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

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Original Citation:

Availability:

This version is available <http://hdl.handle.net/2318/1531260> since 2015-12-04T08:11:08Z

Published version:

DOI:10.1098/rspb.2015.1786

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(Article begins on next page)

PROCEEDINGS B

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Journal:	<i>Proceedings B</i>
Manuscript ID	RSPB-2015-1786.R1
Article Type:	Research
Date Submitted by the Author:	n/a
Complete List of Authors:	Castellano, Sergio; University of Turin, Life Sciences and Systems Biology Cermelli, paolo; University of Torino, Department of Mathematics
Subject:	Evolution < BIOLOGY, Theoretical biology < BIOLOGY, Behaviour < BIOLOGY
Keywords:	decision mechanisms, cognitive bias, mimicry
Proceedings B category:	Theoretical Biology

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23 Running title: The evolution of intimidating deceptions

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

30

31 **ABSTRACT**

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

46

47 Keywords: decision making; cognitive bias; mimicry

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50 INTRODUCTION

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

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

75 Cognitive biases in decision making are systematic errors in the judgment of the world and are widespread
76 in humans and non-humans animals [5]. Although some cognitive biases are likely the side-effect of our
77 limited capacity of processing and storing sensory information [6], other cognitive biases may indeed
78 represent adaptive solutions in the use of the information made available by the environment [7]. For
79 example, when the environment made information uncertain and costly to acquire, natural selection is
80 expected to favour 'fast and frugal' decision rules that bias the probability of decision errors in the less
81 expensive direction [8]. In antagonistic interactions, when the rival quality can be only poorly assessed,
82 overconfidence and bravery is expected to evolve if the costs of 'false-positive' (i.e. the missed reward due
83 to overestimation of risks) overcome (of a certain proportion) the costs of 'false-negative' (i.e. the costs of
84 defeat due to underestimation of risks) [9] (see also supplementary materials A1).

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

93 **The model**

94 Imagine an insectivorous bird, searching for caterpillars in the dense foliage of a forest. As the bird is flying
95 about, it is facing the risk of being spotted by its predator, the Sparrow Hawk. But the search is worth the
96 risk, because if the bird fails to find enough preys today, it will not survive until tomorrow. Suddenly, the
97 bird spots something moving slowly in front of it. If the stimulus is recognized as a caterpillar, the bird will
98 attack. If it is recognized as a snake, the bird will flee away from it. If it is recognized as a millipede (which

99 we assume to be neither an edible prey nor a dangerous predator), the bird will ignore it and pass on. To
 100 decide, the bird needs a cognitive machinery that can process information both rapidly and accurately. But
 101 rapidity and accuracy conflict each other and, under conditions of uncertainty, the cognitive machinery
 102 should make optimal trade-offs between these two opposing demands.

103 To model the bird's decision process, we assume that its cognitive machinery is composed by two
 104 computational modules: the Caterpillar C-module and the Snake S-module, which control, respectively, the
 105 prey-attack and the predator-escape motor responses. By accumulating independent pieces of evidence,
 106 the modules compete against each other for execution of the motor response. Competition terminates
 107 (and choice is made) when the evidence for either one of the motor responses reaches a critical threshold.
 108 Since assessments are uncertain and prone to error, the bird is assumed to obtain a sequence of
 109 $\mathbf{X}_1, \mathbf{X}_2 \dots \mathbf{X}_n$ observations and to assign to each of them a score of "snakeness" (s) and "caterpillarness" (c),
 110 which may be viewed as the perceived perceptual distance from an internal image of snakes and
 111 caterpillars.

112 Let be s_i and c_i the scores obtained from the \mathbf{X}_i observation. Let be $P(s_i|H^S)$ the probability of perceiving
 113 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
 114 either a caterpillar or a millipede). Similarly, let be $P(c_i|H^C)$ the probability of perceiving the stimulus c_i
 115 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-
 116 and C- modules are assumed to compute the log-likelihood ratios of the snake and caterpillar hypotheses,
 117 respectively (see [16] and Figure S1 in the supplementary materials):

$$118 \quad z^S(s_i) = \log \frac{P(s_i|H^S)}{P(s_i|H^{C,m})}, \quad z^C(c_i) = \log \frac{P(c_i|H^C)}{P(c_i|H^{S,m})}.$$

119 $z^S(s_i)$ and $z^C(c_i)$ are thus the coordinates of the observation \mathbf{X}_i in the bi-dimensional decision plane
 120 described by the S- and C- dimensions.

