Optimistic and pessimistic biases: a primer for behavioural ecologists
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To address the adaptive value of optimism/pessimism an operational definition is required. I define a behavioural decision as relatively optimistic if it is consistent with the animal having either, a higher expectation of reward, or a lower expectation of punishment (threat), than the same animal in a different state (or a different animal). Pessimism is the inverse of optimism. Such relative behavioural biases can arise from various cognitive mechanisms, and do not require inaccurate (i.e. biased) cognitive representations of the probabilities of either rewards or punishers. Normative models show that optimistic and pessimistic behavioural biases can be adaptive in the face of risk or uncertainty. Empirical evidence from a range of species can be interpreted as supporting predictions of these models. Behavioural biases are hypothesised to be a key component of affective states, whose evolutionary function is to prioritise the allocation of resources towards the currently most important fitness-relevant activities.

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Introduction
Optimistic and pessimistic biases belong to a group of decision-making phenomena referred to collectively as cognitive biases. These phenomena were first documented by psychologists and behavioural economists studying human judgement and decision making, but have more recently captured the interest of evolutionary biologists and researchers studying non-human animals.1 Interest in optimistic biases has its origins in two findings from humans. The first is that healthy subjects are, on average, optimistic in their future expectations [1], and moreover, that they tend to rate their expectations as better than they objectively are [2]. The second is that there are consistent individual differences in optimism, with more anxious and/or depressed subjects typically being less optimistic than healthy subjects [3,4]. The link between optimism and affective state in humans has inspired applied ethologists and psychopharmacologists interested in identifying behavioural correlates of affective state to develop behavioural tasks for assessing optimism in animals. The result is a growing body of literature on optimistic/pessimistic biases in animals [5,6,7–9].

The above findings have sparked the interest of behavioural ecologists, because cases of apparent irrationality and unexplained individual differences in behaviour are challenges for adaptationist accounts of behaviour [10,11†]. However, attempts to explain the adaptive value of optimism are currently hindered by confusion over the precise phenomenon under discussion: optimism is defined differently by different constituencies of researchers.

A cognitive bias has recently been defined as, ‘A consistent deviation from an accurate perception or judgement of the world’ [12†]. However, this definition is an unsatisfactory starting point for an exploration of the adaptive value of optimism in animals (and probably also humans). The definition focuses on biases in perception and judgement (cognitive processes), but natural selection acts directly on behavioural output, and the patterns of responses recorded in animal judgement and decision-making experiments are behavioural responses, not cognition. As I will show below, there is no simple mapping between biases in cognitive representations and behaviour (Figure 1). Furthermore, the implication that optimistic biases involve flawed decision-making is inapplicable to the measures of optimism obtained from the tasks currently used in animals in which there is no objectively accurate response. Therefore, we need operational definitions of optimism at the level of observed behaviour that are applicable to the data collected on animals.

In the following sections I aim to clarify: first, the set of behavioural phenomena measured in human and animal subjects included under the umbrella of ‘optimistic cognitive biases’, second, the role of cognitive mechanisms in

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1 Henceforth I refer only to optimism and optimistic biases. Pessimism is simply the inverse of optimism — a human or animal that is more optimistic is simultaneously less pessimistic.

2 Henceforth, animals.
the generation of observed optimistic biases and finally whether optimistic biases can be adaptive.

**What are optimistic cognitive biases?**

**Unrealistic optimistic biases**

In popular usage, a bias implies a judgement or decision that is inaccurate. Bias is therefore an appropriate descriptor of the finding that humans are on average unrealistically optimistic when asked to report the likelihood of future events (e.g. their probability of winning a lottery or being diagnosed with cancer) [2]. Data are obtained by requiring subjects to estimate the absolute probability of a future event or to estimate their probability of experiencing a future event compared to an average person [13]. Given that it is possible to obtain estimates of a subject’s true probability of experiencing an event or true position on a distribution, subjects can be classified as unrealistically optimistic or pessimistic. Unrealistic optimism has not been measured in animals because of the difficulty of finding a behavioural measure that reflects a cognitive representation that is just one element of the cognitive machinery underlying decision-making (Figure 1).

