Ecological Processes

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Amur tiger urine enhances the foraging behavior of three major small-bodied mesopredator species in northeastern China

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Abstract

Background Apex predators exert dual effects on mesopredators, including both suppression through lethal encounters and fear, as well as facilitation through providing food via prey remains. While large-scale studies on how apex predators influence mesopredator distributions are abundant, research on how apex predators affect mesopredators at the fine scale—particularly their specific behaviors—remains limited.

Results Using urine from captive Amur tigers as an apex predator cue and captive bird eggs, which served as a food source for mesopredators with minimal odor interference, we evaluated the effects of this apex predator scent on the foraging behavior of mesopredators across a 400 km^2 experimental area in northeastern China over a 3-month period. Our results demonstrate that tiger urine attracted small-bodied mesopredators, increasing their visitation speed and accelerating nest predation. Asian badgers in particular perceived tiger urine as a food resource cue, stimulating their exploration and squat-marking behavior improving egg detection and predation.

Conclusions With the deepening of wildlife conservation efforts, there is a growing recognition of the inherent complexity of ecosystems, underscoring the imperative for greater prudence in formulating wildlife management decisions. Our findings on the behavioral responses of small-bodied mesopredators to Amur tiger urine offer critical insights that reinforce this principle, reshaping conventional understanding of apex-mesopredator interactions in temperate forest ecosystems of Northeast China. The complexity of these interactions is further amplified by the multifaceted ecological roles of apex predators, as documented in global and regional studies. For wildlife management decisions, these insights demand a shift from one-size-fits-all approaches to context-specific, behaviorally informed strategies.

Keywords Amur tiger urine, Mesopredator, Predatory behavior, Marking behavior

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Background

Increasing recognition has been given to the critical role of predator functional groups in ecosystems. Predators not only regulate herbivore populations (Sala et al. 2024; Verma and Kumar 2024), preventing overgrazing, but also maintain biodiversity and ecosystem stability by regulating interactions within predator functional groups. Such regulation manifests prominently in dynamic interactions between apex predators and mesopredators. Apex predators exert top-down control by directly preying on mesopredators and inducing fear-driven behavioral responses, effectively suppressing the 'mesopredator release' (Berger et al. 2008; Jachowski et al. 2020; Newsome et al. 2017). Simultaneously, apex predators can facilitate mesopredators and other micro- and macro-organisms by supplying prey carcasses as vital energy sources. For example, after the reintroduction of the apex predator African lion (*Panthera leo*, ITIS.gov number 183803) into South Africa's Karoo National Park, large prey species were detected with a higher frequency in the feces of black-backed jackals (*Canis mesomelas*, ITIS.gov number 183818) (Daryl et al. 2018). This mechanism of cross-trophic energy transfer enhances the efficiency of material and energy cycling, thereby augmenting an ecosystem's biological carrying capacity and bolstering its resilience to environmental fluctuations (DeVault et al. 2003; Wilmers et al. 2003).

The dual influence of apex predators profoundly shapes the survival strategies of mesopredators, necessitating their adaptation to the ecological contexts of specific environments (Clare et al. 2016; Reustle and Smee 2020). For example, in Alaska, coyotes (*Canis latrans*, ITIS.gov number 180599) spatially avoid areas frequently used by wolves (*Canis lupus*, ITIS.gov number 180596) in summer, as the risk of mortality outweighs the benefits of increased carrion availability; however, in winter, they prefer areas with higher wolf activity, due to elevated metabolic demands and reduced food availability (Klauder et al. 2021). Apex predators, while shaping the life-history strategies of mesopredators, further extend their influence to lower trophic-level specie. As conservation efforts intensify and apex predator populations recover at varying rates, it becomes essential to adopt a more nuanced and holistic understanding of the complex interactions within predator functional groups and effects of apex predator recovery on ecological interactions.

Extensive research has evaluated the influence of apex predators on the distribution and abundance of mesopredators at the landscape scale (She et al. 2023; Letnic et al. 2011), including in Northeast China where Amur tiger (*Panthera tigris altaica*, ITIS.gov number 726472) is the apex predator. However, at finer scales, we still know very little about how Amur tigers influence the distribution of local mesopredators, how these mesopredators behaviorally respond to tigers, and what cascading effects they have on lower trophic level.

Urine, a natural by-product of Amur tigers' daily activities, remains in the environment for extended periods after excretion (Mohorovic and Krofel 2021), serving as olfactory cues that signal predator presence to other species. Unlike auditory or visual signals, these olfactory cues convey both the timing and persistence of predator presence at specific locations. Similar to other predators, Amur tigers cache their kills after hunting and frequently return to feed on the remaining carcasses (Elbroch and Wittmer 2012). When prey resources are abundant, they utilize approximately 65–75% of the prey, leaving a substantial portion of the remains available in the environment (Miller et al. 2013). Amur tigers spend around 30% of their daily activity time near to hunting sites (Miller et al. 2014), and this prolonged activity increases the chance of urination in proximity to hunting sites. Other species modulate their behavioral patterns in response to the perceived information (Osada et al. 2015; Palmer et al. 2021). Species exhibit varying responses to predator cues. For mesopredators, the dynamics are markedly more intricate. While they are vulnerable to predation, they may also exploit apex predator prey remains as valuable food resources. Consequently, mesopredators must judiciously balance the trade-offs informed by these olfactory signals (Haswell et al. 2018; Prange and Gehrt 2007).

