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“Decoding ambiguity”: Asian elephants’ (*Elephas maximus)* use previous experiences and sensory information to make decisions regarding ambiguity

Sagarika Phalke[a,1], Cécile Sarabian[a,b,2], Alice C. Hughes[a,3], Hannah S. Mumby[a,*,4]

[a] Area of Ecology and Biodiversity, School of Biological Sciences, The University of Hong Kong, Hong Kong
[b] Institute for Advanced Study in Toulouse, Toulouse School of Economics, Université Toulouse Capitole, Toulouse, France

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ABSTRACT

Animals rely on sensory information from the environment to make optimal decisions. However, animals are often faced with incomplete or ambiguous information. Some species use sensory information and previous experiences to generate expectations about ambiguity. To test this, we used a cognitive bias test experimentally modified for Asian elephants (*Elephas maximus*) to investigate how they respond to ambiguous cues after positive (rewarded) and negative (unrewarded) experiences. We manipulated the degree of ambiguity by associating the spatial position and colour of the cues to either previously experienced positive or negative experiences. We demonstrate that elephants use previous experiences, and the valence (affective value) attached to those experiences to make decisions regarding ambiguity. Elephants show a positive bias by opening the ambiguous positive box three times as often and twice as quickly compared to the negative cue. Conversely, they are less likely to open and slower to respond to the ambiguous negative cue. These results are consistent with responses of farm animals and captive wild mammals when faced with unconditioned ambiguous cues with perceptual overlaps. Our findings indicate that when making decisions under ambiguity, animals rely on cognitive and sensory mechanisms. A greater understanding of decision-making mechanisms could aid in understanding animals’ responses to their immediate environment with potential implications for conservation and welfare.

1. Main text

1.1. Introduction

Decision-making is necessary for the survival of most animals. Decisions influence essential functions such as foraging, movement, mate choice, and competition, which have fitness consequences. Considering relevant environmental information is paramount because of the high potential costs and benefits certain decisions have. To do this, animals use sensory cues from their surroundings to make decisions (Budaev et al., 2019). However, making decisions in the wild often means responding to environmental cues that are not always straightforward. For example, animals might face novel or ambiguous food sources (Miller et al., 2022). This creates a layer of complexity when making decisions based on incomplete information. Studies have shown that animals often use sensory data and prior experiences to generate beliefs about incomplete and ambiguous cues received from the environment (Crane et al., 2024). To test for this effect, cognitive bias tests are used to investigate the impact of previous positive or negative experiences on animals’ responses to ambiguous cues (Harding et al., 2004).

When animals are presented with unclear or ambiguous choice situations, they use mechanisms to process information and make decisions based on external cues or prior experiences (Hilbert, 2012). This is referred to as a cognitive bias. Cognitive biases have been detected in a wide range of species, such as primates (Ash and Buchanan-Smith, 2016; Bethell et al., 2016), cetaceans (Clegg et al., 2017; Clegg and Delfour,

* Corresponding author.
E-mail address: hsmumby@hku.hk (H.S. Mumby).
[1] https://orcid.org/0000-0001-6385-7157
[2] https://orcid.org/0000-0002-2225-8702
[3] https://orcid.org/0000-0002-4899-3158
[4] https://orcid.org/0000-0002-1774-5688

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2018), and birds (Bateson et al., 2015; Adriaense et al., 2019). The cognitive bias task (or judgment bias task) in animals involves subjects being trained to anticipate a positive or negative event using a particular sensory cue associated with visual, auditory, olfactory, tactile, or spatial orientation information. After learning to associate sensory information with a positive or negative event, they are further exposed to an intermediate sensory cue between the positive and negative event, i.e., the ambiguous cue. The assumption is that experience of prior positive or negative events affects the animal's response to ambiguity. Cognitive bias tests are an exciting tool for studying decision-making in animals in the face of ambiguity. They allow us to manipulate the level of ambiguity, and the quality of sensory information presented to the animal, providing deeper insight into decision-making mechanisms.

Cognitive bias has yet to be studied in any elephant species, despite the animal's use of multiple sensory information to make decisions (Jacobson and Plotnik, 2020) and their extensive cognitive abilities (Bates et al., 2008a; Plotnik and Jacobson, 2022). Elephant species are expected to have the capacity to comprehend and retain information about prior experiences, which is necessary for the completion of cognitive bias tests. Experimental studies on elephant learning and memory retention have successfully used visual discrimination tasks (Markowitz et al., 1975; Jacobson and Plotnik, 2020). In addition, elephants display extensive spatial-temporal memory for resources and conspecifics within landscapes (Hart et al., 2008; Bates et al., 2008b; Polansky et al., 2015). In keeping with these abilities, visual and spatial orientation cues often used in cognitive bias tests can be adapted to create a species-relevant experimental design for elephants.