121 For the sake of simplicity, we assume the likelihoods to be normally distributed. Specifically, $P(s|H^S)$ and
 122 $P(c|H^C)$ 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

123 have mean $-d$ and similar variance σ^2 . Under these simplifying assumptions, the amount of evidence $z^s(s_i)$
 124 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
 125 $z^c(c_i) = 2dc_i/\sigma^2$).

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

131 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,

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

$$136 \quad V_s(n) = V_s(n-1) + \frac{2d}{\sigma^2} s(n), \quad V_c(n) = V_c(n-1) + \frac{2d}{\sigma^2} c(n) \quad \text{EQ. 1}$$

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

138 Eq. 1 describes a random-walk processes on the decision plane, with transition probabilities that depend
 139 only on the type of stimulus processed.

140 Choice depends on V_s and V_c , and the decision is made as soon as one of these variables reaches its critical
 141 threshold. Specifically, we assume that each dimension has two thresholds (a_s and $-b_s$, a_c and $-b_c$). The
 142 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
 143 chooses the escape response, conversely, when $V_s < a_s$ and $V_c \geq a_c$ it chooses the attack response. The
 144 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
 145 and the caterpillar hypotheses are rejected, and the bird concludes that the inspected animal is a millipede.

146 Notice that to choose an action just one of the two upper thresholds must be passed, whereas to choose
 147 no-action both the lower thresholds must be passed (Figure 1).

148 The four decision threshold values ($a_s; -b_s; a_c; -b_c$) identify the bird's decision strategy and directly
 149 affect its fitness, by influencing both the response times and the error probabilities. Suppose the bird is
 150 inspecting a caterpillar. The inspection can have three outcomes: the bird recognizes and attacks the prey
 151 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
 152 probabilities (the subscripts and superscripts refers to, respectively, the true and the perceived stimulus).
 153 The probability of correctly recognizing the prey is thus $(1 - \alpha_c^s - \alpha_c^m)$. Furthermore, we indicate with t_c ,
 154 t_s , and t_m the mean response times during the assessment of caterpillars, snakes and millipedes. Similarly,
 155 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
 156 the probability of confusing a millipede with either a caterpillar or a snake, and with α_s^c and α_s^m the
 157 probabilities of confusing the snake with either a caterpillar or a millipede.

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

160 **(a) The fitness of a decision strategy**

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

168 To compute these quantities, we assume that the bird finds potential preys/predators every τ time units.

169 The spatial distribution of caterpillars, snakes and millipedes is random and the probabilities of finding

170 them coincide with their relative abundances in the forest, which is ϑ_c (caterpillars), ϑ_s (snakes), and
 171 ($\vartheta_m = 1 - \vartheta_c - \vartheta_s$) (millipedes).

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

$$175 \quad p = \frac{\pi}{(1 - \alpha_c^s - \alpha_c^m)\vartheta_c}. \quad \text{EQ. 4a}$$

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

$$179 \quad T = (p - 1)(\tau + T_D), \quad \text{EQ. 4b}$$

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

$$181 \quad T_D = \vartheta_m(t_m + \alpha_m^c \tau_\varepsilon) + \vartheta_c t_c + \vartheta_s \alpha_s^s t_s \quad \text{EQ. 4c}$$

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

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

$$187 \quad h = \alpha_s^c + \alpha_s^m + (1 - \alpha_s^c - \alpha_s^m)g(t_s). \quad \text{EQ. 4d}$$

188 When the bird encounters a snake, it will be killed either if it fails to recognize him (with probability
 189 $\alpha_s^c + \alpha_s^m$) or if it does recognize him (with probability $1 - \alpha_s^c - \alpha_s^m$), but fails to escape (with probability
 190 $g(t_s)$). In the latter case, $g(t_s)$ describes the increasing predation risk with the increasing time response.
 191 This simple choice is computationally less expensive than the more precise estimate of the predation risk

192 involving the mean of g over all decision times. In any case, the probability of surviving to all the snakes
 193 encountered in a day is $(1 - h)^{p\vartheta_s}$.

