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Economic and Social Modulations of Innate Decision-Making in Mice Exposed to Visual Threats

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eLife Assessment

The authors show that innate defensive behavior in mice is shaped by threat intensity, reward value, and social hierarchy, highlighting how value and social context influence instinctive decisions. The authors provide a **valuable** characterization of escape behavior which approximates naturalistic conditions. The evidence is **incomplete** due to indirect measures of vigilance and somewhat misleading characterizations of the looming stimulus.

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Abstract

When confronted by predators, animals make innate decisions with rapid reaction times—a trait shaped by natural selection to maximize survival. However, rapid reactions are effective only when grounded in accurate judgments and appropriate choices, which often require cognitive control. To address how such choices are shaped, we developed a behavioral paradigm to investigate how threat intensity, reward value, and social hierarchy influence decision-making in foraging mice exposed to overhead visual threats. Using a machine learning-based approach, we classified defensive responses into four distinct decision types. We observed rapid habituation to repeated looming threats, with substantial inter-individual variability in the rate of habituation. Across both early and late phases of habituation, threat intensity is the primary determinant of decision-making, strongly driving behavior towards escape. In contrast, the influence of reward is context-dependent and emerges primarily in the late phase: under low-threat conditions, higher rewards suppress defensive responses, consistent with value-based decision theory, whereas under high-threat conditions, higher rewards promote escape, potentially reflecting heightened vigilance. Innate decision-making is further modulated by social hierarchy, with dominant mice showing greater vigilance and a stronger bias towards risk-averse behaviors, while subordinates are more reward-driven. To understand the underlying decision-making process, we developed a drift-diffusion leaky integrator model that successfully captures how threat intensity, reward value, and vigilance are integrated. Together, these findings reveal the economic and social modulation of innate decisions, offering insights into the computational mechanisms underlying the interplay between instinctive reactions and cognitive control.

1 Introduction

How animals make decisions among alternative actions is a key question in neuroscience. In natural environments, decisions arise from the integration of sensory inputs, internal states, and learned experience (Meister, 2022). In the laboratory, both learned and innate paradigms have been used to study decision-making. Some learned paradigms, such as two-alternative forced choice (2-AFC) and GO-NOGO tasks (Andermann et al., 2010; Burgess et al., 2017), often require weeks of training in head-fixed animals; whereas other learned paradigms require less training over several days in freely moving animals, including maze exploration (Barnes, 1979; Morris, 1984; Rosenberg et al., 2021; Small, 1901), foraging decisions (Hayden, 2018; Hayden et al., 2011; Steiner and Redish, 2014), and active avoidance (Bravo-Rivera et al., 2014; Moscarello and LeDoux, 2013; Mowrer and Lamoreaux, 1946). While these paradigms have significantly advanced our understanding of the neural mechanisms underlying learned decisions, the training itself may engage neural circuits that differ from those evolved for innate decision-making (Steinmetz et al., 2019).

In contrast, innate decisions—such as whether to escape from an approaching aerial predator (De Franceschi et al., 2016; Yilmaz and Meister, 2013) or a simulated ground threat like a robogator (Amir et al., 2015; Choi and Kim, 2010)—are executed without prior training and may more directly reflect the function of neural circuits shaped by natural selection. In complex environments, making correct and rapid innate defensive decisions often requires cognitive control to assess risk and evaluate alternative defensive strategies (Evans et al., 2019). Defensive responses to terrestrial predators have been well studied: escape decisions depend on predator–prey distance (Ydenberg and Dill, 1986), and the predatory imminence continuum theory describes a graded set of defensive behaviors tuned to perceived threat level (Fanselow and Lester, 1988). Responses to approaching aerial predators are likely also scaled with the perceived threat intensity, which depends on the physical properties of the threat (De Franceschi et al., 2016; Liden and Herberholz, 2008; Tammero and Dickinson, 2002; Yang et al., 2020; Yilmaz and Meister, 2013), prior experience (Vale et al., 2017), and environmental context, including housing conditions (Lenzi et al., 2022). At the neural level, the superior colliculus (SC) is a central node for processing looming-evoked defensive responses, with distinct output pathways mediating escape versus freezing (Evans et al., 2018; Shang et al., 2018; Wei et al., 2015; Zhou et al., 2019).

Despite this progress, important gaps remain. Mice are social animals, and most predator encounters occur during foraging, yet it is unclear how they weigh perceived risks and rewards when making defensive decisions, or how these decisions are influenced by social hierarchy. To address these questions, we developed an ecologically relevant behavioral paradigm to investigate decision-making in foraging mice exposed to overhead visual threats. Our findings demonstrate that defensive choices are jointly influenced by threat intensity, reward magnitude, and social hierarchy, providing a behavioral framework for future investigations into the neural mechanisms underlying cognitive control of innate decision-making.

2 Results

2.1 A behavioral paradigm for studying innate decision-making in mice

To investigate how animals make innate decisions in natural environments, we designed a behavioral paradigm to simulate the defensive behavior of foraging mice in the wild. In this paradigm, a group of 2–5 co-housed mice was placed in a nest, with each individual identified using a radio frequency identification (RFID) tag. Only one mouse was allowed to enter a linear arena to receive the reward delivered at the end. As the mouse approached the reward, an overhead expanding dark disc that mimics the approach of an aerial predator was triggered (Figure 1A), forcing the animal to decide whether to risk getting the reward or defend itself for safety. Behavioral data were recorded using a ground-mounted camera, and DeepLabCut was used to track the movements of the mouse's nose and tail base (Mathis et al., 2018) (Figure S1A). Compared to the exploratory phase, the presence of looming stimuli significantly increased the frequency of arena entries but decreased the duration of each visit (Figures 1B and 1C).

To identify distinct behavioral patterns in response to the looming stimuli, we defined 19 behavioral features from key body points of the mouse and fed them into a random forest classifier to predict its decisions (Figures 1D and S1B, see Methods and Materials). Animal

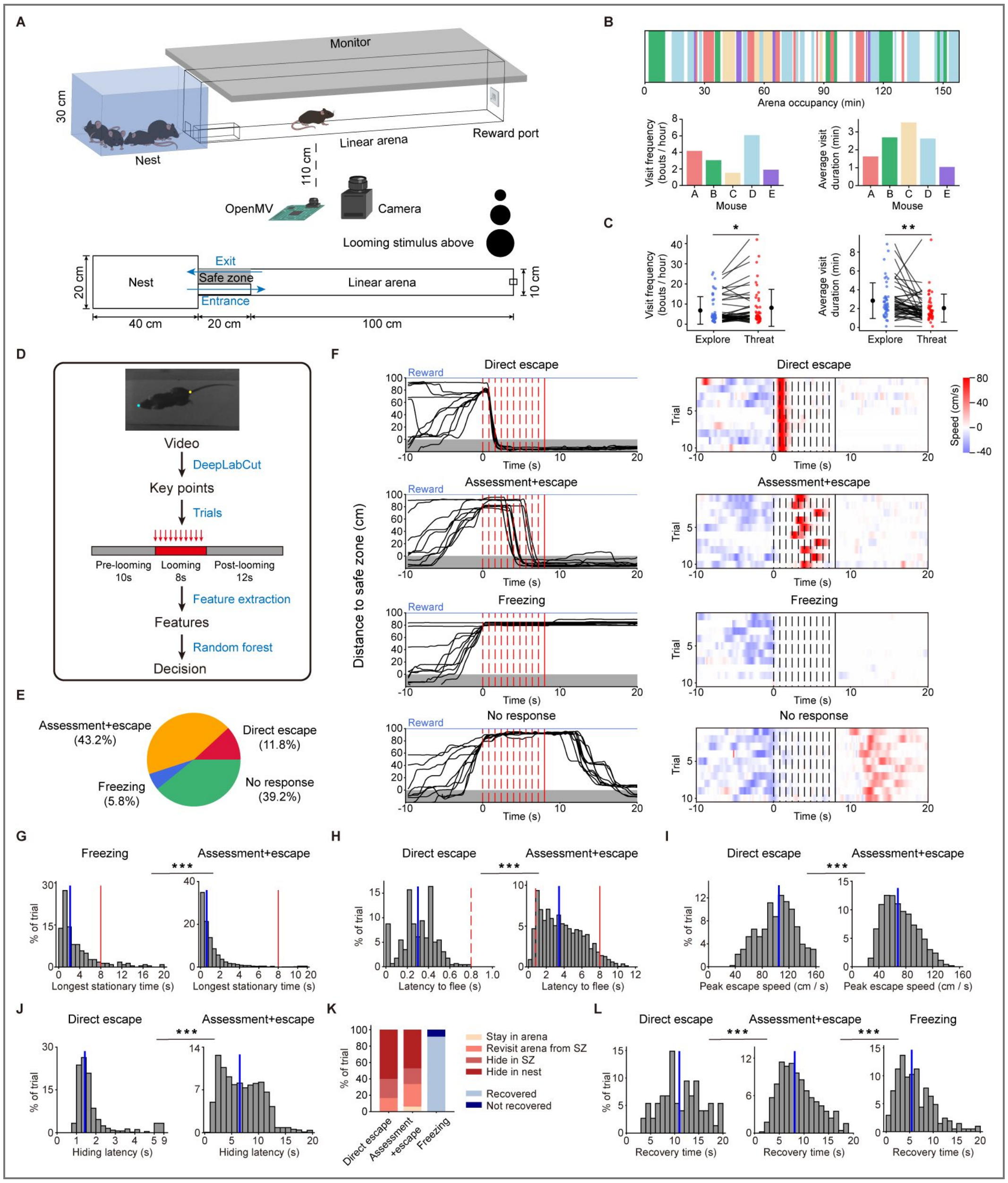


Figure 1. A behavioral paradigm for investigating innate decision-making in mice.

(A) Schematic of the behavioral assay (3D and top-down views). (B) Top: arena occupancy patterns for five example mice in one session. Bottom: visit frequency and average duration for each visit. Colors mark the mouse's identity. (C) Visit frequency and duration under exploration and threat conditions. Error bars represent the standard deviation. N = 46 mice, paired *t*-test. (D) The pipeline for behavioral classification. (E) Distribution of decisions across 3862 trials from 140 mice. (F) Left: distance to the safe zone over time for four decision types (10 example trials each). Red dashed lines mark the onset of each stimulus repetition; solid lines mark the end of the last repetition. Grey shade indicates the safe zone. Right: locomotion speed towards the safe zone over time for the same trials. Positive speed indicates movement towards the safe zone. (G) Distribution of the longest stationary time for "freezing" and "assessment+escape". N = 224 and 1667 trials, Mann-Whitney-Wilcoxon test. Blue lines mark the median; red solid lines mark the end of the last repetition. (H) Distribution of latency to flee for "escape" and "assessment+escape". N = 458 and 1667 trials, Mann-Whitney-Wilcoxon test. Blue lines mark the median; red dashed and solid lines mark the end of the first and last repetitions, respectively. (I) Distribution of peak speed for "escape" and "assessment+escape". N = 458 and 1667, Mann-Whitney-Wilcoxon test. (J) Distribution of hiding latency in the safe zone for "escape" and "assessment+escape". N = 455 and 1563, Mann-Whitney-Wilcoxon test. (K) Distribution of post-decision behavioral states. (L) Distribution of fear recovery time for "escape", "assessment+escape", and "freezing". N = 74, 458, and 205, Kruskal-Wallis test followed by Dunn's post-hoc test with Holm correction. *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

decisions across 3861 trials were categorized into four types: direct escape (11.8%), escape after assessment (43.2%), freezing (5.8%), and no response (39.2%, Figures 1E and 1F). The classification model achieved an accuracy of 95% (Figure S1C). A key distinction between “assessment+escape” and “freezing” decisions was the duration of stationary behavior: mice that decided to freeze remained stationary significantly longer than those in the “assessment+escape” group (Figure 1G). Furthermore, the latency to flee differed significantly between “escape” and “assessment+escape” decisions (Figure 1H).

We hypothesized that fear level increases progressively across the decision types: “freezing”, “escape after assessment”, and “escape”. This is supported by the observations that mice in the “escape” group exhibited higher flee speeds (Figure 1I) and shorter hiding latency (Figure 1J). Additionally, the proportion of mice that recovered within 20 seconds of the stimulus was about 20%, 40%, and 80% for “escape”, “assessment+escape”, and “freezing”, respectively (Figure 1K). Consistently, recovery time decreased progressively across these decision types (Figure 1L). Our findings align with the theory of predatory imminence continuum (Fanselow and Lester, 1988), which proposes that defensive responses become more intense as the perceived threat level increases.

2.2 Mice make economic decisions modulated by vigilance

In the wild, most prey-predator encounters occur while prey animals are foraging, and prey have evolved to maintain high vigilance during foraging to enhance survival. Yet how food value, threat intensity, and vigilance interact to shape defensive decisions remains unclear. To address this question, we developed a behavioral assay that simulates how a foraging animal responds to an approaching aerial predator under different threat and reward conditions (Figure 2A). To maintain a consistent internal state across conditions, mice were not water-deprived. The higher reward value of sucrose over water was validated by measuring consumption during exploration (Figure S3A).

During the first trial, mice showed distinct trajectories and speed profiles across threat and reward conditions (Figures 2B and 2C). These patterns changed rapidly within the first 10 trials, indicating fast habituation to the looming stimulus. This learning was reflected in altered decision patterns (Figure 2D) and changes in escape distance, duration in the reward zone, peak escape speed, and latency to flee (Figures 2E–H). To account for both learning and individual variability, we segmented trials for each mouse into early and late phases using a change-point detection approach on the learning curves (Figures 2I, S3C, and S3D, see Methods and Materials).

In the early phase, behavior was shaped predominantly by the level of threat. Under higher threat, mice were more likely to choose direct escape behaviors (Figure 3A), with longer escape distances (Figure 3B) and less time spent in the reward zone (Figure 3C), suggesting a trade-off between threat avoidance and reward pursuit. Notably, latency to flee decreased with higher threat (Figure 3D), indicating heightened vigilance (Buck, 1966). This threat-dependent change in vigilance was further supported by the longer interval before re-entering the reward zone and slower foraging speed (Figures 3E, 3F, and S4), aligning with findings in birds that elevated predation risk increases vigilance and reduces feeding time (Caraco et al., 1980). In addition, escape speed increased significantly with threat (Figure 3G), reflecting the combined effects of perceived higher risk and heightened vigilance. The analyses restricted to the first trial yielded consistent results (Figures S5).

In the late phase, both threat level and reward value contributed to behavior. Threat remained a dominant factor, while reward exerted a significant, context-dependent influence. Under low-threat conditions, decisions were primarily driven by perceived reward value. As reward value increased, mice exhibited fewer defensive responses (Figure 3H), indicating that they weighed risk and reward to make economic decisions. Higher rewards led to shorter escape distance (Figure 3I) and longer stays in the reward zone (Figure 3J), supporting value-based decision-making strategies. In contrast, vigilance-related metrics, including latency to flee, foraging interval, and foraging speed, were largely unchanged across reward conditions (Figure 3K–M),

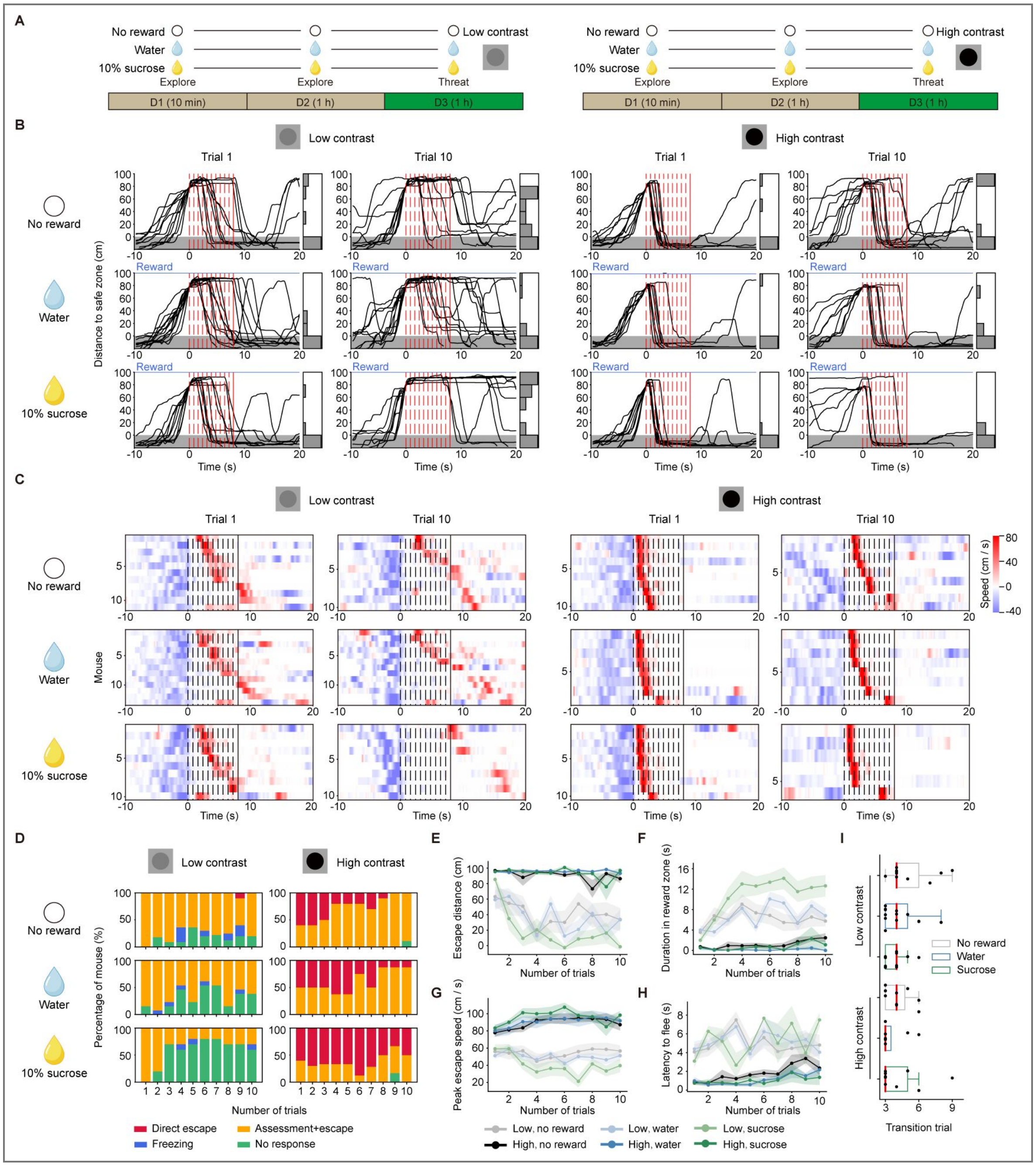


Figure 2. Mice learn quickly from experience.

(A) Schematic of the behavioral assay for studying the economic modulation of innate decision-making. (B-C) Distance to the safe zone and locomotion speed over time for the 1st and 10th trials in response to low- and high-contrast looming stimuli across different reward conditions. Right inset in (B) is the distribution of distance to the safe zone at the end of each trial. Dashed lines mark the start of each stimulus, and solid lines mark the stimulus offset. N = 11 (no reward, low), 13 (water, low), 10 (sucrose, low), 10 (no reward, high), 8 (water, high), 10 (sucrose, high) mice. (D) Summary of the decisions across the first 10 trials under different risk and reward conditions. N = 11, 13, 10, 10, 8, 10 mice. (E-H) Escape distance under threat, duration in reward zone, peak escape speed, and latency to flee across trials in all conditions. Shade denotes the standard error of the mean. (I) Transition trials marking the shift between phases across conditions. Red lines indicate the median; boxes span the interquartile range (IQR); whiskers extend to 1.5 × IQR beyond the box.

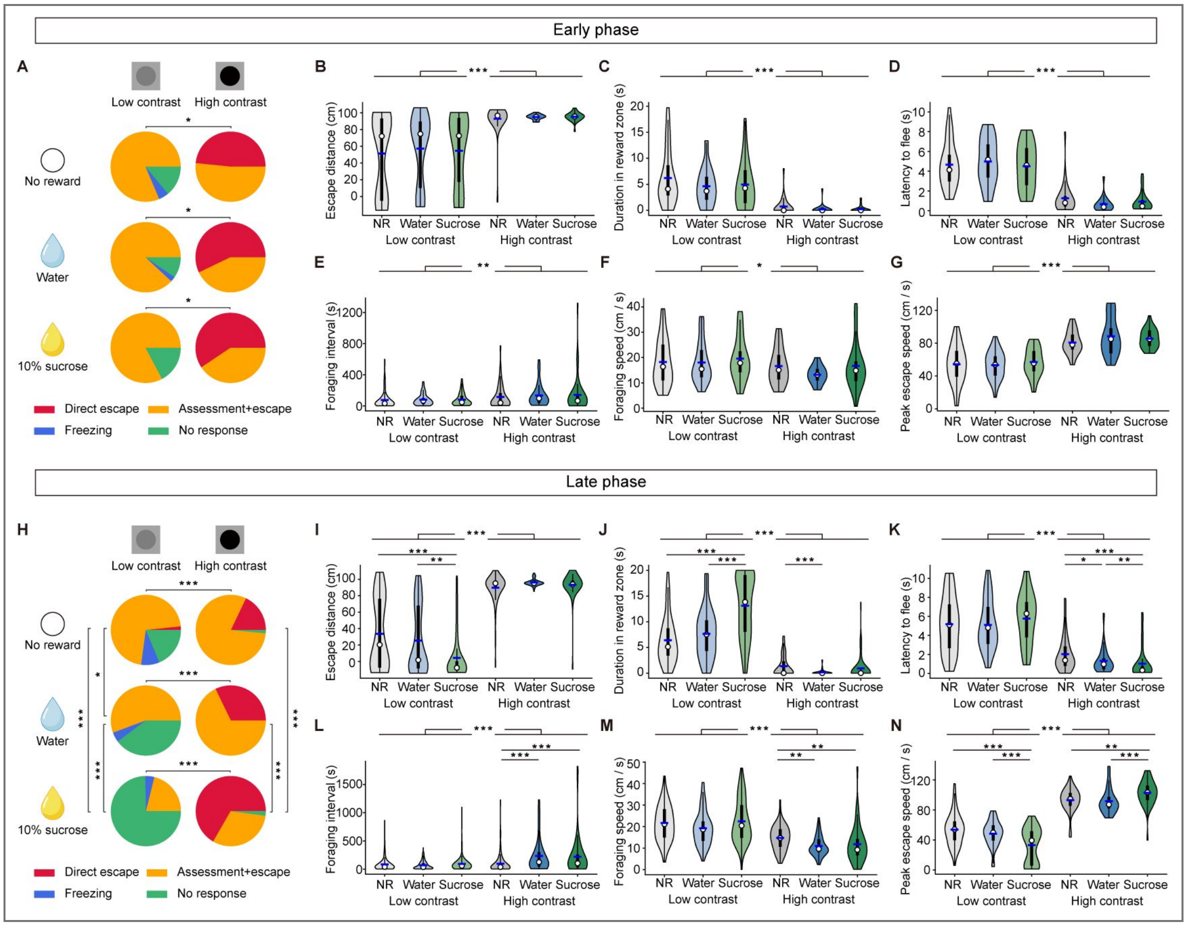


Figure 3. Mice make economic decisions modulated by vigilance.