In this study, we developed a cognitive bias testing protocol suitable for Asian elephants (*Elephas maximus*) to investigate how they respond to ambiguous cues after positive (rewarded) and negative (unrewarded) experiences. We designed a study apparatus that considered their size, perception of distances, and visual acuity. Using boxes with and without food rewards, we gave elephants positive and negative events on which to base their decisions. While other studies used punishment or negative reinforcement, we decided to use the lack of food reward in our study as a negative event as elephants are highly food motivated. We used both spatial separation of the cues and graded colour cues (black to white) for the elephants to access both spatial and visual information in their decision-making process. We assessed which box they were most likely to open to determine whether the elephants exhibited cognitive bias. We classified them as positive, ambiguous, and negative based on colour and spatial location. In addition to understanding elephants' choice of box we also tested how long the elephants took to open a box under positive, ambiguous, and negative conditions. While the action to open a box or not informs us of the animal's choice, latency is more sensitive to specific markers like anticipatory behavior (Ratuski et al., 2021) and motivation (Nematipour et al., 2022). We predicted that elephants would associate ambiguous boxes spatially and visually closer to the positive prior experience as 'positive' and those closer to the negative as 'negative.' Therefore, we predicted that they would prefer to open boxes closer to a previous positive experience and quicker than other boxes.

2. Materials and methods

2.1. Subjects and study site

We conducted cognitive bias tests on eight captive adult female Asian elephants (at Tiger Tops (27.568889°N, 89.103982°E), an eco-tourism facility in Nepal. Females aged between 39 and 70 years and Tiger Tops purchased the elephants from captive facilities in India approximately 20 years ago (see SI Table S1). Elephant handlers and veterinarians managed the animal's well-being. All elephants have a primary (*Phanit)* and secondary (*Pachua)* handler responsible for their care and management. Elephants are housed alone or with preferred associates (groups of two) in naturally vegetated enclosures or *kraals* (ranging from ~0.3–0.6 acres). The handlers feed the elephants *kutchi* (grass sandwiches consisting of hay, chickpeas, molasses, and salt) twice daily. The animals also browse natural fodder in the forest for approximately five hours daily. Handlers provide water and other browse species such as *Mallotus philippinensis*, *Mangifera indica, Saccharum bengalensis, Bombax ceiba*, *ad-libitum* in their *kraals*. Tourism activities are based on demand and occur either in the early morning or evening (maximum duration of three hours). Tourists only observe the elephants and indirectly interact with them through elephant walking safaris (no riding), watching elephants bathe, and grass cutting.

The experiments took place in a section of a field (l x w: 9.50 m x 8.89 m) at the elephant camp, within an area familiar to all the animals. However, this area was not visible to the elephants in their housing *kraals* and there was no influence of social learning. All the experiments occurred between 08:00–10:00 AM, two hours after the morning feed, to ensure an anticipatory response toward the experimental treat without depriving the animals of their regular food routine. While the testing and training phases occurred in the morning, the opening box and habituation phases occurred in the morning and afternoon (16:00–17:00). All elephants were tested approximately over a three-month period which included all the different stages of training and testing. Prior to the study, we conducted an informal poll amongst the elephant handlers to determine high motivating foods. We chose bananas as the preferred food treat as they were rare and highly palatable to all the study animals. Handlers were present to ensure the safety of the experimenter. Handlers were instructed not to use verbal cues and their non-verbal influence over elephant behaviour was restricted by keeping them outside of the testing area. Handlers were kept blind to the experimental objectives to prevent cueing of behaviour.

2.2. Olfactory testing of boxes

We were only interested in assessing the elephants' cognitive responses to ambiguous cues, and to prevent any olfactory cues from affecting the elephants' choices we conducted pre-experimental tests. Elephants strongly rely on olfactory cues to inform behavioral decisions (Rizvanovic et al., 2013). For our experiment we were using wooden boxes and because wood is known to absorb the smell of odorous objects, conducting pre-experiment tests were necessary. None of the ambiguous boxes or the unrewarded boxes contained food treats. If elephants were relying on olfactory cues, there was a possibility of poor box design from influencing the elephants' responses towards the unrewarded and ambiguous boxes because they would determine from olfaction alone whether the box contained food. To prevent this issue, we conducted a test prior to cognitive bias testing to determine whether the opaque wooden boxes used for the experiment were "smell proof". To test this we used the choice task paradigm described by Plotnik and colleagues (Plotnik et al., 2014). The elephants were presented with two visually identical unpainted boxes, one box contained a treat (50 g piece of banana) and the other no food. During the training phase a treat was placed in one of the boxes and the elephant through subsequent trial and error learnt that only one of the boxes was baited with a treat. The elephants had access to both boxes and learnt to look for treat. The elephants were previously trained to open the boxes to access food treat inside (see phase one of training and testing'). During the discrimination phase the elephant was only allowed access to one box based on its choice. Both the boxes were secured with a latch and elephants had to rely on olfactory cues to make a choice. The elephants could use the tip of its trunk to touch the lid, sides, and under-side of the box to smell for the food reward. The elephant's choice was determined by the amount of time spent touching and smelling a particular box which was then opened by the experimenter (see SI Movie S1). Five elephants participated in the olfactory discrimination task using a repeated measures design ($n = 178$ trials). The olfactory test consisted of trials with a 5–7-second interval between trials, during which the experimenter arranged the subsequent trial. We discarded nine trials due to equipment failure or environmental distractions affecting the elephant's choice.

Statistical analysis from a two-tailed binomial test revealed a non-significant effect ($p = 0.487$, 95 % CI [0.45, 0.60]), where the success at choosing the box containing the treat over the no treat box was only 53 % (89 times out of 168 active choice trials). Results indicate that olfactory information did not influence the elephants' box choice.

Supplementary material related to this article can be found online at doi:10.1016/j.applanim.2025.106525.

