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Ecological context modulates the visual detection advantage for snakes

Luiz Biondi [a], Nuno Gomes[a,b], Rafael S. Maior[c], Fábio Silva[a], Samuel Silva[d] and Sandra C. Soares[a]

[a]William James Center for Research, Department of Education and Psychology, University of Aveiro, Aveiro, Portugal; [b]William James Center for Research, ISPA – Instituto Universitário, Lisbon, Portugal; [c]Department of Physiological Sciences, Institute of Biology, Laboratory of Neurosciences Metabolism and Behavior, University of Brasilia, Brasilia, Brazil; [d]Department of Electronics, Telecommunication and Informatics (DETI)/Institute of Electronics and Informatics Engineering (IEETA), University of Aveiro, Aveiro, Portugal

ABSTRACT

Research indicates that the human visual system is highly efficient at detecting snakes, yet less is known about how ecological visual contexts modulate this advantage. We conducted two experiments with university students ($N = 58$ each) to test whether background complexity influences snake-detection efficiency using a dual-task paradigm. In Experiment 1, stimuli were presented on a uniform grey background. Here, snakes were detected and visually fixated significantly faster than non-snake control animals, consistent with previous findings. Crucially, this advantage was not influenced by participants' self-reported fear of snakes or anxiety levels. In Experiment 2, the same stimuli were embedded in a complex leaf-litter background. Under these conditions, non-snake stimuli were detected earlier than snakes, and overall accuracy declined. This indicates that the snake detection advantage is sensitive to changes in perceptual and contextual conditions, which may attenuate or reverse the pattern observed under simplified settings. Subjective fear scores again showed no moderating effect. Overall, these findings are consistent with an evolved sensitivity to snake-related visual features, but show that this advantage is context-dependent and can be attenuated or even reversed under ecologically complex visual conditions, independently of self-reported fear. They underscore the necessity of incorporating ecological variables into threat-detection research.

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1. Introduction

It is widely accepted that living beings that act as predators and/or prey within their ecological niches have developed at least some evolutionary adaptations consistent with these relationships (Dawkins & Krebs, 1979). These adaptations may be physiological, anatomical, behavioural, or, as one might expect, a complex interplay of all three (Burak et al., 2018). For instance, numerous taxa that interact ecologically with venomous snakes, either as prey or predator, have evolved varying levels of resistance to snake venom, illustrating a common outcome of long-term co-evolution (e.g. Daltry et al.,1996; Gibbs et al., 2020; Mancuso et al., 2023; Poran et al., 1987; Robinson et al., 2021; Voss & Jansa, 2012).

In the case of anthropoid primates, numerous studies across disciplines and using diverse methodologies support the notion that their visual system is particularly sensitive to snake-related stimuli (e.g. Gomes et al., 2018; Isbell, 2006; LoBue & DeLoache, 2008; Öhman et al., 2001; Soares et al., 2014; Van Le et al., 2013). This phenotypic trait, frequently discussed within an evolutionary framework, and the behavioural responses associated with it are thought to result from a long evolutionary history in which predatory snakes may have exerted important

CONTACT Sandra C. Soares sandra.soares@ua.pt Department of Education and Psychology, University of Aveiro, Campus Universitário de Santiago, 3810-193, Aveiro, Portugal

selective pressures on primate ancestors. This view is supported by two complementary frameworks: the Fear Module hypothesis (Öhman & Mineka, 2001, 2003), which emphasises the rapid subcortical processing of biologically relevant threats, and the Snake Detection Theory (SDT; Isbell, 2006, 2009), which specifically posits that snakes were a driving force in the evolution of primate visual systems.

According to neurophysiological and behavioural studies, the elongated, sinuous body shape of snakes, along with their threatening nature, may play a key role in triggering visual detection by the primate visual system (e.g. Dinh et al., 2022; LoBue, 2014; Van Strien et al., 2014). This sensitivity is thought to stem from the evolution of a subcortical network, including the amygdala, pulvinar, and superior colliculus, that enables fast, automatic processing of visual information through a neural shortcut that bypasses the cortex (Dinh et al., 2022; Van Le et al., 2013; Van Strien et al., 2016). This so-called *low road* pathway (LeDoux, 1996) allows for the rapid detection of emotionally salient and biologically relevant stimuli, such as snakes (Isbell, 2006, 2009; Öhman & Mineka, 2003). Such expedited detection likely provides a temporal advantage for initiating defensive responses, thereby increasing survival and, ultimately, reproductive success, favouring the maintenance and propagation of this trait within the population (Biondi et al., 2025; Isbell, 2006, 2009, for a review).

However, the effectiveness of these visual mechanisms may depend critically on the visual context in which stimuli are encountered. In natural environments, visual scenes are characterised by high edge density, complex textures, and substantial overlap in visual features between objects and background. Under such conditions, figure-ground segmentation may be more demanding, potentially reducing the salience of diagnostic features such as elongation and curvature that are typically associated with rapid snake detection (LoBue & DeLoache, 2011; Van Strien et al., 2016), particularly when contour segmentation is disrupted by background complexity (Schaefer & Stobbe, 2006; Stevens & Merilaita, 2009). As a result, the perceptual advantage observed under simplified conditions may not generalise to ecologically complex settings.

Consistent with this possibility, although humans often show a detection advantage for snakes, this pattern is not uniformly reported in the literature. Predator-prey interactions frequently drive reciprocal adaptations (Dawkins & Krebs, 1979). In this context, primates and snakes may have co-evolved visual detection and camouflage traits as part of a broader ecological arms race. Therefore, it is reasonable to consider that the evolution of snake species that prey on primates may also have involved strategies that reduce the effectiveness of this visual sensitivity. Importantly, the effectiveness of such adaptations may depend on the ecological and attentional context in which detection occurs, rather than reflecting a uniform advantage across all experimental conditions. Such variability is also consistent with well-documented instances of snakes preying on non-human primates (e.g. Jack et al., 2020; Quintino & Bicca-Marques, 2013; Shine et al., 1998; Valença et al., 2025). Similarly, snake predation and envenomation of humans, particularly among hunter-gatherer or hunter-horticulturalist populations, are not uncommon. Various studies have reported that a significant proportion of individuals in these groups have experienced attempted predation or envenomation (e.g. Headland & Greene, 2011; Jati et al., 2023). Furthermore, the World Health Organization estimates that 4.5–5.4 million people are bitten by snakes annually, with up to 137,000 deaths, numbers considered conservative given widespread underreporting (S. Fox et al., 2006; WHO, 2023).