(A) Distribution of decisions in the early phase for six experimental conditions. N = 43 trials from 11 mice (none, low), 42 trials from 13 mice (water, low), 29 trials from 10 mice (sucrose, low), 31 trials from 10 mice (none, high), 21 trials from 8 mice (water, high) and 32 trials from 10 mice (sucrose, high), Chi-squared test. (B-G) Escape distance under threat, duration in the reward zone, latency to flee, foraging interval, foraging speed, and peak escape speed in the early phase across all conditions. Scheirer–Ray–Hare test with post hoc Dunn's test (Holm correction). N = 43, 42, 29, 31, 21, 32 trials for B, C, F, G; N = 35, 37, 24, 31, 21, 32 trials for D; N = 116, 84, 54, 58, 36, 48 intervals for E. (H) Distribution of decisions in the late phase for six experimental conditions. N = 59 trials from 11 mice (none, low), 88 trials from 13 mice (water, low), 71 trials from 10 mice (sucrose, low), 67 trials from 10 mice (none, high), 59 trials from 8 mice (water, high) and 48 trials from 9 mice (sucrose, high), Chi-squared test. (I-N) Escape distance under threat, duration in the reward zone, latency to flee, foraging interval, foraging speed, and peak escape speed in the early phase across all conditions. Scheirer–Ray–Hare test with post hoc Dunn's test (Holm correction). N = 59, 88, 71, 67, 59, 48 trials for I, J, M, N; N = 43, 49, 15, 66, 59, 47 trials for K; N = 116, 182, 114, 137, 71, 57 intervals for L. For all panels: *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

suggesting that vigilance remains relatively stable. Consistently, escape speed decreased as reward value increased (Figure 3N). The value-based decision-making under low-threat conditions was further validated using within-subject comparisons to control for individual variability (Figure S6).

Under high-threat conditions, however, increasing reward value produced the opposite effect: mice showed more direct escape behaviors (Figure 3H). This shift in decision patterns can be attributed to heightened vigilance driven by reward, as evidenced by shorter latencies to flee, longer foraging intervals, and slower foraging speeds (Figures 3 K–M). This counterintuitive observation suggests that under high threat, reward value indirectly shapes decision-making by modulating vigilance. In contrast, duration in the reward zone did not increase with reward value (Figure 3J). Collectively, these findings reveal how innate decision-making in response to looming stimuli is shaped by the dynamic interplay between perceived threat intensity, reward value, and vigilance.

2.3 Influence of social hierarchy on decision-making under threat

Mice are social animals that live in groups, where social hierarchy often plays a critical role in shaping behavior. To investigate how social rank influences decision-making under threat, we compared the responses of dominant and subordinate mice to looming stimuli. Rank within each mouse pair was determined using the tube test before and after the behavioral experiments (Figure 4A, see Methods and Materials), and only pairs with stable rankings were included in the analysis.

We first verified that behavioral responses to the visual threat were not confounded by the presence of a social partner. Before looming exposure, subordinate mice spent more time exploring the arena than dominant mice (Figures 4B and 4C), which may reflect social avoidance. However, this difference disappeared during and after looming exposure, suggesting that the looming stimulus became the primary driver of behavior. To confirm this, we examined the probability of mice fleeing to the nest. If subordinates were avoiding dominants, they should preferentially escape to the safe zone rather than return to the nest where the dominant was present. Contrary to this prediction, dominant and subordinate mice showed similar probabilities of fleeing directly to the nest (Figure 4D), confirming that defensive responses were driven by the visual threat rather than by social avoidance.

When the threat co-localized with the reward, only dominant mice reduced their relative time spent in the reward zone during the 2-h session (Figures 4E and 4F), indicating greater vigilance and risk aversion compared to subordinates. This heightened vigilance in dominant mice was further supported by reduced habituation to the looming threat (Figures 4G, 4H, and S7), a higher proportion of direct escape decisions (Figure 4I), and shorter latencies to flee (Figure 4J). No rank differences were observed in foraging interval or foraging speed. This may be due to the experimental design, in which only one mouse was allowed in the arena at a time, potentially altering natural foraging dynamics.

Furthermore, dominant mice prioritized threat avoidance over reward, fleeing longer distances with higher escape speed and spending less time in the reward zone (Figures 4M–O). To rule out the possibility that the tube test itself influenced defensive behavior, we conducted additional experiments in which looming sessions occurred both before and after the tube test (Figure S8); the results remained largely consistent. Together, these findings indicate that social hierarchy biases the trade-off between reward seeking and threat avoidance, with dominant mice exhibiting heightened threat vigilance and subordinate mice showing stronger reward-driven behavior.

2.4 A mathematical model for innate decision-making under threat

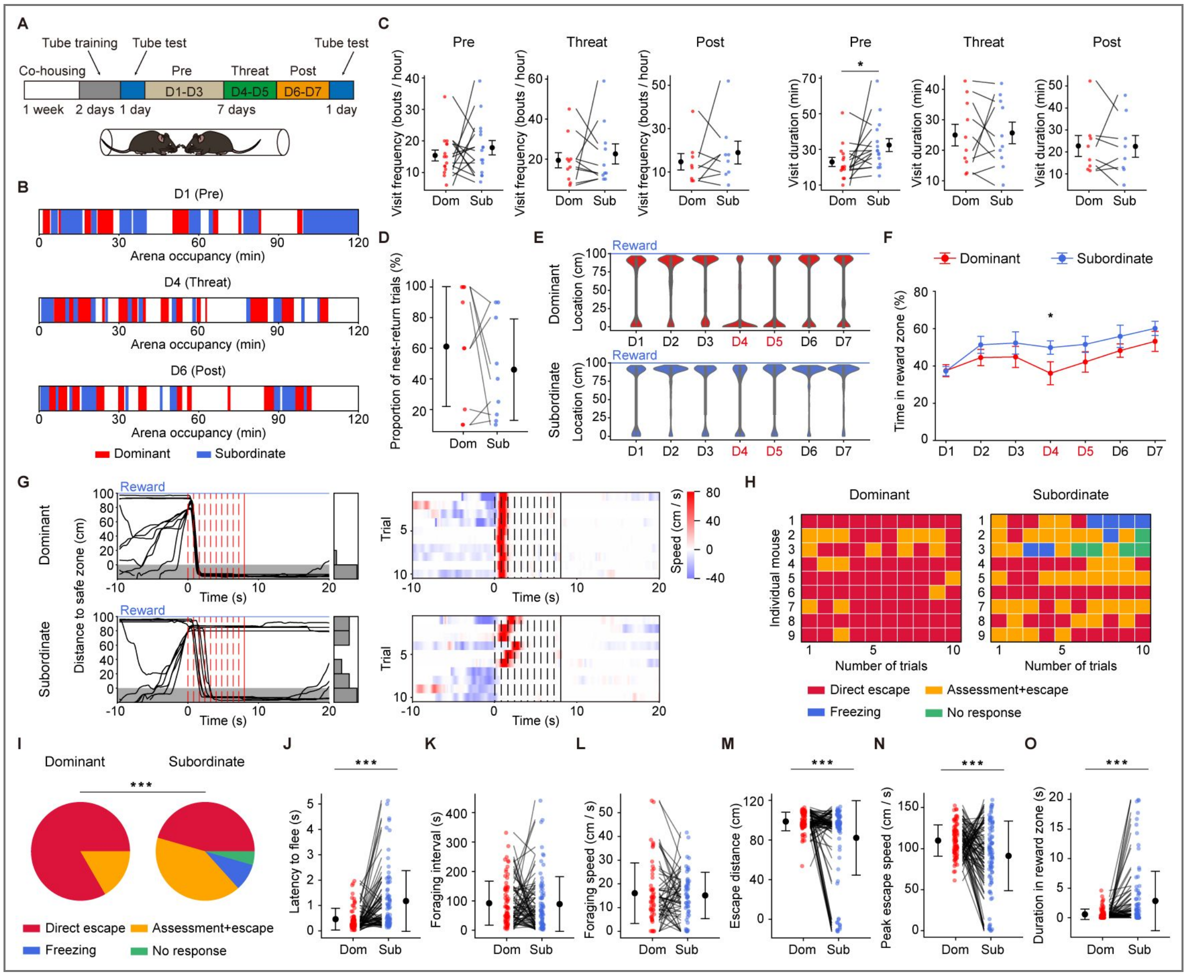


Figure 4. **Influence of social hierarchy on innate decision-making.**

(A) Schematic of the behavioral assay for studying the social modulation of innate decision-making. Top, experimental timeline. Each session lasted 2 hours per mouse pair during the pre-looming, looming, and post-looming phases. Bottom, schematic of the tube test. (B) Arena occupancy for an example pair of mice during the three sessions. (C) Visit frequency and total visit duration for dominant and subordinate mice during the pre-threat, threat, and post-threat sessions. N = 5 pairs (pre), 5 pairs (threat), 4 pairs (post), respectively; paired *t*-test. (D) Proportion of nest-return trials in escape trials for dominant and subordinate mice. N = 9 pairs, paired *t*-test. (E) Distance to the safe zone over seven days for an example pair. Looming stimuli were presented on days 4 and 5. (F) Percentage of time spent in the reward zone across days. Error bars represent SEM. N = 9 pairs, paired *t*-test. (G) Distance to the safe zone (left) and locomotion speed (right) for an example pair. (H) Behavioral decisions across the first 10 trials for 9 mouse pairs. (I) Pie charts showing decision distributions for dominant and subordinate mice. N = 90, 90 trials, Stuart-Maxwell test. (J) Latency to flee for dominant and subordinate mice. N = 78 trials; paired *t* test. (K) Foraging interval for dominant and subordinate mice. N = 75 trials. (L) Foraging speed for dominant and subordinate mice. N = 53 trials. (M–O) Escape distance under threat, peak escape speed, and duration in the reward zone for dominant and subordinate mice. N = 90 trials. *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

Our experimental results demonstrate that innate decision-making in response to visual threats is influenced by perceived threat intensity, reward value, and vigilance. To understand the underlying decision-making process, we developed a mathematical model in which the evidence for escape is accumulated by a drift-diffusion leaky integrator. An escape response is triggered when the evidence level crosses a predefined threshold:

$$\frac{dx_i}{dt} = -\alpha \cdot x_i(t) + \beta \cdot s(t) - r + \delta \cdot \frac{dW}{dt} \qquad (1)$$

$$E(t) = \mathcal{H}\left(x_i(t) - x_{thr}\right) \qquad (2)$$

Here, $x_i(t)$ is the accumulated escape evidence at time t on the ith trial. The leakage rate α drives the evidence towards zero and is the reciprocal of the integration time constant. The stimulus function $s(t)$ denotes the normalized diameter of the looming stimulus (Figure S9A). Together with the threat gain β, which reflects stimulus contrast and the animal's vigilance level, these terms represent the perceived threat level and drive evidence accumulation towards escape. The term r represents the perceived reward value, which suppresses the accumulation of escape evidence. $W(t)$ is a Wiener process, such that $W(t + \Delta t) - W(t) \sim N(0, \Delta t)$, and δ is the diffusion rate. The binary variable $E(t)$ indicates whether an escape decision is made, with H denoting the Heaviside step function and x_{thr} the decision threshold. If a decision is reached within the first expansion of the looming disc, it is classified as a direct escape; otherwise, it is classified as an escape after assessment.

Model parameters were estimated using behavioral data in the late phase of reward-threat experiments in two steps (see Methods and Materials). First, we fit the model to the data under no-reward conditions and identified the optimal leakage rate ($\alpha = 1.78$), threat gain (low threat: $\beta = 1$; high threat: $\beta = 1.44$), diffusion rate ($\delta = 5.6$), and decision threshold ($x_{thr} = 0.71$) (Figure S9B). This revealed distinct decision-making dynamics under low- and high-threat conditions. Under low threat, the average evidence level remained below the escape threshold, and escape decisions emerged from stochastic fluctuations in individual trials (Figure 5A). Under high threat, the average evidence level crossed the threshold, indicating that escape decisions were mainly driven by threat gain (Figure 5B). Notably, threat gain and diffusion rate had distinct effects on latency to flee: threat gain shifted the mean latency, while diffusion rate affected its variance. Thus, the model captured not only the observed decision patterns but also the distributions of latency to flee.

In the second step, we identified the threat gain and reward value across different threat and reward conditions in the late phase (Figures S9C and S9D). Consistent with experimental findings that decisions under low threat were primarily driven by reward value, the fitted reward-value parameter increases with reward magnitude (0, 0.08, and 0.25 for no reward, water, and sucrose, respectively). With these parameters, the model reproduced the observed reduction in escape likelihood without changes in latency to flee (Figures 5A, 5C, and 5E). The same reward-value parameters were then used to model the decision-making process under high-threat conditions. The fitted threat-gain parameter increased across reward conditions (1.44, 1.8, and 2.55 for no reward, water, and sucrose, respectively), counteracting—and ultimately reversing—the influence of reward value. The model again reproduced the experimentally observed increase in escape decisions and decrease in latency to flee (Figures 5B, 5D, and 5F).

To assess the model's predictive power, we simulated how the decision score and latency to flee vary as functions of reward value (r) and threat gain (β). Increasing reward generally reduces escape probability and increases latency to flee, whereas increasing threat gain has the opposite effect (Figures 5G, 5H, and S9E–G). These relationships were confirmed by a simplified deterministic model (Figures S9H–K, see Methods and Materials). Notably, reward can also indirectly promote escape by elevating vigilance, with the magnitude of this effect depending on the level of baseline vigilance, defined as vigilance in the absence of reward (Figure 5I). This dual influence explains the absence of a reward effect in the early phase under both threat conditions: high vigilance shifts the operating range to a region where reward's indirect promoting effect is balanced by its direct suppressing effect on escape decisions.

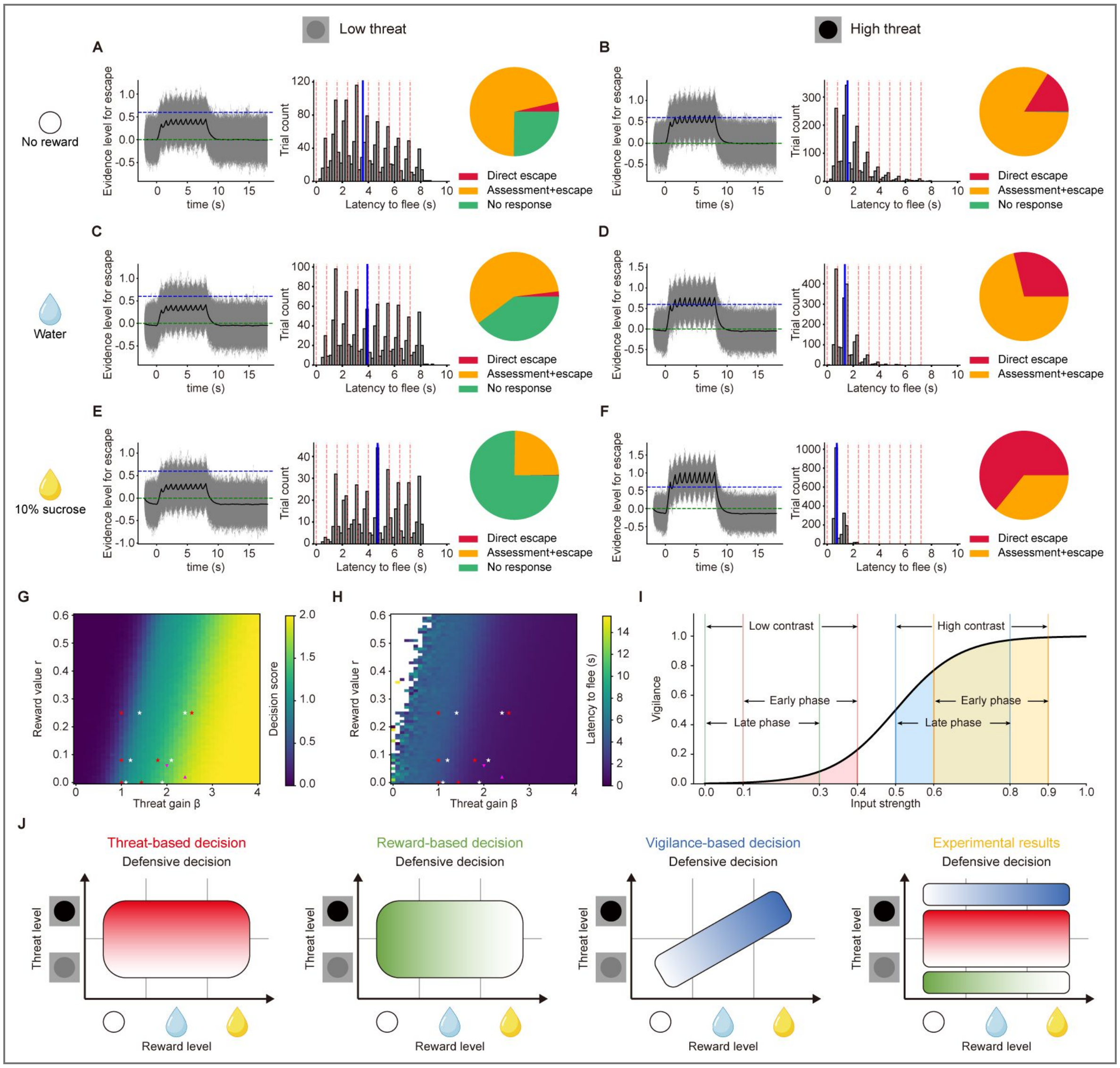


Figure 5. **Drift-diffusion leaky integrator model for escape decisions.**

(A-F) Simulated accumulation of escape evidence, along with predicted latencies to flee and decision distributions across six threat and reward conditions. Green dashed horizontal lines mark the $x = 0$; blue dashed horizontal lines mark the $x = x_{thr}$; red dashed vertical lines mark the onset of each looming stimulus; blue vertical lines mark the median. (G) Heatmap of decision scores as a function of threat gain and reward value. White and red stars indicate fitted parameters for the early and late phases of the reward–threat paradigm, respectively; upward and downward pink triangles indicate fitted parameters for dominant and subordinate mice in the social-threat paradigm, respectively. (H) Heatmap of latencies to flee as a function of threat gain and reward value. (I) Vigilance as a function of input strength, illustrating how the indirect effect of reward on defensive decisions via vigilance depends on the baseline vigilance level. (J) Schematic showing how threat intensity, reward value, and vigilance jointly determine defensive decisions. Color saturation indicates the likelihood of defensive decisions.

We next applied this model to the social-threat paradigm. The behavior of dominant mice was captured by a combination of lower reward value and higher threat gain compared to subordinates (Figures 5G and 5H). This aligns with the experimental finding that dominant animals spent less time in the reward zone and fled more quickly (Figures 4J and 4O). Together, these results demonstrate that the model robustly captures key behavioral features across phases and paradigms, providing a unified mechanistic account of innate decision-making under threat (Figure 5J).

3 Discussion

When confronted by a predator, an animal must rapidly decide whether to escape, freeze, or continue its ongoing behavior. This life-or-death decision is crucial for rodents facing aerial predators. While mice are social animals and most predator encounters occur during foraging, it remains unclear how they integrate perceived risk and reward when making defensive decisions, or how these decisions are influenced by social hierarchy. Using a foraging-based paradigm, we demonstrate that responses to visual threat are shaped by threat intensity, reward value, social rank, and internal state, and this integrated decision process can be captured by a mathematical model.

3.1 Main findings

We designed a behavioral paradigm to simulate how mice respond to visual threats during foraging (Figure 1). Mice rapidly adapted to repeated looming threats, with substantial inter-individual variability in the rate of habituation (Figure 2). While threat intensity robustly shaped behavior in both early and late phases of habituation, reward exerted a clear influence only in the late phase (Figure 3). Specifically, increasing threat intensity shifted behavior towards more defensive responses. In contrast, reward value produced a context-dependent effect: under low-threat conditions, higher rewards suppressed defensive responses, aligning with value-based decision theory; whereas under high-threat conditions, higher rewards promoted escape decisions, potentially reflecting heightened vigilance. Innate decision-making was further shaped by social hierarchy (Figure 4): dominant mice exhibited a stronger tendency towards defensive behaviors, whereas subordinates were reward-driven and less likely to flee. Finally, we developed a drift-diffusion leaky integrator model to simulate the decision-making process, effectively capturing the key features of the observed decision patterns (Figure 5).