2.3. Apparatus and materials for the cognitive bias test

We assessed eight adult female captive Asian elephants on their response to ambiguous cues using the cognitive bias test (see SI Movie S2). For the cognitive bias test, we used the 'Go/No Go' task design (Roelofs et al., 2016), where an animal's response to the positive, negative, and ambiguous cues was assessed on whether they open the box. We used a modification of the spatial cognitive bias task (Burman et al., 2008) where the experimental set-up consisted of five units in a semi-circular design (Briefer and McElligott, 2013) (see Fig. 1 (I)). Each unit consisted of a wooden box (l x w x h: 0.38 m x 0.32 m x 0.32 m), placed on a wooden stand (2 m x 0.45 m x 0.35 m), with a black tarpaulin screen (1.2 m x 1.05 m) hiding the unit from the elephant to prevent cueing of (non) placement of food (see Fig. 1C). The boxes at the extremities (black/white) represented the positive (banana treat) and negative (no treat) cues, and the ambiguous boxes (no treat) were placed in the middle. None of the ambiguous boxes were rewarded with a food treat, which could have influenced the elephants' decision to open the boxes. The position of the boxes was fixed as we were using spatial cues in addition to visual cues. We used a combination of both spatial and visual cues as we wanted to ensure that elephants were able to successfully discriminate between cues within a small experimental area. We placed one ambiguous box close to the positive box (ambiguous positive box resembling the positive cue in a greyscale colour), one at the centre, which was equidistant from both terminal boxes (more ambiguous) and another one close to the negative box (ambiguous negative box resembling the negative cue in a greyscale colour). The experimenter trained half the elephants ($n = 4$) to associate the white box with a food treat (50 g banana) and the other half the black box to counterbalance the effects of location or colour. The wooden boxes had lids that had to be opened by the elephants to access the treat inside. The elephants could open the box or not (*decision*) if they perceived that it contained a food treat or not (*perception of information and experience*). The elephants could access the boxes only after the experimenter slid them along the stands with the help of a pushing pole (measuring 1.9 m in length) attached to the back of the box (see Fig. 1(II)). The experimenter placed the treat in a plastic bucket (1 L) inside the positive box (see Fig. 1 (III)). All boxes had a bucket to ensure cue standardization and to prevent the olfactory contamination of the box with food residues.

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Each ambiguous box represented a greyscale and spatial location within the semi-circular design. We positioned (spatial) the ambiguous boxes between the terminal boxes, which were different shades of grey (colour). The ambiguous boxes partially resembled the positive and negative boxes next to them. The grey shade of the ambiguous box close to the black box was a 2:1 black-to-white mixture. The ambiguous box close to the white box was 1:2 black-to-white, and the middle (more ambiguous) was a 1:1 black-to-white mixture. The ambiguous boxes were present but not visible to the animals and were kept out of accessible range behind the tarpaulin sheets during the habituation and training phase. This was to prevent the effect of changes in the experimental set-up from influencing the response of the animals during the testing phase. They were only made accessible to the animal during the testing phase. A trial began when the experimenter slid the box along the stand, making it accessible to the elephant. It ended after a cut-off time of 120 s or when the animal opened the box, whichever occurred sooner.