**Relative optimistic biases**

In many cognitive bias studies, subjects are required to respond to questions or stimuli to which there is ostensibly no objectively accurate response. There are at least three bodies of such research relevant to optimism, each using different methods.

The first approach involves measuring a personality trait called dispositional optimism using questionnaires such as the life orientation test (LOT), in which subjects indicate their degree of agreement with statements such as, ‘In uncertain times, I usually expect the best’ [3,14]. The second approach involves studying responses to ambiguous linguistic stimuli. For example, assessing spelling of homophones (e.g. die/dye), priming effects of homographs (e.g. batter) or interpretation of ambiguous sentences (e.g. ‘The doctor examined Emily’s growth’) [15]. The third approach also requires subjects to respond to ambiguous stimuli, but differs in not being dependent on language, because simple response latencies [16,17,18], go/no-go responses [19,20] or choices [21–25] are measured.

Due to the lack of a requirement for language, this third approach is the only one currently developed for use in animals, and the only one for which analogous tasks exist in humans and animals [26,27]. In the most common form, known as judgement bias tasks [8,28], subjects are required to respond to ambiguous cues that are intermediate between two anchor cues on some continuous stimulus dimension (e.g. tone frequency [24,25,29], roughness of substrate [21,23], colour saturation [17,19,30], spatial location [31,32]; Figure 2a). The anchors differ in the valence of an associated outcome (typically positive and negative or positive and less positive/neutral), and these valences have been learned during a prior discrimination training phase. The reinforcers used for positive outcomes are typically food (but see [33,34] for the use of conspecific contact), whereas the punishers used for the negative outcomes include unpleasant noises [35], bitter tastes [16,17,36], exposure to potential predators [32,37], water spray [38] or electric shocks [25,39]. In a simpler variant of these tasks, the anchor cues are biologically meaningful to the subjects and require no prior training (e.g. a smiling versus sad face [27,40] or a con-specific image versus a predator image [34]; Figure 2b). Ambiguous cues in these latter tasks are morphed intermediates between the valenced anchors.
Figure 2

Methodology used in standard judgement bias tasks with animal subjects. (a) A task (based on [17,30]) in which there is an arbitrary association between the cues used and the associated outcomes. In such tasks a training phase is required in which subjects learn the cues associated with reward (R) and punishment (P). Subjects are tested by presenting the two trained cues (R and P) and typically three additional ambiguous cues designated NR for near reward, Amb for maximally ambiguous and NP for near punishment. Ambiguous cues are presented at low frequency during the test phase only, and are typically neither rewarded nor punished. (b) A task (based on [33]) in which the cues used are biologically meaningful to the subjects (in this case domestic chicks) and require no training because chicks are attracted to conspecifics but frightened by predators (in this case, an owl). (c) Example data derived from such tasks. The measured variable is typically either the proportion of go responses (shown) or latency to respond. The figure shows two alternative results: the green solid line corresponds to an optimistic subject that responds to NR, Amb and NP similarly to R, whereas the red dotted line corresponds to a pessimistic subject that responds to NR, Amb and NP similarly to P.

Judgement bias tasks typically produce smooth generalisation gradients between the two anchor cues that can be used to measure optimism (Figure 2c).

Since there is no objectively accurate response in any of the above tasks, biases can only be defined relative to the performance of a specified control group. Thus, an animal is defined as relatively optimistic if it displays a greater expectation of reward or a reduced expectation of punishment than, either the same animal in a different state, or another group of animals. Absolute measures of optimism can be obtained from all the above tasks (although these will only be at the group level in tasks where it is necessary to counter-balance the association between cues and valences across individuals [41]), but they are hard to interpret (what does it mean that the 50% morph between a sad and smiling face is classified as sad? [40]). It is debatable whether the phenomena discussed in this section should be called biases at all [42], but the use of the term is now firmly established in the animal literature [8].

Few studies have directly compared different measures of relative optimism within subjects. One study on humans found that dispositional optimism is positively correlated with priors about expectation of reward computed from choices on a novel behavioural task in which probability of reward was relatively uncertain [43**].

