Preys’ exploitation of predators’ fear: when the caterpillar plays the Gruffalo

Sergio Castellano and Paolo Cermelli

1 Department of Life Science and Systems Biology, University of Turin, via Accademia Albertina 13, Turin 10123, Italy
2 Department of Mathematics, University of Turin, Via Carlo Alberto 10, Turin 10123, Italy

Alike the little mouse of the Gruffalo’s tale, many harmless preys use intimidating deceptive signals as anti-predator strategies. For example, several caterpillars display eyespots and face-like colour patterns that are thought to mimic the face of snakes as deterrents to insectivorous birds. We develop a theoretical model to investigate the hypothesis that these defensive strategies exploit adaptive cognitive biases of birds, which make them much more likely to confound caterpillars with snakes than vice versa. By focusing on the information-processing mechanisms of decision-making, the model assumes that, during prey assessment, the bird accumulates noisy evidence supporting either the snake-escape or the caterpillar-attack motor responses, which compete against each other for execution. Competition terminates when the evidence for either one of the responses reaches a critical threshold. This model predicts a strong asymmetry and a strong negative correlation between the prey- and the predator-decision thresholds, which increase with the increasing risk of snake predation and assessment uncertainty. The threshold asymmetry causes an asymmetric distribution of false-negative and false-positive errors in the snake–caterpillar decision plane, which makes birds much more likely to be deceived by the intimidating signals of snake-mimicking caterpillars than by the alluring signals of caterpillar-mimicking snakes.

1. Introduction

‘Silly old owl. Doesn’t he know, there’s no such thing as a Gruffalo!’ [1]

The Gruffalo is a loved children’s tale [1] about a little, harmless mouse, who ventures in a deep dark wood searching for food. During the search, the mouse survives, in turn, to a fox, an owl and a snake by telling them about his friend, the Gruffalo, an imaginary monster, who is coming there to meet the mouse and whose favourite food just happens to be a fox, an owl and a snake. But then the mouse encounters the Gruffalo, who not only appears to be frighteningly real, but also hungry for mice. Once more, the clever mouse manages to survive by convincing the Gruffalo that he, the mouse, is the one to be scared of. In fact, following the mouse back through the forest, the Gruffalo is impressed by the terrified reaction that the mouse (with the Gruffalo) induces from the snake, the owl and the fox, and when the mouse finally announces that his ‘tummy is beginning to rumble’ and that his ‘favourite food is Gruffalo crumble’, the monster quickly turns and flees, leaving the mouse savouring his nuts.

This nice children story is about the ‘irrational’ nature of fear, which makes us (the Gruffaloes) believe the unbelievable, and succumb to the power of intimidating deceptions. In this sense and from an evolutionary point of view, this story is also a metaphor of the defensive strategies that several harmless preys have adopted to deceive their predators. Paradigmatic examples of intimidating deception are the many tropical species of caterpillars and pupae, which display eyespots and other face-like colour patterns that mimic the face of their own predators’ predators: the small insectivorous birds [2]. These morphological traits are often accompanied by postures and locomotory behaviours that reinforce the threat display: for example, when disturbed, some caterpillars inflate their...
anterior segments, improving the resemblance of a snake-head model [3], or even palpitate their posterior eyespots producing the effect of a blinking vertebrate eye [4]. Although spectacular, eyespots and face-like colour patterns do not closely resemble any particular predator model and their evolutionary success as a survival strategy should be found in their ability to exploit a pre-existing bias in the predators’ cognitive mechanisms of decision-making. Alike the mouse of the Gruffalo tale, caterpillars succeed in their deception because natural selection has predisposed their predators to be deceived.

Cognitive biases in decision-making are systematic errors in the judgement of the world and are widespread in humans and non-human animals [5]. Although some cognitive biases are likely the side-effect of our limited capacity to process and store sensory information [6], other cognitive biases may indeed represent adaptive solutions in the use of the information made available by the environment [7]. For example, when the environment makes information uncertain and costly to acquire, natural selection is expected to favour ‘fast and frugal’ decision rules that bias the probability of decision errors in the less expensive direction [8]. In antagonistic interactions, when the rival’s quality can be only poorly assessed, overconfidence and bravery are expected to evolve if the costs of ‘false-positive’ (i.e. the missed reward owing to overestimation of risks) outweigh (to some extent) the costs of ‘false-negative’ (i.e. the costs of defeat owing to underestimation of risks) [9]. (See also electronic supplementary materials, A1.)