We note, however, that unlike non-human primates, humans are generally not typical prey of snakes; snake attacks on humans are rare and often defensive. Nonetheless, humans can provide a valuable model for studying visual detection mechanisms due to our conserved primate visual system.

If it is indeed the case that, in at least some instances, snakes are able to evade the purported visual sensitivity of anthropoid primates, we suggest that an important ecological or physical variable may be overlooked in several studies. This is especially pertinent considering that various work on the subject strongly supports the SDT.

Importantly, although some studies have evaluated the efficiency of snake detection under conditions that impair visibility (e.g. Kawai & He, 2016; Soares et al., 2014), to our knowledge, few studies have attempted to simulate natural environmental conditions in a way that could plausibly camouflage snake stimuli. In fact, many early studies on human snake detection, including the seminal work by Öhman et al. (2001), paid little attention to the background context in which stimuli were presented (e.g. Beligiannis & Van Strien, 2020; Grassini et al., 2016).

From our perspective, given that SDT originates from an ecological and evolutionary framework, it is essential to address the role of snake camouflage on the reported detection advantage humans appear to have for these stimuli.

To address this gap, here we aimed at examining the visual detection of snake images compared to non-elongated, non-curvilinear, and non-threatening animal stimuli under two degrees of background complexity. Based on the likely foraging scenarios frequently reported in ethnographic accounts of snakebite incidents (e.g. Headland & Greene, 2011; Jati et al., 2023), we employed a continuous attention task in which animal stimuli appeared unpredictably in the visual periphery while participants focused on a central, cognitively demanding task. Unlike classical visual search paradigms, this approach does not require participants to actively search for a predefined target, but instead places them in a state of ongoing task engagement while remaining sensitive to unpredictable environmental events. As such, capturing more naturalistic detection conditions necessarily involves the interaction of multiple stimulus and contextual factors, reflecting a trade-off between experimental control and ecological validity.

Based on extensive literature supporting SDT, we tested two hypotheses: (1) snakes would be detected more efficiently than control stimuli in either condition; and (2) the background complexity would attenuate this detection advantage by disrupting visual features (e.g. edge density, contour salience) that facilitate snake recognition.

2. Methods

The present study comprised two experiments. In Experiment 1, we compared the latency and accuracy of detection between snake and non-snake silhouette stimuli presented on a uniform grey screen within a black circular aperture, in the absence of any environmental background context. In Experiment 2, the same stimuli, now incorporating additional visual details such as pigmentation patterns and internal morphological features (e.g. eyes, limbs, feathers), were embedded in a complex leaf-litter background containing dry leaves, twigs, and other natural textures to simulate the ecological niches of many terrestrial and semi-arboreal snakes, and we assessed how this environmental complexity affected detection performance.

2.1. Participants

Experiment 1 included 58 participants (48 women; age range = 19–40 years, $M_{age} = 22.09$, SD = 5.75). Experiment 2 included 58 participants (50 women, age range = 18–36 years, $M_{age} = 20.67$, SD = 3.91), of whom 17 (29.31%) had also participated in Experiment 1, with sessions separated by 10 months. All data were collected at the Neurolab, Department of Education and Psychology, University of Aveiro. Participants were required to have normal or corrected-to-normal vision.

Sample sizes were determined *a priori* following Brysbaert's (2019) recommendations for within-subject designs ($N \geq 50$ to achieve >80% power for effects of $d \geq 0.4$ at $\alpha = 0.05$). We did not base these estimates on effect sizes reported in previous studies due to substantial methodological heterogeneity in visual stimuli, task procedures, and other design features. Post-hoc power calculations using reaction time data (conducted in R using the pwr package – Champely, 2020) confirmed that the sample size of 58 participants per experiment was more than sufficient to detect effects of the magnitude expected in this research paradigm.

All participants gave written informed consent and received either course credit or a €5 voucher. The study protocol was approved by the Research Ethics Committee of the University of Aveiro (10-CED/2022).

2.2. Stimuli

The same set of 12 animal images was used in both experiments: six images of elongated, curvilinear, and potentially threatening animals (i.e. snakes) and six images of non-elongated, non-threatening animals (e.g. tortoises, a semi-aquatic freshwater turtle, birds, and a squirrel), most of which naturally occur in similar habitats to many snake species.

Images were selected for both snake and non-snake categories, and an initial screening ensured they did not differ substantially in terms of contrast and luminance. Care was taken to resize all images to occupy equivalent visual space, maximising the area covered by each animal. As a result, images of highly distended or stretched snakes were excluded. Additionally, animal categories were chosen to minimise differences in colour palette across conditions, ensuring overall chromatic similarity and supporting comparability across stimuli. Following this selection process, the SHINE toolbox (Willenbockel et al.,

2010) was used to equalise the images based on their luminance histograms, using the snake images as templates.

In Experiment 1, stimuli were presented as black silhouettes within a black circular aperture against a uniform mid-grey background. In Experiment 2, the same animals, now presenting additional visual details such as inner contours (e.g. feathers, limbs, eyes, melanisation patterns), were overlaid onto a naturalistic leaf-litter background composed of organic debris with heterogeneous textures and tones. This background was selected based on general structural properties associated with visually complex natural environments, including heterogeneous textures, overlapping elements, and high edge density, rather than to maximise camouflage for a specific stimulus set. The background image subtended approximately 4.57° × 4.57° of visual angle.

The background image for Experiment 2 was selected from photographs of plant remains material and did not fill the entire image frame, resulting in irregular contours. Two criteria guided the selection process: (1) all animal stimuli had to fit entirely within the area occupied by the leaf-litter simulation area without exceeding its boundaries; and (2) the leaf colours had to resemble those of the animal stimuli, creating a perceptually demanding visual environment. The goal was to generate a challenging detection task, in which all animals shared similar colour properties with a complex, naturalistic background.

