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Preys' exploitation of predators' fear: when the caterpillar plays the Gruffalo.

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Running title: The evolution of intimidating deceptions

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

ABSTRACT

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.

Keywords: decision making; cognitive bias; mimicry

INTRODUCTION

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 frightening real, but also hungry for mice. Once more, the clever mouse manages to survive by convincing the Gruffalo to be him, the mouse, 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 to 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, letting the mouse savouring his nuts.

This nice children story is about the "irrational" nature of fear, which makes us (the Gruffaloes) to believe the unbelievable, and to 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 predators of their own 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 to 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 predator's 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 judgment of the world and are widespread in humans and non-humans animals [5]. Although some cognitive biases are likely the side-effect of our limited capacity of processing and storing 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 made 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 quality can be only poorly assessed, overconfidence and bravery is expected to evolve if the costs of 'false-positive' (i.e. the missed reward due to overestimation of risks) overcome (of a certain proportion) the costs of 'false-negative' (i.e. the costs of defeat due to underestimation of risks) [9] (see also supplementary materials A1).

In the present 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].

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 preys 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 is composed by 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 $\boldsymbol{X}_1, \boldsymbol{X}_2 \dots \boldsymbol{X}_n$ observations and to assign to each of them a score of "snakeness" (*s*) and "caterpillarness" (*c*), which may be viewed as the perceived perceptual distance from an internal image of snakes and caterpillars.

Let be s_i and c_i the scores obtained from the $\boldsymbol{X}_i$observation. Let be $P(s_i|H^s)$ the probability of perceiving the stimulus s_i when the inspected animal is a snake and $P(s_i|H^{c,m})$ when it is not a snake (thus, when it is either a caterpillar or a millipede). Similarly, let be $P(c_i|H^c)$ the probability of perceiving the stimulus c_i when the inspected animal is a caterpillar and $P(c_i|H^{s,m})$ 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 Figure S1 in the supplementary materials):

$$z^s(s_i) = \log\frac{P(s_i|H^s)}{P(s_i|H^{c,m})}, \qquad z^c(c_i) = \log\frac{P(c_i|H^c)}{P(c_i|H^{s,m})}.$$

$z^s(s_i)$ and $z^c(c_i)$ are thus the coordinates of the observation $\boldsymbol{X}_i$ 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 $P(c|H^c)$ are assumed to have mean *d* and variance σ^2, whereas $P(s|H^{c,m})$ and $P(c|H^{s,m})$ are assumed to have mean -*d* and similar variance σ^2. Under these simplifying assumptions, the amount of evidence $z^s(s_i)$ supporting H^S (or, equivalently, the amount of evidence $z^c(c_i)$ supporting H^C) is $z^s(s_i) = 2ds_i/\sigma^2$ (or $z^c(c_i) = 2dc_i/\sigma^2$).

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 $G = \begin{bmatrix} \frac{4d^2}{\sigma^2} & 0 \\ 0 & \frac{4d^2}{\sigma^2} \end{bmatrix}$ and means, respectively, $\left[\frac{2d^2}{\sigma^2}, -\frac{2d^2}{\sigma^2}\right]$ if a snake, $\left[-\frac{2d^2}{\sigma^2}, \frac{2d^2}{\sigma^2}\right]$ if a caterpillar, and $\left[-\frac{2d^2}{\sigma^2}, -\frac{2d^2}{\sigma^2}\right]$ if a millipede. Notice that the two axes of the decision plane are assumed orthogonal (i.e. zero covariance between z^s and z^c, but see A2 in the supplementary materials for a discussion of this assumption). After *n* samples, the inspected animal will be represented in the decision plane by a point with coordinates $[V_s(n), V_c(n)]$, where:

$$V_s(n) = V_s(n-1) + \frac{2d}{\sigma^2} s(n), \qquad V_c(n) = V_c(n-1) + \frac{2d}{\sigma^2} c(n) \qquad \text{EQ. 1}$$

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

Eq. 1 describes a random-walk processes on the decision plane, with transition probabilities that depend only 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 and $-b_s$, a_c and $-b_c$). 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.

Notice 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).