Relationships between unrealistic and relative biases
Few studies have directly compared measures of unrealistic optimism and relative optimism within subjects. There is some evidence in humans that unrealistic comparative optimism and dispositional optimism are uncorrelated, suggesting that they are different phenomena [44,45].

What mechanisms cause optimistic biases?

Unrealistic biases
Unrealistic optimistic biases are attributed to inaccurate (overconfident) cognitive representations of the probability of positive events occurring, because this is what subjects are asked to report [46]. Thus an unrealistic optimistic bias can be thought of as a representational bias. However, this assumption should be treated with caution. It has not been proven that people can accurately report the content of their cognitive representation of the probability of an event in isolation of their cognitive
representations of its payoffs. Since behavioural decisions should be informed by the expectation of an event, which is the product of its probability and payoff, it is possible that we do not have access to the contents of the separate representations feeding into decision-making, and hence report expectations as opposed to probabilities (see Figure 1). A more profound criticism of this literature shows that unrealistic optimistic biases can arise as a statistical artefact of sampling procedures, and questions whether they are real biological phenomena at all [47].

Relative biases
Differences in relative optimistic bias typically cannot be attributed to a specific cognitive mechanism (for a misunderstanding of this point see [48]). A change in behavioural output can be due to changes in any of the cognitive mechanisms via which animals acquire, store and utilise information in decision making (Figure 1; [8]), and from studying behaviour alone, it is therefore not straightforward to infer the cognitive process or processes responsible for an optimistic bias [49**] (although see [43**] for a promising approach). A relative optimistic bias could be produced by greater attention to more positive stimuli or positive features of stimuli [24], higher estimates of the probability of a positive outcome or increased pay-off attached to a positive outcome [8]. Recent studies using pharmacological manipulations [22,32,50,51,52] and brain imaging techniques [53] are starting to shed some light on the neurobiological mechanisms underlying cognitive biases in animals.

Can optimistic biases be adaptive?
Many definitions of cognitive bias describe them as flawed or irrational, and this has led to the assumption by some authors that they are, by definition, evolutionarily maladaptive [10]. However, recent theoretical work suggests that biases at both the representational level (e.g. the representational biases assumed to underlie unrealistic optimism) and the behavioural level (e.g. relative optimistic biases) can potentially be adaptive.

Representational biases
Bayesian decision theory shows that optimal decisions should be based on unbiased (i.e. accurate) estimates of the probability of outcomes and their payoffs [49**]. On the face of it, this suggests that biased representations of probability will result in sub-optimal decisions, and be maladaptive. However, theoretical work from the growing evo-mechio field of research, which seeks to find adaptive explanations for cognitive mechanisms [54,55], has shown that this is not necessarily the case. Biased representations of the probability of events, also referred to as self-deception, could evolve given specific assumptions [49**]. For example, it has been argued that self-deception could be a less cognitively costly alternative, particularly when selection pressure exists for animals to deceive each other [56–58]. A recent model that addresses criticisms of previous work in this area [49**,59**] suggests that self-deception can indeed evolve in certain circumstances [60*].

**Behavioural biases**
Normative models exist for predicting how animals should behave when faced with situations involving risk and uncertainty (see [10] for a review of applications to optimism). Although there is no objectively optimal response in the judgement bias tasks used to assess optimism in animals, it is reasonable to assume that animals will respond in such tasks using evolved cognitive mechanisms for tackling risk and uncertainty. Following this logic, the decision about how to respond to an ambiguous cue perceptually intermediate between two cues associated with punishment and reward can be modelled using an area of Bayesian decision theory known as signal detection theory (SDT; [61]). Consider a test trial in a standard go/no-go judgement bias task in which one anchor (R) is associated with food reward and the other (P) with punishment of some type (Figure 2a). On the basis of the evidence available (the similarity of the cue to each of the anchors) the animal must decide whether to approach (go) or stay put/retreat (no-go). The four possible outcomes for the animal given its decision and the true state of the world (whether reward or punishment actually obtains) are shown in Table 1. SDT shows that the optimal decision depends on: first, the strength of the evidence provided by the cue that the true state of the world is rewarding, second, the animal’s estimates of the prior probabilities that reward and punishment will occur, and finally, the payoffs (benefit or cost) for the animal of the four possible outcomes [42,49**]. Each of these quantities must be estimated by the subject via perception of the current environment, prior learning or evolution. Less evidence of reward is required for a go response to be optimal the higher the prior probability of reward and the higher the payoff from reward relative to the costs of punishment. Under this model, a pessimist can be thought of as an animal with a bias towards the no-go response, whereas an optimist is an animal with a bias towards the go response (Figure 3).