3.2 Relation to earlier work

Aerial predators pose a significant threat to rodents. Previous studies have shown that overhead visual stimuli in the laboratory elicit robust defensive behaviors in rodents (Wallace et al., 2013; Yilmaz and Meister, 2013). Because these stimuli can mimic distinct predatory actions, the resulting behavioral responses depend on the specific physical properties of the stimulus. For example, an overhead expanding dark disc that mimics an approaching aerial predator preferentially triggers escape rather than freezing (Yilmaz and Meister, 2013), while a small black moving dot that mimics a cruising predator predominantly induces freezing behavior (De Franceschi et al., 2016). These findings suggest that the response is not a simple reflex but involves a decision-making process. Additional stimulus properties that influence the action selection include contrast, speed, size, and shape (De Franceschi et al., 2016; Evans et al., 2018; Yang et al., 2020). Support for a decision-making process also comes from its modulation by environmental factors and experience: mice freeze more when no refuge is available (Wei et al., 2015) and quickly learn that the looming stimulus poses no real threat (Lenzi et al., 2022; Vale et al., 2017; Zhong et al., 2023). This innate decision-making process is observed across invertebrates and vertebrates (Evans et al., 2019).

Compared with earlier work, the present study differs in two aspects. First, instead of manually annotating behavioral responses, we employed a machine-learning approach to classify behavioral decisions. This approach largely reduced the labor required for labeling and minimized misclassi-fications due to inter-individual variability. Second, unlike previous studies using 2D arenas, we designed a 1D linear arena to simulate foraging conditions, where the nest and reward zone were separated by a long corridor. Decision patterns observed here were similar to those reported in 2D environments (Yang et al., 2020). Consistent with previous findings (Lenzi et al., 2022), mice quickly adapted to the looming stimulus after a few trials.

One concern with the linear arena design is that the looming stimulus is usually presented at the end of the arena, raising the possibility that mice simply retreat upon reaching a physical boundary. To address this, we presented the stimulus between the foraging mice and the nest (Figure S2A). Under this condition, mice quickly escape towards the nest—and thus towards the threat—rather than away from it (Figure S2B). This behavior indicates that their escape responses are not simple reflexes, but instead incorporate the safety of the nest into their decisions.

Fanselow and Lester's predatory imminence continuum theory posits that defensive behaviors are graded according to perceived threat level (Fanselow and Lester, 1988). To test whether this frame-work applies to aerial threats, we varied both prey–threat distance and prey–safety distance. As prey-threat distance increased, mice showed less direct escape behavior, with longer latencies to flee and slower escape speeds (Figures S2C–G), indicating that defensive responses scale with threat proximity. These effects cannot be explained by the failure to detect the stimulus at longer distances; if that were the case, foraging speed would remain unaffected. Instead, mice slowed as they approached the threat in the 75-cm condition (Figure S2D), reflecting lower fear compared to shorter distances. In contrast, prey-safety distance did not significantly influence defensive behaviors (Figures S2H and S2I). One interpretation is that once an aerial threat is detected, the urgency to escape overrides evaluation of refuge proximity. To further verify this, we introduced barriers that lengthened the return path to the nest. Even under these conditions, defensive behaviors remained unaffected by prey-safety distance (Figures S2J and S2K).

3.3 Economic and social modulations of innate decision-making under threat

Value-based decision-making—where choices arise from comparisons of the subjective value of expected outcomes—is a well-established framework for understanding behavior across species (Rangel et al., 2008). Prospect theory, which accounts for decision-making under risk in humans (Kahneman and Tversky, 1979), has been applied to learned decision-making in rodents (Constantinople et al., 2019). Here, we demonstrate that value-based decision-making also extends to innate defensive behaviors: when confronted with threat, mice integrate perceived reward and threat value to make their decisions.

Importantly, perceived value is determined not only by stimulus physical properties but also by internal brain state. In the resting state, for example, perceived stimulus strength scales with physical intensity according to Weber–Fechner laws. In our paradigm, the perceived threat value is strongly modulated by vigilance, a state of heightened and sustained attention to potential danger. This vigilance-dependent modulation substantially alters how the same looming stimulus is evaluated and the resulting decisions.

Consistent with value-based evaluation, increasing threat intensity reliably increased defensive responses across reward conditions and behavioral phases. These changes reflect differences in perceived threat rather than stimulus detection, as evidenced by coordinated changes in escape latency, distance, and speed, and further supported by trial-by-trial inspection confirming reliable stimulus detection across contrast levels (Figure S5).

Reward-dependent behavior also follows value-based principles, but in a vigilance-dependent manner. In nature, foraging often occurs under predation risk, and evolutionary pressure has favored prey that maintain heightened vigilance in the presence of high-value rewards. Consistent with this, increasing the reward magnitude increased both perceived reward value and—via elevated vigilance—perceived threat value. These opposing effects jointly govern the escape decision.

In the early phase, baseline vigilance is already high because looming is an innate threat. Under this high-vigilance condition, reward-driven increases in perceived reward and perceived threat counterbalance each other, resulting in no behavioral differences across reward conditions. With repeated exposure, habituation to looming reduces vigilance, shifting the operating region leftward along a sigmoidal vigilance–intensity function (Figure 5I). Such a sigmoidal form is biologically plausible because vigilance is bounded by a relaxed-state minimum and by cognitive capacity. This shift has opposite consequences under low versus high threat. Under low threat in the late phase, reduced vigilance compresses the dynamic range, weakening the indirect effect of reward on perceived threat and allowing perceived reward value to dominate decisions. Under high threat, the vigilance function remains within a steeper region of the sigmoid, where increases in reward effectively elevate vigilance and thus perceived threat. As a result, reward produces the opposite behavioral effect under high threat. Together, these dynamics explain why reward effects are absent early but emerge after habituation in a strongly threat-dependent manner.

Social rank–dependent differences in defensive behavior also fit within this framework. Even under identical conditions, dominant mice perceived higher threat value due to higher vigilance and lower reward value, consistent with their more risk-averse behavior. Similar status-dependent escape patterns have been reported across species, including voles (Kleiman et al., 2014) and crayfish (Krasne et al., 1997), suggesting an evolutionarily conserved strategy.

Because vigilance declines with habituation, factors that modulate the rate of habituation also influence defensive behavior. Although individuals vary, several patterns are consistent. Mice habituate more rapidly under high-threat or high-reward conditions (Figure 2I). Dominant mice habituate more slowly than subordinates, consistent with their elevated vigilance (Figures 5H and S7A). Housing conditions also alter habituation: group-housed animals adapt more slowly to looming than single-housed animals, and dominant–subordinate pairs habituate even more slowly than group-housed mice (Figures 2I and S7A). These patterns indicate that stable social relationships sustain high vigilance and slow habituation—an evolutionarily conserved strategy that may enhance survival.

One limitation of the present study is that our experiments were conducted exclusively in male mice to avoid the confounding effects of behavioral variability associated with the female estrous cycle. Extending this paradigm to females—with careful control for estrous cycles—will provide a more comprehensive understanding of how economic and social factors modulate defensive decision-making.

3.4 A proposed role for the superior colliculus in value integration

What neural circuits underlie the economic and social modulations of decision-making under threat? A growing body of research implicates the SC as a key node in looming-evoked defensive behaviors (Evans et al., 2018; Shang et al., 2015; Wei et al., 2015). In parallel, reward is encoded by dopaminergic neurons in the ventral tegmental area (VTA) (Cohen et al., 2012; Schultz, 1998) and serotonergic neurons in the dorsal raphe nucleus (Liu et al., 2014; Miyazaki et al., 2011), which project widely to regions such as ventral striatum (Schultz et al., 1992), orbitofrontal cortex (Tremblay and Schultz, 2000), cerebellum (Wagner et al., 2017). Furthermore, social status modulates behavior via circuits involving the medial prefrontal cortex (mPFC) (Kingsbury et al., 2019; Wang et al., 2011) and serotonergic signaling (Edwards and Kravitz, 1997; Raleigh et al., 1991; Yeh et al., 1997).

We propose the SC as a central hub for mediating the economic and social modulations of decision-making for several reasons. First, while neurons in the superficial (sSC) and intermediate (iSC) layers of the medial SC are involved in detecting looming threats and triggering defensive responses (Li et al., 2023, 2020), they also express receptors for both dopamine and serotonin (Mooney et al., 1996; Woolrych et al., 2021), indicating they can receive reward- and social-related information. Notably, dopamine receptor expression is layer-specific, with D1 receptors enriched in the sSC and D2 receptors in the iSC, suggesting layer-dependent processing of reward signals. Consistently, reward-related signals have been observed in the medial sSC (Baruchin et al., 2023). Second, the deep layers of SC receive from the retrosplenial cortex (RSC) (Campagner et al., 2023) and indirectly from the hippocampus (Benavidez et al., 2021), which may convey spatial and contextual information relevant to reward (Calvin et al., 2025). In parallel, the lateral SC mediates approach behaviors towards rewarding stimuli such as food or prey (Comoli et al., 2012; Krauzlis et al., 2013). These findings suggest that medial–lateral interactions within the SC may play a critical role in resolving threat–reward trade-offs during decision-making. Third, the deep-layer SC receives inputs from the mPFC (Benavidez et al., 2021), providing a pathway through which social and contextual signals can modulate defensive decisions. Finally, these SC deep layers are strongly and reciprocally connected with the periaqueductal gray (PAG) and project to dopaminergic neurons in the substantia nigra (Comoli et al., 2003), enabling efficient translation of integrated sensory, economic, and social signals into action execution. They also project to the lateral amygdala via the lateral posterior nucleus (LP) (Wei et al., 2015) to rapidly elicit the fear state.

Taken together, these anatomical and functional studies support the view that the SC serves as a central hub for the economic and social modulation of decision-making evoked by visual threat. In particular, cross-layer processing and medial–lateral interactions within the SC may provide key circuit mechanisms through which reward value and social context shape innate defensive decisions.

3.5 Mathematical modeling

The proposed drift-diffusion leaky integrator model builds on an integrator model of internal state (Gibson et al., 2015) and extends it by incorporating a reward-driven drift-diffusion process (Ratcliff, 1978). Conceptually, the integrator part in our model aligns with Lorenz's “hydraulic” model of motivation, which describes how internal drives shape behavior (Lorenz, 1950). While our model resembles the leaky integrator used to model escape behavior in flies (Gibson et al., 2015), it differs in several ways. First, the earlier model lacks a reward-related drift component. Second, while they modeled the looming effect as a delta function, our model allows the evidence level to vary continuously with the stimulus size. Third, the influence of vigilance is absent in that model. A similar model has been proposed (Evans et al., 2018), but it did not incorporate reward and vigilance. Note that the evidence level for escape in our model is not equivalent to the fear level (Anderson and Adolphs, 2014); rather, when it crosses a threshold, the animal may enter a fear state.

Below, we briefly discuss the roles of individual parameters. The leakage rate α represents a drive towards the resting state. Perceived threat was modeled as the product of the threat gain β and the sensory input $s(t)$ and promotes escape decisions, whereas perceived reward r drives the decision away from escape. The threat gain increases not only with threat intensity but also with reward value via its influence on vigilance. The effect of reward on vigilance depends on the operating region of the sigmoidal vigilance function. This operating region is set by the baseline vigilance level (Figure 5I) and reflects habituation to repeated looming threats. Furthermore, threat gain and reward value have distinct effects on escape latency: higher threat gain exponentially shortened latency, whereas higher reward value increased it linearly (Figure S9F and S9G). These effects are confirmed using a simplified deterministic version of the model (Figure S9J and S9K; see Methods and Materials).

Lastly, the diffusion rate δ plays a critical role, particularly under low-threat conditions where the average evidence trajectory fails to reach the threshold. This parameter may reflect the fluctuation of the animal's internal state. The diffusion rate captures the trial-to-trial variability: even small amounts of noise can accumulate over time, resulting in large differences across individual trials and contributing to variability in escape latency. Overall, this computational framework not only accounts for our experimental observations but also offers a quantitative foundation for studying innate decision-making across species. Understanding how these parameters are implemented at the circuit level is an exciting direction for future research.

4 Methods and Materials

4.1 Animal

Male C57BL/6J mice were group-housed on a 12-hour light / 12-hour dark cycle and used at ages 2-3 months. Behavioral experiments were conducted during the light phase. All experimental procedures were performed under the animal welfare guidelines and approved by the Institutional Animal Care and Use Committee at the Chinese Institute for Brain Research, Beijing.

4.2 Behavioral platform

The behavioral platform consisted of a nest, a linear arena, a radio frequency identification (RFID) system, a real-time mouse position detection system, and a reward delivery port. As illustrated in Figure 1A, the nest (40 cm (L) × 20 cm (W) × 30 cm (H)) and the linear arena (100 cm × 10 cm × 30 cm) were made with infrared transmitting acrylic to allow unobtrusive behavioral monitoring. They were connected by a one-way tunnel (20 cm × 3 cm × 3 cm) for entering the arena and a 20 cm × 5 cm × 30 cm safe zone with a 5 cm × 5 cm one-way door for returning to the nest. Because it wasn't directly under the monitor, the safe zone was darker than the arena. Mice were labeled via implanted RFID tags, which were detected by an RFID reader placed around the tunnel. Only one mouse was allowed to enter the arena at a time. Specifically, when all mice were in the nest, the door between the nest and the tunnel was open, while the door between the tunnel and the arena remained closed. When a single mouse entered the tunnel, as detected by the RFID system, the door to the nest closed and the door to the arena opened, allowing the mouse to enter the arena. The mice were rewarded at the end of the arena with water or sucrose. Licking time and reward volume were recorded.

To track mouse position in real time, an OpenMV camera with a 90° field-of-view lens was mounted on the ground, 110 cm beneath the arena. The mouse position was used to control the tunnel doors and to trigger stimulus presentation when the mouse entered the arena. Specifically, the tunnel had two doors: the first connected the tunnel to the nest, and the second door connected the tunnel to the arena. Once a mouse entered the tunnel, the first door closed and the second door opened. A second camera (LBAS-U350-74M) with a lens (FA0615A) was also placed on the ground to record animal behavior at 30 frames per second.

4.3 Visual stimulation

Looming stimuli were presented on a 55-inch monitor (121 cm × 68 cm) suspended 32 cm above the arena. Visual stimulation was implemented using Psychopy in Python and was aligned to the mouse's real-time location. The stimulus was a black disc that expanded ten times on a gray background ($\sim$ 65 cd / cm^2). For each time, the disc expanded from 0° to 20° of visual angle at a speed of 40°/s, followed by a stationary phase lasting 0.3 s. The inter-stimulus interval was randomized between 1 and 2 minutes. Two stimulus contrasts at 20% and 99% were displayed by adjusting the luminance of the disc.

4.4 Economic modulation of innate decision-making

All mice were habituated to the behavioral platform for two days before the looming experiment. On the first day, five mice from the same home cage were placed in the nest for 30 minutes with all doors closed. Each mouse was then placed individually in the nest and allowed to explore the arena for 10 min under normal door operation; if a mouse entered the arena fewer than two times, the exploration period was extended until at least two arena visits were completed. Subsequently, all five mice were returned to the nest with all doors open and allowed to freely explore the arena for 2 h to ensure that each mouse learned the reward location at the end of the linear arena. On the second day, each mouse was placed individually in the nest and given an additional 1 h of exploration under normal door operation to further acclimate to the environment. The looming experiment was conducted the following day. An overhead looming stimulus of either low (20%) or high (99%) contrast was triggered when the mouse entered the trigger zone, defined as the region within 20 cm of the reward port. For each mouse, both the looming contrast and reward type remained constant across trials. In total, we collected and analyzed behavioral data from 590 trials across 62 mice.

To control for individual variation in decision-making, we compared the same animal's behavior under reward and no-reward conditions. Two groups of mice were used in the experiment. In the first group (n = 5), mice were first tested under the reward condition, followed by the no-reward condition. In the second group (n = 4), the order was reversed. For the reward condition, mice were water-deprived one day before the exploration, and water was provided via the reward port. In the no-reward condition, mice were not water-deprived, and the reward port was removed. Before the looming experiment, mice were acclimated to the linear arena for two days as described above. On the third day, a looming stimulus with 20% contrast was displayed for five trials. In total, behavioral data from 84 trials across nine mice were recorded and analyzed.

4.5 Social modulation of innate decision-making

To investigate the impact of social hierarchy on decision-making, we first determined the social rank of each mouse pair using the tube test (Wang et al., 2011). Mice were co-housed with a glass tube (3 cm diameter, 10 cm long) for one week, then trained to cross a 30 cm tube 10 times per day over two consecutive days. On the third day, a pair was tested for up to six trials; if one mouse achieved four consecutive wins, it was designated the dominant individual; otherwise, the pair (1 out of 6 pairs) was excluded from further experiment.

Before the looming experiment, mice were water-deprived and allowed to explore the linear arena for two hours per day over three days, during which water rewards were delivered at the end of the arena. Over the following two days, the looming experiment with a stimulus contrast of 99% was performed for two hours per day. After the looming experiment, mice continued to explore the arena for an additional two days, after which their social rank was reassessed with the tube test. All remaining pairs maintained a stable rank order.

To assess whether the tube test itself influenced defensive decision-making, additional looming experiments were conducted on four mouse pairs before and after introducing the tube test. Specifically, the first looming experiment was conducted prior to the tube test in Figure 4A. The behavioral patterns in a total of 180 trials from 18 mice were recorded and analyzed.

4.6 Behavioral quantification

Animal behaviors were quantified in three steps. First, two key points—the nose and tail base—were labeled and tracked in the recorded videos using DeepLabCut (Figure S1A). Tracked points with likelihood scores below 0.6 were excluded and filled via linear interpolation. Locomotion speed was calculated for each frame and smoothed using a 0.3 s moving average window. Unless otherwise specified, the speed of the tail base was used for subsequent analyses. Second, individual 30 s trials were extracted, each consisting of 10 seconds before, 8 seconds during, and 12 seconds after the looming stimulus. Multiple episodes of these states could occur within a single trial.

Third, we defined 19 behavioral features related to locomotion speed, distance, and state transitions. Eleven features were related to speed and distance: (1) peak speed towards the reward port before stimulus onset; (2-4) maximum, mean, and coefficient of variation of speed after stimulus onset; (5) latency to peak speed; (6) hiding latency, defined as the time between stimulus onset and arrival at the safe zone (set to 20 s if the mouse did not reach the safe zone by the end of the trial); (7) escape distance, defined as the distance covered between stimulus onset and offset; (8) distance to the nest at the end of the trial; (9) total distance traveled at speeds greater than 90% of the peak speed; (10) duration of movement at speeds greater than 90% of the peak speed; and (11) duration of time with both key points moving slower than 1 cm / s. Eight features were related to state transitions: (12) latency to flee, defined as the time from stimulus onset to the first escape state, where an escape state was identified when the animal moved more than 10 cm at a speed exceeding 10 cm / s; (13-15) average speed, distance traveled, and acceleration during the fastest escape episode; (16) latency to the fastest escape episodes; (17) latency to the first stationary state, where a stationary state was defined when both key points moved less than 1 cm / s for more than 0.3 s; (18,19) total and longest stationary duration.

Finally, these features were fed into a random forest model with a maximum depth of 5 to classify animal behaviors. For trials in which neither escape nor stationary states were identified, latencies (feature 12,16,17) were set to 20 s, distance (14) to 0 cm, speed (13) to 0 cm / s, acceleration (15) to 0 cm / s^2, and duration (18,19) to 0 s. The model was trained on 238 trials and tested on 102 trials, achieving an accuracy of 0.95 on the test set. Using this classifier, behavioral decisions in 3862 trials across 140 mice were categorized into four types: direct escape, escape after assessment, freezing, and no response (Figure S1). A decision score was calculated for each condition as $S = 3p_e + 2p_{fe} + p_f$, where p_e, p_{ae}, p_f denote the proportion of direct escape, escape after assessment, and freezing, respectively. To quantify how quickly animals recovered from a fear state, we measured recovery time. For escape trials, recovery time was defined as the hiding duration, measured from entry into the safe zone to re-entry into the arena. For freezing trials, recovery time was defined as the interval between the onset of the first freezing episode and the termination of the last freezing episode.

To quantify the influence of reward, the reward zone was defined as a region within 10 cm of the reward port, and the duration in the reward zone was defined as the time spent within this zone during the 20 seconds following stimulus onset. Vigilance was assessed using latency to flee, foraging interval (time between two consecutive entries into the trigger zone), and foraging speed (average speed heading to the trigger zone before the looming exposure).

To segment the trials into two phases, we performed principal component analysis on a feature matrix containing decision score, escape distance, time spent in the reward zone, peak escape speed, and latency to flee across the first 10 trials. We extracted the first principal component (Figure S3), which captured the majority of the variance, and used its learning curve to detect transitions in behavior. Change points of the learning curve were detected by the ruptures approach (Gallistel et al., 2004; Truong et al., 2020).

4.7 Behavioral modeling

Parameters in the drift-diffusion leaky integrator model were estimated in two steps by minimizing a loss function using a grid search. In the first step, we fit our model to behavioral data in the no-reward condition, setting $r = 0$ and $\beta = 1$ for the low-threat condition, and estimated α, δ, x_{thr}, and β for the high-threat condition. In the second step, we estimated β and r for water and sucrose conditions under both threat conditions. The loss function combines fitting errors in the distribution of behavioral decisions ($\mathscr{L}_{\text{dec}}$), the median latency to flee ($\mathscr{L}_{\text{med}}$), and the variability of latency ($\mathscr{L}_{\text{sd}}$):

$$\mathcal{L} = 100\mathcal{L}_{\text{dec}} + 2\mathcal{L}_{\text{med}} + \mathcal{L}_{\text{sd}} \tag{3}$$

The decision-distribution mismatch is quantified using a mean cosine distance:

$$\mathcal{L}_{\text{dec}} = \frac{1}{C}\sum_{c=1}^{C}\left(1 - \frac{\mathbf{d}_c \cdot \hat{\mathbf{d}}_c}{\|\mathbf{d}_c\|\|\hat{\mathbf{d}}_c\|}\right) \tag{4}$$

where $\mathbf{d}_c$ and $\mathbf{d}^{\wedge}{}_c$ denote the observed and model-predicted decision distributions for contrast level c, and $C = 2$ is the number of threat conditions.