In this paper, we explore the hypothesis that ‘irrational fear’ (the psychological condition induced by an overestimation of risks) has been favoured by natural selection because of the disproportional high costs of ‘false-negative’ relative to ‘false-positive’ errors in predator recognition. To investigate this hypothesis, we develop a sequential-sampling model of decision-making [10–12]. In this model, decision-makers integrate noisy evidence over time and make decisions when the accumulated evidence reaches a given threshold. Sequential-sampling models are dynamic variants of signal detection models [13], which have long been the classic approach in behavioural ecology for investigating optimal animal decisions under perceptual uncertainty [14,15].

2. The model

Imagine an insectivorous bird searching for caterpillars in the dense foliage of a forest. As the bird is flying about, it is facing the risk of being spotted by its predator, the Sparrow Hawk. But the search is worth the risk, because if the bird fails to find enough prey today, it will not survive until tomorrow. Suddenly, the bird spots something moving slowly in front of it. If the stimulus is recognized as a caterpillar, the bird will attack. If it is recognized as a snake, the bird will flee away from it. If it is recognized as a millipede (which we assume to be neither an edible prey nor a dangerous predator), the bird will ignore it and pass on. To decide, the bird needs a cognitive machinery that can process information both rapidly and accurately. But rapidity and accuracy conflict each other and, under conditions of uncertainty, the cognitive machinery should make optimal trade-offs between these two opposing demands.

To model the bird’s decision process, we assume that its cognitive machinery comprises two computational modules: the Caterpillar C-module and the Snake S-module, which control, respectively, the prey-attack and the predator-escape motor responses. By accumulating independent pieces of evidence, the modules compete against each other for execution of the motor response. Competition terminates (and choice is made) when the evidence for either one of the motor responses reaches a critical threshold. Since assessments are uncertain and prone to error, the bird is assumed to obtain a sequence of \( X_1, X_2, \ldots, X_n \) observations and to assign to each of them a score of ‘snakiness’ (s) and ‘caterpillarness’ (c), which may be viewed as the perceived perceptual distance from an internal image of snakes and caterpillars.

Let be \( s \) and \( c \) the scores obtained from the \( X_i \) observation.

Let \( P(s|H^s) \) be the probability of perceiving the stimulus \( s \) when the inspected animal is a snake and \( P(s|H^m) \) when it is not a snake (thus, when it is either a caterpillar or a millipede). Similarly, let \( P(c|H^s) \) be the probability of perceiving the stimulus \( c \) when the inspected animal is a caterpillar and \( P(c|H^m) \) when it is either a snake or a millipede. The S- and C-modules are assumed to compute the log-likelihood ratios of the snake and caterpillar hypotheses, respectively (see [16] and electronic supplementary material, figure S1):

\[
z^s(s_i) = \log \frac{P(s_i|H^s)}{P(s_i|H^m)}
\]

and

\[
z^c(c_i) = \log \frac{P(c_i|H^s)}{P(c_i|H^m)}.
\]

\( z^s(s_i) \) and \( z^c(c_i) \) are thus the coordinates of the observation \( X_i \) in the bi-dimensional decision plane described by the S- and C-dimensions.