Predictions from the SDT model are broadly supported by empirical results derived from judgement bias tasks mainly published within the applied ethology literature,

| Table 1 |
| --- |
| **Payoffs** of possible outcomes in a go/no-go judgement bias task. |
| | True state of the world |
| | Reward (R) | Punishment (P) |
| Decision | Go | No-go |
| Payoff | b | −c | 0 | 0 |

*Where b is the fitness benefit derived from obtaining the reward and c is the fitness cost suffered as a result of being punished.*
Optimistic and pessimistic biases are hypothesised to be a key component of affective states, whose evolutionary function is hypothesised to be to prioritise the allocation of resources towards the current most important fitness-relevant activities [42,66]. The link between optimistic biases and affect is strengthened by results showing that optimistic biases measured using judgement bias tasks correlate with established measures of subjective mood in human subjects [26,27].

Conclusions
Different methods are used to measure optimism in human and animal subjects, and different claims are made about what is measured. It is important to distinguish between optimistic biases in the cognitive representations of quantities, such as the probability of obtaining a future reward (representational biases), and optimistic biases in observable behaviour (behavioural biases). Behavioural biases are hard to define in absolute terms since there is no objectively accurate response in the tasks used to measure them. However, a relative definition is possible, with an animal being defined as relatively optimistic if it makes behavioural decisions consistent with it having either, a higher expectation of reward, or a lower expectation of punishment, than either the same animal in a different state, or a different animal. Thus far, only behavioural biases have been measured in animals and the evidence for representational biases in humans is weak.

Theoretical modelling has demonstrated that both representational biases and behavioural biases can be adaptive. The adaptive account of behavioural biases is supported by empirical results from experiments in which either the past experiences or current environments of animals are manipulated and predicted shifts in optimism are measured. However, a formal meta-analysis of published results is needed to test these associations properly, because not all results are in line with predictions [24,67].

Behavioural biases are hypothesised to be a key functional component of affective states and play a role in allocating behavioural decisions towards the most important terms. For example, manipulating an animal’s early developmental experience of food availability might alter its priors about the availability of food in the world, and hence reduce optimism that ambiguous cues predict food [17*,23]. Reducing feather condition might impair flight and increase the costs of dealing with a predation attempt, and hence increase pessimism that ambiguous cues predict punishment [62]. In general, it appears that a wide range of manipulations that are likely to either alter perceived prior probabilities of punishment and reward and/or alter the state of the animals so as to alter their payoffs from reward and punishment, produce predicted shifts in optimism (for recent examples see [17*,19,20,25,29,31,32,36–38,41,63–65]).

Although few papers discuss their results within this framework (see [17*] for an exception). As predicted, the proportion of ‘go’ responses increases as the ambiguous cue becomes more similar to R yielding the smooth generalisation gradients typical in judgement bias results (Figure 2c). Although most existing experiments in the applied ethology literature do not explicitly manipulate either, the prior probabilities of reward or punishment or, the payoffs of reward and punishment, many of the manipulations conducted can be construed in these

![Figure 3](https://www.sciencedirect.com)
current fitness-relevant priorities [42, 65]. Thus far, there are only a few cases where comparable judgement bias tasks to those used in animals have been applied to human subjects [26, 27]. Further work of this type is needed to clarify the links between the subjective components of affective states measurable only in humans and the objective measures of optimistic behavioural bias measurable across species.

Conflict of interest
Nothing declared.

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