Previous studies have shown that direct killing among predators is most likely to occur when the body size ratio falls between 2 and 5.4 (Donadio and Buskirk 2006; Palomares and Caro 1999). For example, in the carnivore community of the African savanna, lions are the primary cause of mortality for spotted hyenas (*Crocuta crocuta*, ITIS.gov number 621907) (Trinkel and Kastberger 2005); however, when the target shifts to black-backed jackals—whose body size is much smaller than their own—their role turns to a facilitative one (Welch et al. 2023). We hypothesize that the attraction effect of Amur tiger urine on small-bodied mesopredators outweighs its fear—inducing effect—this assumption was derived from preliminary field observations, where we occasionally noticed mesopredators lingering near areas with potential apex predator traces rather than avoiding them outright, suggesting a possible "attraction-driven" response rather than pure fear. Nest predators are typically small-bodied mesopredators, and using bird eggs in experiments allows for a focus on specific species. Additionally, bird eggs have minimal scent, which reduces potential interference in the experiment, enabling the results to better reflect the unique effects of tiger urine on small mesopredators.

This study aimed to examine the impact of apex predator chemical cues on the foraging behavior of small-bodied mesopredators at a fine scale by deploying Amur tiger urine near artificial bird nests. Through hypothesis testing, we found that Amur tiger urine accelerated the visitation speed of small-bodied mesopredators; in particular, Asian badgers (*Meles leucurus*, ITIS.gov number 726279) increased resource-based marking around the urine, which ultimately reduced the survival rate of bird eggs. This result indicates that small-bodied mesopredators were not deterred by the apex predator's chemical cues but instead used the area more actively, confirming that the positive effect of apex predators on small-bodied mesopredators outweighs the potential negative impact of fear in this specific ecological context, which deepens our understanding of the interaction relationships between predators.

Methods

Study area

The study area (400 km^2) is situated within Hunchun district of the Northeast China Tiger and Leopard National Park (~14,600 km^2) (Fig. 1). This region in Northeast China serves as the primary habitat for Amur tigers within the country (Wen et al. 2024). The area shares a border with Russia's Land of the Leopard National Park and represents the region with the highest frequency and density of cross-border movements by Amur tigers between China and Russia (Vitkalova et al. 2018). In recent years, concerted efforts by the Chinese government and societal stakeholders have led to a steady recovery of Amur tiger populations (Qi et al. 2021; Wen et al. 2022).

Key apex predators inhabiting the area comprise Amur tigers, Amur leopard (*Panthera pardus orientalis*, ITIS.gov number 726471), Ussuri brown bear (*Ursus arctos lasiotus*, ITIS.gov number 726992), and Ussuri black bear (*Ursus thibetanus ussuricus*, ITIS.gov number 727001).