The median-latency loss is defined as

$$\mathcal{L}_{\text{med}} = \frac{1}{C}\sum_{c=1}^{C}\frac{\left|\hat{L}_c^{\text{med}} - L_c^{\text{med}}\right|}{\hat{L}_c^{\text{med}} + L_c^{\text{med}}}, \tag{5}$$

and the latency-variability loss is

$$\mathcal{L}_{\text{sd}} = \frac{1}{C}\sum_{c=1}^{C}\frac{\left|\hat{L}_c^{\text{sd}} - L_c^{\text{sd}}\right|}{\hat{L}_c^{\text{sd}} + L_c^{\text{sd}}}. \tag{6}$$

For the final fitted model (Equation 1), $\alpha = 1.78$ and $\delta = 5.6$. Under low-threat conditions, $\beta = 1$ for all conditions; under high-threat conditions, $\beta = 1.44, 1.8, 2.55$ for no reward, water, and sucrose, respectively. The reward values were $r = 0, 0.08, 0.25$ for no reward, water, and sucrose, respectively, under both threat conditions. In Equation 2, the decision threshold was $x_{thr} = 0.71$.

To further understand how threat and reward shape decisions, we analyze a deterministic simplification of the model:

$$\frac{dx}{dt} = -\alpha \cdot x(t) + n \cdot t - p \tag{7}$$

where $p > 0$ denotes the perceived reward value and $n \cdot t < 0$ denotes the perceived threat strength, which grows linearly over time.

With the initial condition $x(0) = 0$, the solution is

$$x(t) = \frac{n}{\alpha}t + \left(\frac{p}{\alpha} + \frac{n}{\alpha^2}\right)\left(e^{-\alpha t} - 1\right) \tag{8}$$

This reveals a competition between two components. First, a linear term driven by threat accumulation promotes escape over time. Second, an exponentially decaying component reflects the combined influence of reward and threat.

4.8 Quantification and statistical analysis

No statistical method was used to predetermine sample size. The Shapiro-Wilk test was applied to assess the normality of data distributions. For comparison between two groups, a two-sample *t*-test or paired *t*-test was used for normally distributed data; otherwise, the Mann–Whitney U-test or one-sample Wilcoxon signed-rank test was applied. For multi-group comparisons, one-way or two-way analysis of variance (ANOVA) was used when data were normally distributed, followed by Tukey's post hoc test. For non-parametric multi-group comparisons, the Kruskal–Wallis test (for one factor) or the Scheirer–Ray–Hare test (for two factors) was applied, followed by Dunn's post hoc test with Holm correction. The chi-square test was conducted to analyze categorical variables, while paired categorical comparisons were assessed using the Stuart–Maxwell test. Detailed statistical information for each experiment is provided in the Results section and figure legends.

5 Supplemental information

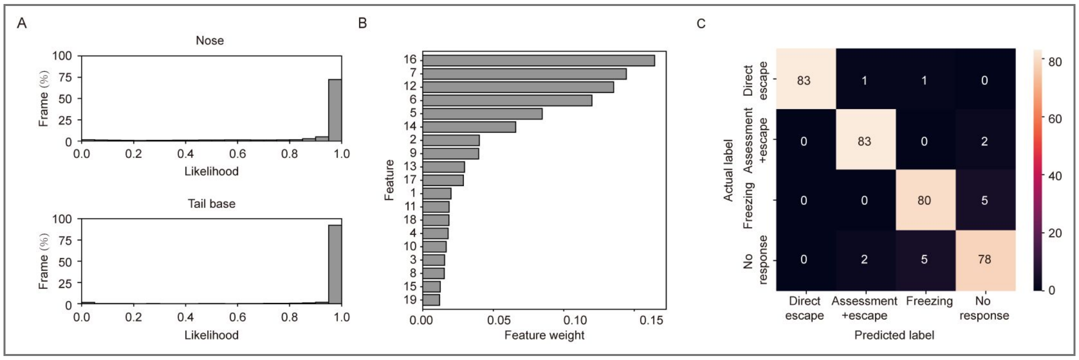


Figure S1. **Model validation and feature analysis for automated behavioral classification.** (A) Tracking accuracy of the mouse nose and tail base using DeepLabCut. (B) Weights of the 19 behavioral features in the random forest classifier. (C) Model performance evaluated by a confusion matrix on the test dataset.

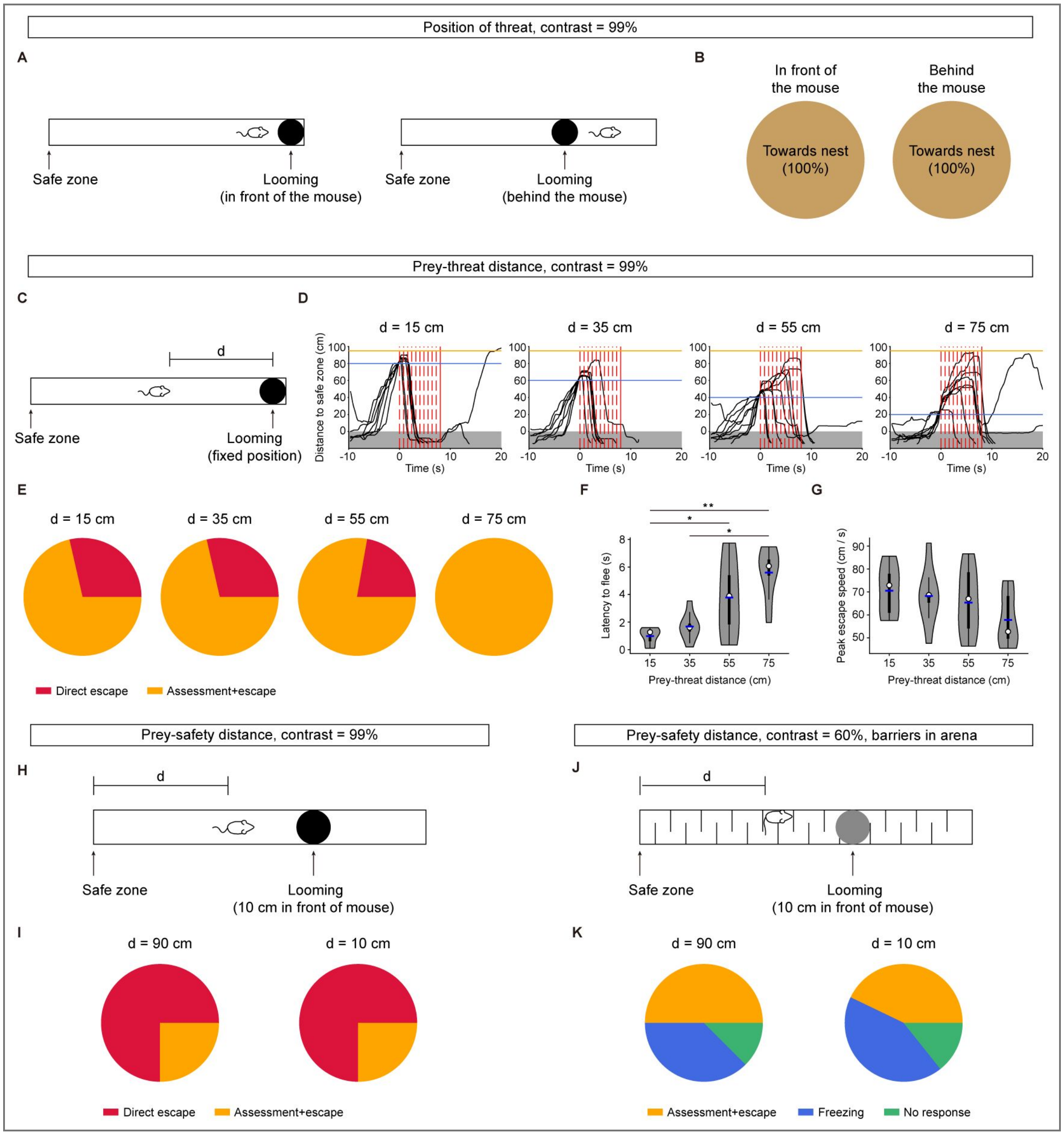


Figure S2. **Effects of threat position, prey–threat distance, and prey–safety distance on defensive responses to looming stimuli.**

(A) Schematic of the experiment in which looming stimuli were presented either in front of or behind mice during foraging. (B) Distribution of escape direction for front and behind stimulus positions. N = 97, 16 trials. (C) Schematic of the experiment in which looming stimuli were presented at the end of the linear arena with varying distances between the mouse and the threat. (D) Distance to the safe zone over time for four prey-threat distances. Red dashed lines mark the onset of each stimulus repetition; solid lines mark the end of the last repetition. Grey shade indicates the safe zone. Blue lines mark the mouse's position when the looming stimulus was triggered; orange lines mark the location of the looming stimulus. N = 7 (15 cm), 7 (35 cm), 9 (55 cm), and 8 (75 cm) trials from 5 mice. (E) Distribution of decisions across prey-threat distances. (F–G) Latency to flee and peak escape speed across prey-threat distances. Kruskal-Wallis test with post hoc Dunn's test (Holm correction). (H) Schematic of the experiment in which looming stimuli were presented in front of the mouse at varying distances between the mouse and the safe zone. (I) Distribution of decisions across prey-safety distances. N = 4, 4 trials. (J) Schematic of the experiment in which low-contrast looming stimuli were presented at varying distances between the mouse and the safe zone in the linear arena with barriers. (K) Distribution of decisions across prey-safety distances in the barrier condition. N = 8, 7 trials. *$p < 0.05$, **$p < 0.01$.

Figure S3.

(A) Water or sucrose consumption during exploration and looming experiments at low and high contrasts. N = 10, 10, 5, 5, 5, 5 sessions; Mann–Whitney–Wilcoxon test. Boxes represent the interquartile range (IQR), and whiskers show the full data range. (B) Pie chart showing the proportion of looming stimuli detected by mice in no-response trials under low- and high-threat conditions. Low contrast: N = 117 trials from 29 mice; high contrast: N = 2 trials from 2 mice (high contrast). (C) Proportion of total behavioral variance explained by principal component 1 (PC1) for individual mice across all conditions. N = 11, 13, 10, 10, 8, 10. (D) Cumulative PC1 score for an example mouse in each condition. Red dashed lines mark the transition from the early to the late phase. *$p < 0.05$, **$p < 0.01$.

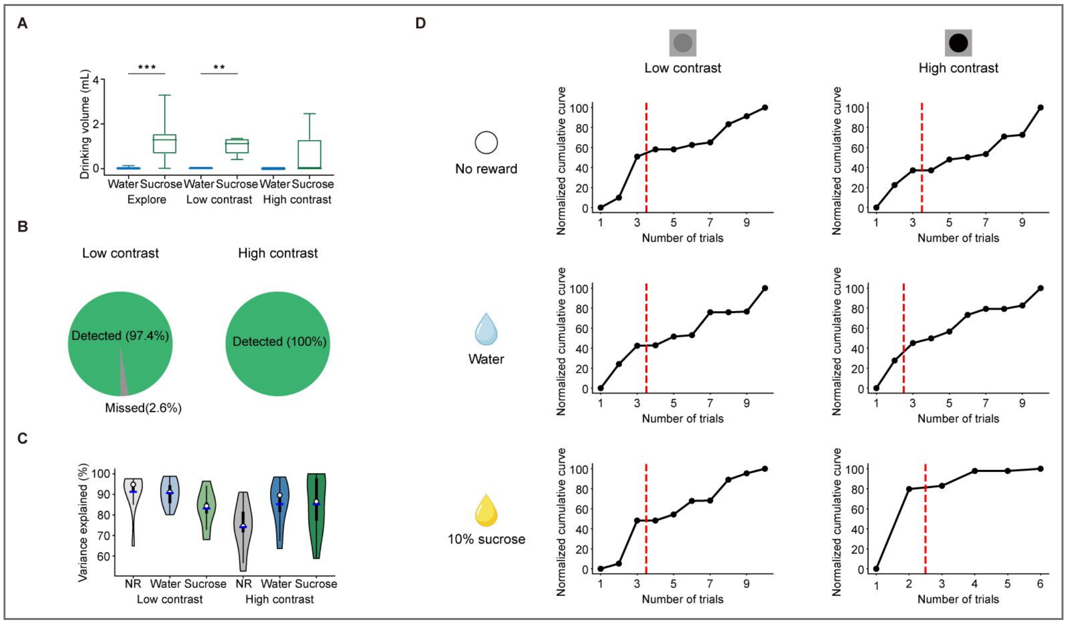


Figure S4. **Distribution of foraging speed.**

(A) Distribution of foraging speed relative to distance from the safe zone in the early phase across different risk and reward conditions. (B) Distribution of foraging speed in the late phase. Data are from 11 mice (no reward, low contrast), 13 mice (water, low contrast), 10 mice (sucrose, low contrast), 10 mice (no reward, high contrast), 8 mice (water, high contrast), and 10 mice (sucrose, high contrast).

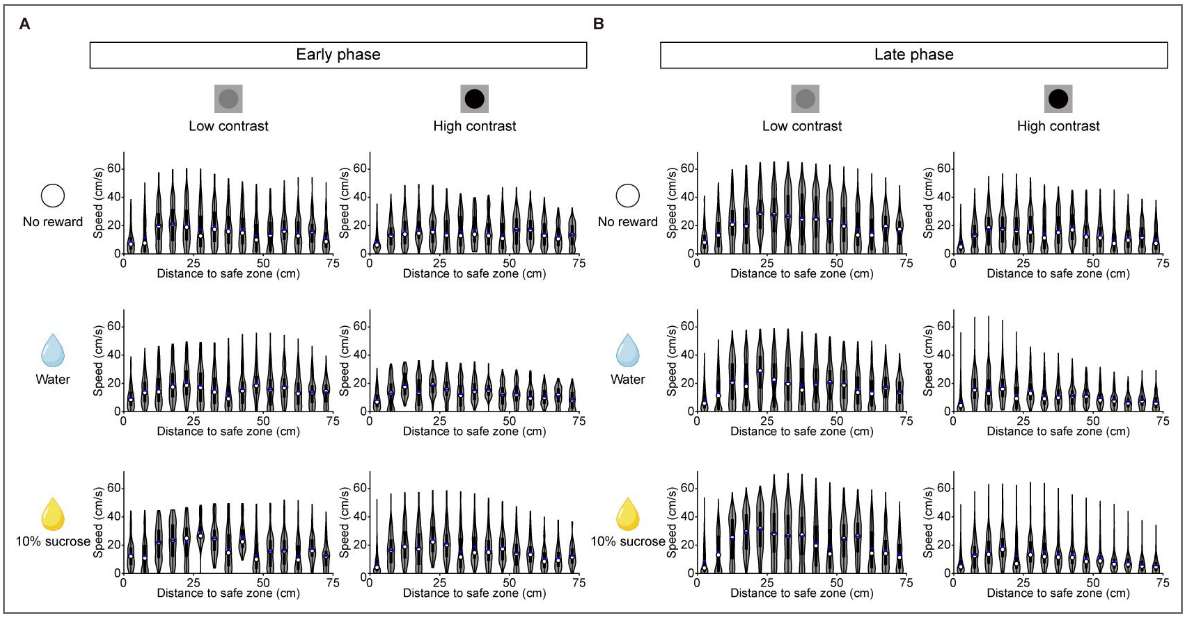


Figure S5. **Behavioral responses to looming stimuli across risk and reward conditions in the first trial.**

(A) Distribution of decisions for each mouse under six conditions. N = 11 (no reward, low contrast), 13 (water, low contrast), 10 (sucrose, low contrast), 10 (no reward, high contrast), 8 (water, high contrast), 10 (sucrose, high contrast); Chi-squared test. (B–F) Escape distance under threat, duration in the reward zone, latency to flee, foraging speed, and peak escape speed across conditions. Scheirer–Ray–Hare test with post hoc Dunn's test (Holm correction). N = 11, 13, 10, 10, 8, 10 trials for B, C, E, F; N = 11, 11, 10, 10, 8, 10 trials for D. *$p < 0.05$, ***$p < 0.001$.

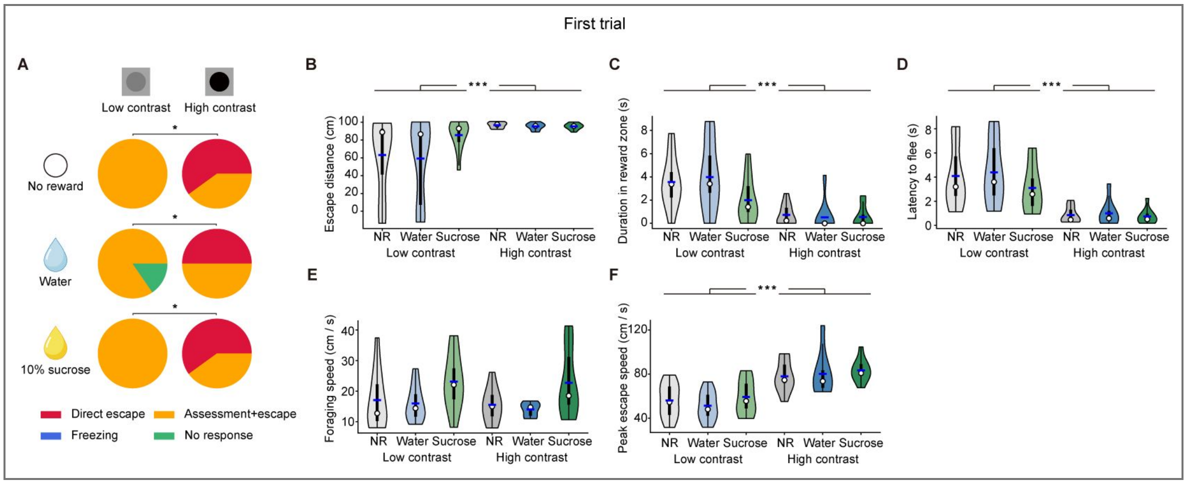
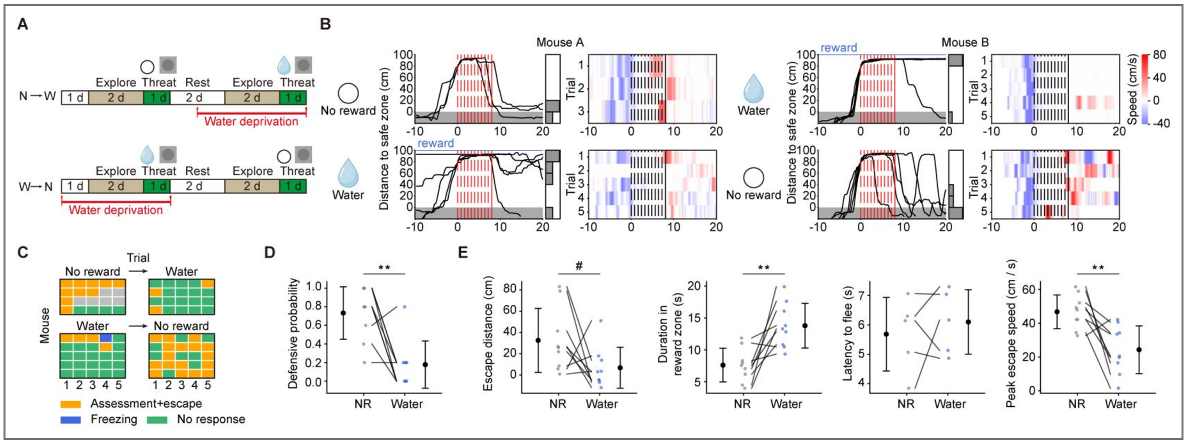


Figure S6. **Reward modulation of defensive behavior to looming stimuli in the same mouse.**

(A) Experimental timeline illustrating how water reward influences innate decision-making within the same animal. (B) Distance to the safe zone and locomotion speed towards the safe zone across trials in response to low-contrast looming stimuli with and without water reward in two example mice. Left: no-reward condition followed by water-reward condition; Right: water-reward condition followed by no-reward condition. (C) Decision patterns of nine mice across two sessions with 5 trials for each. Gray squares indicate trials where the mouse did not enter the arena within 30 minutes. (D) Defensive probability in no-reward and water-reward conditions. N = 9 mice, paired t-test. (E) Escape distance under threat, duration in the reward zone, latency to flee, and peak escape speed in no-reward and water-reward conditions. N = 5 mice for latency to flee and 9 mice for other measures, paired t-test, two-sided. #$p < 0.1$, *$p < 0.05$, **$p < 0.01$.