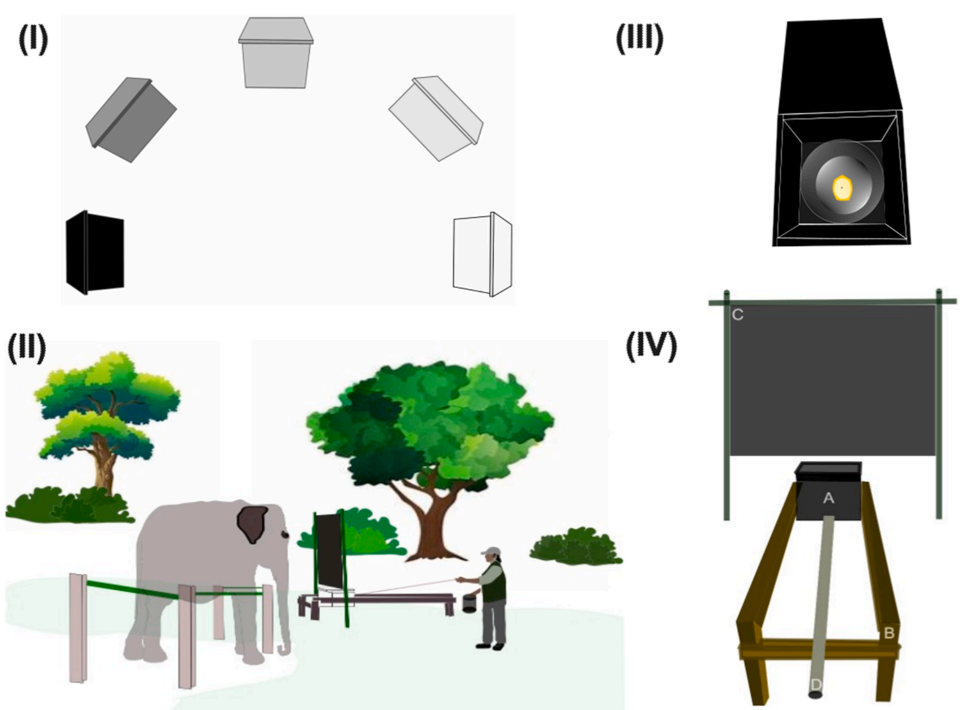

Fig. 1. Experimental design (I) A representational view of the boxes showing the black and white boxes (positive/ negative) at the extreme with the ambiguous boxes in shades of grey placed in a semi-circular design. (II) Elephants were placed within a barricaded area, preventing them from accessing the experimenter and the boxes. The boxes were made accessible to the animals with the help of a pushing pole. All boxes were placed behind black tarpaulin screens between trials. (III) Internal representation of the box with the banana treat. The banana is placed inside a bucket to prevent food contamination, and the bucket is placed within the box. (IV) Experimenters view from behind the screen (A) showing the black box placed on (B) a wooden stand with (C) a black tarpaulin screen hiding the unit from the elephant to prevent cueing of food placement and the experimenter behavior of (D) pushing the pole.

The cut-off time was chosen based on the average time taken for the study animals to walk a particular distance in a previous experiment (*Phalke et al. in prep.*). During the training and the testing phase, the experimenter randomized the order in which they approached the boxes. This was to prevent the experimenter's movement from acting as a cue for the elephant toward a particular direction in which they received/did not receive a reward. Experimenter behavior was also standardized to prevent signalling the elephant to a rewarded v/s unrewarded box. The experimenter pretended to put food in the non-rewarded box and the ambiguous boxes (sham reward).

2.4. Training and testing

All the elephants (n = 8) underwent two phases of the cognitive bias test. *Phase one* consisted of (A) learning to *open the box,* (B) *habituating* the elephant to the experiment area, and (C) *discriminating* between positive and negative cued boxes. *Phase two* consisted of *testing* the elephants' decision toward the ambiguous cue.

2.4.1. Phase one (A) opening box

In this first step, elephants learned how to open boxes. The phase consisted of three sessions, with ten trials each, conducted over two days. Trials occurred between 08:00–10:00 a.m. and 16:00–17:00 p.m., two hours after their regular food routine. The experimenter placed a 10 g piece of banana in a bucket inside the box to encourage learning. The learning criterion for this phase was when elephants successfully opened the box in six or more consecutive trials (Nissani, 2008). This phase took place away from the main experimental area, with an unpainted wooden box to prevent association with the cued boxes.

2.4.2. Phase one (B) habituation

To prevent the effect of novelty influencing animals' decisions in the training and testing phases of the study, the animals were habituated to the experimental area. Habituation consisted of four sessions of 10–15 min each, where the experimenter released the animals into the experimental area. Sessions were conducted in the morning between 08:00–10:00 a.m. and 4:00–5:00 p.m. During the sessions, the experimenter randomly placed treats (10 g banana) around the experimental site to encourage exploratory behavior (trunk touching, moving freely around the site) and reduce alarm behavior (ears spread out, trunk in the air, tail raised). The experimenter also spent equal time (60 seconds each) around the different units to acclimate the animal to the experimenter's movement around the experimental area.

2.4.3. Phase one (C) pre-training and training

The third step of phase one consisted of two stages, the *pre-training* and the *training* phase (Briefer and McElligott, 2013). The *pre-training stage* involved encouraging the animal to interact with the positive and the negative boxes. It consisted of the experimenter initially encouraging the animals to interact with both the extreme boxes by tapping the boxes three times after 30 s during a trial. This was done to ensure that the animals knew that the positive box contained a food treat, and the negative box did not. Once elephants started responding to the boxes with no prompt (group average = six sessions) (see SI Table S1), the experimenter moved to the training step. The positive and the negative boxes were presented one at a time to assess elephants' responses to the positive and the negative boxes. Each pre-training session consisted of eight trials, where animals were presented with two positive and two negative cues and then randomized positive and negative (e.g. +, +, -, -, +, -, +, +, +, -). Both the pre-training and the training stage were only conducted between 08:00–10:00 in the morning to prevent animal fatigue.

Once the animal responded without prompts, the experimenter moved to the training stage. During the training stage, the experimenter used a pseudo-random sequence for the session, which did not sequentially have more than two consecutive positive or negative cues (e.g., +, -, +, -, -, +, -, + or +, -, -, +, +, -, -, +). The primary aim of this stage was for the animal to discriminate between positive and negative boxes. Elephants had to learn to discriminate between the positive and negative boxes to pass into the testing phase. This was to ensure that elephants could perceive the concept of ambiguity upon presenting the ambiguous cues. Sessions always began and ended with a positive cue to encourage the participation of the animals in the sessions. The experimenter created a new pseudo-randomized sequence for the elephants each day. Their performance over two consecutive sessions was recorded to assess whether elephants learned to discriminate between the positive and negative boxes. For the discrimination learning criterion, elephants had to choose the positive box ≥ 80 % across two consecutive sessions or across 16 consecutive trials (Plotnik et al., 2019) (see SI Table S1). Once the animals passed the learning criterion, they advanced to the testing phase.