For the sake of simplicity, we assume the likelihoods to be normally distributed. Specifically, \( P(s|H^s) \) and \( P(c|H^s) \) are assumed to have mean \( d \) and variance \( \sigma^2 \), whereas \( P(s|H^m) \) and \( P(c|H^m) \) are assumed to have mean \(-d\) and similar variance \( \sigma^2 \). Under these simplifying assumptions, the amount of evidence \( z^s(s) \) supporting \( H^s \) (or, equivalently, the amount of evidence \( z^c(c) \) supporting \( H^c \)) is

\[
z^s(s) = 2ds/\sigma^2 \quad (or \quad z^c(c) = 2dc/\sigma^2).
\]

So far, we have described how the C- and S-computational modules are assumed to process a single piece of information. However, since the acquired information is often noisy and the evaluation often uncertain (i.e. \( \sigma^2 \gg 0 \)), the bird may need several pieces of information before committing to one of the alternative hypotheses (thus, before either attacking, fleeing or ignoring the stimulus). For this reason, we assume that the computational modules accumulate over time-independent pieces of evidence, which are normally distributed in the two-dimensional decision plane with covariance matrices

\[
G = \begin{bmatrix}
4d^2/\sigma^2 & 0 \\
0 & 4d^2/\sigma^2
\end{bmatrix}
\]

and means, respectively, \([2d^2/\sigma^2, -2d^2/\sigma^2]\) if a snake, \([-2d^2/\sigma^2, 2d^2/\sigma^2]\) if a caterpillar, and \([-2d^2/\sigma^2, -2d^2/\sigma^2]\) if a millipede. Note that the two axes of the decision plane are assumed orthogonal (i.e. zero covariance between \( z^s \) and \( z^c \), but see electronic supplementary material, A2, for a discussion of this assumption). After \( n \) samples, the inspected animal will be represented in the decision plane by a point.
be passed (figure 1). whereas to choose no-action both the lower thresholds must only on the type of stimulus processed. 

Decision plane, with transition probabilities that depend

The amounts of evidence for the snake and caterpillar distributions (concentric circles). Coloured arrows show the direction and the drift of the diffusion process that describes the decision-making mechanism. The bird will flee if the decision variable enters the ‘snake’ region, attack if in the ‘caterpillar’ region and it will simply stop the assessment and start a new case that the decision variable falls in either the top-left or the top-right or the bottom-right rectangle, we assume there is a 0.5 probability, respectively, to attack or to ignore the stimulus, to attack or flee from the stimulus, and to flee or ignore the stimulus. The concatenated black arrows show an example of how evidence accumulates over time during a decision: after four time units, the decision variable has crossed the snake threshold, activating the flee motor response. (Online version in colour.)

The four decision threshold values \((a_s, -b_s; a_c, -b_c)\) identify the bird’s decision strategy and directly affect its fitness, by influencing both the response times and the error probabilities. Suppose the bird is inspecting a caterpillar. The inspection can have three outcomes: the bird recognizes and attacks the prey or it confuses the caterpillar with either a snake or a millipede. We indicate with \(a_s^c\) and \(a_c^c\) the two error probabilities (the subscripts and superscripts refer to, respectively, the true and the perceived stimulus). The probability of correctly recognizing the prey is thus \((1 - a_s^c - a_c^c)\).

Furthermore, we indicate with \(a_s^c\) the probability of confusing a snake with a caterpillar or a millipede, with \(a_m^c\) the probability of confusing a millipede with either a caterpillar or a snake, and with \(a_s^m\) and \(a_c^m\) the probabilities of confusing the snake with either a caterpillar or a millipede.

The fitness of a decision strategy depends on the four threshold values and can be represented as a function of both the error probabilities and the inspection times.

**Figure 1.** Graphical representation of the decision-making mechanism. The decision plane is defined by the snake and the caterpillar axes. Since assessment is uncertain, single pieces of sensory information about snakes (square), caterpillars (triangle) and millipedes (circle) have bi-normal, overlapping distributions (concentric circles). Coloured arrows show the direction and the drift of the diffusion process that describes the decision-making mechanism. The bird will flee if the decision variable enters the ‘snake’ region, attack if in the ‘caterpillar’ region and it will simply stop the assessment and start a new search if the decision variable reaches the ‘millipede’ region. In the unlikely case that the decision variable falls in either the top-left or the top-right or the bottom-right rectangle, we assume there is a 0.5 probability, respectively, to attack or to ignore the stimulus, to attack or flee from the stimulus, and to flee or ignore the stimulus. The concatenated black arrows show an example of how evidence accumulates over time during a decision: after four time units, the decision variable has crossed the snake threshold, activating the flee motor response. (Online version in colour.)

\[
\begin{align*}
V_s(n) &= V_s(n-1) + \frac{2d}{\sigma_s^2} s(n), \\
V_c(n) &= V_c(n-1) + \frac{2d}{\sigma_c^2} c(n)
\end{align*}
\]

are the amounts of evidence for the snake and caterpillar hypotheses, respectively.