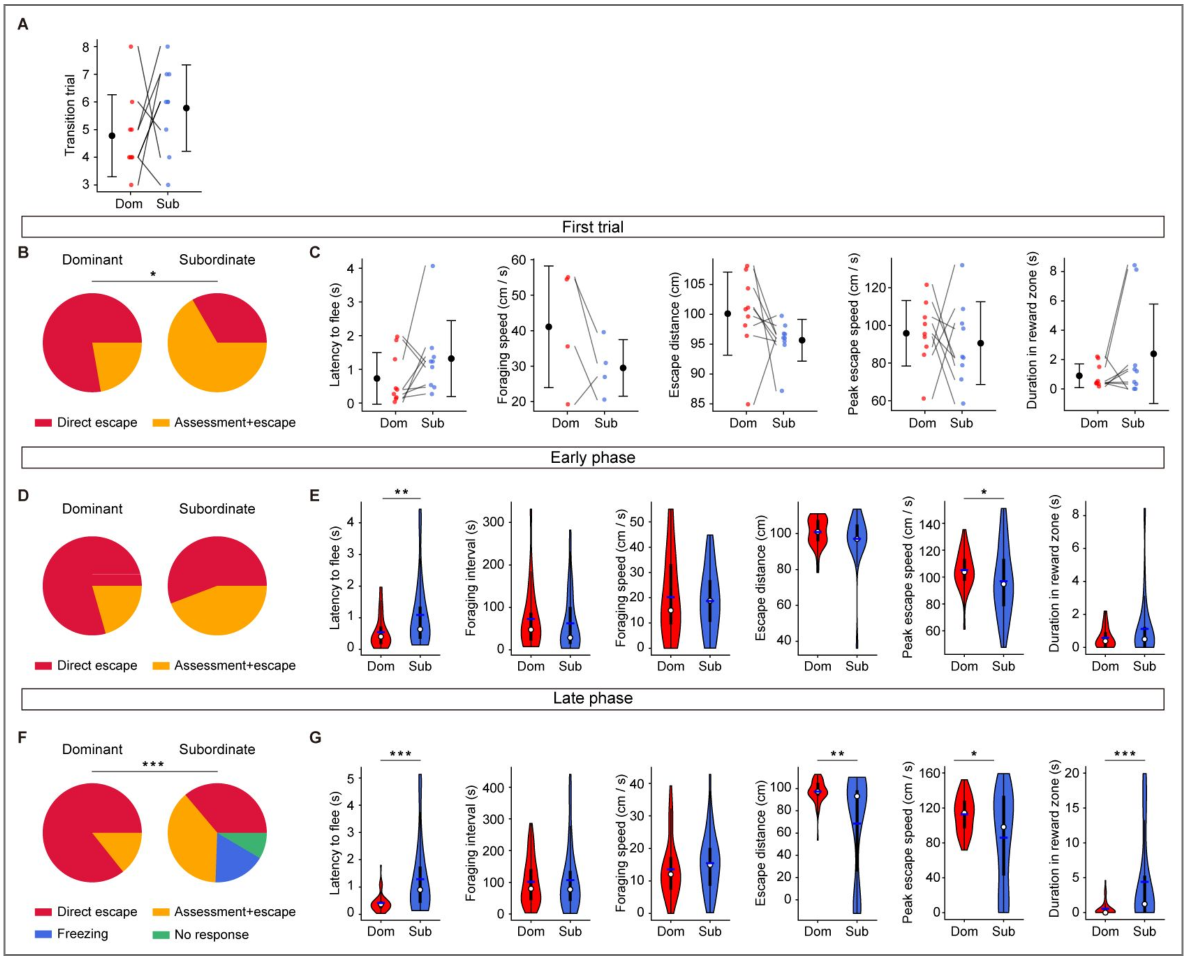


Figure S7. Behavioral responses to looming stimuli for dominant and subordinate mice in different phases.

(A) Transition trial marking the start of the late phase for dominant and subordinate mice. N = 9 pairs. (B) Behavioral decisions for dominant and subordinate mice during their first exposure to threat. Stuart-Maxwell test. N = 9 pairs. (C) Latency to flee, foraging speed, escape distance under threat, peak escape speed, and duration in the reward zone during the first threat exposure. N = 4 pairs for foraging speed; N = 9 pairs for other features. Paired *t* test (D) Behavioral decisions for dominant and subordinate mice in the early phase. Chi-squared test. N = 34, 43 trials, respectively. (E) Violin plots showing latency to flee, average foraging interval, foraging speed, escape distance under threat, peak escape speed, and duration in the reward zone for dominant and subordinate mice in the early phase. N = 34, 43 trials, respectively. Mann-Whitney-Wilcoxon test. (F) Behavioral decisions for dominant and subordinate mice in the late phase. Chi-squared test. N = 56, 47 trials, respectively. (G) Violin plots showing latency to flee, average foraging interval, foraging speed, escape distance under threat, peak escape speed, and duration in the reward zone for dominant and subordinate mice in the late phase. N = 56, 35 trials for latency to flee; N = 56, 47 trials for other measures. Mann-Whitney-Wilcoxon test. $*p < 0.05$, $**p < 0.01$, $***p < 0.001$.

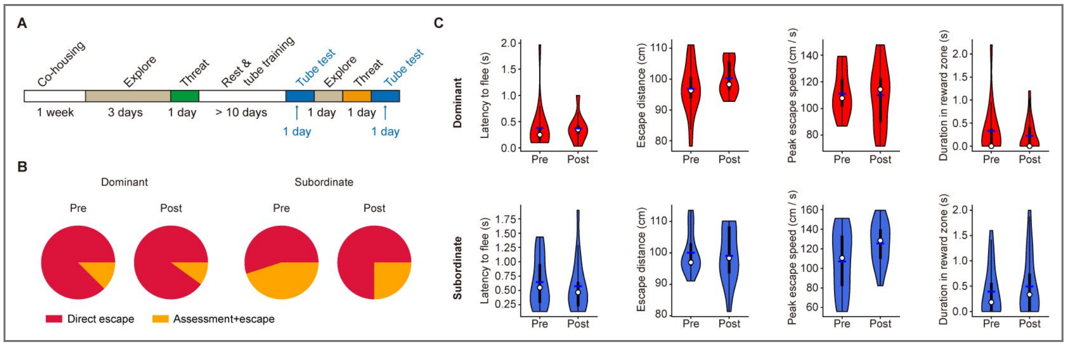


Figure S8. **Comparison of behavioral responses to looming stimuli before and after the tube test.**

(A) Schematic timeline of the looming experiments before and after the tube test. (B) Behavioral decisions for dominant and subordinate mice before and after the tube test. Chi-squared test. Dominant: N = 16 (pre) and 20 (post) trials from 4 mice; Subordinate: N = 20 (pre) and 16 (post) trials from 4 mice. (C) Violin plots showing latency to flee, escape distance under threat, peak escape speed, and duration in the reward zone for dominant (top) and subordinate (bottom) mice before and after the tube test. Mann-Whitney-Wilcoxon test.

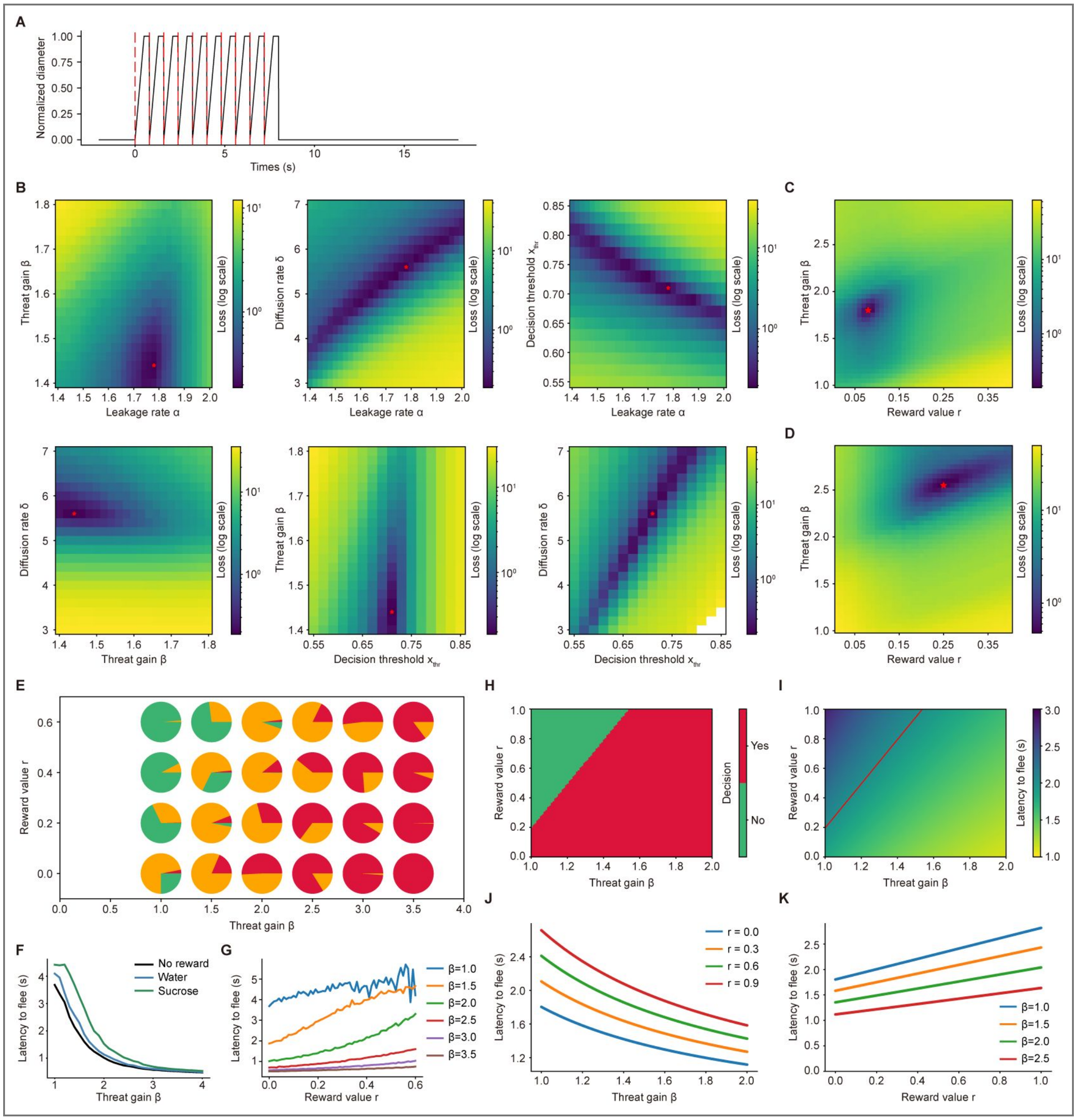


Figure S9. **Fitting loss in the drifting–diffusion leaky integrator model.**

(A) Temporal profile of the normalized looming stimulus diameter. (B) Loss landscapes across the parameter space for estimating the leakage rate, high-contrast threat gain, diffusion rate, and decision threshold during the first-stage fitting. Red stars indicate the optimal parameter estimates based on experimental data in the late phase of the reward-related paradigm under the no-reward condition. (C) Loss landscapes across the parameter space for estimating the reward value and high-contrast threat gain under the water-reward condition. Red stars mark the optimal fits to experimental data in the late phase of the reward-related paradigm. (D) Same as (C), for the sucrose-reward condition. (E) Model-predicted distribution of decisions across threat gain and reward values. (F) Predicted latency to flee as a function of threat gain for varying reward values. (G) Predicted latency to flee as a function of reward value for varying threat gain. (H–I) Decisions and latency to flee across threat gain and reward values predicted by a simplified deterministic model. (J–K) Same as (F–G), but for the simplified deterministic model.

Data availability

Data and code are available in a public GitHub repository (*https://github.com/YatangLiLab/Li_Innate_Decision_Making_2025*).

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Additional information

Author contributions

Ya-tang Li supervised the project; Ya-tang Li, Zhe Li, and Yidan Sun designed the experiments; Zhe Li collected all the data; Zhe Li, Jiahui Wang, and Jialin Li analyzed the data; Ya-tang Li carried out the neural modeling; Zhe Li and Ya-tang Li prepared figures; Ya-tang Li, Ling-yun Li, and Zhe Li wrote the manuscript.

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References

1. **Amir A.,** Lee S.-C., Headley D. B., Herzallah M. M., Pare D (2015) Amygdala signaling during foraging in a hazardous environment. *Journal of Neuroscience* **35**:12994-13005
2. **Andermann M. L.,** Kerlin A. M., Reid C (2010) Chronic cellular imaging of mouse visual cortex during operant behavior and passive viewing. *Frontiers in Cellular Neuroscience* **4**
3. **Anderson D. J.,** Adolphs R (2014) A framework for studying emotions across species. *Cell* **157**:187-200
4. **Barnes C. A** (1979) Memory deficits associated with senescence: a neurophysiological and behavioral study in the rat. *Journal of Comparative and Physiological Psychology* **93**:74-104

5. **Baruchin L. J.,** Alleman M., Schröder S (2023) Reward modulates visual responses in the superficial superior colliculus of mice. *Journal of Neuroscience* **43**:8663-8680

6. **Benavidez N. L.,** Bienkowski M. S., Zhu M., Garcia L. H., Fayzullina M., Gao L., Bowman I., Gou L., Khanjani N., Cotter K. R., *et al.* (2021) Organization of the inputs and outputs of the mouse superior colliculus. *Nature Communications* **12**:4004

7. **Bravo-Rivera C.,** Roman-Ortiz C., Brignoni-Perez E., Sotres-Bayon F., Quirk G. J (2014) Neural structures mediating expression and extinction of platform-mediated avoidance. *Journal of Neuroscience* **34**:9736-9742

8. **Buck L** (1966) Reaction time as a measure of perceptual vigilance. *Psychological Bulletin* **65**:291-304

9. **Burgess C. P.,** Lak A., Steinmetz N. A., Zatka-Haas P., Reddy C. B., Jacobs E. A. K., Linden J. F., Paton J. J., Ranson A., Schröder S., *et al.* (2017) High-yield methods for accurate two-alternative visual psychophysics in head-fixed mice. *Cell Reports* **20**:2513-2524

10. **Calvin O. L.,** Erickson M. T., Walters C. J., Redish A. D (2025) Dorsal hippocampus represents locations to avoid as well as locations to approach during approach-avoidance conflict. *PLOS Biology* **23**:e3002954

11. **Campagner D.,** Vale R., Tan Y. L., Iordanidou P., Pavón Arocas O., Claudi F., Stempel A. V., Keshavarzi S., Petersen R. S., Margrie T. W., *et al.* (2023) A cortico-collicular circuit for orienting to shelter during escape. *Nature* **613**:111-119

12. **Caraco T.,** Martindale S., Pulliam H. R (1980) Avian flocking in the presence of a predator. *Nature* **285**:400-401

13. **Choi J.-S.,** Kim J. J (2010) Amygdala regulates risk of predation in rats foraging in a dynamic fear environment. *Proceedings of the National Academy of Sciences* **107**:21773-21777

14. **Cohen J. Y.,** Haesler S., Vong L., Lowell B. B., Uchida N (2012) Neuron-type-specific signals for reward and punishment in the ventral tegmental area. *Nature* **482**:85-88

15. **Comoli E.,** Coizet V., Boyes J., Bolam J. P., Canteras N. S., Quirk R. H., Overton P. G., Redgrave P (2003) A direct projection from superior colliculus to substantia nigra for detecting salient visual events. *Nature Neuroscience* **6**:974-980

16. **Comoli E.,** Das Neves Favaro P., Vautrelle N., Leriche M., Overton P. G., and Redgrave P. (2012) Segregated anatomical input to sub-regions of the rodent superior colliculus associated with approach and defense. *Frontiers in Neuroanatomy* **6**

17. **Constantinople C. M.,** Piet A. T., Brody C. D (2019) An analysis of decision under risk in rats. *Current Biology* **29**:2066-2074

18. **De Franceschi G.,** Vivattanasarn T., Saleem A., Solomon S. (2016) Vision guides selection of freeze or flight defense strategies in mice. *Current Biology* **26**:2150-2154

19. **Edwards D. H.,** Kravitz E. A (1997) Serotonin, social status and aggression. *Current Opinion in Neurobiology* **7**:812-819

20. **Evans D. A.,** Stempel A. V., Vale R., Branco T (2019) Cognitive control of escape behaviour. *Trends in Cognitive Sciences* **23**:334-348

21. **Evans D. A.,** Stempel A. V., Vale R., Ruehle S., Lefler Y., Branco T (2018) A synaptic threshold mechanism for computing escape decisions. *Nature* **558**:590-594

22. **Fanselow M. S.,** Lester L. S (1988) A functional behavioristic approach to aversively motivated behavior: predatory imminence as a determinant of the topography of defensive behavior. In: Bolles R. C., Beecher M. D (Eds). *Evolution and Learning* Lawrence Erlbaum Associates. pp. 185-212

23. **Gallistel C. R.,** Fairhurst S., Balsam P (2004) The learning curve: Implications of a quantitative analysis. *Proceedings of the National Academy of Sciences* **101**:13124-13131

24. **Gibson W. T.,** Gonzalez C. R., Fernandez C., Ramasamy L., Tabachnik T., Du R. R., Felsen P. D., Maire M. R., Perona P., Anderson D. J. (2015) Behavioral responses to a repetitive visual threat stimulus express a persistent state of defensive arousal in *drosophila*. *Current Biology* **25**:1401-1415

25. **Hayden B. Y** (2018) Economic choice: the foraging perspective. *Current Opinion in Behavioral Sciences* **24**:1-6

26. **Hayden B. Y.,** Pearson J. M., Platt M. L (2011) Neuronal basis of sequential foraging decisions in a patchy environment. *Nature Neuroscience* **14**:933-939

27. **Kahneman D.,** Tversky A (1979) Prospect theory: an analysis of decision under risk. *Econo-metrica* **47**:263-291

28. **Kingsbury L.,** Huang S., Wang J., Gu K., Golshani P., Wu Y. E., Hong W (2019) Correlated neural activity and encoding of behavior across brains of socially interacting animals. *Cell* **178**:429-446.

29. **Kleiman M.,** Bodek S., Eilam D (2014) Who are the bosses? Group influence on the behavior of voles following owl attack. *Behavioural Processes* **108**:183-190

30. **Krasne F. B.,** Shamsian A., Kulkarni R (1997) Altered excitability of the crayfish lateral giant escape reflex during agonistic encounters. *Journal of Neuroscience* **17**:709-716

31. **Krauzlis R. J.,** Lovejoy L. P., Zénon A (2013) Superior colliculus and visual spatial attention. *Annual Review of Neuroscience* **36**:165-182

32. **Lenzi S. C.,** Cossell L., Grainger B., Olesen S. F., Branco T., Margrie T. W (2022) Threat history controls flexible escape behavior in mice. *Current Biology* **32**:2972-2979

33. **Li C.,** Kühn N. K., Alkislar I., Sans-Dublanc A., Zemmouri F., Paesmans S., Calzoni A., Ooms F., Reinhard K., Farrow K. (2023) Pathway-specific inputs to the superior colliculus support flexible responses to visual threat. *Science Advances* **9**:eade3874

34. **Li Y.-t.,** Turan Z., Meister M. (2020) Functional architecture of motion direction in the mouse superior colliculus. *Current Biology* **30**:3304-3315.

35. **Liden W. H.,** Herberholz J (2008) Behavioral and neural responses of juvenile crayfish to moving shadows. *The Journal of Experimental Biology* **211**:1355-1361

36. **Liu Z.,** Zhou J., Li Y., Hu F., Lu Y., Ma M., Feng Q., Zhang J.-E., Wang D., Zeng J., *et al.* (2014) Dorsal raphe neurons signal reward through 5-HT and glutamate. *Neuron* **81**:1360-1374

37. **Lorenz K. Z** (1950) The comparative method in studying innate behavior patterns. *Symposia of the Society for Experimental Biology* **4**:221-268

38. **Mathis A.,** Mamidanna P., Cury K. M., Abe T., Murthy V. N., Mathis M. W., Bethge M (2018) DeepLabCut: markerless pose estimation of user-defined body parts with deep learning. *Nature Neuroscience* **21**:1281-1289

39. **Meister M** (2022) Learning, fast and slow. *Current Opinion in Neurobiology* **75**:102555

40. **Miyazaki K.,** Miyazaki K. W., Doya K (2011) Activation of dorsal raphe serotonin neurons underlies waiting for delayed rewards. *Journal of Neuroscience* **31**:469-479

41. **Mooney R. D.,** Huang X., Shi M. Y., Bennett-Clarke C. A., Rhoades R. W (1996) Serotonin modulates retinotectal and corticotectal convergence in the superior colliculus. *Progress in Brain Research* **112**:57-69

42. **Morris R** (1984) Developments of a water-maze procedure for studying spatial learning in the rat. *Journal of Neuroscience Methods* **11**:47-60

43. **Moscarello J. M.,** LeDoux J. E (2013) Active avoidance learning requires prefrontal suppression of amygdala-mediated defensive reactions. *Journal of Neuroscience* **33**:3815-3823

44. **Mowrer O. H.,** Lamoreaux R. R (1946) Fear as an intervening variable in avoidance conditioning. *Journal of Comparative Psychology* **39**:29-50

45. **Raleigh M. J.,** McGuire M. T., Brammer G. L., Pollack D. B., Yuwiler A (1991) Serotonergic mechanisms promote dominance acquisition in adult male vervet monkeys. *Brain Research* **559**:181-190

46. **Rangel A.,** Camerer C., Montague P. R (2008) A framework for studying the neurobiology of value-based decision making. *Nature Reviews Neuroscience* **9**:545-556

47. **Ratcliff R** (1978) A theory of memory retrieval. *Psychological Review* **85**:59-108

48. **Rosenberg M.,** Zhang T., Perona P., Meister M (2021) Mice in a labyrinth show rapid learning, sudden insight, and efficient exploration. *eLife* **10**:e66175 https://doi.org/10.7554/eLife.66175
49. **Schultz W** (1998) Predictive reward signal of dopamine neurons. *Journal of Neurophysiology* **80**:1-27
50. **Schultz W.,** Apicella P., Scarnati E., Ljungberg T (1992) Neuronal activity in monkey ventral striatum related to the expectation of reward. *Journal of Neuroscience* **12**:4595-4610
51. **Shang C.,** Chen Z., Liu A., Li Y., Zhang J., Qu B., Yan F., Zhang Y., Liu W., Liu Z., *et al.* (2018) Divergent midbrain circuits orchestrate escape and freezing responses to looming stimuli in mice. *Nature Communications* **9**:1232
52. **Shang C.,** Liu Z., Chen Z., Shi Y., Wang Q., Liu S., Li D., Cao P (2015) A parvalbumin-positive excitatory visual pathway to trigger fear responses in mice. *Science* **348**:1472-1477
53. **Small W. S** (1901) Experimental Study of the Mental Processes of the Rat. II. *The American Journal of Psychology* **12**:206-239
54. **Steiner A. P.,** Redish A. D (2014) Behavioral and neurophysiological correlates of regret in rat decision-making on a neuroeconomic task. *Nature Neuroscience* **17**:995-1002
55. **Steinmetz N. A.,** Zatka-Haas P., Carandini M., Harris K. D (2019) Distributed coding of choice, action and engagement across the mouse brain. *Nature* **576**:266-273
56. **Tammero L. F.,** Dickinson M. H (2002) Collision-avoidance and landing responses are mediated by separate pathways in the fruit fly, Drosophila melanogaster. *The Journal of Experimental Biology* **205**:2785-2798
57. **Tremblay L.,** Schultz W (2000) Reward-related neuronal activity during go-nogo task perfor-mance in primate orbitofrontal cortex. *Journal of Neurophysiology* **83**:1864-1876
58. **Truong C.,** Oudre L., Vayatis N (2020) Selective review of offline change point detection methods. *Signal Processing* **167**:107299
59. **Vale R.,** Evans D. A., Branco T (2017) Rapid spatial learning controls instinctive defensive behavior in mice. *Current Biology* **27**:1342-1349
60. **Wagner M. J.,** Kim T. H., Savall J., Schnitzer M. J., Luo L (2017) Cerebellar granule cells encode the expectation of reward. *Nature* **544**:96-100
61. **Wallace D. J.,** Greenberg D. S., Sawinski J., Rulla S., Notaro G., Kerr J. N. D (2013) Rats maintain an overhead binocular field at the expense of constant fusion. *Nature* **498**:65-69
62. **Wang F.,** Zhu J., Zhu H., Zhang Q., Lin Z., Hu H (2011) Bidirectional control of social hierarchy by synaptic efficacy in medial prefrontal cortex. *Science* **334**:693-697
63. **Wei P.,** Liu N., Zhang Z., Liu X., Tang Y., He X., Wu B., Zhou Z., Liu Y., Li J., *et al.* (2015) Processing of visually evoked innate fear by a non-canonical thalamic pathway. *Nature Communications* **6**:6756
64. **Woolrych A.,** Vautrelle N., Reynolds J. N. J., Parr-Brownlie L. C (2021) Throwing open the doors of perception: The role of dopamine in visual processing. *European Journal of Neuroscience* **54**:6135-6146
65. **Yang X.,** Liu Q., Zhong J., Song R., Zhang L., Wang L (2020) A simple threat-detection strategy in mice. *BMC Biology* **18**:93
66. **Ydenberg R. C.,** Dill L. M (1986) The economics of fleeing from predators. *Advances in the Study of Behavior* **16**:229-249
67. **Yeh S.-R.,** Musolf B. E., Edwards D. H (1997) Neuronal adaptations to changes in the social dominance status of crayfish. *Journal of Neuroscience* **17**:697-708
68. **Yilmaz M.,** Meister M (2013) Rapid innate defensive responses of mice to looming visual stimuli. *Current Biology* **23**:2011-2015
69. **Zhong J.,** Liu Q., Yang X., Su J., Li X., Luo M., Wang L (2023) Mice learn from the predator-attack experience to accelerate flight behavior via optimizing the strategy of environment exploration. *Biochemical and Biophysical Research Communications* **665**:26-34

70. **Zhou Z.,** Liu X., Chen S., Zhang Z., Liu Y., Montardy Q., Tang Y., Wei P., Liu N., Li L., *et al.* (2019) A VTA GABAergic neural circuit mediates visually evoked innate defensive responses. *Neuron* **103**:473-488.