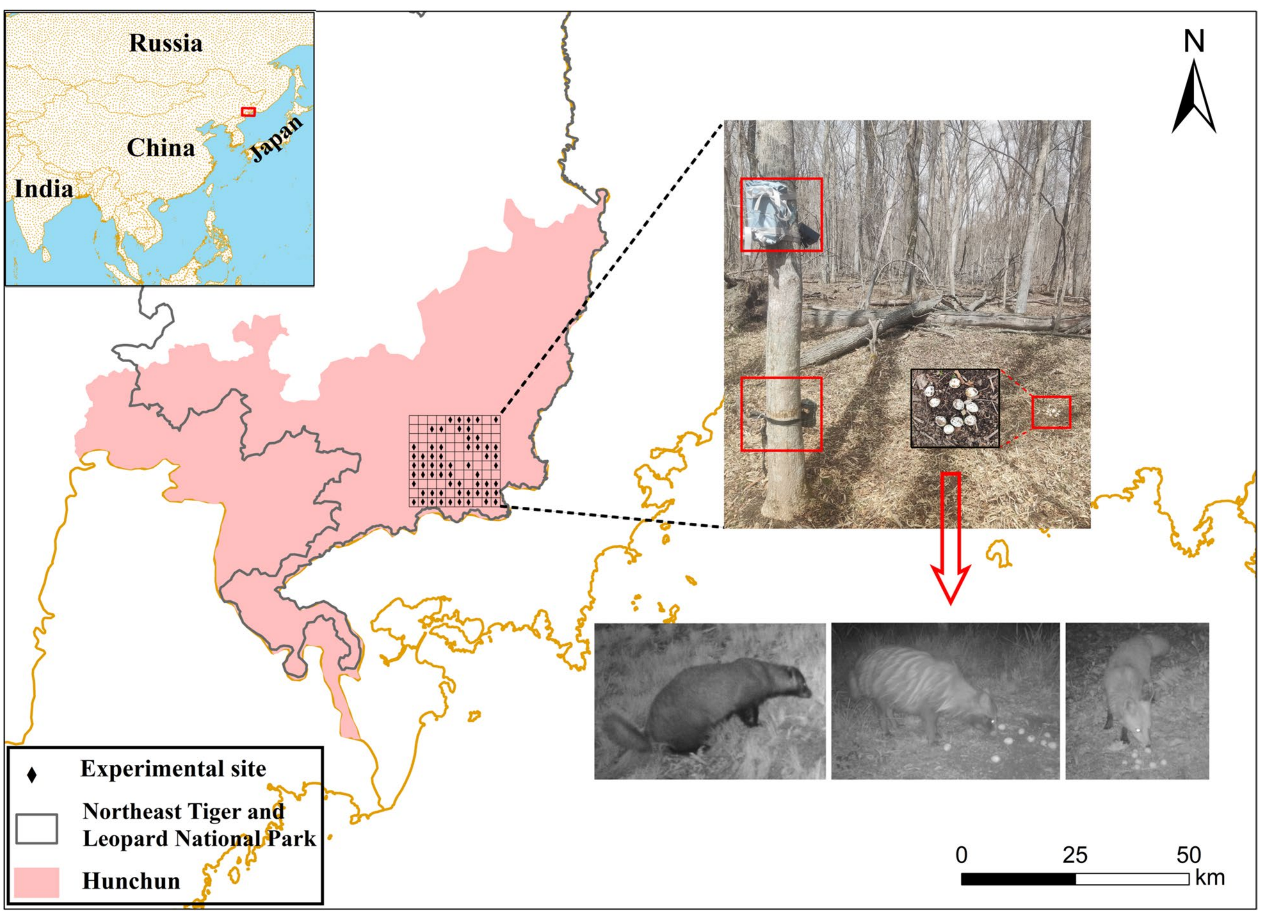

Fig. 1 Experimental site in the study area in Northeast China. The left side shows the spatial distribution of the experimental sites, and the right side shows the actual view on the experimental sites. The three photos respectively show the predation scenes of bird eggs by the Asian badger, raccoon dog, and red fox

Mesopredators include Asian badger, Raccoon dogs (*Nyctereutes procyonoides*, ITIS.gov number 183821), Yellow-throated martens (*Martes flavigula*, ITIS.gov number 621940), Siberian weasel (*Mustela sibirica*, ITIS.gov number 621955), Red foxes (*Vulpes vulpes*, ITIS.gov number 180604), and Amur hedgehogs (*Erinaceus amurensis*, ITIS.gov number 633538). Terrestrial avifauna include Common pheasants (*PhAsianus colchicus*, ITIS.gov number 175905) and Northern hazel grouse (*Tetrastes bonasia*, ITIS.gov number 677536) (Qi and Zhong 2004).

Urine collection

Tiger urine utilized in this study was sourced from captive Amur tigers housed at the Northeast Tiger Park in Mudanjiang City, Heilongjiang Province. The enclosures have cement flooring and a specialized drainage system designed to direct urine out of enclosures. Keepers cleaned cement floors and drainage channels daily using high-pressure water jets, and each evening, sterile absorbent cotton was placed at the drainage outlets; urine-soaked cotton was retrieved the following morning. Urine was subsequently extracted from the absorbent cotton into 200 ml plastic containers and preserved in an ultra-low-temperature freezer at −80 °C. A total of 4 Amur tiger urine samples was collected in October 2022. All tigers were born in 2016 (6 years old at the time of collection), including 2 females and 2 males, none of which were in estrus. The urine samples were stored at −80 °C for 6 months before the formal experiment was conducted in April 2023.

Field design and tiger urine set-up

A total of 86 infrared cameras were deployed across the study area, arranged in a 2×2 km grid configuration, designed to minimize scent dispersion between experimental sites and to reduce the likelihood of recording the same foraging event across multiple locations (Legendre 1993; Silveira et al. 2003). The trails or ridges most frequently utilized by mammals were identified and selected as the optimal camera installation sites within each grid. Infrared cameras were mounted on tree trunks at a height of 40–50 cm above ground level, ensuring the capture of both large species such as Amur tigers and small species such as Asian badgers. Infrared cameras were configured to capture three consecutive photographs followed by a 30-s video, operating with no interval between captures. To minimize the potential for missing species detections, due to the sensitivity limitations of infrared cameras, an additional 24-h surveillance camera was deployed at each experimental site, mounted on the same tree, ensuring that the bird eggs were positioned at the focal center of the monitored field of view. The 24-h surveillance cameras are equipped with built-in solar panels and an additional 300,000 mAh mobile power supply. Boasting 1080P video resolution and night vision capability, they can ensure continuous monitoring throughout the entire experimental period.

Of these, 60 locations were selected as experimental sites for the present study and were deliberately positioned away from human settlements and agricultural lands to mitigate the impact of human interference. The preliminary experiment provided a reference for selecting urine as the apex predator cue, avoiding potential behavioral changes of mesopredators induced by other odors—we compared two odors in the preliminary experiment and found that only urine exerted an attractive effect on mesopredators (Additional file 1: Figure S1). Meanwhile, to avoid residual interference from previously deployed Amur tiger urine, we calculated the duration during which the urine remained perceptible to animals. We defined the effective duration of tiger urine as the time when animals first failed to exhibit sniffing behavior at the urine placement site. The results showed that the perceptibility of Amur tiger urine to other animals mostly disappeared after approximately 15 days (Additional file 1: Figure S2). Therefore, the experimental period was uniformly set to 15 days. The formal experiment was conducted from April to June 2023, consisting of 4 rounds, which coincided with the natural breeding season of ground-nesting birds (Duan and Zhang 2017). For details of the preliminary experiment, please refer to the supplementary materials.