Equation (2.1) describes a random-walk process on the decision plane, with transition probabilities that depend on the type of stimulus processed.

Choice depends on \(V_s\) and \(V_c\), and the decision is made as soon as one of these variables reaches its critical threshold. Specifically, we assume that each dimension has two thresholds \(a_s, a_c\) and \(-b_s, -b_c\). The lines \(V_s = a_s, V_c = a_c\) are the upper absorbing barriers for the process: when \(V_s \geq a_s\) and \(V_c < a_c\), the bird chooses the escape response; conversely, when \(V_s < a_s\) and \(V_c \geq a_c\), it chooses the attack response. The lines \(V_s = -b_s, V_c = -b_c\) are the lower decision thresholds: when \(V_s \leq -b_s\) and \(V_c \leq -b_c\), both the snake and the caterpillar hypotheses are rejected, and the bird concludes that the inspected animal is a millipede. Note that to choose an action just one of the two upper thresholds must be passed, whereas to choose no-action both the lower thresholds must be passed (figure 1).

\[
p = \frac{\pi}{(1 - a_s^c - a_c^m) \Phi}.
\]

This quantity indirectly affects the probability that the bird will survive its predators. In fact, the larger the number of items that the bird must inspect, the longer the time it must be exposed to the attack of the sparrow hawk, which is

\[
T = (p - 1)(\tau + T_D)
\]

where \(T_D\) is the mean decision time, defined as the weighted sum of the times of all possible decisions:

\[
T_D = \Phi t_m + \Phi a_m \tau_s + \Phi c_a \tau_c + \Phi a_m \alpha_m t_c.
\]
Figure 2. Decision-strategy pay-offs. A decision strategy is defined by four variables, which are, respectively, the bottom- and the top-decision thresholds along the caterpillar and the snake dimension. In (a), we compute the pay-offs of all the combinations of the four decision variables and plot their maximum values against the two bottom thresholds. Maximum pay-offs increase monotonically with the decrease of both the snake and the caterpillar bottom thresholds. In (b), we set the bottom thresholds at their optimal values (i.e. $b_a = -b_c = -5$) and show pay-offs variation as a function of the two top thresholds ($a_c$ and $a_s$). Optimal decisions are made when the caterpillar top threshold is much greater than the snake top threshold, making false-negative errors in prey recognition much more likely than false-positive errors. All the simulations were run using the following set of parameters: $d = 1$; $a^2 = 1$; $\partial_m = 0.4$; $\partial_t = 0.1$; $\pi = 20$; $\tau = 15$; $\varphi = 10^{-3}$; $g(t) = t/(t_i + 10)$. (Online version in colour.)

The number of preys inspected daily, $p$, will also affect the probability that the bird will be killed by a snake. In fact, every day, the bird is expected to inspect $p\partial_t$ snakes. During each encounter, we approximate the probability that the bird will be eaten by the snake by the expression

$$h = a_c^s + a_s^m + (1 - a_c^s - a_s^m)g(t_i).$$

When the bird encounters a snake, it will be killed either if it fails to recognize him (with probability $a_c^s + a_s^m$) or if it does recognize him (with probability $1 - a_c^s - a_s^m$), but fails to escape (with probability $g(t_i)$). In the latter case, $g(t_i)$ describes the increasing predation risk with the increasing time response. This simple choice is computationally less expensive than the more precise estimate of the predation risk involving the mean of $g$ over all decision times. In any case, the probability of surviving to all the snakes encountered in a day is $(1 - h)^p\partial_t$.