Peer reviews

Reviewer #1 (Public review):

This study by Li and colleagues examines how defensive responses to visual threats during foraging are modulated by both reward level and social hierarchy. Using a naturalistic paradigm, the authors test how the availability of water or sucrose, with sucrose being more rewarding than water, shapes escape behavior in mice exposed to looming stimuli of different intensities, which are used to probe perceived threat level and defensive responses. In parallel, the study compares dominant and subordinate animals to assess how social rank biases the trade off between reward seeking and threat avoidance. By combining detailed behavioral analyses with computational modeling, the work addresses how reward level and social context jointly influence escape decisions in an ethologically relevant setting.

Across the different experimental conditions, perceived threat level is the main determinant of behavior. The authors show that looming stimuli associated with higher threat (contrast) consistently elicit faster and more robust escape responses than lower threat stimuli. This effect is particularly evident during early exposures, when animals are highly vigilant and have not yet habituated to the looming stimulus (learned that it is not dangerous). Later they described that as animals gain experience and habituate, behavior becomes more flexible, and reward level begins to exert a graded modulation of the escape response. Importantly, the authors show that under high threat conditions increasing reward value leads to more frequent and faster escape rather than greater reward pursuit. This finding is particularly relevant, as it suggests that highly valued rewards can heighten vigilance and thereby enhance responsiveness to threat, highlighting that reward does not simply compete with defensive behavior but can also reshape it depending on the perceived level of danger, in contrast to low threat conditions, where threat can be more easily outweighed by reward. Thus, an important conceptual contribution of the study is the introduction of vigilance as a useful framework to interpret these effects. Vigilance is treated as a behavioral state reflecting heightened attention to potential danger. In line with what is known from natural foraging, mice initially maintain high vigilance when confronted with an innate threat. This perspective helps clarify a finding that might otherwise appear counterintuitive. One might expect higher rewards to motivate animals to tolerate risk, explore more, and habituate faster in any scenario. Instead, the data suggest that highly rewarding outcomes can elevate vigilance, making animals more responsive to threat and leading to faster or more frequent escape under high threat conditions. In this sense, reward does not simply compete with threat but can also amplify sensitivity to it, depending on the internal state of the animal.

The social results are particularly interesting in this context as well. Dominant mice consistently prioritize avoidance over reward, showing stronger escape responses and slower habituation than subordinates. This behavior is well captured by the vigilance framework proposed by the authors: dominant animals appear to maintain higher vigilance, which biases decisions toward threat avoidance. The authors further suggest that stable social relationships sustain high vigilance and slow habituation, framing this as an evolutionarily conserved strategy that may enhance survival. This interpretation provides a valuable perspective on how social structure shapes defensive behavior beyond immediate physical interactions. At the same time, there are important limitations to this interpretation. All experiments were conducted in male mice, and it is possible that the relationship between social hierarchy, vigilance, and defensive behavior would differ substantially in females. In addition, the idea that stable social relationships maintain elevated vigilance does not straightforwardly align with broader views of social stability as protective for mental health and as a buffer against anxiety and stress. These points do not undermine the findings but suggest that the social effects described here should be interpreted with caution and within the specific context of the task and sex studied.

Another important limitation is that the neural mechanisms underlying these effects remain speculative. The manuscript includes an extensive discussion of candidate circuits, particularly involving the superior colliculus and downstream structures, but this section is necessarily based on prior literature rather than on data presented in the study. Given the complexity of the circuits involved in integrating internal state, reward, social context, and vigilance, the current work should be viewed as providing a strong behavioral and conceptual framework rather than direct insight into underlying neural mechanisms.

Methodologically, the behavioral paradigm is well suited for studying escape decisions in socially housed animals, and the machine learning based classification of defensive responses is a clear strength. The computational model provides a useful formalization of how threat level, reward level, and vigilance interact and may be valuable for other laboratories studying escape, approach avoidance, or conflict situations, particularly as a way to classify behavioral outcomes after pose estimation. More generally, the work will be of interest to the neuroethology community for its detailed characterization of escape behavior under naturalistic conditions.

Given the ethological nature of the study and the high inter individual variability reported by the authors, clarity and precision in the methods are especially important for reproducibility. While the revised manuscript addresses many earlier concerns, some aspects remain slightly difficult to follow. For example, the main text states that animals were not water deprived to avoid differences in internal state, whereas parts of the methods describe conditions in which animals were water deprived, suggesting that internal state manipulation may differ across experiments. Clearer separation and explanation of these conditions would further strengthen confidence in the work.

Overall, this study provides a rich and thoughtful analysis of how reward level and social hierarchy modulate defensive behavior through changes in vigilance. It offers a useful conceptual advance for thinking about escape behavior in naturalistic settings and lays a solid foundation for future work aimed at linking these behavioral states to underlying neural circuits.

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Reviewer #2 (Public review):

Zhe Li and colleagues investigate how mice exposed to visual threats and rewards balance their decisions in favour of consuming rewards or engaging in defensive actions. By varying threat intensity and reward value, they first confirm previous findings showing that defensive responses increase with threat intensity and that there is habituation to the threat stimulus. They then find that water-deprived mice have a reduced probability of escaping from low contrast visual looming stimuli when water or sucrose are offered in the environment, but that when the stimulus contrast is high, the presence of sucrose or water increases the probability of escape. By analysing behaviour metrics such as the latency to flee from the threat stimulus, they suggest that this increase in threat sensitivity is due to increased vigilance. Analysis of this behaviour as a function of social hierarchy shows that dominant mice have higher threat sensitivity, which is also interpreted as being due to increased vigilance. These results are captured by a drift diffusion model variant that incorporates threat intensity and reward value.

The main contribution of this work is quantifying how the presence of water or sucrose in water-deprived mice affects escape behaviour. The differential effects of reward between the low and high contrast conditions are intriguing, but I find the interpretation that vigilance plays a major in this process not supported by the data. The idea that reward value exerts some form of graded modulation of the escape response is also not supported by the data. In addition, there is very limited methodological information, which makes assessing the quality of some of the analyses difficult, and there is no quantification on the quality of the model fits.

(1) The main measure of vigilance in this work is reaction time. While reaction time can indeed be affected by vigilance, reaction times can vary as a function of many variables, and be different for the same level of vigilance. For example, a primate performing the random dot motion task exhibits differences in reaction times that can be explained entirely by the stimulus strength. Reaction time is therefore not a sound measure of vigilance, and if a goal of this work is to investigate this parameter, then it should be measured. There is some attempt at doing this for a subset of the data in Figure 3H, by looking at differences in the action of monitoring the visual field (presumably a rearing motion, though this is not described) between the first and second trials in the presence of sucrose. I find this an extremely contrived measure. What is the rationale for analysing only the difference between the first and second trials? Also, the results are only statistically significant because the first trial in the sucrose condition happens to have zero up action bouts, in contrast to all other conditions. I am afraid that the statistics are not solid here. When analysing the effects of dominance, a vigilance metric is the time spent in the reward zone. Why is this a measure of vigilance? More generally, measuring vigilance of threats in mice requires monitoring the position of the eyes, which previous work has shown is biased to the upper visual field, consistent with the threat ecology of rodents.

(2) In both low and high contrast conditions, there are differences in escape behaviour between no reward and water or sucrose presence, but no statistically significant differences between water and sucrose (eg: Figure 3B). I therefore find that statements about reward value are not supported by the data, which only show differences between the presence or absence of reward. Furthermore, there is a confound in these experiments, because according to the methods, mice in the no-reward condition were not water-deprived. It is thus possible that the differences in behaviour arise from differences in the underlying state.

(3) There is very little methodological information on behavioural quantification. For example, what is hiding latency? Is this the same are reaction time? Time to reach the safe zone? What exactly is distance fled? I don't understand how this can vary between 20 and 100cm. Presumably, the 20cm flights don't reach the safe place, since the threat is roughly at the same location for each trial? How is the end of a flight determined? How is duration measured in reward zone measures, e.g., from when to when? How is fleeing onset determined?

(4) There is little methodological information on how the model was fit (for example, it is surprising that in the no reward condition, the r parameter is exactly 0. What this constrained in any way), and none of the fit parameters have uncertainty measures so it is not possible to assess whether there are actually any differences in parameters that are statistically significant.

Comments on the revised manuscript:

The manuscript has been revised and improved significantly by the addition of methodological details and new analysis. I remain, however, unconvinced by the argument that increased vigilance in the presence of reward leads to heightened escape behaviour.

In response to my criticism that the work does not measure vigilance directly, the authors have included measures of foraging interval and foraging speed, which they state are "two direct behavioral analyses of vigilance". I disagree - like reaction time, foraging speed and foraging interval can be modulated, for example, by changes in threat sensitivity. Increased threat sensitivity comes with diverse behavioral changes that may well include increased vigilance, but foraging interval and foraging speed can certainly change without the animal expressing increased vigilance behaviors. A bigger issue I still have though, is with the conclusion that the presence of reward increases "direct escape behaviors". Comparing the no reward, water and sucrose groups indeed shows a difference (which is now clear after the split into early and late phases), but the issue is that these are different mice. As the text is written, is sounds like introducing reward will acutely increase escape. But if we look at the raw data show in Figure 2C, what I think is happening is that the presence of reward is decreasing habituation to the stimulus. The data for trials 1 and 10 in the three conditions show this - there is habituation with no reward (reaction times are all shifting to the right), a bit less with water and very little with sucrose. This is interesting in its own right and we can speculate why it might be happening, but I think this is conceptually different from what the authors are proposing.

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Reviewer #3 (Public review):

Male mice were tested in a classic behavioral "flee the looming stimulus" paradigm. This is a purely behavioral study; no neural analyses were done. Mice were housed socially, but faced the looming stimulus individually, using an elegant automated tunnel (see videos for clarity).

The additional changes made to the paper clarify the work done. While there are some limitations (male mice, weird stimulus), the general results are interesting and a valuable addition to the experimental literature. The main claim of the paper is that the different rewards (none, water, sucrose) did not change the escape properties early in learning, but did late, particularly that in the late (already experienced) conditions, reward value (assuming sucrose > water > no reward) interacted with the salience of the looming stimulus (light gray, dark gray). (Panels 3D, 3G, 3K, 3N).

For readers, I want to note that one of the most interesting results is actually in Figure S2, where they find that a looming stimulus behind the mouse still makes a mouse run to the nest. In these conditions, the mouse runs past the looming stimulus to get to safety! (I also do love the video of the mouse running around the barriers like a snake to get home.)

I have a few minor clarification questions and a few notes that I think would be useful additions for authors and readers to think about.

Dominance: What does the mouse social science literature say about the "test tube" test? What can we conclude from this test? This would be useful when trying to understand what is causing the dominance/submissive difference in responses. Figure 4 shows that the dominant mice are more risk-averse than the submissive mice. Is "dominance" in the test-tube actually a measure of risk-seeking? Is the issue that the submissive mice don't think they can get back to the food-site easily, so they are less willing to sacrifice the current (if dangerous) foraging opportunity? Is the issue that the submissive mice can't get back to the nest? As I understand it, the nest was always available to all the mice, so I suspect inability to get to the nest is an unlikely hypotheses. Is the issue that the submissive mice also don't feel safe in the nest?

Limitations of the study: There is an acknowledged limitation to male mice, and the limitations of the small data sets that are typical of such experiments. In addition, however, it is also worth noting the strangeness of the looming stimulus, which is revealed clearly in the videos. The stimulus is a repeating growing circle, growing in a single location within the environment. The stimulus repeats 10 times, once per second. This is not what an attacking hawk or owl would look like. (I now have this image of an owl diving down, and then teleporting up and diving down again.) Note - I am fine with this stimulus. It produces an interesting experiment and interesting results. I do not think the authors need to change anything in their paper, but readers need to recognize that this is not a "looming predator".

These "limitations" are better seen as "caveats" when folding these results in with the rest of the literature that has gone before and the literature to come. (Generally, I do not believe that science works by studies making discoveries that change how we think about problems - instead, science works by studies adding to the literature that we integrate in with the rest of the literature.) Thus, these caveats should not be taken as problems with the study or as fixes that need to be done. Instead, they are notes for future researchers to notice if differences are found in any future studies.

Thus, my only suggestion is that I think authors could write a more careful paper by using the past and subjunctive tense appropriately. Experimental observations should be in past tense, as in "the influence of reward was context-dependent and emerged in the late phase" instead of "the influence of reward is context-dependent and emerges in the late phase" - it emerged in the late phase this once - it might not in future experiments, not due to any fault in this experiment nor due to replicability problems, but rather due to unexpected differences between this and those future experiments. At which point, it will be up to those future experiments to determine the difference. Similarly, large conclusions should be in the subjunctive tense, as in "these data suggest that threat intensity is likely to be the primary determinant of decision making" rather than "threat intensity is the primary determinant of decision making", because those are hypotheses not facts.

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Author response:

The following is the authors' response to the current reviews.

> ***Public Reviews:***
>
> ***Reviewer #1 (Public review):***
>
> *This study by Li and colleagues examines how defensive responses to visual threats during foraging are modulated by both reward level and social hierarchy. Using a naturalistic paradigm, the authors test how the availability of water or sucrose, with sucrose being more rewarding than water, shapes escape behavior in mice exposed to looming stimuli of different intensities, which are used to probe perceived threat level and defensive responses. In parallel, the study compares dominant and subordinate animals to assess how social rank biases the trade off between reward seeking and threat avoidance. By combining detailed behavioral analyses with computational modeling, the work addresses how reward level and social context jointly influence escape decisions in an ethologically relevant setting.*
>
> *Across the different experimental conditions, perceived threat level is the main determinant of behavior. The authors show that looming stimuli associated with higher threat (contrast) consistently elicit faster and more robust escape responses than lower threat stimuli. This effect is particularly evident during early exposures, when animals are highly vigilant and have not yet habituated to the looming stimulus (learned that it is not dangerous). Later they described that as animals gain experience and habituate, behavior becomes more flexible, and reward level begins to exert a graded modulation of the escape response. Importantly, the authors show that under high threat conditions increasing reward value leads to more frequent and faster escape rather than greater reward pursuit. This finding is particularly relevant, as it suggests that highly valued rewards can heighten vigilance and thereby enhance responsiveness to threat, highlighting that reward does not simply compete with defensive behavior but can also*

> *reshape it depending on the perceived level of danger, in contrast to low threat conditions, where threat can be more easily outweighed by reward. Thus, an important conceptual contribution of the study is the introduction of vigilance as a useful framework to interpret these effects. Vigilance is treated as a behavioral state reflecting heightened attention to potential danger. In line with what is known from natural foraging, mice initially maintain high vigilance when confronted with an innate threat. This perspective helps clarify a finding that might otherwise appear counterintuitive. One might expect higher rewards to motivate animals to tolerate risk, explore more, and habituate faster in any scenario. Instead, the data suggest that highly rewarding outcomes can elevate vigilance, making animals more responsive to threat and leading to faster or more frequent escape under high threat conditions. In this sense, reward does not simply compete with threat but can also amplify sensitivity to it, depending on the internal state of the animal.*
>
> *The social results are particularly interesting in this context as well. Dominant mice consistently prioritize avoidance over reward, showing stronger escape responses and slower habituation than subordinates. This behavior is well captured by the vigilance framework proposed by the authors: dominant animals appear to maintain higher vigilance, which biases decisions toward threat avoidance. The authors further suggest that stable social relationships sustain high vigilance and slow habituation, framing this as an evolutionarily conserved strategy that may enhance survival. This interpretation provides a valuable perspective on how social structure shapes defensive behavior beyond immediate physical interactions. At the same time, there are important limitations to this interpretation. All experiments were conducted in male mice, and it is possible that the relationship between social hierarchy, vigilance, and defensive behavior would differ substantially in females. In addition, the idea that stable social relationships maintain elevated vigilance does not straightforwardly align with broader views of social stability as protective for mental health and as a buffer against anxiety and stress. These points do not undermine the findings but suggest that the social effects described here should be interpreted with caution and within the specific context of the task and sex studied.*

We thank the reviewer for raising this important point. In the context of repeated looming exposure, slower habituation reflects more sustained vigilance over time. Compared to individually housed mice, group-housed mice exhibit slower habituation (Lenz et al., 2022), and pair-housed mice showed even slower habituation in our current work. Importantly, this pattern does not indicate that pair-housed mice have higher overall vigilance than individually housed animals. Although individually housed mice habituate more quickly, they display higher initial vigilance, as reflected by their increased probability of escaping in response to looming stimuli (Lenz et al., 2022). Thus, pair-housed mice exhibited reduced defensive responses compared to individually housed animals, consistent with a social buffering effect.

Furthermore, in a separate study (Rank- and Threat-Dependent Social Modulation of Innate Defensive Behaviors; Li, Gao, Li, 2026, eLife 15:RP109571), we directly compared responses to looming stimuli when mice were tested alone versus in the presence of a social partner and observed clear evidence of social buffering.

> *Another important limitation is that the neural mechanisms underlying these effects remain speculative. The manuscript includes an extensive discussion of candidate circuits, particularly involving the superior colliculus and downstream structures, but this section is necessarily based on prior literature rather than on data presented in the study. Given the complexity of the circuits involved in integrating internal state, reward, social context, and vigilance, the current work should be viewed as providing a strong*

> *behavioral and conceptual framework rather than direct insight into underlying neural mechanisms.*

We fully agree that the proposed neural mechanisms remain speculative and that the circuits involved in integrating internal state, reward, and social context are likely far more complex. We have revised the manuscript to acknowledge this limitation.

> *Methodologically, the behavioral paradigm is well suited for studying escape decisions in socially housed animals, and the machine learning based classification of defensive responses is a clear strength. The computational model provides a useful formalization of how threat level, reward level, and vigilance interact and may be valuable for other laboratories studying escape, approach avoidance, or conflict situations, particularly as a way to classify behavioral outcomes after pose estimation. More generally, the work will be of interest to the neuroethology community for its detailed characterization of escape behavior under naturalistic conditions.*
>
> *Given the ethological nature of the study and the high inter individual variability reported by the authors, clarity and precision in the methods are especially important for reproducibility. While the revised manuscript addresses many earlier concerns, some aspects remain slightly difficult to follow. For example, the main text states that animals were not water deprived to avoid differences in internal state, whereas parts of the methods describe conditions in which animals were water deprived, suggesting that internal state manipulation may differ across experiments. Clearer separation and explanation of these conditions would further strengthen confidence in the work.*

To improve clarity, we have revised the Methods section to clearly distinguish between experimental conditions that involved water deprivation and those that did not.