2.4.4. Phase two: testing

After the animals learned to discriminate between the positive and negative boxes, during the testing phase the experimenter introduced the intermediate ambiguous cues. Each elephant was tested over four days, with nine trials (three positive, three negative and one trial for each of the three ambiguous cues) per session. Again, the boxes were presented one at a time as we were interested in the response of the animals to the boxes. Sessions began with presenting a positive and negative cue as a reminder (Briefer and McElligott, 2013), followed by a pseudo-random order of the other cues. For each elephant, equal positive and negative cues preceded the ambiguous cues on different test days, such that each of the three ambiguous cues followed two positive and two negative cues across the four test days. This prevented the influence of either a positive or negative expectation in response to the ambiguous cue. The experimenter recorded the elephants' responses to each of the cued boxes. Information such as which box was opened and if the elephant opened the box, the time taken to do so.

2.5. Statistical analyses

The models were fit using the glmmTMB package (Brooks et al., 2017). The relative fits of the models were estimated using the package lmtest (Zeileis and Hothron, 2002) which uses the likelihood ratio tests (LRT). While goodness of fit model selection recommended using lognormal distribution for the model involving the time taken to open boxes, since our trials were restricted to 120 s (censored trail time), we used a gamma distribution to analyze the data (Gygax, 2014). After model selection, we used the DHARMa package (Hartig, 2022) to evaluate model assumptions, homogeneity of residuals, and homoscedasticity of variables. Data was analysed using the statistical software R v. 4.1.2 (R Core Team, 2022). To analyze the elephants' decision, i.e., which boxes were opened (Model 1), and the time taken to open the boxes (Model 2) based on visual and spatial cues, we constructed two generalized linear mixed models (GLMMs). The outcome for boxes opened during testing was a binary response (Yes = box opened/ No = box not opened; *Model 1*), and the time taken to open boxes was a continuous response (ranging from 2 to 120 s; *Model 2*). We tested the effect of the boxes (factor with five levels: positive, negative, and three different ambiguous) and session number (factor with four levels: sessions 1, 2, 3, and 4) on the probability of opening a particular box which followed a binomial distribution (logit link; *Model 1*); and on the time taken to open a box which followed a gamma distribution (log link; *Model 2*). The term session number was included to test if there was learning that ambiguous boxes did not contain a food treat. For all our analyses, we included the date nested within elephant identity as a random effect to control for variance in individual elephants across the different testing days.

3. Results

We found a significance of the main effect, i.e., the cued boxes in the model, by using the likelihood ratio test of the full model against the model without the term. This was significant for both models; probability of opening cued boxes (LRT $\chi^2(4) = 122.71$, $p < 0.001$) and time taken to open the boxes (LRT $\chi^2(4) = 67.45$, $p < 0.001$). We also tested the significance of the covariate session number by removing them from the full model and testing for significance against the model without the term. Session number did not significantly improve the fit of the model for both Model 1 (LRT χ^2 (7) = 1.86, p = 0.6) and Model 2 (LRT $\chi^2(8) = 4.39$, p = 0.22). We also tested for an interaction between the main effect – boxes and covariate session numbers and compared them against an association between effects. The interaction did not improve the fit of either model, probability of opening boxes (LRT $\chi^2(12) = 9.53$, p = 0.65) and time taken to open cued boxes (LRT $\chi^2(12) = 13.64$, p = 0.32). Thus, they were dropped to ensure parsimony and better interpretation of the main effects.

3.1. Which boxes were more likely to be opened? (Model 1)

We analysed the elephants' decision to open the different boxes across all trials (n = 288). The effect of boxes significantly improved the fit of the model (LRT, $\chi^2(4) = 122.71$, $p < 0.001$). In contrast, the session number did not significantly improve the model (LRT, $\chi^2(3) = 1.41$, p = 0.70), indicating there was no learning effect that the ambiguous boxes were not baited with food across sessions. Looking at elephants' decision to open boxes, we found that the predicted probability of opening the ambiguous positive box was 68 % compared to 19 % for the negative box (see Fig. 2). Elephants were 3.2 times more likely to open the positive box compared to the negative box (GLMM, z = -7.63, $p < 0.001$) (see SI Table S2). They were only 1.3 times more likely to open the positive box than the ambiguous positive box (GLMM, z = -3.45, $p < 0.001$). When looking at the more ambiguous box equidistant to the positive and the negative, we find that elephants were 3.5 times more likely to open the positive box than the more ambiguous box (GLMM, z = -6.31, $p < 0.001$). In contrast, there was no difference in opening the more ambiguous box compared to the negative box (GLMM, z = -0.11, p = 0.90).

3.2. How much time did elephants take when they decided to open boxes? (Model 2)

We used a subset of the total trials (n = 288) in which the elephants opened the boxes (n = 154). Like Model 1, the main effect of boxes significantly improved the fit of the model (LRT, $\chi^2(4) = 67.45$,