By combining equations (2.2b) and (2.2d), we obtain the probability that the bird that adopts a decision strategy $D = (a_c, -b_c, a_s, -b_s)$ will survive until the next day:

$$W(D) = [1 - \varphi(p(D) - 1)(\tau + T_D(D))][(1 - h(D))^p\partial_t].$$

(b) Solution procedure
In order to compute the error probabilities $a_c^s, a_c^m$ and $a_s^c, a_s^m$ as well as the expected decision times $t_c, t_s$, and $t_{cr}, t_{sm}$, we replace the random-walk processes in equation (2.1) by continuous-time diffusion processes in the decision plane. Actually, we have three distinct random walks, and thus diffusion processes, characterized by the probability distributions of the snake, caterpillar and millipede signals, described in the previous section. For a given initial signal in the decision plane, a decision is taken by the animal when the sample path reaches the boundary of the uncertainty region bounded by the decision thresholds. This is a first-exit problem, and, for a given initial signal, the probability that the first exit occurs at a particular threshold, as well as the first exit times, can be computed as explained in electronic supplementary material, A2. Taking the averages with respect to the initial point distributions (either a snake, a caterpillar or a millipede) yields the error probabilities and the mean decision times for each choice of the decision thresholds $(a_c, -b_c, a_s, -b_s)$, which in turn allows us to compute the fitness of each strategy.

3. Results
In our model, the decision strategy is defined by the bottom- and the top-decision thresholds. Figure 2a shows the effect of the two bottom thresholds. The maximum pay-offs of a decision strategy increase monotonically with the decrease of both, because the lower their values the lower the risk of mistaking either a caterpillar or a snake for a millipede. However, since the model assumes that a millipede is recognized only when both the bottom thresholds are crossed, their effect is synergistic: the risk of false negatives is high only when both of the bottom thresholds are high. In figure 2b, we set the bottom thresholds at their optimal values and analyse the effect of the two top thresholds. In this case, the expected pay-offs show a strongly asymmetric distribution. In fact, the highest pay-offs are found when the caterpillar top threshold ($a_c^s = 2$) is about one order of magnitude greater than the snake top threshold ($a_s^m = 0.2$).

The choice of the decision thresholds is the mechanism by which the decision maker can adjust false-positive and false-negative errors in relation to their costs on survival, which depend on the environment. We focus on two environmental factors: the predator pressure and the uncertainty of prey assessment.

(a) The snake predation pressure
In figure 3a,c, we show the effect of the relative abundance of snakes and caterpillars on the optimal decision strategy. In
these simulations, the hawk predation risk is kept constant at a moderately low level ($w = 10^{-2}$, but see electronic supplementary material, figure S2, for the effect of an increase in the hawk predation risk). When there are no snakes and caterpillars are abundant, snake false-positives are much more costly than caterpillar false-positives. For this reason, the optimal top threshold is high along the snake dimension and lower along the caterpillar dimension (i.e. $a_s/C^2 > a_c/C^3$). However, a very low risk of snake predation is sufficient ($q_s = 0.01$) to bias decision to the opposite direction and to make snake false-positives much more likely than caterpillar false-positives. As the snake abundance increases, the decision bias increases as well: under disproportionally high risks of snake predation (i.e. $q_s > 0.15$), a caterpillar has a 50% probability of being mistaken for a snake (figure 3c). The higher the rate of snake false-positives, the higher the number of prospective preys to be assessed, the longer the time the bird spends searching for food and, thus, the higher his risk of being predated by the hawk.

(b) Uncertainty during prey assessment

Figure 3b,d shows the effect of assessment uncertainty on the optimal decision strategy. In our model, uncertainty is described by $\sigma^2$, the variance of the independent pieces of information acquired during inspection. Independent of the assessment accuracy, the optimal snake threshold is always lower than the optimal caterpillar threshold, making snake false-negatives less likely than caterpillar false-negatives. However, when the assessment is accurate, the two types of errors do not conflict strongly against each other and the optimal decision strategy keeps both low. As the uncertainty increases, so does their conflict, because to keep the snake false-negatives low, the caterpillar false-negatives must necessarily increase. Indeed, the increasing uncertainty causes an increase in the difference between the likelihoods of the two types of errors and, consequently, an increasing overestimation of the snake predation risk. An increasing uncertainty in the decision process has the same effect of an increasing risk of snake predation: in both cases, the snake false-negatives become much costlier than the caterpillar false-negatives, favouring an overestimation of the former.

