



Of mice and cats: interspecific variation in prey responses to direct and indirect predator cues

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Abstract

Prey behavioral responses to predation risk cues may vary between species; moreover, the strength of these behaviors may differ depending on risk cue. In northwestern Taiwan, we used the giving up density (GUD) framework supported with camera trap observations to test how two wild murid rodents that differ by up to fivefold in body size (striped field mouse, *Apodemus agrarius*, and lesser rice-field rat, *Rattus losea*) altered their foraging behavior depending on microhabitat characteristics (indirect predator cues) and exposure to predator odors (direct predator cues) of three felids: the native leopard cat (*Prionailurus bengalensis*), the introduced domestic cat (*Felis catus*), and the exotic bobcat (*Lynx rufus*). GUD was not affected by predator odors but rather by microhabitat type; rodents removed more seeds under the cover of vegetation compared to exposed food stations, which may reflect a proactive approach to avoiding high-risk areas in a heterogeneous environment. The smaller mouse, *A. agrarius*, spent more time foraging in experimental food patches compared to the larger rat, *R. losea*, irrespective of predator odor. Conversely, *R. losea* spent more time investigating stations and exhibiting vigilance compared to *A. agrarius*. Species-level differences are consistent with behavioral phenomenon that smaller, “faster” species confer more boldness compared to larger, “slower” species, which reinforces the connection between behavior and pace of life, and further elucidates how the behavior of different prey species may not be interchangeable in contexts of risk.

Significance statement

In the wild, animals eat while trying not to be eaten. Therefore, preys often change their behavior in response to risk cues, but the intricacies of these behavioral shifts can be complex and vary between species. With the use of camera trap monitoring and experimental food patches, we were able to examine fine-scale species-specific behaviors and test for dissimilarities. Two species of wild rodents did not change their foraging behavior to the addition of predator odors, but we did observe an interspecific behavioral variation. The smaller, “faster” rodent species spent more time foraging, while the larger, “slower” species spent more time vigilant with more thorough investigation. These interspecific behavioral differences likely indicate the smaller species demonstrated more boldness, whereas the larger rodent was more cautious, which is consistent with the association between pace of life (POL) and behavior.

Keywords Behaviors · Giving up density (GUD) · Vigilance · Foraging · Microhabitat · Predation risk

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Introduction

Ubiquitously, preys navigate their environments while exposed to risks that can have far-reaching effects. The strong selective force of predation can govern the morphological, physiological, and life history and behavioral traits of prey (Anson et al. 2013; Hermann and Thaler 2014; Bedoya-Perez et al. 2019). Many mammalian prey species have highly developed chemosensory systems and use olfaction to discriminate predators (Eisenberg and Kleiman 1972; Dielenberg and McGregor 2001). Predator cues, such as odors, have been found to induce antipredator responses in mammalian prey (Apfelbach et al. 2005, 2015; Parsons and Blumstein 2010). These responses may include modulating space use, decreased activity, cessation of foraging, increased vigilance, immobility, and hiding (Blanchard and Blanchard 1989; Lima and Bednekoff 1999; Preisser et al. 2005; Takahashi et al. 2005). According to the landscape of fear framework, the perception of predation risk for prey is spatially heterogeneous throughout their habitat, with certain areas of a home range perceived as riskier than others, generating an unbalanced trade-off between risk and reward for foraging behavior (Laundré et al. 2001). However, if prey continuously face high predation risk, bold or risky foraging endeavors may be necessary to meet their energetic demands and avoid starvation (Lima and Bednekoff 1999; Moll et al. 2017; Bedoya-Perez et al. 2019).

Small mammals, specifically rodents, are preyed upon by mammalian, avian, and reptilian predators. To address different sources of danger, rodents may utilize environmental cues for assessing contexts of risk (Lima and Dill 1990; Wolff and Sherman 2008). While direct risk cues typically involve stimuli from a predator, such as odors, indirect cues include microhabitat features and illumination (Thorson et al. 1998; Farnworth et al. 2019). For example, rodents may view vegetation cover as a safe refuge and factor in the distance from these sheltered areas when making decisions concerning activity (Brown and Morgan 1995; Searle et al. 2008). Intuitively, in exposed microhabitats, prey can be at higher risk to various predators and may attenuate their foraging behavior (Orrock et al. 2004; While and McArthur 2005). Moreover, there is mounting evidence supporting the importance of indirect cues as drivers of predation risk (Orrock et al. 2004; Verdolin 2006; Preisser et al. 2007; Farnworth et al. 2020). Therefore, indirect risk cues, namely, uncovered microhabitat, may reflect a high predation risk due to exposure to multiple predator taxa including birds of prey, mammalian carnivores, and reptiles (Orrock et al. 2004; Verdolin 2006; Hunter and Barrett 2015).

Prey responses to direct cues, specifically predator odors, may vary depending on the community structure of predators and prey, evolutionary history between

focal predator and prey, and behavioral variation of prey (Apfelbach et al. 2005; Réale et al. 2007; Parsons et al. 2018). To date, many risk-related foraging behavior studies have focused on a single prey species (Orrock et al. 2004; Verdolin 2006 (review); Carthey and Banks 2018; Farnworth et al. 2019). In real-world field conditions with multiple prey species, interspecific variations in behavioral responses to risk may exist; therefore, comparative approaches should be incorporated to better understand the importance of risk cues in prey communities.