In Experiment 2, stimuli were presented as dynamic video clips at 10 frames per second. Each animal image began fully transparent and gradually increased in opacity until reaching 100% over a 4-second interval (40 frames). In Experiment 1, the stimuli increased in opacity from 0% to 5% over a 7-second period. The discrepancy in both final opacity and presentation duration was implemented to equate task difficulty, given that in Experiment 2 the stimuli were embedded within a background context that could potentially obscure the animals.

Snake images exhibited low variability in luminance and contrast, consistent with the histogram equalisation procedure. Specifically, mean luminance was 79.65 (±1.00), ranging from 77.78 to 80.44. RMS contrast had a mean of 55.35 (±0.33), with a range of 55.14–56.05. Mean object coverage (i.e. proportion of the image area occupied by the animal) was 28.61% (±0.38%). For the other animal categories, mean luminance was 80.23 (±6.19), with a range of 68.26–85.90; RMS contrast averaged 54.27 (±2.14), ranging from 51.68 to 57.88; and object coverage was 28.60% (±2.58%). These values confirm that the stimuli were well-matched across categories in terms of low-level visual features.

In both experiments, the background image (either the circular aperture in Experiment 1 or the leaf-litter background in Experiment 2) was displayed around the centre of the screen in eight spatial locations arranged in an octagonal configuration, and remained visible throughout each trial (see Figure 1). Background images were positioned at angular orientations spaced at 45° intervals, corresponding to cardinal (0°, 90°, 180°, 270°) and intercardinal (45°, 135°, 225°, 315°) directions.

Due to screen resolution and display calibration, radial eccentricity varied slightly across positions. Stimuli located along the vertical and horizontal axes (0°, 90°, 180°, 270°) were placed approximately 6.46° of visual angle from the centre of the screen. Stimuli along the diagonal axes (45°, 135°, 225°, 315°) were positioned slightly closer, at approximately 5.76° of visual angle from the centre of the screen. In both experiments, the background image remained visible throughout each trial.

2.3. Procedure

Participants first provided informed consent and filled out the State-Trait Inventory for Cognitive and Somatic Anxiety (STICSA; Barros et al., 2022; Ree et al., 2008). They were then seated 55 cm away from a 23.8-inch widescreen monitor (EIZO FlexScan EV2451; resolution: 1920 × 1080 pixels). Experimental instructions were presented on the screen, followed by a 15-trial practice block to familiarise participants with the procedure and address any questions. Both the practice block and the experimental tasks were performed with participants' heads stabilised in a chin rest to ensure consistent viewing conditions.

Eye-tracking data were recorded using a Tobii Pro Spectrum System (Tobii Technology, Stockholm, Sweden), which captures binocular gaze using the Pupil Center Corneal Reflection method at a sampling rate of 300 Hz. A standard 9-point calibration procedure was performed prior to the experimental session. Calibration quality was assessed visually based on the alignment between gaze points and calibration targets, and repeated when necessary to ensure adequate accuracy. One participant was

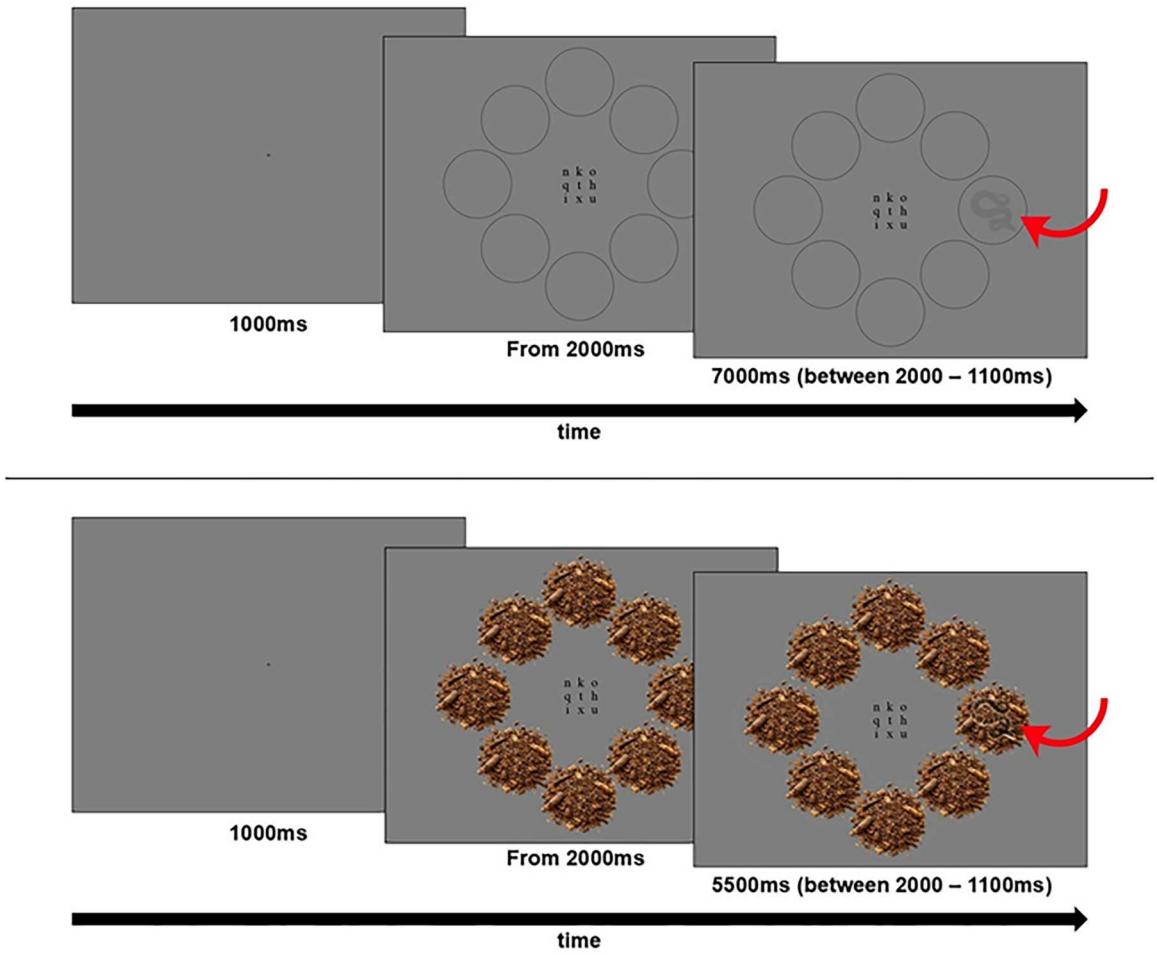

Figure 1. Schematic illustration of the experimental design across conditions. The upper panel depicts Experiment 1 (plain background), and the lower panel depicts Experiment 2 (leaf-litter simulation background). Each panel illustrates the temporal sequence of a target trial, including fixation, central task, and the final visibility level of a peripheral stimulus following gradual onset. The red arrow indicates the location at which the animal stimulus appears.

excluded due to insufficient calibration accuracy, which prevented reliable gaze recording.