> *Overall, this study provides a rich and thoughtful analysis of how reward level and social hierarchy modulate defensive behavior through changes in vigilance. It offers a useful conceptual advance for thinking about escape behavior in naturalistic settings and lays a solid foundation for future work aimed at linking these behavioral states to underlying neural circuits.*
>
> ***Reviewer #2 (Public review):***
>
> *Zhe Li and colleagues investigate how mice exposed to visual threats and rewards balance their decisions in favour of consuming rewards or engaging in defensive actions. By varying threat intensity and reward value, they first confirm previous findings showing that defensive responses increase with threat intensity and that there is habituation to the threat stimulus. They then find that water-deprived mice have a reduced probability of escaping from low contrast visual looming stimuli when water or sucrose are offered in the environment, but that when the stimulus contrast is high, the presence of sucrose or water increases the probability of escape. By analysing behaviour metrics such as the latency to flee from the threat stimulus, they suggest that this increase in threat sensitivity is due to increased vigilance. Analysis of this behaviour as a function of social hierarchy shows that dominant mice have higher threat sensitivity, which is also interpreted as being due to increased vigilance. These results are captured by a drift diffusion model variant that incorporates threat intensity and reward value.*
>
> *The main contribution of this work is quantifying how the presence of water or sucrose in water-deprived mice affects escape behaviour. The differential effects of reward between the low and high contrast conditions are intriguing, but I find the interpretation that vigilance plays a major in this process not supported by the data. The idea that reward value exerts some form of graded modulation of the escape response is also not supported by the data. In addition, there is very limited methodological information,*

> *which makes assessing the quality of some of the analyses difficult, and there is no quantification on the quality of the model fits.*
>
> *(1) The main measure of vigilance in this work is reaction time. While reaction time can indeed be affected by vigilance, reaction times can vary as a function of many variables, and be different for the same level of vigilance. For example, a primate performing the random dot motion task exhibits differences in reaction times that can be explained entirely by the stimulus strength. Reaction time is therefore not a sound measure of vigilance, and if a goal of this work is to investigate this parameter, then it should be measured. There is some attempt at doing this for a subset of the data in Figure 3H, by looking at differences in the action of monitoring the visual field (presumably a rearing motion, though this is not described) between the first and second trials in the presence of sucrose. I find this an extremely contrived measure. What is the rationale for analysing only the difference between the first and second trials? Also, the results are only statistically significant because the first trial in the sucrose condition happens to have zero up action bouts, in contrast to all other conditions. I am afraid that the statistics are not solid here. When analysing the effects of dominance, a vigilance metric is the time spent in the reward zone. Why is this a measure of vigilance? More generally, measuring vigilance of threats in mice requires monitoring the position of the eyes, which previous work has shown is biased to the upper visual field, consistent with the threat ecology of rodents.*

We agree that reaction time can be influenced by multiple factors, including stimulus strength. Consistent with this, reaction times (i.e. latencies to flee) were substantially shorter under high-contrast conditions (Figure 3E). However, even under the same high-contrast condition, reaction times were significantly shorter in the water condition compared to the no-reward condition, suggesting that other factors such as vigilance may contribute.

Upward-directed attention includes rearing, up-stretching, and upward head orientation, which will be clarified in the Method section. To address concerns about statistical validity, we will quantify these behaviors across the first 10 trials rather than limiting the analysis to the first two.

As for the dominance-related results, we interpret them as reflecting both enhanced vigilance and reduced reward-seeking behavior. Time spent in the reward zone is not a measure of vigilance but an indicator of reward-seeking motivation. We will clarify this in the revised manuscript.

> *(2) In both low and high contrast conditions, there are differences in escape behaviour between no reward and water or sucrose presence, but no statistically significant differences between water and sucrose (eg: Figure 3B). I therefore find that statements about reward value are not supported by the data, which only show differences between the presence or absence of reward. Furthermore, there is a confound in these experiments, because according to the methods, mice in the no-reward condition were not water-deprived. It is thus possible that the differences in behaviour arise from differences in the underlying state.*

In Figure 3B, the difference between water and sucrose conditions did not reach statistical significance ($p = 0.08$). We plan to collect additional data to determine whether this is due to limited statistical power. It is also possible that some behavioral readouts are more sensitive to the differences between water and sucrose conditions. For example, Figure 3F shows that escape speed was significantly higher in the sucrose than in the water condition under high-contrast stimulation.

Thank you for pointing this out. To control for the potential confounds related to internal state, mice were not water-deprived under any of the three conditions in Figures 3A-3H. We will clarify this in the main text and Methods. For Figures 3I-3M, which compare decision-making under no-reward and water conditions, we will conduct additional experiments using non-deprived mice in the water condition.

> *(3) There is very little methodological information on behavioural quantification. For example, what is hiding latency? Is this the same are reaction time? Time to reach the safe zone? What exactly is distance fled? I don't understand how this can vary between 20 and 100cm. Presumably, the 20cm flights don't reach the safe place, since the threat is roughly at the same location for each trial? How is the end of a flight determined? How is duration measured in reward zone measures, e.g., from when to when? How is fleeing onset determined?*

Hiding latency was defined as the time from stimulus onset to the animal's arrival at the safe zone. Reaction time was quantified as the latency to flee, measured from stimulus onset to the initiation of the first flight state. The flight state was defined as locomotion exceeding 10 cm at a speed greater than 10 cm/s. Distance fled was defined as the distance covered between stimulus onset and offset for all trials. However, in trials classified as no reaction or freezing, this measure does not accurately reflect escape behavior. We will therefore rename it as distance under threat to better capture its meaning. The reward zone was defined as the region within 15 cm of the reward port at the end of the arena. Duration in the reward zone was measured as the time spent within this region during the 20 seconds following stimulus onset. In Figure 4E, the percentage of time spent in the reward zone was calculated relative to the total time the mouse remained in the arena during the 2-hour social session.

All definitions and additional details on behavioral quantification will be included in the revised Methods section.

> *(4) There is little methodological information on how the model was fit (for example, it is surprising that in the no reward condition, the r parameter is exactly 0. What this constrained in any way), and none of the fit parameters have uncertainty measures so it is not possible to assess whether there are actually any differences in parameters that are statistically significant.*

We appreciate the comment and agree that further clarification is needed. We will provide a more detailed description of the model fitting procedure in the revised Methods section. Specifically, the drift rate parameter (r), which reflects the perceived reward value, was constrained to zero in the no-reward condition. To enable statistical comparison across conditions, we will report uncertainty measures for all fit parameters.

> *Comments on the revised manuscript:*
>
> *The manuscript has been revised and improved significantly by the addition of methodological details and new analysis. I remain, however, unconvinced by the argument that increased vigilance in the presence of reward leads to heightened escape behaviour.*
>
> *In response to my criticism that the work does not measure vigilance directly, the authors have included measures of foraging interval and foraging speed, which they state are "two direct behavioral analyses of vigilance". I disagree - like reaction time, foraging speed and foraging interval can be modulated, for example, by changes in threat sensitivity. Increased threat sensitivity comes with diverse behavioral changes that may well include increased vigilance, but foraging interval and foraging speed can certainly change without the animal expressing increased vigilance behaviors. A bigger issue I still have though, is with the conclusion that the presence of reward increases "direct escape behaviors". Comparing the no reward, water and sucrose groups indeed shows a difference (which is now clear after the split into early and late phases), but the*

> *issue is that these are different mice. As the text is written, is sounds like introducing reward will acutely increase escape. But if we look at the raw data show in Figure 2C, what I think is happening is that the presence of reward is decreasing habituation to the stimulus. The data for trials 1 and 10 in the three conditions show this - there is habituation with no reward (reaction times are all shifting to the right), a bit less with water and very little with sucrose. This is interesting in its own right and we can speculate why it might be happening, but I think this is conceptually different from what the authors are proposing.*

We agree that vigilance is not directly observable as a single variable. Our intent was not to claim that foraging speed and foraging interval provide a direct measure of vigilance, but rather to suggest that they may serve as indirect behavioral correlates.

We also considered an alternative interpretation: these two measures could reflect perceived reward value under high-threat conditions across distinct reward types. If that were the case, animals would be expected to exhibit shorter intervals and faster speeds across no reward, water, and sucrose conditions. However, our data do not support this interpretation (Figures 3L and 3M), suggesting that these measures are more likely correlated with vigilance.

Furthermore, it is unlikely that changes in foraging interval and speed are driven by altered threat sensitivity, as animals could not see the threat during most of the foraging bout and only encountered it at the end.

Regarding the conclusion that the presence of reward increases direct escape behaviors, our interpretation is that increased reward value reduces habituation, thereby maintaining higher vigilance during the late phase. This was discussed in the second-to-last paragraph of the "Economic and social modulations of innate decision-making under threat" subsection in the Discussion.

> ***Reviewer #3 (Public review):***
>
> *Male mice were tested in a classic behavioral "flee the looming stimulus" paradigm. This is a purely behavioral study; no neural analyses were done. Mice were housed socially, but faced the looming stimulus individually, using an elegant automated tunnel (see videos for clarity).*
>
> *The additional changes made to the paper clarify the work done. While there are some limitations (male mice, weird stimulus), the general results are interesting and a valuable addition to the experimental literature. The main claim of the paper is that the different rewards (none, water, sucrose) did not change the escape properties early in learning, but did late, particularly that in the late (already experienced) conditions, reward value (assuming sucrose > water > no reward) interacted with the salience of the looming stimulus (light gray, dark gray). (Panels 3D, 3G, 3K, 3N).*
>
> *For readers, I want to note that one of the most interesting results is actually in Figure S2, where they find that a looming stimulus behind the mouse still makes a mouse run to the nest. In these conditions, the mouse runs past the looming stimulus to get to safety! (I also do love the video of the mouse running around the barriers like a snake to get home.)*
>
> *I have a few minor clarification questions and a few notes that I think would be useful additions for authors and readers to think about.*
>
> *Dominance: What does the mouse social science literature say about the "test tube" test? What can we conclude from this test? This would be useful when trying to understand what is causing the dominance/submissive difference in responses. Figure 4 shows that the dominant mice are more risk-averse than the submissive mice. Is "dominance" in the*

> *test-tube actually a measure of risk-seeking? Is the issue that the submissive mice don't think they can get back to the food-site easily, so they are less willing to sacrifice the current (if dangerous) foraging opportunity? Is the issue that the submissive mice can't get back to the nest? As I understand it, the nest was always available to all the mice, so I suspect inability to get to the nest is an unlikely hypotheses. Is the issue that the submissive mice also don't feel safe in the nest?*

The tube test is a widely used assay in the rodent social behavior literature to assess dominance hierarchies, operationally defined by the ability of one animal to force its opponent to retreat from a narrow tube. Importantly, this assay does not directly measure risk-seeking or anxiety-related traits, but rather competitive outcomes during social conflict. Furthermore, our data indicate that the behavioral responses of subordinate mice to looming stimuli are primarily driven by the visual threat itself rather than by social avoidance. This point was elaborated in the second paragraph of the “Social modulation of innate decision-making” subsection in the Results section.

> *Limitations of the study: There is an acknowledged limitation to male mice, and the limitations of the small data sets that are typical of such experiments. In addition, however, it is also worth noting the strangeness of the looming stimulus, which is revealed clearly in the videos. The stimulus is a repeating growing circle, growing in a single location within the environment. The stimulus repeats 10 times, once per second. This is not what an attacking hawk or owl would look like. (I now have this image of an owl diving down, and then teleporting up and diving down again.) Note - I am fine with this stimulus. It produces an interesting experiment and interesting results. I do not think the authors need to change anything in their paper, but readers need to recognize that this is not a "looming predator".*
>
> *These "limitations" are better seen as "caveats" when folding these results in with the rest of the literature that has gone before and the literature to come. (Generally, I do not believe that science works by studies making discoveries that change how we think about problems - instead, science works by studies adding to the literature that we integrate in with the rest of the literature.) Thus, these caveats should not be taken as problems with the study or as fixes that need to be done. Instead, they are notes for future researchers to notice if differences are found in any future studies.*
>
> *Thus, my only suggestion is that I think authors could write a more careful paper by using the past and subjunctive tense appropriately. Experimental observations should be in past tense, as in "the influence of reward was context-dependent and emerged in the late phase" instead of "the influence of reward is context-dependent and emerges in the late phase" - it emerged in the late phase this once - it might not in future experiments, not due to any fault in this experiment nor due to replicability problems, but rather due to unexpected differences between this and those future experiments. At which point, it will be up to those future experiments to determine the difference. Similarly, large conclusions should be in the subjunctive tense, as in "these data suggest that threat intensity is likely to be the primary determinant of decision making" rather than "threat intensity is the primary determinant of decision making", because those are hypotheses not facts.*

We thank the reviewer for the helpful suggestions and have revised the Abstract accordingly.

The following is the authors’ response to the original reviews.

> ***Public Reviews:***
>
> ***Reviewer #1 (Public review):***
>
> *Summary:*

> *This study investigates how mice make defensive decisions when exposed to visual threats and how those decisions are influenced by reward value and social hierarchy. Using a naturalistic foraging setup and looming stimuli, the authors show that higher threat leads to faster escape, while lower threat allows mice to weigh reward value. Dominant mice behave more cautiously, showing higher vigilance. The behavioral findings are further supported by a computational model aimed at capturing how different factors shape decisions.*
>
> *Strengths:*
>
> *(1) The behavioral paradigm is well-designed and ethologically relevant, capturing instinctive responses in a controlled setting.*
>
> *(2) The paper addresses an important question: how defensive behaviors are influenced by social and value-based factors.*
>
> *(3) The classification of behavioral responses using machine learning is a solid methodological choice that improves reproducibility.*
>
> *Weaknesses:*
>
> *(1) Key parts of the methods are hard to follow, especially how trials are selected and whether learning across trials is fully controlled for. For example, it is unclear whether animals are in the nest during the looming stimulus presentations. The main text and methods should clarify whether multiple mice are in the nest simultaneously and whether only one mouse is in the arena during looming exposure. From the description, it seems that all mice may be freely exploring during some phases, but only one is allowed in the arena at a time during stimulus presentation. This point is important for understanding the social context and potential interactions, and should be clearly explained in both the main text and methods.*

We agree that these details are essential and have clarified them in the Methods. When the door system operated normally, only one mouse was allowed in the arena during looming exposure. Specifically, when all mice were in the nest, the nest-tunnel door was open and the tunnel-arena door was closed. Once a single mouse entered the tunnel, as detected by an OpenMV camera, the nest-tunnel door closed and the tunnel-arena opened, ensuring that only that mouse could enter the arena.

Habituation was conducted over two days. On day 1, five mice were placed together in the nest for 30 minutes with all doors closed. Each mouse was then placed individually in the nest and allowed to freely explore the arena for 10 minutes under normal door operation. Finally, all mice were returned to the nest with all doors open and allowed for free exploration for 2 hours. On day 2, each mouse was placed individually in the nest and given an additional 1 hour of exploration under normal door operation.

> *(2) It is often unclear whether the data shown (especially in the main summary figures) come from the first trial or are averages across several exposures. When is the cut-off for trials of each animal? How do we know how many trial presentations were considered, and how learning at different rates between individuals is taken into account when plotting all animals together? This is important because the looming stimulus is learned to be harmless very quickly, so the trial number strongly affects interpretation.*

We observed substantial inter-individual variability in habituation to looming stimuli, with a sharp decline in defensive responses over the first few trials followed by more gradual changes. To account for this, we segmented trials for each animal into two phases: an early rapidhabituation phase and a later stable phase. Analyzing these phases separately revealed that threat intensity dominates behavior in the early phase, whereas both threat and reward significantly influence behavior in the late phase. These results are now presented in revised Figures 2 and 3. Analyses restricted to first trials are included in Figure S5.

> *(3) The reward-related effects are difficult to interpret without a clearer separation of learning vs first responses.*

As noted above, we have re-analyzed our data to account for learning effects.

> *(4) The model reproduces observed patterns but adds limited explanatory or predictive power. It does not integrate major findings like social hierarchy. Its impact would be greatly improved if the authors used it to predict outcomes under novel or intermediate conditions.*

We have substantially revised the modeling analysis. The model is now fitted to behavioral data from the late phase and used to predict outcomes across additional conditions, including the early phase behavior and rank-dependent behavioral differences. The model successfully captures behavioral patterns across these conditions, supporting its predictive value beyond descriptive fitting.

> *(5) Some conclusions (e.g., about vigilance increasing with reward) are counterintuitive and need stronger support or alternative explanations. Regarding the interpretation of social differences in area coverage, it's also possible that the observed behavioral differences reflect access to the nesting space. Dominant mice may control the nest, forcing subordinates to remain in the open arena even during or after looming stimuli. In this case, subordinates may be choosing between the threat of the dominant mouse and the external visual threat. The current data do not distinguish between these possibilities, and the authors do not provide evidence to support one interpretation over the other. Including this alternative explanation or providing data that addresses it would strengthen the conclusions.*

To support the interpretation of increased vigilance with reward under high-threat conditions, we analyzed additional behavioral measures beyond latency to flee. Rewarded mice showed longer foraging interval and slower foraging speed, both consistent with elevated vigilance (Figures 3L and 3M).

To address the alternative explanation that subordinate mice may remain in the arena due to restricted nest access, we compared arena occupancy before, during, and after looming exposure. Although subordinates spent more time in the arena before looming, this difference disappeared during and after looming exposure (Figures 4C). Moreover, dominant and subordinate mice were

equally likely to flee to the nest during escape trials. These findings rule out nest access restrictions as an explanation for the observed rank-dependent differences in defensive behaviors.

> *(6) While potential neural circuits are mentioned in the discussion, an earlier introduction of candidate brain regions and their relevance to threat and value processing would help ground the study in existing systems neuroscience.*

We have revised the Introduction to incorporate relevant brain regions and neural circuits.

> *(7) Some figures are difficult to interpret without clearer trial/mouse labeling, and a few claims in the text are stronger than what the data fully support. Figure 3H is done for low contrast, but the interesting findings will be to do this experiment with high contrast. Figure 4H - I don't understand this part. If the amount of time in the center after the loom changes for subordinate mice, how does this lead to the conclusion that they spend*

> *most of their time in the reward zone?. Figure 3A - The example shown does not seem representative of the claim that high contrast stimuli are more likely to trigger escape. In particular, the 10% sucrose condition appears to show more arena visits under low contrast than high contrast, which seems to contradict that interpretation. Also, the plot currently uses trials on the Y-axis, but it would be more informative to show one line per animal, using only the first trial for each. This would help separate initial threat responses from learning effects and clarify individual variability.*

We have substantially revised the figures. Results from trial segmentation based on individual habituation are now explicitly presented in Figures 2 and 3, and analyses using only the first trials are provided in Figure S5 to separate initial responses from learning effects.

Regarding the original Figure 4H, we are not entirely certain about the concern. In this panel, we measured time spent in the reward zone, which is defined as the region within 10 cm of the reward port at the end of the arena, not the center of the arena, during looming exposure. Subordinate mice spent significantly more time in the reward zone than dominant mice. We have further clarified this in the revised manuscript.

> *(8) The analysis does not explore individual variability in behavior, which could be an important source of structure in the data. Without this, it is difficult to know whether social hierarchy alone explains behavioral differences or if other stable traits (e.g., anxiety level, prior experiences) also contribute.*

We observed substantial individual variability in both dominant and subordinate mice, even on the first trial (Figure S7). Paired dominant–subordinate comparisons were used to isolate rankdependent effects.

> *(9) The study shows robust looming responses in group-housed animals, which contrasts with other studies that often require single housing to elicit reliable defensive responses. It would be valuable for the authors to discuss why their results differ in this regard and whether housing conditions might interact with social rank or habituation.*

Robust looming-evoked defensive responses have been reported in both group- and singlehoused mice (Yilmaz and Meister, 2013, Lenzi et al., 2022), although single-housed mice habituate more rapidly. We have now discussed the potential interactions between housing conditions, social rank, and habituation in defensive behaviors in the revised manuscript.

> ***Reviewer #2 (Public review):***
>
> *Zhe Li and colleagues investigate how mice exposed to visual threats and rewards balance their decisions in favour of consuming rewards or engaging in defensive actions. By varying threat intensity and reward value, they first confirm previous findings showing that defensive responses increase with threat intensity and that there is habituation to the threat stimulus. They then find that water-deprived mice have a reduced probability of escaping from low contrast visual looming stimuli when water or sucrose are offered in the environment, but that when the stimulus contrast is high, the presence of sucrose or water increases the probability of escape. By analysing behaviour metrics such as the latency to flee from the threat stimulus, they suggest that this increase in threat sensitivity is due to increased vigilance. Analysis of this behaviour as a function of social hierarchy shows that dominant mice have higher threat sensitivity, which is also interpreted as being due to increased vigilance. These results are captured by a drift diffusion model variant that incorporates threat intensity and reward value.*
>
> *The main contribution of this work is to quantify how the presence of water or sucrose in waterdeprived mice affects escape behaviour. The differential effects of reward between the low and high contrast conditions are intriguing, but I find the interpretation that*

> *vigilance plays a major role in this process is not supported by the data. The idea that reward value exerts some form of graded modulation of the escape response is also not supported by the data. In addition, there is very limited methodological information, which makes assessing the quality of some of the analyses difficult, and there is no quantification of the quality of the model fits.*
>
> *(1) The main measure of vigilance in this work is reaction time. While reaction time can indeed be affected by vigilance, reaction times can vary as a function of many variables, and be different for the same level of vigilance. For example, a primate performing the random dot motion task exhibits differences in reaction times that can be explained entirely by the stimulus strength. Reaction time is therefore not a sound measure of vigilance, and if a goal of this work is to investigate this parameter, then it should be measured. There is some attempt at doing this for a subset of the data in Figure 3H, by looking at differences in the action of monitoring the visual field (presumably a rearing motion, though this is not described) between the first and second trials in the presence of sucrose. I find this an extremely contrived measure. What is the rationale for analysing only the difference between the first and second trials? Also, the results are only statistically significant because the first trial in the sucrose condition happens to have zero up action bouts, in contrast to all other conditions. I am afraid that the statistics are not solid here. When analysing the effects of dominance, a vigilance metric is the time spent in the reward zone. Why is this a measure of vigilance? More generally, measuring vigilance of threats in mice requires monitoring the position of the eyes, which previous work has shown is biased to the upper visual field, consistent with the threat ecology of rodents.*

We agree that reaction time can be influenced by multiple factors, including stimulus strength. Consistent with this, reaction times (i.e. latencies to flee) were substantially shorter under highcontrast conditions. However, even under the same high-contrast condition, reaction times were significantly shorter in the reward conditions compared to the no-reward condition, suggesting that other factors such as vigilance may contribute.