194 By combining Eq. 4b and 4d, we obtain the probability that the bird that adopts a decision strategy

195 $D = (a_s, -b_s, a_c, -b_c)$ will survive until the next day:

$$196 \quad W(D) = [1 - \varphi(p(D) - 1)(\tau + T_D(D))] [(1 - h(D))^{\vartheta_s p(D)}]. \quad \text{EQ. 5}$$

197 (b) Solution procedure

198 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
 199 and t_m , we replace the random walk processes in Eq. 1 by continuous-time diffusion processes in the
 200 decision plane. Actually, we have three distinct random walks, and thus diffusion processes, characterized
 201 by the probability distributions of the snake, caterpillar and millipede signals, described in the previous
 202 section. For a given initial signal in the decision plane, a decision is taken by the animal when the sample
 203 path reaches the boundary of the uncertainty region bounded by the decision thresholds. This is a first-exit
 204 problem, and, for a given initial signal, the probability that the first exit occurs at a particular threshold, as
 205 well as the first exit times, can be computed as explained in A2 of the supplementary materials. Taking the
 206 averages with respect to the initial point distribution (either a snake, a caterpillar or a millipede) yields the
 207 error probabilities and the mean decision times for each choice of the decision thresholds
 208 $(a_s; -b_s; a_c; -b_c)$, which in turn allows to compute the fitness of each strategy.

209 RESULTS

210 In our model, the decision strategy is defined by the bottom and the top decision thresholds. Figure 2a
 211 shows the effect of the two bottom thresholds. The maximum payoffs of a decision strategy increase
 212 monotonically with the decrease of both, because the lower their values the lower the risk of mistaking
 213 either a caterpillar or a snake with a millipede. However, since the model assumes that a millipede is

214 recognized only when both the bottom thresholds are crossed, their effect is synergistic: the risk of false
215 negatives is high only when both the bottom thresholds are high. In Figure 2b, we set the bottom
216 thresholds at their optimal values and analyse the effect of the two top thresholds. In this case, the
217 expected payoffs shows a strongly asymmetric distribution. In fact, the highest payoffs are found when the
218 caterpillar top threshold ($a_c^* = 2$) is about one order of magnitude greater than the snake top threshold
219 ($a_s^* = 0.2$).

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

223 **(a) The snake predation pressure**

224 In Figure 3a,c, we show the effect of the relative abundance of snakes and caterpillars on the optimal
225 decision strategy. In these simulations, the hawk predation risk is kept constant at a moderately low level
226 ($\varphi = 10^{-4}$, but see Fig. S2 in the supplementary materials for the effect of an increase in the hawk
227 predation risk). When there are no snakes and caterpillars are abundant, snake false positives are much
228 more costly than caterpillar false positives. For this reason, the optimal top threshold is high along the
229 snake dimension and lower along the caterpillar dimension (i.e. $a_s^* \gg a_c^*$). However, it suffices a very low
230 risk of snake predation ($\vartheta_s = 0.01$) to bias decision to the opposite direction and to make snake false
231 positives much more likely than caterpillar false positives. As the snake abundance increases, the decision
232 bias increases as well: under disproportionately high risks of snake predation (i.e. $\vartheta_s > 0.15$), a caterpillar
233 has a 50% probability of being mistaken for a snake (Figure 3c). The higher the rate of snake false positives,
234 the higher the number of prospective preys to be assessed, the longer the time the bird spends searching
235 for food and, thus, the higher his risk of being predated by the hawk.