(c) The evolutionary effects of an overestimation of predation risk

When selection favours the evolution of decision mechanisms that overestimate the predation risk in intermediate predators, preys can take advantage of this bias by evolving...
phenotypic traits that increase the probability of false negatives in their predators. In figure 4, we show the distribution of the caterpillar false-negatives in the prey– predator decision space, when the bird adopts the optimal strategy $D^* = (a^*_c, -b^*_s, a^*_s, -b^*_c) = (-0.2, -5, 2, -5)$. The probability that the bird gets the caterpillar confused with a snake or a millipede is 0.39. A mutation that shifts the position of the caterpillar in either the snake or the millipede directions is positively selected because of the survival benefits it provides to the mutant (i.e. the increased rate of false negatives induced in its predator). Indeed, the model suggests that the maximum benefits are expected when the mutant changes along both dimensions. If selection can favour the evolution of intimidating deception strategies in caterpillars, it makes very unlikely the evolution of aggressive mimicry in snakes. In the bird decision space, in fact, snakes lie at the centre of a plateau where the probability of being mistaken for a caterpillar is extremely low. A mutation that shifts the snake towards the caterpillar position would only marginally increase the probability that the snake be confused with a caterpillar.

4. Discussion

In an uncertain world, decision errors are unavoidable, but their negative effects can be at least mitigated by biasing the probability of error in the least costly direction [8]. For example, when there is uncertainty about the dangerousness of a prospective prey, a predator is expected to overestimate the risk of attacking the prey if the costs of false positives (i.e. the perceived prey is actually a predator) are higher than the costs of false negatives (i.e. the perceived predator is actually a prey). Our model of decision-making has been devised to explore this hypothesis by studying the optimal trade-offs between false-positive and false-negative errors in prey and predator detection. Results are consistent with the predictions of the ‘error management theory’ [8]. Decisions, in fact, are strongly biased in the direction that minimizes the probability of failing to recognize a snake (predator), even if this makes very likely the failure of recognizing a caterpillar (prey). Furthermore, the model predicts the bias to increase with both the increasing risks of snake predation and the increasing assessment uncertainty and to decrease with the increasing costs of prey searching.

Since we aimed at exploring the adaptive significance of decision biases and their evolutionary effects, our modelling approach has been that of integrating function and mechanism within a coherent theoretical framework [17]. In fact, adaptive decision biases can be viewed only in the light of the constraints imposed by the cognitive machinery of decision-making [16]. The theoretical model, thus, should be based on some explicit assumptions about not only the rules of decision-making but also the mechanisms of information processing. We made two main assumptions about these mechanisms. First, we assume that noisy evidence for the testing hypotheses is accumulated over time and that a decision is made when the evidence for one of the hypotheses reaches a critical threshold [10–12,18–20]. Second, we assume that, during assessment of prospective preys/predators, the bird makes the two alternative hypotheses (caterpillar/not-caterpillar; snake/not-snake) to compete against each other. Both these assumptions have a robust biological foundation that comes from studies on the neurophysiology of decision-making [21–23]. In particular, Cisek and co-workers [21,23] have provided theoretical and empirical evidence that perceptual, cognitive and motor processes, rather than interacting serially, work in parallel. According to this model, the sensory–motor system accumulates information supporting alternative motor responses, which compete against each other for execution. Although we use the model in a rather specific context (the bird–caterpillar interaction), this same decision mechanism can be extended to a diversity of choice contexts. In our model, the bird had to choose among three alternative actions (flee, attack or ignore) and the decision is basically a three-dimensional process (the caterpillar, the snake and the time dimensions). If the choice had been between two alternative actions (e.g. stay or abandon the foraging patch; approach or ignore a prospective mate), then the decision would have been a two-dimensional process. Finally, if we had reduced decisions to one dimension, by assuming a fixed evaluation time, then our model would have been simply a variant of a classic signal-detection model [13].

