situations (e.g., the presence of a predator). Given a one-dimensional cue, optimal thresholds for detection systems can be set according to signal detection theory (SDT; Green and Swets, 1966). SDT makes use of the likelihood ratio of available evidence: the likelihood of a particular situation (e.g., a predator being present) given the evidence, divided by the likelihood of the alternative situation (no predator) given the evidence. In conjunction with the costs of different types of error, the likelihood ratio can be used to set an optimal threshold, whereby signals exceeding that threshold are dealt with in a different way to signals below the threshold (e.g., running away or not).

Without considering the costs of each type of error, animals (or detection systems in general) may appear optimistic or pessimistic. For instance, Nesse's (2005) smoke detector principle asserts that fire alarms should go off far more often than fires occur. This is because the cost of a false alarm is much smaller than the cost of an undetected fire. If the probabilities of the outcomes (fire or no fire) are considered alone, without taking account of expected pay-offs, smoke detectors would appear pessimistic. But if we consider the asymmetric fitness consequences of false alarms and undetected fires, this bias is clearly rational. Similarly, in the context of predation, the optimal response to a possible predator cue (such as a snapping twig) depends on the relative costs of fleeing unnecessarily versus ignoring a genuine predator (see Nesse, 2005; Trimmer et al., 2008).

Haselton and Buss (2000) and Haselton and Nettle (2006) use SDT—under the heading of error management theory (EMT)—to consider the decision of whether or not to respond to a signal, when it is assumed that natural selection maximises expected future reproductive success. Haselton and Nettle term any threshold where the possibilities are not equally likely as *biased* and so state (p. 48) that 'a wide variety of biases, both positive (optimistic) and negative (paranoid), may be brought under a single explanatory umbrella.' Although this terminology means that non-zero biases may evolve, it does not mean that the threshold or resulting decisions are non-optimal. Indeed, EMT assumes that natural selection favours optimal decisions. Thus, from a wider perspective than considering biases only in terms of probabilities, EMT is not concerned with optimism or pessimism as we define them here.

2.2. Uncertainty regarding the pay-offs from current actions

Apparently optimistic behaviour might be favoured as a strategy for dealing with uncertainty about the consequences of current actions. For example, when individuals interact directly with one another, they may be uncertain about their own capabilities and about how other individuals are going to behave. In the context of reproductive decisions, individuals may be uncertain about the conditions for raising their offspring. In these cases, selection can produce behaviour that is associated with more favourable outcomes, as discussed below.