236 **(b) Uncertainty during prey assessment**

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

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

250 When selection favours the evolution of decision mechanisms that overestimate the predation risk in
251 intermediate predators, preys can take advantage of this bias by evolving phenotypic traits that increase
252 the probability of false negatives in their predators. In Figure 4, we show the distribution of the caterpillar
253 false negatives in the prey-predator decision space, when the bird adopts the optimal strategy $D^* =$
254 $(a_s^*, -b_s^*, a_c^*, -b_c^*) = (-0.2, -5, 2, -5)$. The probability that the bird gets the caterpillar confused with
255 either a snake or a millipede is 0.39. A mutation that shifts the position of the caterpillar in either the snake
256 or the millipede directions is positively selected because of the survival benefits it provides to the mutant
257 (i.e. the increased rate of false negatives induced in its predator). Indeed, the model suggests that the
258 maximum benefits are expected when the mutant changes along both dimensions. If selection can favour
259 the evolution of intimidating deception strategies in caterpillars, it makes very unlikely the evolution of
260 aggressive mimicry in snakes. In the bird decision space, in fact, snakes lay at the centre of a plateau where

261 the probability of being mistaken for a caterpillar is extremely low. A mutation that shifts the snake
262 towards the caterpillar position would only marginally increase the probability that the snake be
263 confounded with a caterpillar.

264 **Discussion**

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

277 Since we aimed at exploring the adaptive significance of decision biases and their evolutionary effects, our
278 modelling approach has been that of integrating function and mechanism within a coherent theoretical
279 framework [17]. In fact, adaptive decision biases can be viewed only in the light of the constraints imposed
280 by the cognitive machinery of decision making [16]. The theoretical model, thus, should be based on some
281 explicit assumptions about not only the rules of decision making but also the mechanisms of information
282 processing. We made two main assumptions about these mechanisms. First, we assume that noisy
283 evidence for the testing hypotheses is accumulated over time and that a decision is made when the
284 evidence for one of the hypotheses reaches a critical threshold [10-12,18-20]. Second, we assume that,

285 during assessment of prospective preys/predators, the bird makes the two alternative hypotheses
286 (caterpillar/not-caterpillar; snake/not-snake) to compete against each other. Both these assumptions have
287 a robust biological foundation that comes from studies on the neurophysiology of decision making [21-23].
288 In particular, Cisek and colleagues [21,23] have provided theoretical and empirical evidence that
289 perceptual, cognitive and motor processes, rather than interacting serially, work in parallel. According to
290 this model, the sensory-motor system accumulates information supporting alternative motor responses,
291 which compete against each other for execution. Although we used the model in a rather specific context
292 (the bird-caterpillar interaction), this same decision mechanism can be extended to a diversity of choice
293 contexts. In our model, the bird had to choose among three alternative actions (flee, attack or ignore) and
294 the decision is basically a three-dimension process (the caterpillar, the snake and the time dimensions). If
295 the choice had been between two alternative actions (e.g. stay or abandon the foraging patch; approach or
296 ignore a prospective mate), then decision would have been a two-dimension process. Finally, if we had
297 reduced decisions to one dimension, by assuming a fixed evaluation time, then our model would have been
298 simply a variant of a classic signal-detection model [13].

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

310 between the snake and the caterpillar decision thresholds is the adaptive side-effect of the parallel
311 processing.

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

334 As the little, clever mouse of the Gruffalo's tale teaches us, fear is in the eyes of beholder and frightened
335 eyes are predisposed to overestimate the real risks. Thus, when natural selection favours fear in predators,

336 it may also favour intimidating bluffs in preys, as long as the expected costs that predators pay by calling an
337 erroneously-suspected bluff are much higher than those they pay by being eventually bluffed. Our model
338 suggests that the asymmetric costs of decision errors might have a double effect on the prey-predator
339 interaction: it may favour the evolution of intimidating-deception strategies in preys, but constrain the
340 evolution of alluring-deception strategies in predators. In our model, in fact, the bird is more likely to be
341 frightened by a snake-mimicking caterpillar than to be lured by a caterpillar-mimicking snake. Put another
342 words, our model makes the testable prediction that a bluff is more likely to succeed if it threatens costs
343 than if it promises benefits. However, the evolutionary success of a deception strategy depends not only on
344 the probability of succeeding in deception, but also on the costs of failing. The caudal luring of a snake
345 might have a low success probability in attracting lizards or birds [32], but the costs of failure are so low
346 that natural selection might still favour this predator strategy despite the constraining cognitive biases. In
347 contrast, the intimidating-deception strategy of a prey has very high failure costs and it may evolve
348 precisely because the cognitive biases have always maintained a high probability of success.