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 α_c^s and α_c^m the two error probabilities (the subscripts and superscripts refers to, respectively, the true and the perceived stimulus). The probability of correctly recognizing the prey is thus $(1 - \alpha_c^s - \alpha_c^m)$. Furthermore, we indicate with t_c , t_s , and t_m the mean response times during the assessment of caterpillars, snakes and millipedes. Similarly, we indicate with α_s^c, α_s^m the probabilities of confusing a snake with a caterpillar or a millipede, with α_m^c, α_m^s the probability of confusing a millipede with either a caterpillar or a snake, and with $\alpha_s^c$and α_s^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.

(a) The fitness of a decision strategy

We define the fitness of a decision strategy as the probability that the bird that adopts this strategy will survive until the next day. The bird will survive if (i) it manages to catch π caterpillars and, concomitantly, if it avoids being predated by both (ii) the sparrow hawk, and (iii) the snake. We assume that the probability of being predated by the sparrow hawk is directly proportional to the total time spent in searching for food, with φ being the proportionality constant; whereas the probability of being predated by the snake depends on the ability of recognizing the snake and on the number of snakes that the bird is expected to inspect every day.

To compute these quantities, we assume that the bird finds potential preys/predators every τ time units. The spatial distribution of caterpillars, snakes and millipedes is random and the probabilities of finding them coincide with their relative abundances in the forest, which is ϑ_c (caterpillars), ϑ_s (snakes), and $(\vartheta_m = 1 - \vartheta_c - \vartheta_s)$ (millipedes).

Depending on the decision strategy, the bird will have a probability α_c^s and α_c^m of confounding a caterpillar with a snake or a millipede, and thus the expected number of items that the bird will inspect in order to obtain the daily ratio π of caterpillars is:

$$p = \frac{\pi}{(1-\alpha_c^s-\alpha_c^m)\vartheta_c}. \qquad \text{EQ. 4a}$$

This quantity indirectly affects the probability that the bird will survive to 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:

$$T = (p-1)(\tau + T_D), \qquad \text{EQ. 4b}$$

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

$$T_D = \vartheta_m(t_m + \alpha_m^c \tau_\varepsilon) + \vartheta_c t_c + \vartheta_s \alpha_s^s t_s \qquad \text{EQ. 4c}$$

τ_ε is a constant and represents the penalty paid by the bird when it erroneously attacks a millipede. The probability that the bird will be not predated by the sparrow hawk is $(1 - \varphi T)$.

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

$$h = \alpha_s^c + \alpha_s^m + (1 - \alpha_s^c - \alpha_s^m)g(t_s). \qquad \text{EQ. 4d}$$

When the bird encounters a snake, it will be killed either if it fails to recognize him (with probability $\alpha_s^c + \alpha_s^m$) or if it does recognize him (with probability $1 - \alpha_s^c - \alpha_s^m$), but fails to escape (with probability $g(t_s)$). In the latter case, $g(t_s)$ 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 $(1-h)^{p\vartheta_s}$.

By combining Eq. 4b and 4d, we obtain the probability that the bird that adopts a decision strategy $D=(a_s,-b_s,a_c,-b_c)$ will survive until the next day:

$$W(D)=\left[1-\varphi(p(D)-1)\left(\tau+T_D(D)\right)\right]\left[\left(1-h(D)\right)^{\vartheta_s p(D)}\right]. \qquad \text{EQ. 5}$$

(b) Solution procedure

In order to compute the error probabilities α_c^s, α_c^m, and α_s^c, α_s^m as well as the expected decision times t_s, t_c and t_m, we replace the random walk processes in Eq. 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 A2 of the supplementary materials. Taking the averages with respect to the initial point distribution (either a snake, a caterpillar or a millipede) yields the error probabilities and the mean decision times for each choice of the decision thresholds $(a_s;-b_s;a_c;\ -b_c)$, which in turn allows to compute the fitness of each strategy.

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 payoffs 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 with 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 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 payoffs shows a strongly asymmetric distribution. In fact, the highest payoffs are found when the caterpillar top threshold ($a_c^* = 2$) is about one order of magnitude greater than the snake top threshold ($a_s^* = 0.2$).