In front of the camera at each experimental site, we placed 10 Japanese quail (*Coturnix japonica*, ITIS.gov number 176013) eggs on the ground as artificial nests, similar in size to the eggs of natural ground-nesting birds (pheasants and hazel grouse). Tiger urine was placed 20 cm to the right of the artificial nests, relative to the camera's position. Among the 60 sites, 20 were designated as "control" where no tiger urine was applied during any of the four experimental rounds, allowing for the observation of nest predator behavior in the absence of tiger urine and insight into the effects of repeated trials on nest predators. An additional 20 sites constituted "Urine Group 1" where tiger urine was deployed during the second round only, while the remaining 20 sites formed "Urine Group 2" with tiger urine applied during the third round only. In the first round, no urine was applied in either "Urine Group 1" or "Urine Group 2" to observe the behavior of nest predators in the absence of tiger urine (Additional file 1: Figure S3). Similarly, no urine was applied in the fourth round to examine whether the behavior of nest predators returned to the pre-urine baseline after the suspension of tiger urine addition. To minimize potential interference as much as possible, all personnel received unified training and followed standardized operating procedures to ensure consistent human-induced interference across all groups. Meanwhile, before entering the mountain each day, all individuals were inspected for personal items: the use of perfume or insect repellent was prohibited, no food was allowed to be carried, and smoking was forbidden. Disposable gloves were worn during equipment installation, bird egg placement, and Amur tiger urine deployment. Upon departure, all human-related items in the surrounding area were inspected and removed. Following the conclusion of each experimental round, fresh eggs were replaced at all sites, irrespective of whether the previous eggs had been predated.

Data collection

Following the conclusion of each experimental round, memory cards and batteries of both cameras were replaced, and egg predation events documented according to photographic records.

Experimental sites with malfunctioning equipment that failed to capture predation events were excluded, resulting in a total of 55 sites (Control: $n=19$; Urine group 1: $n=19$; Urine group 2: $n=17$) with valid records covering the entire experimental duration. A 30-min interval was adopted as the criterion for independent events, and animal behavior data were screened based on these independent events (Kolowski and Oley 2021). First, we identified independent events of animal visits using infrared cameras. Based on the time of each event, we retrieved 5 min of video footage before and after the corresponding time from the 24-h surveillance recordings and documented the animals' behaviors. If bird eggs disappeared without any recorded animal visits, we reviewed the surveillance footage to trace the process around the time of the disappearance and documented the relevant animal behaviors. Predator species and their corresponding predatory behaviors were recorded according to the following term definitions:

Species Relative Abundance (RAI): quantitative measure for evaluating species activity: $\mathrm{RAI}=(A_i/T)\times 100$, where A_i denotes the count of independent valid photographs of species i, and T refers to the cumulative number of continuous operational days for that camera (Martin-Garcia et al. 2022; Liu et al. 2013).

Mesopredator Visitation Speed: The elapsed time from the start of the experimental round to the first recorded visit by mesopredators at the site.

Note that considering the effect of species distribution, we excluded sites where mesopredators did not appear in any of the four rounds of experiments, assumed to indicate minimal mesopredator activity in those areas; all remaining sites were retained to facilitate an analysis of variability within the same region. According to the experimental design, sampling plots with no mesopredator visitation within 15 days (360 h) were assigned a value of 360 h. This avoids statistical bias caused by mesopredators that would have originally visited after 360 h (before tiger urine was placed) being recorded within 360 h due to attraction by tiger urine. For example, in some areas where mesopredator activity was originally low, no visits were recorded during the experimental period without tiger urine; however, mesopredators began to appear after tiger urine was placed, though their arrival time was still relatively late. In contrast, in areas where mesopredators were more active, their visit speed was already fast even before tiger urine was placed. If we had ignored the data where no mesopredator visits were recorded, the effect of tiger urine would have been obscured. To verify the reliability of this assignment method, we used the Cox Proportional Hazards Model. Results from this model (Additional file 1: Figure S4) showed that the probability of mesopredator visits was significantly higher in plots treated with Amur tiger urine compared to control plots. If a significant difference can be detected using 360 h as the threshold, the actual difference would be even more pronounced.

Badger Marking Frequency: The frequency of squatting marking behaviors exhibited by Asian badgers at the site.

Egg Predation: A binary variable indicating whether at least one bird eggs at the site were predated by mesopredators, coded as 0 (eggs survived) or 1 (eggs predated).