349 **Competing interests**

350 We have no competing interests.

351 **Authors' contributions**

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

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425 **FIGURE CAPTIONS**

426 **Figure 1.** Graphical representation of the decision-making mechanism. The decision plane is defined by the
 427 snake and the caterpillar axes. Since assessment is uncertain, single pieces of sensory information about
 428 snakes (red), caterpillars (green) and millipedes (gray) show bi-normal, overlapping distributions
 429 (concentric circles). Colored arrows show the direction and the drift of the diffusion process that describes
 430 the decision-making mechanism. The bird will flee if the decision variable enter the 'snake' region, attack if
 431 in the 'caterpillar' region and it will simply stop the assessment and start a new search, if the decision
 432 variable reaches the 'millipede' region. In the unlikely case that the decision variable falls in either the top-
 433 left or the top-right or the bottom-right rectangle, we assume there is a 0.5 probability respectively to
 434 attack or to ignore the stimulus, to attack or flee from the stimulus, and to flee or ignore the stimulus. The
 435 concatenated black arrows show an example of how evidence accumulates over time during a decision:
 436 after four time units, the decision variable has crossed the snake threshold, activating the flee motor
 437 response.

438 **Figure 2.** Decision-strategy payoffs. A decision strategy is defined by four variables, which are, respectively,
 439 the bottom and the top decision thresholds along the caterpillar and the snake dimension. In (a), we
 440 compute the payoffs of all the combinations of the four decision variables and plot their maximum values
 441 against the two bottom thresholds. Maximum payoffs increase monotonically with the decrease of both
 442 the snake and the caterpillar bottom thresholds. In (b), we set the bottom thresholds at their optimal
 443 values (i.e. $-b_s = -b_c = -5$), and show payoffs variation as a function of the two top thresholds (a_s and
 444 a_c). Optimal decisions are made when the caterpillar top threshold is much greater than the snake top
 445 threshold, making false-negative errors in prey recognition much more likely than false-positive errors. All
 446 the simulations were run using the following set of parameters: $d = 1$; $\sigma^2 = 1$; $\vartheta_m = 0.4$; $\vartheta_s = 0.1$; $\pi =$
 447 20 ; $\tau = 15$; $\varphi = 10^{-4}$; $g(t_s) = \frac{t_s}{t_s+10}$.

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

455 **Figure 4.** Contour plot of the bird's decision landscape. Isolines show the probabilities that the object
456 described by the bi-normal density function $\mathbf{N}(s, c, \varepsilon_s = \varepsilon_c = 1)$ be perceived either as a snake (thus,
457 eliciting a flee motor response) or as a millipede (thus, eliciting no motor response). The positions of the
458 "normal" caterpillar in the bird's decision plane have the binormal distribution $\mathbf{N}(s = -1, c = 1, \varepsilon_s = \varepsilon_c =$
459 $1)$. A "mutant" caterpillar with $\mathbf{N}(s = -1 + \tau, c = 1 + \omega, \varepsilon_s = \varepsilon_c = 1)$ will be favoured by natural
460 selection if the mutation increases the probability of bird's false negatives. The three arrows from the
461 "normal" caterpillar show the increase in false negatives of a mutant when (i) $\tau = 1$ and $\omega = 0$, horizontal
462 arrow; (ii) $\tau = 0$ and $\omega = -1$, vertical arrow; and (iii) $\tau = 1$ and $\omega = -1$, oblique arrow. Analogously, the
463 arrow from the "normal" snake shows the increase in false negatives due to a mutation that causes a shift
464 in the snake bi-normal distribution of $\tau = 1$ and $\omega = -1$.