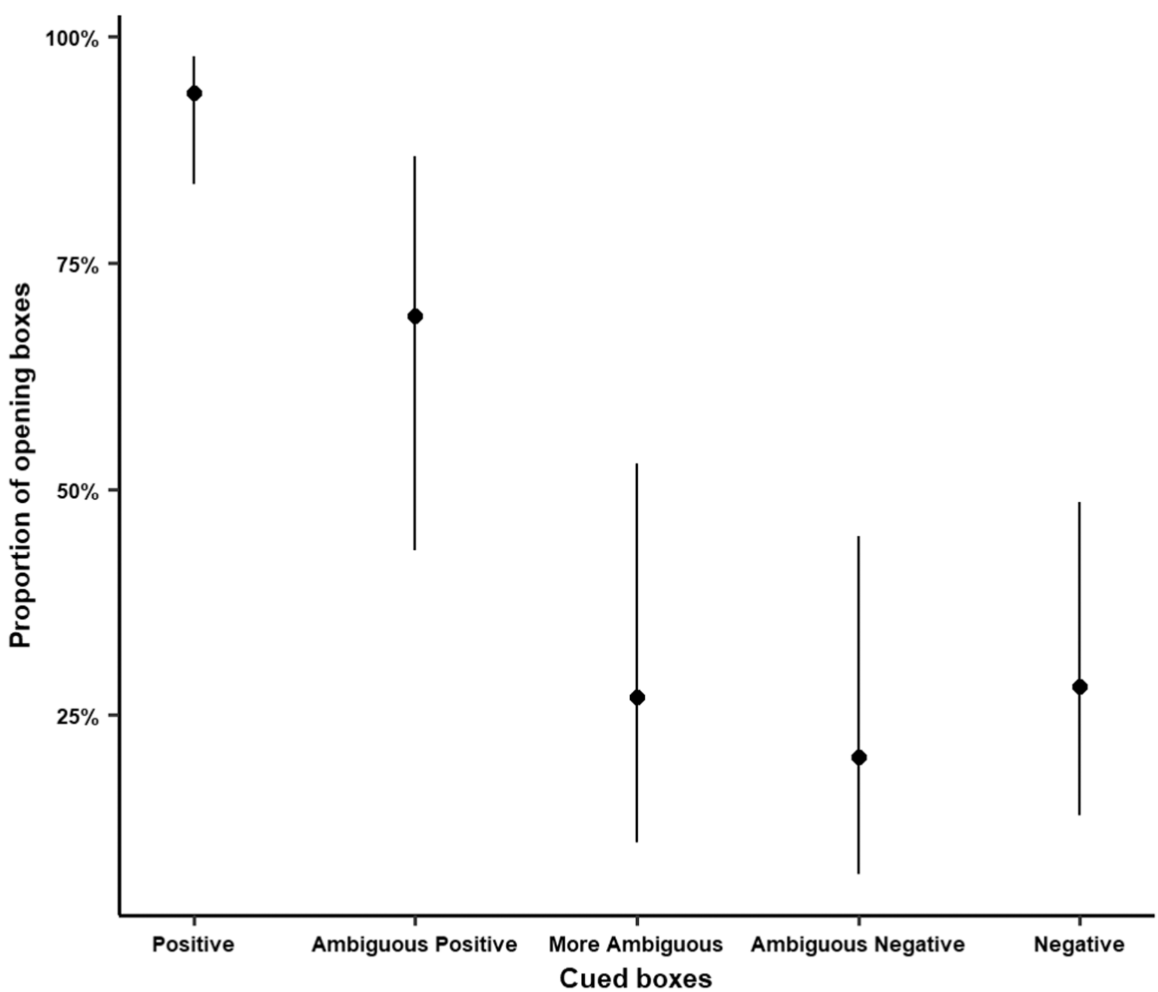

Fig. 2. The predicted probability of elephants (n = 8) opening the different cued boxes was assessed through collective responses (n = 288) across the four testing days. The probability of opening the boxes in percentages is represented on the y-axis against the cued boxes on the x-axis. The black dots indicate the predicted percentage of opening each of the boxes. The error bars indicate the range of the confidence intervals at 95 % based on the predicted values for each of the cued boxes. We found the elephants were more likely to open the positive box than the other boxes ($p < 0.001$). Elephants were also more likely to open the ambiguous positive compared to the other ambiguous boxes ($p \leq 0.001$) and the negative box ($p < 0.001$). We did not find a difference between the negative, more ambiguous and the ambiguous negative box.

$p < 0.001$), while session number did not significantly improve the model (LRT, $\chi^2(3) = 4.39$, $p = 0.22$). When comparing the time taken to open the boxes, we found that elephants took longer as they moved from the positive to the negative box (see Fig. 3). The predicted time to open the positive box was on average, 13 seconds versus the 42 seconds when animals decided to open the negative box (GLMM, $z = 8.25$, $p < 0.001$) (see SI Table S2). While subjects took less time to open the positive box than the ambiguous positive (GLMM, $z = 1.93$, $p = 0.05$), there was, on average, only a difference of five seconds between the two. Comparing the more ambiguous box to the positive and ambiguous negative boxes we did not find a significant difference between both: ambiguous positive (GLMM, $z = -0.99$, $p = 0.32$) and ambiguous negative (GLMM, $z = 0.85$, $p = 0.39$). However, we found a significant difference between the positive and ambiguous negative boxes (GLMM, $z = 1.91$, $p = 0.05$), where elephants took 1.7 times longer to respond to the latter. Comparing the two models, elephants showed no difference in the probability of opening the more ambiguous box compared to the negative box (Model 1; GLMM, $z = -0.11$, $p = 0.90$). However, when they did open it, on average, they opened it 20 s faster than the latter (Model 2; GLMM, $z = -2.43$, $p = 0.01$).