Modelling methods

First, we recorded bird egg predation events to identify the predominant nest predators in the region and to assess the effects of tiger urine on egg survival probabilities. To explore the influence of tiger urine on mesopredator predation behaviors in greater depth, we then applied Random Forest (RF) to optimize dataset fitting. Recent studies have shown that machine learning methods may outperform traditional regression-based algorithms (Karthik et al. 2025; Mi et al. 2017; Surendran et al. 2025). Random Forest effectively mitigates the overfitting risk of single decision trees through Bootstrap sampling and random feature selection at each node. Its generalization error converges to a stable limit as the number of trees increases, eliminating concerns about performance degradation caused by excessive model complexity. The model exhibits strong robustness to label noise and outliers in training data and flexibly supports both classification and regression tasks without strict normality assumptions or complex preprocessing (Breiman 2001; Elith et al. 2006).

In the Random Forest fitting process, visitation speed was used as the response variable to reflect the predatory behavior of mesopredators. We assume that the distributions of Amur tigers and mesopredators themselves will also affect the behavior of mesopredators. We use RAI to assess species distributions and incorporate the results into model fitting (Li and Wang 2013). Due to the limited observation data available for most known species in the region, the analysis of the random forest model for individual species is restricted to badgers, raccoon dogs, and red foxes. To minimize the influence of both preliminary and current experiments on species RAI in the study area, we utilized data from the year prior to the experiment. Additionally, we observed that Asian badgers, the primary nest predators, exhibited pronounced marking behaviors after sniffing tiger urine or predating eggs. We hypothesize that the urine of Amur tigers and the occurrence of predation would affect the marking behavior of Asian badgers. Accordingly, marking frequency was incorporated as an additional variable in badger-specific modeling.

Since the response variables in the four models are not binomially distributed data, we used the caret package in R to calculate the coefficient of determination (R^2) to test the predictive ability of the models, and computed the importance ranking of variables in each model (Kuhn 2008). To further describe the correlation between predictor variables and response variables, we conducted correlation analysis for different types of variables. For continuous variables, Spearman's correlation analysis was adopted (Yang et al. 2015); for categorical variables, the Wilcoxon test was used (Fay and Proschan 2010; Yu 2004). Additionally, boxplots were plotted to visualize the positive or negative correlations between categorical variables and the response variable. All statistical analyses were conducted in R version 4.4.2.

Results

Main mesopredators and the survival rate of bird eggs

Over the 60-day experimental period, 404 predation events were documented, with 1,812 eggs consumed. Excluding avian predators, the major mesopredators in the study area were Asian badgers (690 eggs), raccoon dogs (54 eggs), red foxes (38 eggs), hedgehogs (33 eggs), weasels (15 eggs) and yellow-throated martens (8 eggs) (Additional file 1: Table S1). Egg survival rate declined markedly ($p=0.03$) following the application of tiger urine. After 15 days, the survival rate in the control group was 20.94 ± 3.96%, whereas that in the tiger urine treatment group dropped to just 5.48 ± 2.09% (Fig. 2).

The attraction of tiger urine to mesopredators

We calculated the RAI of these avian egg predators in the region: the average RAI was 3.00 for Asian badgers, 0.81 for red foxes, 0.12 for raccoon dogs, 0.15 for yellow-throated martens, 0.09 for hedgehogs, and 0.03 for Siberian weasels (Additional file 1: Table S2).

In the random forest models for the visit speeds of three mesopredator species, tiger urine emerged as a key influencing factor across all models, and there was a significant negative correlation between mesopredators' visit speed (lower values indicate faster arrival) and the presence of tiger urine (Table 1; Fig. 3). For Asian badgers, the sampling round also constituted an important factor, which may be attributed to the development of spatial memory in this species.

The effect of tiger urine on the marking behavior and food-searching of badgers

Of the 22 camera sites where tiger urine was placed and badgers preyed on bird eggs, 18 sites (82%) showed that badgers initially identified the tiger urine, explored, then preyed on the eggs. The average time spent sniffing the urine at fixed points was 24.68 ± 4.74 s.

In the random forest model for the marking frequency of badger, predation occurrence was the primary influencing factor, followed by tiger urine. Marking frequency of badger was significantly positively related to bird egg predation, the presence of tiger urine (Table 1; Fig. 4).

Discussion

Mesopredator attraction to Amur tiger urine

Mesopredator visitation speed

In our study area, the Amur tiger, as the apex predator in the temperate forests of the Northern Hemisphere, functions as both an umbrella and flagship species, playing a critical role in maintaining the stability of the local ecosystem (Gao et al. 2023; Miller et al. 2014). Its considerable body size creates a stark size disparity with local mesopredators. The body mass ratio of Amur tigers to these mesopredators ranged from 13.6 to 305.0, which is far beyond the 2–5.4 range where direct killing between predators is most likely to occur (Additional file 1: Table S3). The ecological niche overlap between Amur tigers and these small mesopredators is minimal, and the energy returns from preying on such small mesopredators would be negligible. Previous dietary studies of Amur tigers in Hunchun revealed that mesopredators contribute less than 5% to their overall diet, suggesting that Amur tigers exert limited suppressive effects on local small mesopredators (Gu et al. 2018; Kerley et al. 2015).