The main task consisted of 100 trials: 48 target trials, in which an animal stimulus (snake or non-snake) appeared in the visual periphery, and 52 no-target trials, in which no animal stimulus was presented. Each no-target trial had a total duration of 18 s in Experiment 1 and 16.5 s in Experiment 2. Each trial began with a 1-second fixation cross, followed by a continuous stream of 3×3 letter matrices shown in the centre of the screen. The quadrilateral formed by this letter matrix, considering side segments that intersect the centres of the letters, has side lengths of 1.71° of visual angle. Each matrix contained either the letter "p" or "q" (never both), along with eight randomly selected distractor letters. Participants were instructed to press the corresponding key ("p" or "q") as quickly and accurately as possible while maintaining visual focus on the central letter matrix. They were instructed to shift gaze away from the central task only if they detected a potentially relevant peripheral event.

In the target trials, a peripheral stimulus gradually appeared in one of eight possible locations. The stimulus onset occurred randomly between 2 and 11 s after trial start, with the image fading in from

full transparency to a predefined level of visibility, depending on the experiment (Figure 1). This gradual onset was designed to minimise abrupt exogenous attentional capture and to ensure that detection depended more on the perceptual characteristics of the stimuli and their integration with the background rather than on a transient onset signal. The differences in fade-in parameters between experiments were introduced following pilot testing to avoid ceiling effects in Experiment 1 and floor effects in Experiment 2.

In Experiment 1, the stimulus (either a snake or a non-snake animal) gradually emerged over a period of 7 s, reaching only 5% opacity. In Experiment 2, by contrast, the stimulus faded in to full opacity over 4 s. Once the fade-in was complete, the image remained onscreen for an additional 1.5 s, resulting in a total visibility duration of 5.5 s in Experiment 2.

This difference in fade-in duration required each trial in Experiment 1 to last 18 s, compared to 16.5 s in Experiment 2. In both experiments, stimuli were presented randomly across the eight peripheral locations. Each participant was exposed to 24 snake and 24 non-snake stimuli, presented in a pseudo-randomized order and balanced across positions.

Participants were instructed to press the spacebar upon detecting the appearance of an animal stimulus. If the spacebar was pressed during stimulus presentation, both the peripheral image and the letter matrix disappeared, and the participant used the mouse to indicate the location of the stimulus. This response procedure ensured that participants truly perceived the stimulus visually, confirming that the spacebar press was not made arbitrarily. If no response was registered within 7 s in the first experiment, or 5.5 s in the second one, the image disappeared and a message ("You did not detect the animal") was displayed.

In no-target trials, no stimulus appeared, and the sequence continued before ending automatically. The number of letter matrices shown per trial varied depending on the participant's response time and, in target trials, the stimulus onset. A short break (up to three minutes) was given midway through the experiment, followed by a second calibration before resuming the task. For eye-tracking analyses, predefined Areas of Interest (AOIs) were used. A central AOI was defined around the letter matrix to capture fixation behaviour associated with the primary task. In addition, eight peripheral AOIs were defined around the possible stimulus locations, extending approximately 0.15° of visual angle beyond the boundaries of the background images. These peripheral AOIs were activated dynamically and were only considered in the analyses from the moment the stimulus began to appear.

Two main dependent variables were recorded: (1) detection accuracy (i.e. whether the animal stimulus was detected) and (2) response time (i.e. the latency between the onset of the fade-in period and keypress). In parallel, eye-tracking data were used to assess whether the first visual fixation landed within the area of interest, mirroring detection accuracy, and to measure the latency of this first fixation, analogous to response time. We labelled this variable as "first" visual fixation because it is possible for a visual fixation to occur without a corresponding detection report via keyboard. Such a report may never occur, may occur only following subsequent fixations, or may occur later without an immediately preceding fixation. These complementary measures enabled a direct comparison of detection efficiency between snake and non-snake stimuli using both behavioural (keyboard) and eye-tracking data. This dual approach was intended to enhance measurement reliability and allow methodological triangulation. After completing the task, participants filled out the Snake Fear Questionnaire (SNAQ; Klorman et al., 1974) and signed a debriefing form. The SNAQ was administered post-task to avoid influencing participants' emotional state during the experimental phase.

All questionnaires were implemented via the UA Forms platform, which uses LimeSurvey software. The experimental task was programmed using PsychoPy (version 2023.1.0), integrated with the eye-tracking system.

2.4. Statistical analyses

All statistical analyses were conducted using Jamovi (version 2.6.26.0; The jamovi project, 2024) with the GAMLj 3 module (Gallucci, 2024), which builds on the lme4 R package (Bates et al., 2015). For both models, effects were interpreted as statistically significant when $p \leq .050$. The random-effects structure was selected following the recommendations of Matuschek et al. (2017), which emphasise selecting the most complex model supported by the data to balance statistical power and control of Type I error. Specifically, likelihood ratio tests (LRTs) were used to compare nested models, adopting a liberal threshold of $p < .200$ to favour more complex structures when justified.

In Experiment 1, accuracy in target detection was close to ceiling (approximately 98% in both conditions), and no formal analyses were conducted on this variable. However, the accuracy of first visual fixations, recorded via eye tracker, was substantially lower, and these data were analysed using a generalised linear mixed-effects model with a binomial distribution and a logit link function. The model predicted the likelihood of a correct first fixation as a function of stimulus type (Snake vs. Non-Snake). A likelihood ratio test comparing a model with random intercepts only to one including random slopes for stimulus type revealed no significant improvement in model fit [$\Delta_{\text{Log Likelihood}} = 0.66$, $\chi^2(2) = 1.31$, $p = .519$]; therefore, the simpler model was retained.