4. Discussion

The elephants in our study exhibited cognitive bias in their responses towards ambiguous cues. Subjects showed a positive bias whereby they were three times more likely to open the ambiguous box resembling the positive cue and almost twice as fast as the ambiguous box resembling the negative cue. They showed a negative bias by opening the ambiguous cue resembling the negative cue less frequently and slower than the positive cue. Even though the ambiguous boxes were never rewarded with food, the subjects showed repeatable patterns of cognitive bias (false positives) based on their expectations. Our results correspond with cognitive bias tests conducted on farm cattle (Kremer et al., 2021) and captive wild mammals such as pigs (Oliveira et al., 2016), rodents (Krakenberg et al., 2019), and primates (Bethell et al., 2016). In these studies, animals were more likely to behave as they would have to a previously learned condition cue (either positive or negative) when faced with unconditioned ambiguous cues with perceptual overlaps.

We found that the elephants in our study may have used a category-based response rule with cue classification based on the colour and spatial location of the positive and negative cues. Animals can categorize and form expectations (positive or negative) about ambiguous cues based on perceptual similarities with their previous experiences (Roelofs

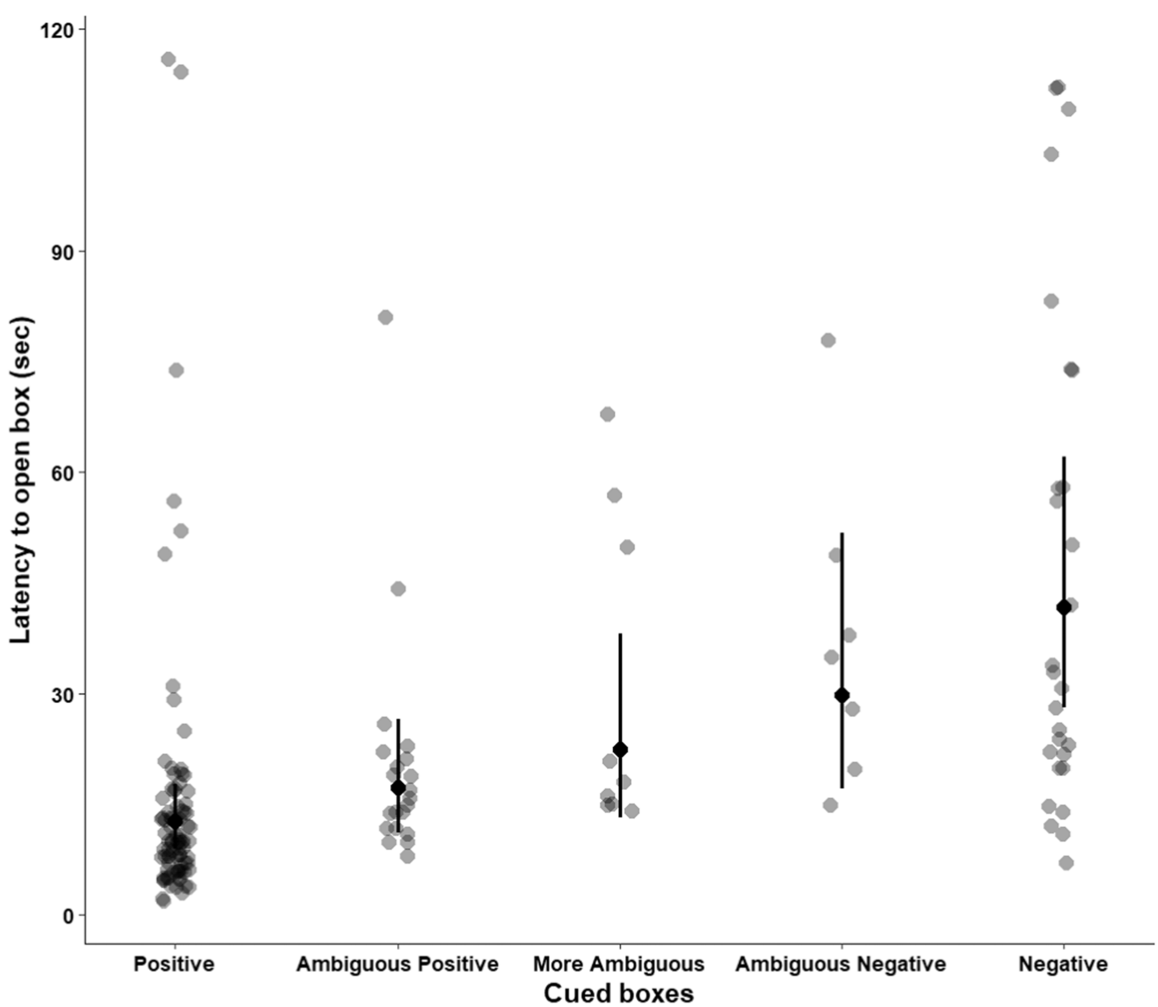

Fig. 3. The predicted time taken by the elephants (n = 8) to open the differently cued boxes (in seconds) was assessed through the collective responses (n = 154) across the four testing days. The latency to open boxes is represented on the y-axis, and the differently cued boxes are depicted on the x-axis. The predicted value is a black dot, and individual raw data points are grey dots. The error bars indicate the range of the confidence intervals at 95 % based on the predicted latency values for each of the cued boxes. The positive box was opened more quickly compared to the ambiguous positive ($p = 0.05$), more ambiguous ($p = 0.013$), and the ambiguous negative and the negative ($p < 0.001$). We did not find a difference in time taken to open the more ambiguous compared to the ambiguous positive and ambiguous negative boxes. However, we found that elephants opened the more ambiguous box quicker than the negative box ($p = 0.01$).

et al., 2016). For example, Brajon and colleagues (Brajon et al., 2015) found that pigs (*Sus scrofa*) remembered perceptual characteristics of humans with whom they had previous positive or negative experiences and used these characteristics to inform future interactions with strangers. Our findings suggest that elephants may retain specific sensory cues and attach positive or negative values (valences) to previous experiences, which influence animals' expectations and subsequent responses to ambiguous cues.