As the main mesopredators in this analysis—Asian badgers, red foxes, and raccoon dogs—exhibit differences in foraging strategies, behaviors, and population distributions, we conducted separate model analyses for each species. Although Asian badgers are generally regarded as generalist predators primarily feeding on invertebrates, they are adept at utilizing local resources

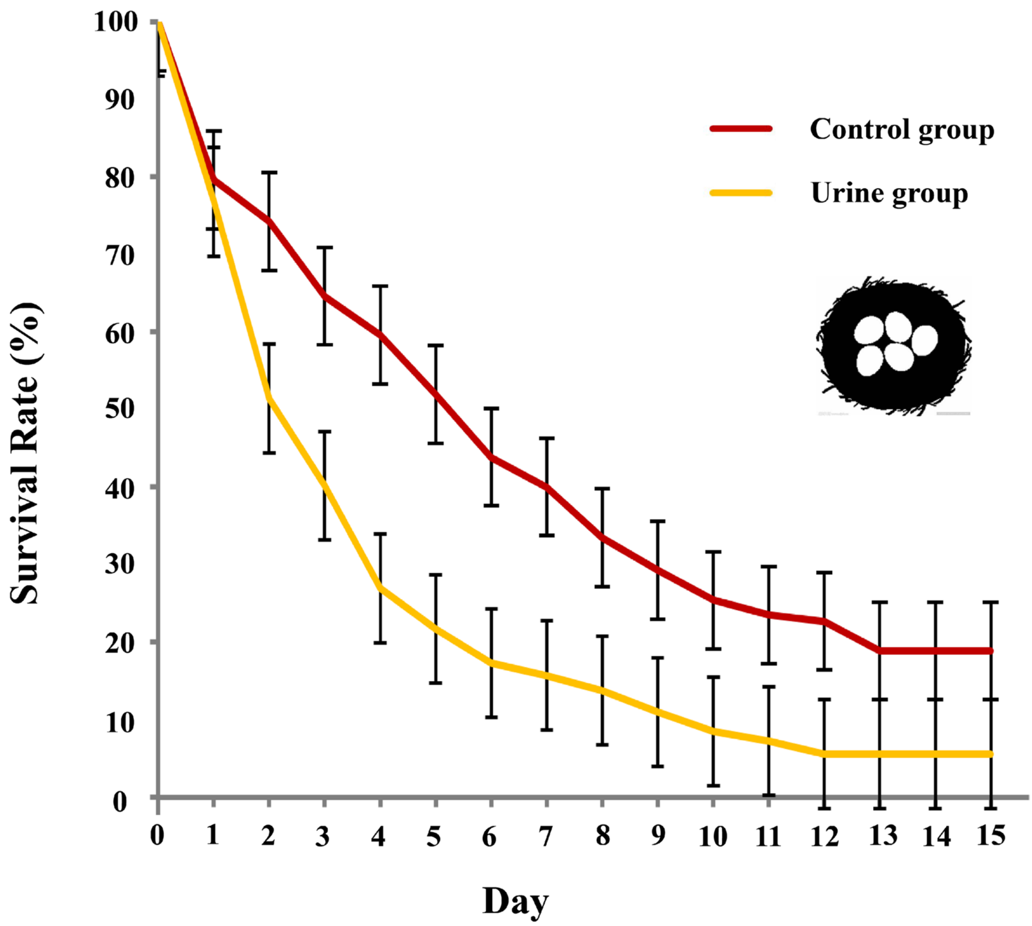

Fig. 2 Changes in bird egg survival rates before and after tiger urine placement. Blank: (*n* = 129). Urine: (*n* = 36)

and display opportunistic foraging behavior throughout their distribution range (James and Suuri 2010; Li et al. 2013). Their diet also varies significantly with temperature and latitude. In winter and high-latitude regions, where food resources are relatively scarce, animals tend to utilize all available resources; increased carnivory may be a common adaptation among omnivorous mammals (Castañeda et al. 2022; Egle et al. 2009). Compared to other regions lacking apex predators or located at lower latitudes, the dietary analysis of Asian badgers in the Hunchun area showed that the occurrence frequency of large ungulates in their diet exceeded 40%, while that for red foxes was over 50% (Wu 2025). Red foxes and raccoon dogs have been repeatedly documented to exhibit obvious scavenging behavior in other studies, which is more pronounced in high-latitude regions (Elmeros et al. 2018; Meisner et al. 2014).

Our results confirm this hypothesis. The urine of Amur tigers can attract small-bodied mesopredators such as Asian badgers, red foxes, and raccoon dogs and accelerate their visit speed; Particularly for the relatively abundant Asian badgers, the application of Amur tigers RAI also demonstrates the impact of tigers' actual distribution on badgers' behavior. In areas with higher tiger densities, badgers may be more familiar with the odor of apex predators, further illustrating the reliability of tiger urine as an apex predator behavioral cue. However, for the relatively scarce red foxes and raccoon dogs, Amur tigers' relative abundance did not affect their visitation speed, possibly due to sample limitations. The visit speed of Asian badgers showed an acceleration as the number of experiments increased. This may be because Asian badgers developed a degree of spatial memory (Mellgren and Roper 1986).