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 ($\varphi = 10^{-4}$, but see Fig. S2 in the supplementary materials 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. $a_s^* \gg a_c^*$). However, it suffices a very low risk of snake predation ($\vartheta_s = 0.01$) 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. $\vartheta_s > 0.15$), 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

Figures 3b and 3d show the effect of assessment uncertainty on the optimal decision strategy. In our model, uncertainty is described by σ^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 it does their conflict, because to keep low the snake false negatives, the caterpillar false negatives must necessarily increase. Indeed, the increasing uncertainty causes an increase of 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 $D^* = (a_s^*, -b_s^*, a_c^*, -b_c^*) = (-0.2, -5, 2, -5)$. The probability that the bird gets the caterpillar confused with either 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 lay 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 confounded with a caterpillar.

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 colleagues [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 used 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-dimension 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 decision would have been a two-dimension 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 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, trying 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 preys, 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 bluffed. 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.

Competing interests

We have no competing interests.

Authors' contributions

SC designed the model, analyzed the results and drafted the manuscript. PC provided a mathematical solution of the model and helped draft the manuscript. Both authors gave final approval for publication.

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FIGURE CAPTIONS

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 (red), caterpillars (green) and millipedes (gray) show bi-normal, overlapping distributions (concentric circles). Colored 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 enter 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.

Figure 2. Decision-strategy payoffs. 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 payoffs of all the combinations of the four decision variables and plot their maximum values against the two bottom thresholds. Maximum payoffs 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. $-b_s = -b_c = -5$), and show payoffs variation as a function of the two top thresholds (a_s and a_C). 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: $d = 1;\ \sigma^2 = 1;\ \vartheta_m = 0.4; \vartheta_s = 0.1;\ \pi = 20;\ \tau = 15; \varphi = 10^{-4};\ g(t_s) = \frac{t_s}{t_s+10}$.

Figure 3. The effect of predation risk and assessment uncertainty on the optimal decision strategy. The optimal top-decision thresholds along the snake (filled circles) and the caterpillar (open circles) dimension is shown as a function, respectively, of the predation risk (a) and the uncertainty level (b). An increase of either the predation risk or the uncertainty causes a decrease of the snake thresholds and an increase of the caterpillar thresholds. As a consequence, the false negative errors in snake recognition decrease and the false negative errors in caterpillar recognition increase with the increasing of both the predation risk (c) and the uncertainty level (d). In these simulations, the parameters are those reported in Figure 2.

Figure 4. Contour plot of the bird's decision landscape. Isolines show the probabilities that the object described by the bi-normal density function $\mathbf{N}(s, c, \varepsilon_s = \varepsilon_c = 1)$ be perceived either as a snake (thus, eliciting a flee motor response) or as a millipede (thus, eliciting no motor response). The positions of the "normal" caterpillar in the bird's decision plane have the binormal distribution $\mathbf{N}(s = -1, c = 1, \varepsilon_s = \varepsilon_c = 1)$. A "mutant" caterpillar with $\mathbf{N}(s = -1 + \tau, c = 1 + \omega, \varepsilon_s = \varepsilon_c = 1)$ will be favoured by natural selection if the mutation increases the probability of bird's false negatives. The three arrows from the "normal" caterpillar show the increase in false negatives of a mutant when (i) $\tau = 1$ and $\omega = 0$, horizontal arrow; (ii) $\tau = 0$ and $\omega = -1$, vertical arrow; and iii) $\tau = 1$ and $\omega = -1$, oblique arrow. Analogously, the arrow from the "normal" snake shows the increase in false negatives due to a mutation that causes a shift in the snake bi-normal distribution of $\tau = 1$ and $\omega = -1$.