Regarding the measurement of vigilance, in addition to the latency to flee, we analyzed two additional behavioral measures related to vigilance. First, we examined the foraging interval. Our hypothesis was that more vigilant animals would wait longer before re-entering the reward zone following threat exposure. Consistent with this prediction, mice under sucrose and water reward conditions showed significantly longer foraging intervals than those under no-reward conditions (Figure 3L). Second, we analyzed the foraging speed as mice approached the reward. Increased vigilance should lead to more cautious and therefore slower movements. Our results support this, as mice moved more slowly towards the reward under sucrose conditions (Figure 3M). Taken together, these three measures consistently indicate that mice exhibit increased vigilance under sucrose reward in high-threat conditions.

> *(2) In both low and high contrast conditions, there are differences in escape behaviour between no reward and water or sucrose presence, but no statistically significant differences between water and sucrose (eg, Figure 3B). I therefore find that statements about reward value are not supported by the data, which only show differences between the presence or absence of reward. Furthermore, there is a confound in these experiments, because according to the methods, mice in the no-reward condition were not water deprived. It is thus possible that the differences in behaviour arise from differences in the underlying state.*

Our new analysis, which segments behavior into an early adaptive phase and a late stable phase, reveals a statistically significant difference between water and sucrose rewards in the late phase (Figure 3H), supporting a graded effect of reward value.

To control for the potential confounds related to internal state, mice were not water-deprived in all reward conditions. We have clarified this in the revised manuscript.

> *(3) There is very little methodological information on behavioural quantification. For example, what is hiding latency? Is this the same are reaction time? Time to reach the safe zone? What exactly is distance fled? I don't understand how this can vary between 20 and 100cm. Presumably, the 20cm flights don't reach the safe place, since the threat is roughly at the same location for each trial? How is the end of a flight determined? How is duration measured in reward zone measures, e.g., from when to when? How is fleeing onset determined?*

Hiding latency was defined as the time from stimulus onset to the animal's arrival at the safe zone. Reaction time was quantified as the latency to flee, measured from stimulus onset to the initiation of the first flight state. The flight state was defined as locomotion exceeding 10 cm at a speed greater than 10 cm/s. Distance fled was defined as the distance covered between stimulus onset and offset for all trials. However, in trials classified as no reaction or freezing, this measure does not accurately reflect escape behavior. We will therefore rename it as distance under threat to better capture its meaning. The reward zone was defined as the region within 10 cm of the reward port at the end of the arena. Duration in the reward zone was measured as the time spent within this region during the 20 seconds following stimulus onset. In Figure 4E, the percentage of time spent in the reward zone was calculated relative to the total time the mouse remained in the arena during the 2-hour social session.

All definitions and additional details on behavioral quantification have been included in the revised Methods section.

> *(4) There is little methodological information on how the model was fit (for example, it is surprising that in the no reward condition, the r parameter is exactly 0. What this constrained in any way), and none of the fit parameters have uncertainty measures so it is not possible to assess whether there are actually any differences in parameters that are statistically significant.*

We have provided a detailed description of the model fitting procedure in the revised Methods section. Specifically, the reward-value parameter (r) was constrained to zero in the no-reward condition. We have plotted how the overall loss varies with differeent parameters (Figure S9).

> ***Reviewer #3 (Public review):***
>
> *Male mice were tested in a classic behavioral "flee the looming stimulus" paradigm. This is a purely behavioral study; no neural analyses were done. Mice were housed socially, but faced the looming stimulus individually. Drift-diffusion modeling found that reward-level interacted with threat level such that at low-threat levels, reward contrasted with threat as classically expected (high reward overwhelms low threat, low threat overwhelms low reward), but that reward aligned with threat at higher threat levels.*
>
> *Note that they define threat level by the darkness of the looming stimulus. I am not sure that darker stimuli are more threatening to mice. But maybe. Figure 3 shows that mice react more quickly to high contrast looming stimuli, but can the authors distinguish between the ability to detect the visual signal from considering it a more dangerous threat? (The fact that vigilance makes a difference in the high contrast condition, not the low contrast condition, actually supports the author's hypotheses here.)*

Regarding the interpretation of stimulus contrast as a proxy for threat level, we agree it is crucial to distinguish improved detection from heightened threat perception. To address this, we examined not only latency to flee but also escape distance and peak escape speed, two measures that reflect the intensity of the defensive response. If contrast only influenced detection, we would expect differences in latency but not in escape distance or speed. All three measures differed significantly across contrast conditions, supporting the interpretation that high-contrast stimuli are perceived as more threatening rather than simply more detectable. Furthermore, manual review of "no response" trials confirmed reliable detection in both conditions, with only three potential "missed" trials out of 117 under low contrast (Figure S3B). We have included this discussion in the revised manuscript.

> *The drift-diffusion model (DDM) is fine. I note that the authors included a "leakage rate", which is not a standard DDM parameter (although I like including it). I would have liked to see more about the parameters. What were the distributions? What did the parameters correlate with behaviorally? I would have liked to see distributions of the parameters under the different conditions and different animals. Figure 2C shows the progression of learning. How do the fit parameters change over time as mice shift from choice to choice? How do the parameters change over mice? How do the parameters change over distance to the threat/distance to safety (as per Fanselow and Lester 1988)? They did a supplemental experiment where the threat arrived halfway along the corridor - we could get a lot more detail about that experiment - how did it change the modeling?*
>
> *Because our model is fit to the variance of latency distributions, it cannot be applied to singletrial data. Instead, we analyzed how decisions and latencies vary as functions of the fitted threat gain and reward value parameters (Figures 5G and 5H). We have also introduced a simplified deterministic model to further elucidate the decision-making process.*
>
> *Regarding the influence of distance to the threat, we conducted additional experiments, presenting the looming stimulus at the end of the arena when the mouse was at different distances from it (Figures S2C–G). We found that as the prey-threat distance increased, mice showed less direct escape behavior, with longer latencies to flee and slower escape speeds. This is consistent with the predatory imminence continuum theory (Fanselow and Lester, 1988), which describes graded defensive behaviors tuned to perceived threat level.*
>
> *Regarding the influence of distance to safety, our data indicate that it did not significantly affect defensive responses (Figures S2H and S2I). To test this further, we introduced barriers that lengthened the return path to the safe zone. We found that defensive decisions were not correlated with the distance to the safe zone (Figures S2J and S2K), suggesting that once a threat is detected, animals prioritize escape initiation over evaluating the exact path to safety.*
>
> *Overall, this is a reasonable study showing mostly unsurprising results. I think the authors could do more to connect the vigilance question to their results (which seems somewhat new to me).*

We have expanded our analysis of vigilance. In addition to escape latency, we examined the foraging interval and foraging speed. We hypothesized that more vigilant animals would wait longer before re-entering the reward zone following a threat and would approach the reward more slowly. Consistent with this prediction, mice in the sucrose- and water-reward conditions exhibited significantly longer foraging intervals and slower foraging speeds compared to those in the no-reward condition (Figures 3M and 3N). Together, these three measures consistently demonstrate that mice display heightened vigilance under high-threat, high-reward conditions.

> *Although the data appear generally fine and the modeling reasonable, the authors do not do the necessary work to set themselves within the extensive literature on decision-making in mice retreating from threats.*

> *First of all, this is not a new paradigm; variants of this paradigm have been used since at least the 1980s. There is an *extensive* literature on this, including extensive theoretical work on the relation of fear and other motivational factors. I recommend starting with the classic Fanselow and Lester 1988 paper (which they cite, but only in passing), and the reviews by Dean Mobbs and Jeansok Kim, and by Denis Paré and Greg Quirk, which have explicit theoretical proposals that the authors can compare their results to. I would also recommend that the authors look into the "active avoidance" literature. Moreover, to talk about a mouse running from a looming stimulus without addressing the other "flee the predator" tasks is to miss a huge space for understanding their results. Again, I would start with the reviews above, but also strongly urge the authors to look at the Robogator task (work by June-Seek Choi and Jeansok Kim, work by Denis Paré, and others).*
>
> *Similarly, in their anatomical review, they do not mention the amygdala. Given the extensive literature on the role of the amygdala in retreating from danger, both in terms of active avoidance and in terms of encoding the danger itself, it would surprise me greatly if this behavior does not involve amygdala processing. (If there is evidence that the amygdala does not play a role here, but that the superior colliculus does, then that would be a *very* important result that needs to be folded into our understanding of decision-making systems and neural computational processing.)*
>
> *Second, there is an extensive economic literature on non-human animals in general and on rodents in particular. Again, the authors seem unaware of this work, which would provide them with important data and theories to broaden the impact of their results (by placing them within the literature). First, there are explicit economic literatures in terms of positively-valenced conflicts (e.g., neuroeconomics within the primate literature, sequential foraging and delaydiscounting tasks within the rodent literature), but also there is a long history within the rodent conditioning world, such as the classic work by Len Green and Peter Shizgal. I would strongly urge the authors to explore the motivational conflict literature by people like Gavin McNally, Greg Quirk, and Mark Andermann. Again, putting their results into this literature will increase the impact of their experiment and modeling.*

We have substantially revised the manuscript to contextualize our findings within the extensive literature on defensive behavior and decision-making. The revised Introduction and Discussion now integrate key theoretical frameworks, such as the predatory imminence continuum, and cite relevant work on active avoidance and other "flee the predator" paradigms (e.g., the Robogator task).

We have also incorporated perspectives from neuroeconomics and motivational conflict, including literature on sequential foraging, delay-discounting tasks, and relevant rodent studies. Furthermore, we now discuss the potential contributions of specific brain regions, including the superior colliculus and the amygdala, to the economic and social modulation of innate defensive decisions in response to visual threats.

> ***Recommendations for the authors:***
>
> ***Reviewing Editor Comments:***
>
> *These additional recommendations are generally consistent and overlapping across reviewers, particularly Reviewer #1 and 2, so it is advisable to undertake these changes/additions.*
>
> ***Reviewer #1 (Recommendations for the authors):***
>
> *(1) Experimental methods and trial structure need clarification: It is often unclear how many trials were included per condition, per mouse, and whether the key behavioral*

> *effects (especially reward-related changes) were observed early in the session or after repeated stimulus exposure. For example, in several reward-related plots (e.g., Figure 3), it is not specified whether results are driven by early or later trials. Since the authors themselves report rapid learning of the looming stimulus (habituation), it is critical to state how many trials were included in each comparison, and to analyze whether effects hold on the first exposure and not the rest. Otherwise, conclusions about value-based behavior are hard to separate from learning effects, which may also differ between individuals. Specifically, the methods section is vague and hard to follow.*

We have substantially expanded the Methods section with additional details to improve clarity.

To account for individual variability in habituation to the looming stimulus, we segmented trials for each animal into early and late phases. We demonstrate that threat level is the dominant factor driving behavioral responses in the early phase, while both threat level and reward condition shape behavior in the late phase. We have substantially revised Figures 2 and 3 to reflect these changes.

> *(2) Add a summary of experimental design: A table or schematic summarizing the trial structure, experimental groups, reward/threat conditions, and the timeline of exposures would greatly improve clarity.*

We have added a schematic to Figure 2 summarizing the trial structure, experimental groups, reward and threat conditions, and the overall timeline.

> *(3) Replot key results using only the first trial per mouse: This would allow readers to assess the first (not learned) responses and help control for habituation/suppression.*

We have replotted behavioral results using only the first trial from each mouse and included these analyses in Figure S5. These results confirm that threat level is the dominant factor driving the initial response to looming stimuli.

> *(4) The model needs stronger justification and predictive value: As it stands, the model primarily fits the existing data and does not offer new insights beyond what is already evident from the behavioral results.*
>
> *Important findings, such as social hierarchy effects and habituation dynamics, are not captured in the model, reducing its relevance to the full dataset.*
>
> *The drift-diffusion framework is widely used, and in this implementation appears to have been adjusted post hoc to fit the observed data rather than generating new conceptual advances. No comparison with simpler models is included. Without testing simpler or alternative models, it is not clear whether the added complexity is necessary or justified.*
>
> *Use the model to generate and test predictions: to increase the model's contribution, the authors could simulate new conditions. Suggested experiments include:*
>
> *a) Predicting escape probability and latency at intermediate threat intensities to test whether behavior shifts gradually or abruptly.*
>
> *b) Using the model's habituation parameters to predict changes in escape behavior over repeated exposures.*
>
> *c) Adjusting vigilance or threat gain parameters to simulate dominant versus subordinate animals, and comparing model predictions to actual behavioral differences based on social rank.*

We have substantially revised the modeling section to address these concerns. The updated model is now fitted to behavioral data from the late phase of the reward–threat experiments and used to generate predictions for the early phase and for rank-dependent behavioral differences.

The model accurately captures behavioral patterns across these conditions, demonstrating predictive power beyond descriptive fitting. Accordingly, we have removed the habituation component. Furthermore, we have introduced a simplified deterministic model in the revised manuscript to further understand the decision-making process.

> *(5) Clarify housing and arena access conditions: It is unclear from the text whether all mice are in the nest during looming presentations and whether only one mouse is in the arena during the stimulus. This is important for understanding the social context of each trial and should be explained in the main text and methods.*

We have clarified this point in the Methods section. Under normal door operation, only one mouse was allowed in the arena during looming exposure. Specifically, when all mice were in the nest, the nest-tunnel door was open and the tunnel-arena door was closed. Once a single mouse entered the tunnel, as detected by an OpenMV camera, the nest-tunnel door closed and the tunnel-arena opened, ensuring that only that mouse could enter the arena.

> *(6) Alternative interpretation of subordinate behavior: differences in area coverage and time in the reward zone may not reflect reduced vigilance, but rather avoidance of dominant mice. Subordinates may remain in the open arena to avoid conflict. The authors do not provide evidence distinguishing between these interpretations, and this should be addressed.*

To address the alternative explanation that subordinate mice may remain in the arena due to restricted nest access, we compared arena occupancy before, during, and after looming exposure (Figure 4C). Before looming exposure, subordinate mice spent significantly more time in the arena, consistent with the idea that they may perceive a social threat from the dominant mouse in the absence of any external threat. However, this difference disappeared during and after looming exposure. This shift suggests that the presence of an external threat alters the social dynamic, reducing the influence of dominance on nest access.

To further assess whether dominant mice blocked subordinate access to the nest during threatdriven escapes, we analyzed the fraction of escape trials in which mice returned to the nest (Figure 4D). We found no significant difference between dominant and subordinate mice, indicating that dominant mice did not restrict nest access during these trials. Importantly, rank differences in reward-zone occupancy cannot be explained by nest exclusion, as mice do not need to return to the nest when escaping the threat—they can flee directly to the safe zone. Thus, nest access limitations do not account for the observed rank-dependent patterns.

We agree with the reviewer that reward-zone occupancy should not be interpreted as reduced vigilance in subordinate mice; instead, it likely reflects higher perceived reward value. The manuscript has been revised accordingly.

> *(7) Address why robust looming responses were observed in group-housed mice: previous studies often require single housing to elicit strong defensive responses. The authors should explain why their setup yields robust results in group-housed animals and whether housing conditions may interact with dominance or habituation.*

Looming exposure elicits robust defensive behaviors in both group- and single-housed mice (Yilmaz and Meister, 2013, Lenzi et al., 2022), with single-housed animals habituating more quickly to the stimulus (Lenzi et al., 2022). We have now discussed how housing conditions may interact with social rank and habituation to shape defensive behaviors in the revised manuscript.

For the social-rank experiments, we intentionally co-housed dominant and subordinate mice to maintain a stable hierarchy. This choice was motivated by two considerations. First, our goal was to investigate how social rank modulates defensive responses under ethologically relevant conditions, where mice naturally live in groups. Single housing would remove this social context. Second, singly housing mice can destabilize or eliminate rank relationships, making it difficult to interpret rank-dependent behavioral differences.

> *(8) Add analysis of individual variability: trial-by-trial variability or stable behavioral tendencies in individual animals are not explored. This could explain part of the variation currently attributed to social rank.*

We have analyzed individual variability in both dominant and subordinate mice. We observed substantial variability across all behavioral measurements for each group (Figure S7). To attribute the observed behavioral differences to social hierarchy rather than to other individual traits, we conducted paired comparisons between dominant and subordinate mice (Figure 4).

> *(9) Improve figure labeling and readability: some plots are ambiguous in terms of whether rows represent trials or animals. Overlapping points obscure the data in several figures, for example, Figure 3H, sucrose is n=4?- consider using jittered scatter plots, boxplots, or individual traces to improve clarity. Also same Figure axis Y is missing an 'e'.*

We have revised figures to improve clarity and corrected the typos.

> *(10) Avoid overinterpretation of causal explanations: Statements such as "reward increases vigilance due to evolutionary pressure" or that "subordinates are less vigilant" go beyond what the current data can demonstrate and should be rephrased more cautiously.*

We have revised the manuscript to tone down the statement.

> ***Reviewer #2 (Recommendations for the authors):***
>
> *(1) Provide much more extensive methodological details on analyses and model fitting*

We have thoroughly revised the Methods section to provide extensive detail on both behavioral analyses and computational modeling, as outlined in our responses to points (3) and (4) of the Public Review.

> *(2) Perform experiments or analyses that directly measure vigilance, if vigilance is to remain as a key explanation for the data.*

As detailed in our response to point (1) of the Public Review, we have supplemented the escape latency measure with two direct behavioral analyses of vigilance: foraging interval and foraging speed. This multi-metric approach robustly supports the interpretation of heightened vigilance.

> *(3) Provide extra evidence for an effect of reward value, as opposed to the presence or absence of reward. Control for differences arising from the water deprivation state by performing the no reward condition experiments in water-deprived mice.*

All behavioral data in the reward–threat experiment were collected on normal (non-deprived) mice (Figures 2 and 3), which have been clarified in the revised manuscript. We have reanalyzed the data by segmenting trials into early and late phases for each animal. In the late phase, under low-threat conditions, the effect of reward value is reflected in significant differences between water and sucrose in terms of escape distance and time spent in the reward zone (Figures 3I and 3J). Under high-threat conditions, the reward value effect is reflected in significant differences in latency to flee and peak escape speed (Figures 3K and 3N).

> *(4) Using drift rate to describe the "r" variable is confusing because the drift rate of the drift diffusion process is also determined by terms alpha, beta, and h-terms.*

We have termed “r” as the reward value in the revised manuscript.

> ***Reviewer #3 (Recommendations for the authors):***
>
> *(1) I would tone down some of the extreme statements about the problems of previous experiments (such as that most decision-making is on 2AFC). Lots of people do decision-making in serial foraging, fleeing, and other behavioral tasks. The classic Morris water-maze or Barnesmaze are decision-making tasks that aren't 2AFC. Serial foraging tasks, such as the Restaurant Row task aren't 2AFC. And, actually, lots of mouse behavior tasks are deciding when to stop on a treadmill for a reward. And, for that matter, your task isn't all that "realistic" - mice aren't evolved to flee looming disks, they are evolved to flee hawks and owls. This doesn't invalidate your task at all. I just recommend making it about your work in a positive way rather than others in a negative way.*

We have revised the manuscript to adopt a more positive framing of our work.

> *(2) I also don't think there's much use in bringing in crayfish in a mouse task. Spend your time connecting to the other rodent data (mice and rats) instead.*

We agree and have revised the manuscript accordingly, focusing our discussion on relevant rodent literature to provide a more appropriate context for our findings.

> *Minor concerns:*
>
> *(1) The authors use the term "cognitive control" without making clear what they mean. In general, the authors seem to have a view on decision-making as either being "reflexes" or "cognitive control". This is a very outdated perspective. Modern perspectives include multiple decision-making systems competing, separating these based on their computational properties, such as planning, procedural, instinctual, and, yes, reflexive. Current views on the kinds of behaviors they are discussing generally see fleeing as a transition from reflexive (tonic immobility, freezing) and instinctual responses (freezing, fleeing) to deliberative (anxiety) and procedural (habit). The authors might take a look at the recent Calvin and Redish (2025) paper for some ideas on this.*

We appreciate the reviewer’s insight regarding the term “cognitive control.” In our study, we used this term to emphasize that defensive responses to looming threats are not purely reflexive. Mice exhibit four distinct types of defensive decisions within a short time window, and these decisions are systematically modulated by reward value and social rank. Notably, reward modulation is bidirectional: high reward suppresses defensive responses under low-threat conditions but enhances them under high-threat conditions, indicating that animals integrate multiple sources of information rather than relying solely on instinctive mechanisms.

We did not observe mid-trajectory aborts in mice, as reported in rats by Calvin & Redish (2025). This difference may reflect species-specific behavior or the nature of the threat: our looming stimulus is purely visual and non-harmful, whereas the robotic predator in their study presents a physical threat. We have revised the Discussion to clarify our use of “cognitive control” and to incorporate these perspectives.

> *(2) Only male mice were used. This limits the conclusions that can be drawn.*

We acknowledge the limitation of using only male mice and have discussed this limitation in the revised manuscript.

> *(3) Did the authors observe darting behavior? (Gruene...Shansky 2015).*

We did not observe darting behavior, characterized by rapid movement, as reported during inescapable fear conditioning. In our experiment, the mice consistently escaped towards the nest, in most trials, ran directly to the nest without stopping. Occasionally, under low contrast conditions, mice paused once or twice but never moved towards the reward.

> *(4) How was only one mouse allowed into the linear arena at a time?*

When all mice were in the nest, the nest-tunnel door was open while the tunnel-arena door remained closed. When a single mouse entered the tunnel, as detected by the RFID and OpenMV camera system, the nest-tunnel door closed and the tunnel-arena door opened, allowing only that mouse to enter the arena. We have clarified this protocol in the Methods section.

> *(5) I would like to see more extensive analyses of the animal's responses as a function of distance to the threat (as per Fanselow and Lester 1988).*

As detailed in our response to the public review, we conducted new experiments analyzing behavior as a function of prey–threat distance. The finding that defensive responsiveness decreases with increasing prey–threat distance is now presented in Figures S2C–G and discussed in the context of the predatory imminence continuum.

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