It is important to note that weather conditions are likely to affect the effective duration of tiger urine. For instance, higher temperatures, stronger wind speeds, and increased precipitation can accelerate urine volatilization and reduce its effective duration. However, due to the complexity of the wild environment—even in areas not far apart, significant variations in weather can occur at the same time on the same day—we did not incorporate

Table 1 Random Forest model showing the effects of Amur tiger urine, Amur tiger RAI, egg predation and mesopredator RAI on the foraging behavior of mesopredators

Response variable	Predictor variable	Importance ranks	Rho	R^2
Asian badger visitation speed	Urine	20.73	NA	0.37
	Sampling round	19.01	−0.34	
	Tiger RAI	10.29	−0.29	
	Badger RAI	7.17	−0.26	
Red fox visitation speed	Urine	8.33	NA	0.65
	Fox RAI	3.36	0.22	
	Sampling round	1.91	0.07	
	Tiger RAI	1.49	−0.17	
Racoon dog visitation speed	Urine	13.20	NA	0.71
	Sampling round	9.86	−0.07	
	Racoon dog RAI	2.86	−0.23	
Badger marking frequency	Predation	32.16	NA	0.31
	Urine	11.93	NA	
	Tiger RAI	10.69	0.29	
	Badger RAI	7.59	0.25	

Rho represents the direction (positive or negative) of the correlation

weather into the model here. Further research on this aspect can be conducted in the future.

Specific marking behavior of the Asian badger

The foraging efficiency hypothesis posits that animal scent marking is closely tied to food resources, functioning to signal resource ownership to conspecifics. This behavior facilitates resource partitioning and enhances foraging efficiency. Such food resource marking behaviors have been documented in Eurasian otters (*Lutra lutra*) and honey badgers (*Mellivora capensis*) (Begg et al. 2003; Remonti et al. 2011). In this study, after badgers obtained food (i.e., predated on bird eggs), they frequently marked the surrounding area. Additionally, it was first observed that when badgers were exposed to tiger urine, they exhibited the same squat-marking behavior as when they obtained food—characterized by squatting on their hind limbs and rubbing. Previous research has demonstrated that badgers possess caudal glands which secrete glandular substances used for squatting marking (Kruuk 1989). This marking behavior was more frequent in the presence of tiger urine. Notably, this marking behavior was also observed at sites without tiger urine, albeit at a lower frequency. This may be because scent marking by badgers along their travel routes could aid navigation and efficient food localization, thereby enhancing their spatial memory. We propose that badgers perform squatting marking behavior at key resource sites.

As a chemical cue from the region's apex predator, tiger urine likely serves as an indicator of predator activity (Burger et al. 2008; Prange and Gehrt 2007). Although these scent marks do not guarantee Asian badgers access to food resources, they significantly enhance the likelihood of Asian badgers locating them within 15 days of tiger urination, inferred as recent activity (Amur tigers spend around 30% of their daily activity time near to hunting sites), and this prolonged activity increases the chance of urination in proximity to hunting sites. This finding suggests that Asian badgers benefit from following larger apex predators, as it increases their likelihood of accessing prey carcass resources, with the associated benefits outweighing the risks of predation (Sun et al. 2024; Wilmers et al. 2003).

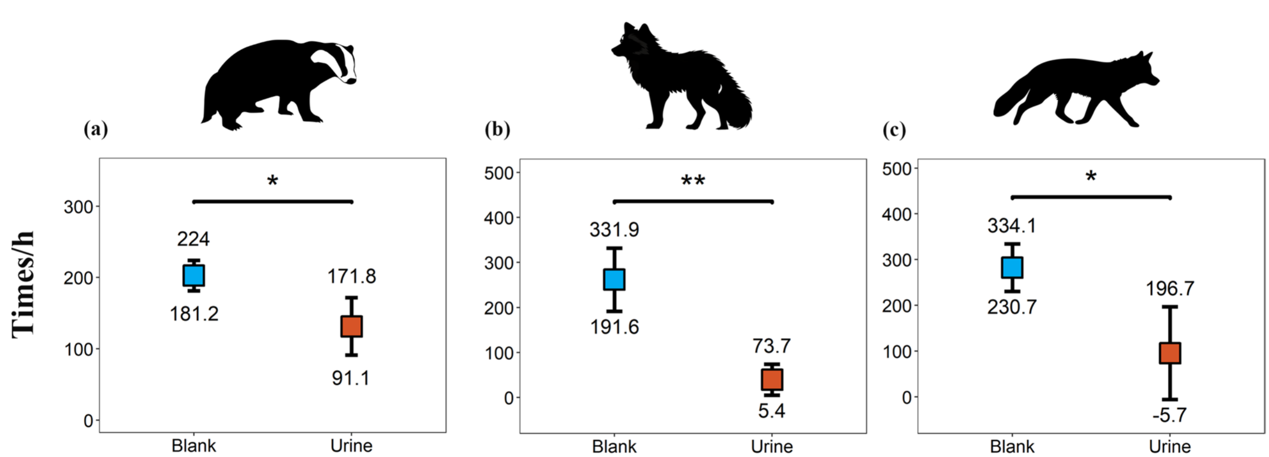

Fig. 3 The impact of tiger urine on the visitation speed of three small-bodied mesopredator species. **a** Asian badgers ($n = 220$); **b** Racoon dogs ($n = 20$); **c** Red foxes ($n = 24$). The values represent the 95% confidence interval