For the reaction time data (in correctly detected target trials), a general linear mixed-effects model with a Gaussian distribution and identity link function was employed. Due to mild violations of normality (visually assessed via Q-Q plots) and homoscedasticity (evaluated using residuals vs. predicted values plots), the dependent variable was log-transformed (base 10) to meet model assumptions. For ease of interpretation, results are presented both on the log-transformed scale and back-transformed into seconds using the bias-corrected formula: Estimated mean (seconds) $= 10^{\hat{\mu}+\frac{\hat{\sigma}^2}{2}}$, where $\hat{\mu}$ is the estimated mean in $\log_{10}$ scale, and σ^2 is the residual variance.

The random-effects structure was again defined via LRTs, which showed no significant benefit from including random slopes [$\Delta_{\text{Log Likelihood}} = 0.03$, $\chi^2(2) = 0.06$, $p = .971$], and thus the more parsimonious model (random intercepts only) was retained. A second model was fitted to assess whether individual differences in anxiety (STICSA) or snake fear (SNAQ) modulated the effect of stimulus type, including these scores as covariates. The same analytic approach was applied to the latency to first fixation data, which was also log-transformed (base 10) due to assumption violations. Once again, the more complex random structure did not significantly improve model fit [$\Delta_{\text{Log Likelihood}} = 0.68$, $\chi^2(2) = 1.37$, $p = .505$].

In Experiment 2, three main dependent variables were analysed: detection accuracy, reaction time, and eye-tracking measures (first fixation accuracy and latency).

Detection accuracy was modelled using a generalised linear mixed-effects model with a binomial distribution and logit link function, predicting the log odds of a correct detection as a function of stimulus type (Snake vs. Non-Snake). A likelihood ratio test comparing a model with random intercepts only to one including random slopes indicated a significant improvement in model fit [$\Delta_{\text{Log Likelihood}} = 2.41$, $\chi^2(2) = 4.82$, $p = .090$], and the more complex model (random intercepts and slopes by participant) was retained. An additional model included participants' STICSA and SNAQ scores as covariates.

The same analytic strategy was applied to first visual fixation accuracy, defined as whether the participant's first fixation fell within the stimulus region. In this case, the likelihood ratio test did not indicate a significant improvement in fit from the more complex model [$\Delta_{\text{Log Likelihood}} = 0.03$, $\chi^2(2) = 0.06$, $p = .970$], so the simpler model was retained.

Reaction time (in seconds) for correct detections was analysed using a general linear mixed-effects model with a Gaussian distribution and identity link function. Stimulus type was included as a fixed effect, and participant ID as a random effect. The comparison between models showed no significant improvement from including random slopes [$\Delta_{\text{Log Likelihood}} = 0.99$, $\chi^2(2) = 1.98$, $p = .371$]. An additional model was fitted including anxiety (STICSA) and fear of snakes (SNAQ) scores as covariates.

Finally, latency to first visual fixation was analysed using the same model structure. The likelihood ratio test again showed no significant benefit of the more complex model [$\Delta_{\text{Log Likelihood}} = 0.49$, $\chi^2(2) = 0.97$, $p = .615$]. It is also important to note that six data points were excluded due to a software issue that resulted in response times exceeding the time window provided to participants (i.e. 5.5 s).

No participants were excluded based on behavioural performance or task compliance. No systematic trimming of reaction time data was applied, and no responses were considered implausibly fast. Eye-tracking analyses were conducted using valid gaze samples as defined by the tracking system, and no formal a priori exclusion criteria based on gaze behaviour were applied.

The data and analysis scripts associated with this research are available at https://osf.io/gavjc/?view_only=6f09f1e50dc7499282cc818978853bb3.

3. Results

3.1. Experiment 1

3.1.1. Reaction time reported on the keyboard

The linear mixed-effects model for reaction time data ($R^2_{\text{Conditional}} = .30$, $R^2_{\text{Marginal}} = .02$), fitted to 2732

observations from 58 participants, revealed a significant main effect of stimulus type [$F(1, 2673.06) = 77.99$, $p < .001$]. Snake stimuli were detected significantly faster than non-snake stimuli. Specifically, mean reaction times were lower for snake stimuli ($\log_{10}$ scale: $M = 0.33$, SE = 0.01; original scale: $M = 2.28$ s) than for non-snake stimuli ($\log_{10}$ scale: $M = 0.38$, SE = 0.01; original scale: $M = 2.56$ s). A graphical representation of this result is shown in Figure 2.

3.1.2. Accuracy and latency for visual fixation on the stimuli reported by the eye-tracker

Regarding the accuracy data measured by the eye tracker through the recording of the first visual fixations on animal stimuli, a generalised linear mixed model ($R^2_{\text{Conditional}} = .50$; $R^2_{\text{Marginal}} = .001$), fitted to 2784 valid target trials from 57 participants (one participant did not have any visual fixation recorded on the animal stimuli), revealed no significant effect of the type of stimulus [$\chi^2(1) = 2.30$, $p = .130$]. Participants were not significantly more likely to visually fixate on targets involving non-snake ($M = .44$, SE = .06) or snake stimuli ($M = .41$, SE = .06).

The linear mixed-effects model for the latency to first visual fixation on animal stimuli data ($R^2_{\text{Conditional}} = .28$, $R^2_{\text{Marginal}} = .01$), fitted to 1235 observations from 57 participants, revealed a significant main effect of stimulus type [$F(1, 1185.55) = 25.28$, $p < .001$]. Similarly to the reaction time data, snake stimuli were detected significantly faster than non-snake stimuli. Mean latency to first visual fixation was lower for snake stimuli ($\log_{10}$ scale: $M = .24$, SE = .02; original scale: $M = 1.90$ s, SE = .08) than for non-snake stimuli ($\log_{10}$ scale: $M = 0.29$, SE = .02; original scale: $M = 2.14$ s, SE = .08). A graphical representation of this result is shown in Figure 2.