While the animals in our study used the cognitive strategy of categorization to make sense of the ambiguous positive and negative cues, for the more ambiguous cue (box in the middle), there appeared to be other influencing factors. For the more ambiguous cue, animals varied their responses between opening the box and the time taken to respond (see SI Fig. 3). Elephants were twice as quick to open the more ambiguous box as the negative cue, indicating that the animals treated the cues differently. While there were observed differences in individual responses of animals towards the cued boxes across the different test days, these variations did not contribute to the overall fit of the model. Conducting similar experiments with a larger sample size could offer insights into whether the nature of true ambiguity or individual animal differences (e.g., age, sex, personality) cause these variations in responses. Specific personality traits have been found to induce positivity or negativity bias in domestic and farmed mammals' responses (Lagisz et al., 2020; Gray and Webster, 2023). The individual variation in responses towards the more ambiguous cue could also be linked to risk-taking behavior. Our study did not explore the impact of negative reinforcement but only a lack of food reward. In natural ecological settings, the frequency and costs of risks could affect animals' responses toward more ambiguous cues (Gray and Webster, 2023), which need to be further explored.

Most previous cognitive bias studies utilize a single sensory cue: auditory, visual, spatial, or olfactory (Roelofs et al., 2016). Due to species-specific accommodations of the experimental design, we needed to ensure that the animals within a limited space could effectively learn to discriminate between positive and negative cues to perceive ambiguity – as weak discrimination performance of the positive and negative cues has been found to decrease the likelihood of detecting a cognitive bias (Roelofs et al., 2016; Lagisz et al., 2020). We decided to use more than one cue (visual and spatial) to increase the likelihood of discrimination. While we achieved learning discrimination between cues, we cannot parse out if one cue (location or colour) had a more significant impact on elephant decision-making. However, based on the ability of mammals to extract different sensory features to make a single percept (Choi et al., 2023) elephants in our study may have shown a more substantial bias due to the presence of both visual and spatial cues. Future studies must focus on the quality and quantity of sensory cues, which may provide greater insight into animals' perceptual mechanisms when responding to ambiguity.

We provide the first evidence of cognitive bias in elephants and highlight the effect of previous experiences in influencing decision-making. Captive elephant welfare researchers have been emphasizing the need for validating cognitive bias tests in order to assess the presence of positive welfare experiences in captivity (Mason and Veasey, 2010). Positive experiences within environments lead to positivity biases which could be considered indicators for good animal welfare (Clegg, 2018). While the cognitive abilities of all extant species of elephants has been demonstrated (Bates, 2020), the cognitive mechanisms underlying elephants behavioural responses is still being investigated (Plotnik and Jacobson, 2022). This study provides baseline information about the potential link between elephant cognition and their affective states, and the need to explore the impact of valence of experiences on learning and decision-making. Since we had a small sample size, we were unable to use affective manipulation used in traditional cognitive bias studies. However, based on the individual responses of the elephants to the more ambiguous cue we believe our study could be used to further understand how factors such as personality and risk-taking have the potential to affect decision-making under ambiguity. We believe that our methods could create an opportunity for future studies to explore cognitive bias in elephants.

Given the wide-ranging evidence for cognitive bias across species and taxa, it clearly plays a critical role in fast and efficient decision-making which allows animals to adapt to environments, which can be rewarding or dangerous (Norbury et al., 2018; Nguyen et al., 2020). For example, anthropogenic changes in their immediate environment has the potential to influence elephants' decisions to engage in crop-foraging behavior which can lead to conflict with humans or death (Srinivasaiah et al., 2012). Therefore, understanding how animals respond to uncertainty has important implications for species fitness, conservation, and welfare.

Ethics Statement

The study followed the ethical guidelines of The University of Hong Kong's 'Committee on the Use of Live Animals in Teaching and Research' (CULATR application 5692–21). The Department of National Parks and Wildlife Conservation (DNPWC) in Nepal granted permission to conduct the study at Tiger Tops.

Author Contributions

SP and HSM were involved in conceptualization; SP developed the methodology and conducted the research; SP and CS worked on the formal analysis; SP wrote the original draft and created the visualizations; SP, CS, ACH and HSM contributed to review and editing of subsequent drafts, HSM was responsible for supervision and funding acquisition.

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CRediT authorship contribution statement

Sagarika Phalke: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Hannah Mumby:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition. **Cécile Sarabian:** Writing – review & editing, Methodology, Investigation. **Alice Hughes:** Writing – review & editing, Methodology, Investigation.

Declaration of Generative AI and AI-assisted technologies in the writing process

The authors declare that no AI or AI assisted technology was used as part of the study or writing of the manuscript.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.applanim.2025.106525.

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