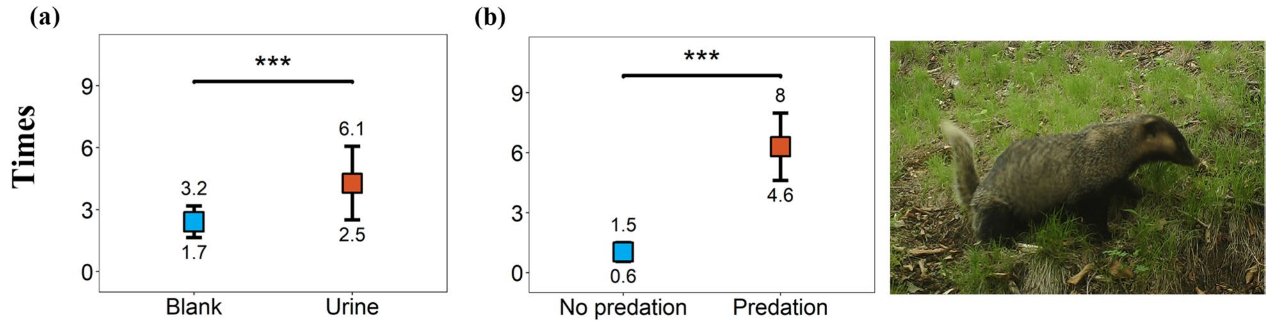

Fig. 4 **a** Effect of tiger urine on badger marking frequency. Blank: (*n* = 181). Urine: (*n* = 35); **b** Effect of egg predation on badger marking frequency. No predation: (*n* = 147). Predation: (*n* = 69). The values represent the 95% confidence interval

Considerations on the cascade effect

In this study, tiger urine increased the likelihood of egg predation by attracting nest predators. This phenomenon may trigger cascading effects within the ecosystem via the mechanism of the nutritional linkage effect (Baker et al. 2025). Asian badgers, red foxes, and raccoon dogs have been repeatedly documented as nest predators of ground-nesting birds (Elmeros et al. 2018; Kemink et al. 2023). The survival rate of nest eggs is critical to the population dynamics of birds (Hancock et al. 2023; Ward et al. 2022). In natural environments, bird nests typically depend on camouflage, concealment, and the sparse spatial distribution of nest predators to mitigate predation pressure (Meyer et al. 2024; Paris and Studds 2024). However chemical cues emitted by apex predators may destabilize this equilibrium by reshaping the spatial dynamics between predators and prey, consequently amplifying predation rates on bird eggs. Due to the lack of data on the nests of ground-dwelling birds in the wild, the reliability of this part of the results needs to be verified by further research. Our research findings can only provide certain insights.

Conclusion

With the deepening of wildlife conservation efforts, there is a growing recognition of the inherent complexity of ecosystems, underscoring the imperative for greater prudence in formulating wildlife management decisions. This study's findings on the behavioral responses of small-bodied mesopredators to Amur tiger urine offer critical insights that reinforce this principle, reshaping conventional understanding of apex-mesopredator interactions in temperate forest ecosystems of Northeast China. The complexity of these interactions is further amplified by the multifaceted ecological roles of apex predators, as documented in global and regional studies. For wildlife management decisions, these insights demand a shift from one-size-fits-all approaches to context-specific, behaviorally informed strategies.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s13717-026-00678-5.

Additional file 1.

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Author contributions

G.J., X.X. designed the study. W.C., C.C., X.L., S.G., D.L., B.H., D.W. and Z.L. contributed to field survey. W.C., W.S., W.B., J.Q., J.G., H.B. contributed to data analysis. W.C. contributed to paper writing, and G.J., X.X., N.J.R. contributed to paper revisions.

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Data availability

The dataset supporting the conclusions of this article is available in the Figshare database: https://doi.org/10.6084/m9.figshare.30804482.v1. We present the core metadata following the ISO 15836:2017 standard. Metadata Element: Dataset. Identifier: https://doi.org/10.6084/m9.figshare.30804482.v1. Title: Amur tiger urine enhances the foraging behavior of three major small-bodied mesopredator species in northeastern China. figshare. Dataset. Creator: Wannian Cheng. Temporal Coverage: 2023-04 to 2023-06. Spatial Coverage: 42.888537°–43.053368°, 130.772259°–130.998136°. Data quality: Outliers have been removed from the data. Code Dependencies: R version 4.4.2. License: CC BY 4.0.

Declarations

Ethics approval and consent to participate

This study has obtained the field research permit from the Hunchun Nature Reserve Administration, and strictly adheres to the Wild Animal Protection Law of the People's Republic of China and the IUCN Guidelines for Ethical Wildlife Research. All procedures involving animals were approved and followed the Animal Care Guidelines issued by the Science and Technology Ethics Committee of Northeast Forestry University (Permit No.: 2025110).

Consent for publication
Not applicable.

Competing interests
The authors declare no competing interests.

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