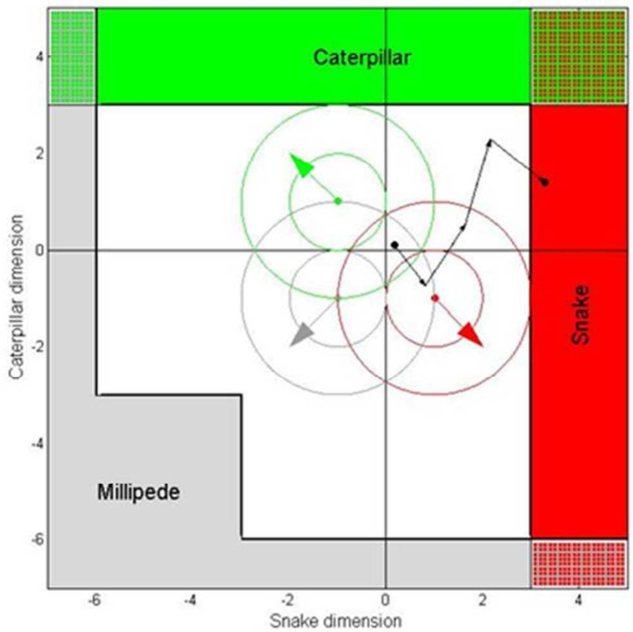

Figure 1
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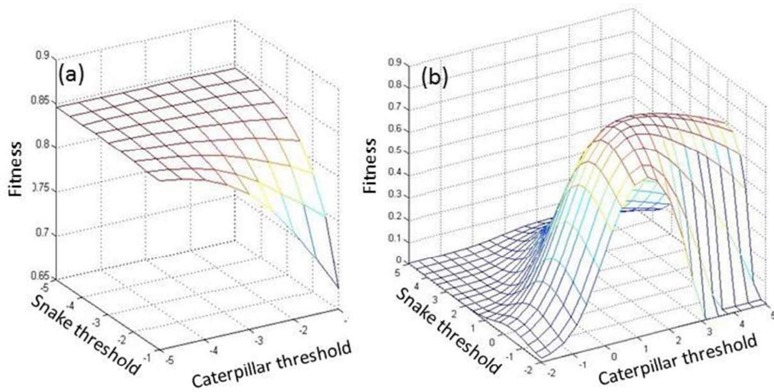

Figure 2
254x190mm (96 x 96 DPI)

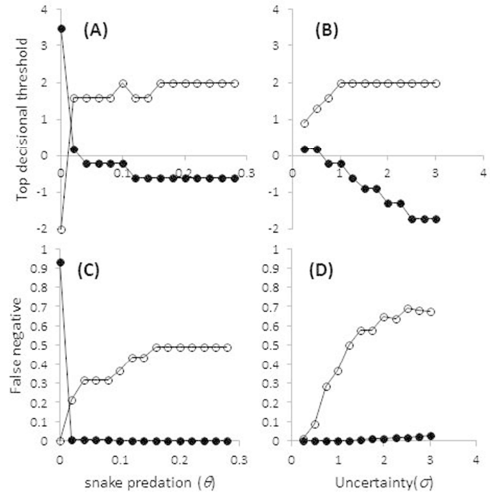

Figure 3
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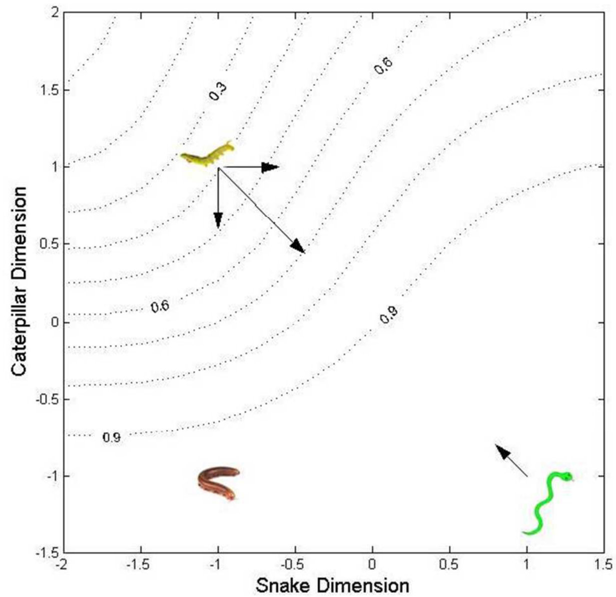

Figure 4
254x190mm (96 x 96 DPI)