The decision mechanism is at the same time a result and a constraint of adaptive evolution. If the parallel processing of alternative actions has been favoured by selection for survival in uncertain and unpredictable environments, this same mechanism might constrain the evolution of adaptive decision rules. For example, when the predation risk increases, our model predicts that: (i) the optimal snake decision threshold should decrease, to keep low the snake false-negatives; and (ii) the optimal caterpillar decision threshold should increase, to...
keep low the caterpillar false-positives. However, this latter change in the decision rules is adaptive only within the constraints imposed by the decision mechanism. If the predator and prey hypotheses were tested in a serial rather than in a parallel fashion, so that the ‘caterpillar’ hypothesis was tested only once the ‘snake’ hypothesis had been rejected, then the optimal caterpillar threshold would have depended only on the costs of confounding a caterpillar with a millipede and would have been much lower than the optimal threshold observed in the parallel processing. In this sense, the negative association between the snake and the caterpillar decision thresholds is the adaptive side-effect of the parallel processing.

While, from the bird’s point of view, the asymmetry of the decision thresholds might be adaptive, from the caterpillar’s point of view, it is a salient feature of the predator’s ‘psychology’ [24], which the caterpillar can exploit to increase its chances of survival in case of detection. In particular, our model shows that the asymmetry of the decision thresholds causes an asymmetric distribution of false-negative errors in the snake–caterpillar decision plane so that the caterpillar resides on the steepest hillside of the decision landscape. If we assume that the prey fitness is strictly associated with its probability to induce false negatives in the predator, then small changes in the position of the prey may be expected to have strong effects on its fitness. Changes can involve traits perceived along either the snake or the caterpillar dimension, but the model suggests that the most effective ones are those that occur along both dimensions. Eye-like markings in many terrestrial [25,26] and aquatic animals [27] are thought to have evolved as an anti-predator adaptation. Three hypotheses have been proposed to explain their functional significance [26]. According to the ‘deflection hypothesis’, eyespots are fake eyes that evolved to draw predators’ attacks to the least vulnerable regions of the prey’s body. In this case, they are thought to modify the form, but not the quality of the perceived prey [28,29]. The other two hypotheses, in contrast, suggest that eyespots evolved to modify the perceived identity of a prospective prey. The mimicry hypothesis suggests that eyespots intimidate predators because they perceive these traits as the eyes of their own predators, whereas the conspicuous signal hypothesis suggests that eyespots intimidate predators simply because they fail to recognize the animal as a palatable prey. These latter two hypotheses are often seen as alternative to each other and some empirical studies have tried to discriminate between them, with contrasting results [30,31]. Our model, however, suggests that conspicuousness and mimicry act simultaneously and synergistically on the decision-making process, so that it might be difficult, if not meaningless, to try to disentangle their effects.

As the little, clever mouse of the Gruffalo’s tale teaches us, fear is in the eyes of beholder and frightened eyes are predisposed to overestimate the real risks. Thus, when natural selection favours fear in predators, it may also favour intimidating bluffs in prey, as long as the expected costs that predators pay by calling an erroneously suspected bluff are much higher than those they pay by being eventually bluff. Our model suggests that the asymmetric costs of decision errors might have a double effect on the prey–predator interaction: it may favour the evolution of intimidating-deception strategies in preys, but constrain the evolution of alluring-deception strategies in predators. In our model, in fact, the bird is more likely to be frightened by a snake-mimicking caterpillar than to be lured by a caterpillar-mimicking snake. Put another words, our model makes the testable prediction that a bluff is more likely to succeed if it threatens costs than if it promises benefits. However, the evolutionary success of a deception strategy depends not only on the probability of succeeding in deception, but also on the costs of failing. The caudal luring of a snake might have a low success probability in attracting lizards or birds [32], but the costs of failure are so low that natural selection might still favour this predator strategy despite the constraining cognitive biases. In contrast, the intimidating-deception strategy of a prey has very high failure costs and it may evolve precisely because the cognitive biases have always maintained a high probability of success.

Authors’ contributions. S.C. designed the model, analysed the results and drafted the manuscript. P.C. provided a mathematical solution of the model and helped draft the manuscript. Both authors gave final approval for publication.

Competing interests. We have no competing interests.

Funding. We received no funding for this study.

References