3.1.3. STICSA and SNAQ as covariates

To assess the potential influence of individual differences in anxiety and fear of snakes, participants' scores on the STICSA (anxiety) and SNAQ (snake fear) were included as covariates in all models. Across the three analyses, reaction time, accuracy of the first visual fixation, and latency of the first visual fixation, the inclusion of these covariates did not substantially alter the pattern of results. Significant main effects of stimulus type remained in the reaction time [$F(1, 2673.02) = 78.02$, $p < .001$] and latency analyses [$F(1, 1185.20) = 25.23$, $p < .001$], indicating that individual differences in anxiety or fear of snakes do not account for the observed effects. As in the original model, no significant effect of stimulus type was found in the accuracy of first fixations [$\chi^2(1) = 2.29$, $p = .130$].

3.2. Experiment 2

3.2.1. Accuracy and reaction time reported on the keyboard

Regarding the accuracy data, a generalised linear mixed-effects model ($R^2_{\text{Conditional}} = .32$, $R^2_{\text{Marginal}} = .02$), fitted to 2778 valid target trials from 58 participants, revealed a significant main effect of stimulus type [$\chi^2(1) = 23.81$, $p < .001$]. Participants were significantly more likely to detect non-snake stimuli ($M = .77$, SE = .03) than snake stimuli ($M = .66$, SE = .04), indicating reduced detection performance for snakes when presented against a camouflage background. This pattern is illustrated in Figure 2.

Regarding the reaction time data, a linear mixed-effects model ($R^2_{\text{Conditional}} = .27$, $R^2_{\text{Marginal}} = .09$), based on 1894 correctly detected target trials from 58 participants, revealed a significant main effect of stimulus type [$F(1, 1840.37) = 239.33$, $p < .001$]. Contrary to Experiment 1, participants detected non-snake stimuli significantly faster ($M = 3.72$ s, SE = 0.05) than snake stimuli ($M = 4.20$ s, SE = 0.05), suggesting a reversal of the pattern observed when the stimuli were presented on a plain background. (see Figure 2).

3.2.2. Accuracy and latency for visual fixation on the stimuli reported by the eye-tracker

Regarding the accuracy data measured by the eye-tracker through the registration of first visual fixations on animal stimuli, a generalised linear mixed-effects model ($R^2_{\text{Conditional}} = .30$; $R^2_{\text{Marginal}} = .004$), fitted to 2778 valid target trials from 58 participants, revealed a significant main effect of stimulus type [$\chi^2(1) = 10.26$, $p = .001$]. Participants were significantly more likely to fixate on non-snake stimuli ($M = .67$, SE = .04) than on snake stimuli ($M = .61$, SE = .04), indicating reduced visual fixation performance for snakes when presented against the leaf-litter background. This data pattern is illustrated in Figure 2.

Regarding the latency to first visual fixation on animal stimuli, a linear mixed-effects model ($R^2_{\text{Conditional}} = .19$, $R^2_{\text{Marginal}} = .06$), based on 1723 visually fixated target trials from 58 participants, revealed

a significant main effect of stimulus type [$F(1, 1{,}664.79) = 119.13$, $p < .001$]. First fixations on non-snake stimuli occurred faster ($M = 3.05$ s, SE = 0.05) than on snake stimuli ($M = 3.50$ s, SE = 0.06), corroborating the suggestion of a reversal of the pattern observed in Experiment 1 (see Figure 2).

3.2.3. STICSA and SNAQ as covariates

Across the four analyses, accuracy and reaction time for keyboard responses, as well as accuracy and latency of the first visual fixation, the inclusion of these covariates did not alter the overall pattern of results. Significant main effects of stimulus type consistently remained [Accuracy keyboard: $\chi^2(1) = 23.71$, $p < .001$; Reaction Time Keyboard: $F(1, 1840.69) = 239.10$, $p < .001$; Accuracy first fixation: $\chi^2(1) = 10.25$, $p = .001$; Latency first fixation: $F(1, 1665.31) = 118.93$, $p < .001$], indicating that the observed effects cannot be accounted for by individual differences in anxiety or fear of snakes.

4. Discussion

To the best of our knowledge, this was the first study to manipulate stimuli used to test the SDT in conjunction with an environmental context resembling the forest floor. Critically, our findings do not challenge the existence of evolved primate visual templates for snake-like stimuli (Isbell, 2006, 2009; Mineka & Öhman, 2002; Öhman & Mineka, 2001, 2003). Instead, they suggest that ecological context, defined by the interaction between background structure and stimulus properties, can modulate the effectiveness of these mechanisms in visually complex settings, introducing a previously overlooked ecological variable to the SDT literature. Importantly, these interpretations do not require assuming that humans are typical prey for snakes; rather, the argument is that primate visual biases, including those conserved in humans, arose under ancestral conditions in which snake camouflage would have conferred adaptive benefits across a range of predator-prey interactions. This perspective situates snake detection within a broader evolutionary-ecological framework linking primate visual evolution, predator-prey dynamics, and camouflage.

In line with classical SDT studies (e.g. Gomes et al., 2018; Le et al., 2016; Öhman et al., 2001; Soares et al., 2014; Soares et al., 2017; Van Le et al., 2013), Experiment 1 (plain background) revealed faster reaction times and shorter latencies for snakes compared to non-snake animals. These results reinforce the role of elongation and curvature as critical features enabling rapid, preattentive snake detection (e.g. Almeida et al., 2015; LoBue & DeLoache, 2011; Van Strien et al., 2016). On the other hand, the total number of animal stimuli detected did not differ significantly between stimulus types, as this measure was subject to ceiling effects. At the same time, many participants detected animals peripherally without gaze shifts, so the eye-tracker registered fewer fixations than detections reported via keyboard. Since peripheral vision is efficient for coarse shapes but less for detailed contours (Gomes et al., 2018), snakes could be rapidly detected without foveal fixation in the simplified context as suggested in other studies (e.g. LoBue et al., 2014).