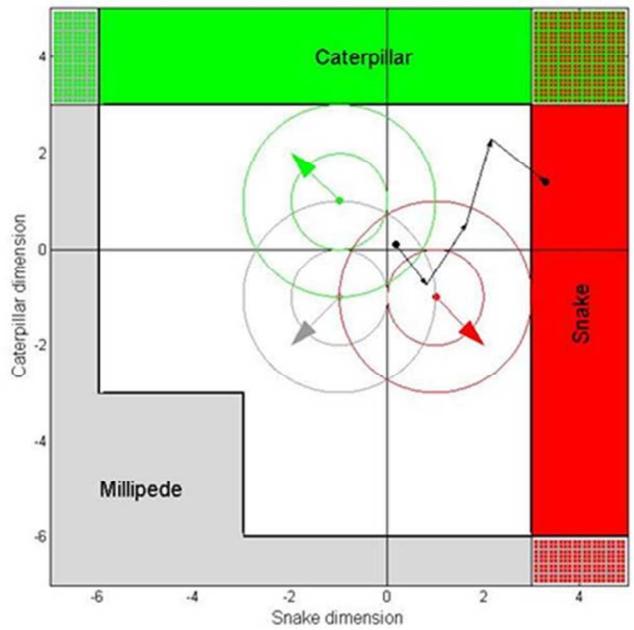


Figure 1
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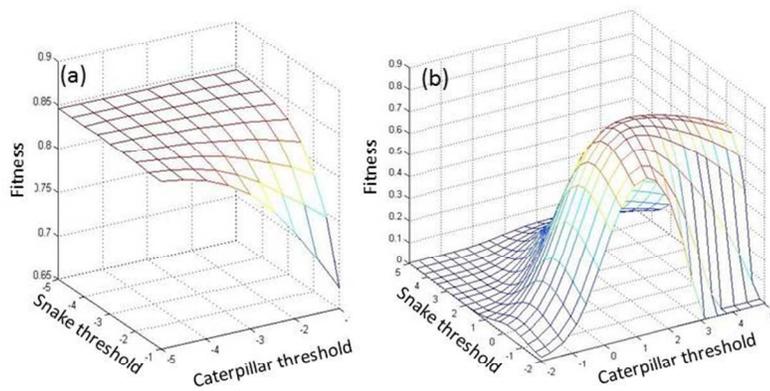


Figure 2
254x190mm (96 x 96 DPI)

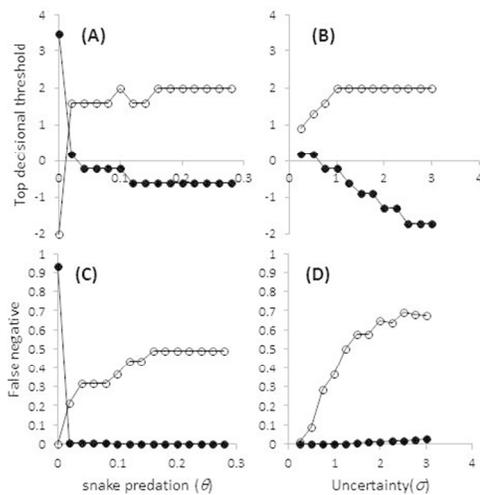


Figure 3
254x190mm (96 x 96 DPI)

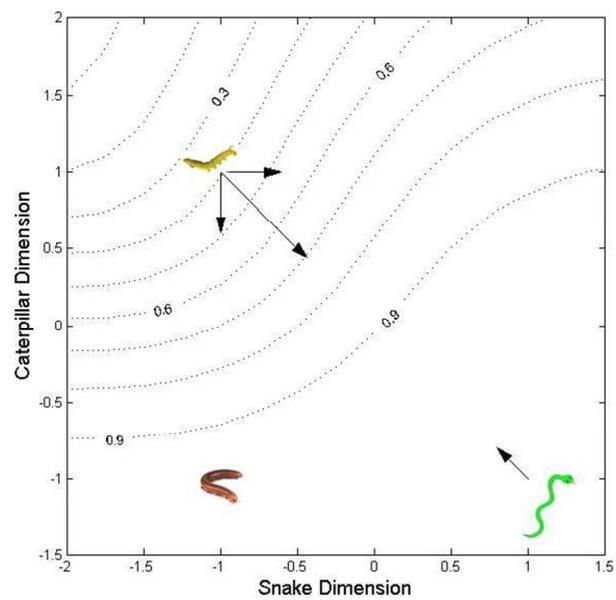


Figure 4
254x190mm (96 x 96 DPI)