However, this advantage did not extend to the second experiment, where stimuli were embedded in a complex forest-floor simulation background. Here, snakes were detected less frequently and with longer latencies than non-threatening animals, contrary to our hypotheses and much of the SDT literature (e.g. Almeida et al., 2015; Dinh et al., 2022; LoBue et al., 2014; Öhman et al., 2001). Notably, Experiment 2 differed from Experiment 1 not only in background context, but also in stimulus visibility and detail (e.g. opacity and internal features), indicating that the two experiments reflect distinct perceptual conditions rather than a single-factor manipulation. Importantly, similar patterns have been reported in other paradigms using complex visual search tasks (e.g. Zsido et al., 2024), suggesting that this reversal may reflect a more general perceptual phenomenon rather than a task-specific effect. This interpretation is also broadly consistent with critiques of snake-detection research emphasising a mismatch between laboratory-based findings and ecologically valid conditions, in which snakes are often difficult to detect despite their putative salience (Coelho et al., 2019).

One plausible interpretation is that increased visual complexity constrains figure-ground segmentation, particularly for elongated and curvilinear shapes, thereby reducing the detectability of features typically associated with snakes. In visually cluttered environments, high edge density and overlapping textures can obscure contours, especially when posture and contrast patterns disrupt boundary segmentation (Allen et al., 2013; Egan et al., 2016; Schaefer & Stobbe, 2006; Stevens & Merilaita, 2009; Troscianko et al., 2009). In addition, snakes can

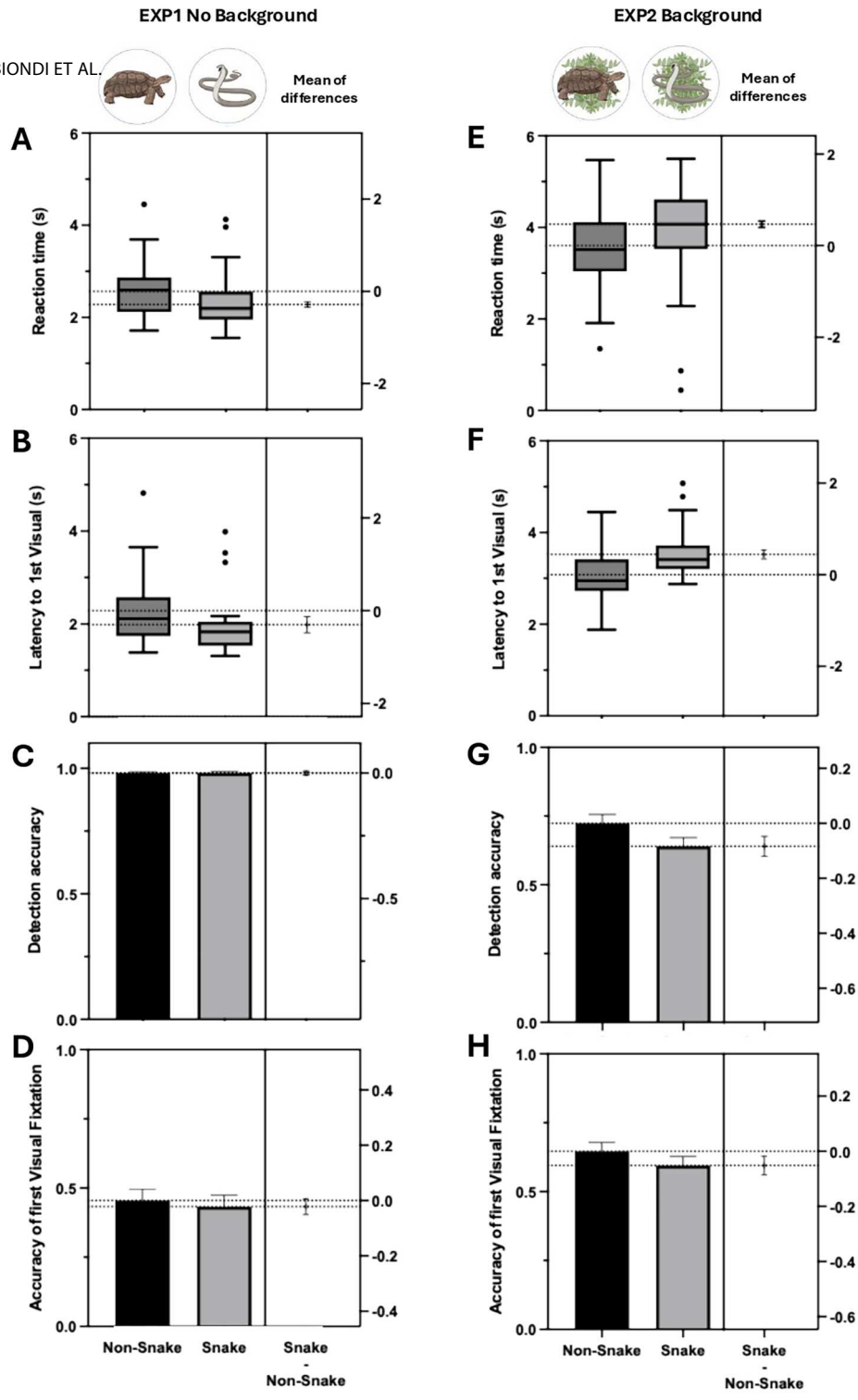

Figure 2. Comparison between "No-background" (Experiment 1; panel A–D) and "Background" (Experiment 2; panel E–H) conditions on stimuli detection. Panels A, B, E and F depict Tukey box and whisker plot showing median values, lower and upper quartile, and outliers. Panels C, D, G and H depict the mean ratio of accurate responses (+SEM). The plot to the right in each panel represents effect size (mean of differences between stimuli with 95% CIs). Snake stimuli induced faster reactions and visual responses than non-snake stimuli in the "No-background" condition (panels A and B, respectively; $p < 0.001$, paired *t*-test). In the "Background" condition, the results were reversed (panels E and F, respectively; $p < 0.001$, paired *t*-test). There was no difference in Detection accuracy or Accuracy of first visual fixation in the "No-background" condition (panels C and D, respectively). In the "Background" condition, accuracy responses to snake stimuli were significantly lower than to non-snake stimuli (panels G and H, respectively; $p < 0.01$, paired *t*-test).

Note: Images of snake and tortoise are for illustration only and do not correspond to the stimuli used in the experiments.

adopt flexible, asymmetrical postures, similar to those used in the present stimuli, that further disrupt perceptual grouping and enhance camouflage (Allen et al., 2013). This interpretation is consistent with empirical evidence showing that snakes can achieve both chromatic and achromatic crypsis by matching the spectral properties of their natural backgrounds, thereby reducing their detectability to both predators and human observers (Isaac & Gregory, 2013).

At the same time, this effect may not be exclusively perceptual. Response-related processes, such as hesitation or transient freezing associated with threat processing, may also contribute to slower detection (Gladwin et al., 2016; Roelofs, 2017). In this sense, threat-related stimuli do not uniformly facilitate responding, but may instead induce inhibitory or action-preparatory states that delay overt responses. More broadly, interactions between emotional salience and executive control can modulate decision processes in complex and context-dependent ways (Pessoa, 2009). Accordingly, the observed reversal likely reflects the joint influence of perceptual constraints and higher-level decisional processes.

Within this broader perspective, ecological and evolutionary accounts remain relevant. Rather than assuming a uniform detection advantage, these findings suggest that the effectiveness of snake-related visual biases depends on whether concealment can be successfully disrupted under specific environmental conditions. This aligns with Isbell's argument (2006) that foveal processing may be critical for resolving camouflaged threats once they enter central vision. From this perspective, the key question is not absolute detection speed across species, but whether snake camouflage can be effectively disrupted.

Beyond visual context, individual variation in emotional responses is thought to modulate detection, and some studies suggest that more threatening stimuli elicit faster visual detection and orienting responses (e.g. Brosch & Sharma, 2005; E. Fox et al., 2007; Zsido et al., 2020), although such effects appear to depend critically on task structure and stimulus conditions. In the present study, however, the SNAQ and STICSA scores did not reliably interact with stimulus type in either experiment, suggesting that the observed pattern of detection was not consistently moderated by individual differences in affective reactivity. Instead, early detection in the present paradigm appears to depend more strongly on stimulus-driven processes operating under conditions of ongoing attentional engagement. In line with theories of a subcortical visual route for biologically relevant stimuli (Öhman & Mineka, 2003; Van Le et al., 2013; Van Strien et al., 2016), our results are consistent with the idea that simple visual features such as elongation and curvature may be sufficient to capture attention independently of subjective fear. At the same time, we found no evidence that this early attentional capture was intrinsically accompanied by anxiety or fear, further suggesting that affective modulation of detection may depend on specific task demands and stimulus configurations (see also Thrasher & LoBue, 2016). Indeed, it has been suggested that heightened attention to snakes may constitute part of the mechanism that facilitates fear learning in a sequential process, but is not necessarily accompanied by the emotional response itself (LoBue, 2013; LoBue & Rakison, 2013; Öhman & Mineka, 2003). While informative, these conclusions are limited by our reliance on self-report measures of fear and anxiety, as no physiological indices of arousal (e.g. SCR, pupil dilation) were collected. This distinction between preattentive detection and affect-driven appraisal supports the notion of a species-wide adaptation rather than individual variability (Almeida et al., 2015; Biondi et al., 2025; Mineka & Öhman, 2002; Öhman & Mineka, 2001, 2003).

Ultimately, by demonstrating that ecological context and perceptual conditions jointly modulate detection performance, our findings are compatible with evolutionary accounts emphasising reciprocal pressures between snake camouflage and primate visual processing. While the human visual system appears sensitive to snake-like features, camouflage may exploit habitat complexity in ways that reduce detectability under specific perceptual conditions. This interpretation applies even though modern humans rarely experience snake predation; camouflage remains adaptive for snakes because it enhances success in hunting prey and avoiding predators, including humans, regardless of whether humans are prey items. Importantly, these results do not demonstrate that primate vision evolved solely in response to snake predation (cf. Andrews et al., 2002; Gould & Lewontin, 1979; Gould & Vrba, 1982). Rather, they suggest that ecological context can influence whether snake features become salient or remain concealed in visually complex environments.

Naturalistic backgrounds may increase ecological validity while also introducing uncontrolled visual properties such as variation in lighting, edge

density, and texture (cf. Biondi et al., 2025). In the present study, the use of a single forest-floor background improved experimental consistency but limits generalizability across different habitats and camouflage conditions.

In addition, several stimulus parameters differed between Experiment 1 and Experiment 2, including opacity, internal visual detail, and temporal dynamics of stimulus presentation. Consequently, the observed differences between experiments should be interpreted as reflecting broader perceptual conditions shaped by the interaction between stimulus and contextual properties, rather than background context alone. At the same time, these design choices were intended to examine detection under more ecologically plausible perceptual conditions.

A further limitation concerns the partial overlap of participants between experiments (29.31%), which may introduce familiarity effects related to repeated exposure to the task. Finally, the gradual onset of stimuli introduces variability in the point at which stimuli become perceptually detectable, although this factor is unlikely to account for the primary within-experiment comparisons. Future studies should employ more tightly controlled within-participant designs that systematically manipulate both stimulus characteristics and environmental context across a wider range of ecological conditions.

Taken together, the contrast between rapid detection on plain backgrounds and impaired detection in complex settings suggests that snake detection emerges from the interaction between evolved visual biases and ecologically structured perceptual conditions. Situating SDT within a broader evolutionary-ecological perspective, one that acknowledges both ancestral predation pressures on primates and the ecological significance of snake camouflage, may provide a more flexible account of the conditions under which snake salience emerges. From this perspective, camouflage and habitat structure are not peripheral variables, but factors that can substantially influence detectability under naturalistic conditions. Future research should continue integrating ecological complexity into experimental designs in order to better capture the perceptual dynamics underlying predator-prey interactions.

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Use of AI-assisted tools

The authors used AI-assisted language tools exclusively for minor language editing, grammar correction, and fluency improvement. No AI tools were used for data analysis, interpretation of results, or generation of scientific conclusions.

Data availability statement

The data associated with this research are available on Open Science Framework (OSF): https://osf.io/gavjc/?view_only=6f09f1e50dc7499282cc818978853bb3.

ORCID

Luiz Biondi http://orcid.org/0000-0002-4568-7315

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