Behavioral variations of prey may arise from differences in pace-of-life (POL). The POL hypothesis posits that closely related species should differ in a collection of physiological, such as metabolic rate, and morphological, such as body size, traits that have coevolved with life histories (Stearns 1983; Wikelski and Ricklefs 2001). These variations in life history fit a fast-slow continuum (Wikelski et al. 2003; Dammhahn et al. 2018). In mammals, small species have been documented to exemplify fast-paced life histories with a prioritization of current reproduction over survival due to their short life spans, whereas larger species with longer life spans adopt slower life history strategies favoring survival over reproduction (Ricklefs and Wikelski 2002; Dobson and Oli 2007). There is growing evidence that behavior is associated with POL (Sih et al. 2004; Réale et al. 2007; Stamps 2007; Dammhahn et al. 2018). For instance, smaller species with fast life histories are expected to demonstrate behaviors conferring boldness, fast exploration, and exploitation of resources, whereas larger species with slower life histories may be more cautious in response to risk (Ricklefs and Wikelski 2002; Stamps 2007; Réale et al. 2010; Sol et al. 2018). Studies have tested both intra- and interspecific behavioral variations of small mammals to risk in artificial conditions (Martin and Réale 2008; Cremona et al. 2015; Best et al. 2020), but few studies have examined interspecific variations of fine-scale behaviors in the prey species' natural habitat.

Prey responses to predator cues may also depend on the evolutionary history of the predator-prey relationship. Invasive species pose severe risks to their native counterparts due to the absence of heritable experiences in the form of biological interactions, which include competition and predation (Dickman 1996; Stokes et al. 2009). For instance, native prey may lack adequate antipredator defenses to introduced predators (Kovacs et al. 2012; Jolly et al. 2018). Without sufficient evolutionary and ecological experiences between a novel predator and native prey, the prey may be naïve to predator cues and unable to respond accordingly, adhering to the naïveté hypothesis (Carthey and Banks 2018; Carthey and Blumstein 2018). Therefore, native prey, such as rodents, may have differential responses to the olfactory

cues of a native predator, an introduced predator, and an exotic, unfamiliar predator.

A common approach to testing the impact of predation risk on the foraging behavior of wild, free-ranging prey involves giving up density (GUD) experiments. GUD can be defined as the density of food remaining in a patch after foraging has ceased and where the risk of predation outweighs the benefit of acquiring food (Brown 1988). These methods are often used to assess the trade-offs between risk and energetic rewards (Brown 1988; Bytheway et al. 2013; Cremona et al. 2014; Welch et al. 2017). Although GUD experiments can provide an overall quantitative assessment of perceived predation risk of prey, when operated alone, there are limitations toward the finer-scale behaviors of prey in response to risk (Bedoya-Perez et al. 2013). These behaviors may have considerable ecological importance and shed light on any risk-related behavioral variations, especially in systems with multiple prey species. Therefore, complementing the GUD framework with video observations via remote sensing camera traps provides a more in-depth analysis of the behavioral traits of foragers and the processes involved in foraging versus risk trade-offs (Bedoya-Perez et al. 2013; Caravaggi et al. 2017; Smith et al. 2020). For instance, species-specific GUD responses to varying risk contexts (e.g., different predator odors) may be concealed by the net result of the community-level GUD responses if different prey species have opposing responses exemplified by one species foraging and the other not. This caveat could be resolved with the addition of camera traps to the GUD design.

In northwestern Taiwan, where the only viable population of the endangered leopard cat (*Prionailurus begalensis*) can be found (Pei et al. 2014), free-ranging domestic cats (*Felis catus*) have become more widespread and abundant. Moreover, efforts to control the growing free-ranging population of domestic cats through programs such as trap-neuter-release (TNR) have remained largely unsuccessful in Taiwan (KJC Pei, personal communication), which is consistent with programs enacted in other countries (Winter 2004). Not only do the two cat species share similarities in their diets with rodents as a major constituent (Chuang 2012; Hunter and Barrett 2015), but in parts of northwestern Taiwan there is overlap in their distribution (INB, unpublished data). Therefore, understanding the effects the two felid predators have on rodent prey could provide implications for the ecological importance of their cues.

This study combined the capabilities of camera trap monitoring with the GUD framework to assess how direct (predator odors from a native predator, i.e., leopard cat, an introduced predator, i.e., domestic cat, and an unfamiliar, exotic predator, i.e., bobcat *Lynx rufus*) and indirect (microhabitat) risk cues affected rodent behaviors representative of two prey species, *Apodemus agrarius* and *Rattus losea*, with the latter up to five-fold larger in body size. Prey may

be expected to have the strongest responses to cues of predators that they share the most evolutionary and ecological history, in this case the leopard cat (Carthey and Blumstein 2018); however, the responses of prey may vary depending on risk context and with dissimilarities in morphological and life history traits of the respective prey species (Réale et al. 2010; Sol et al. 2018). Therefore, our hypotheses included: (1) predator odors will inhibit rodent foraging activity, specifically affecting GUD, and leopard cat odor will have the strongest effect; (2) rodent GUD will be higher in exposed versus covered microhabitat; (3) predator odors will elicit antipredator behaviors such as increased vigilance and decreased foraging; (4) there will be interspecific behavioral differences between the prey species, with *A. agrarius* demonstrating more boldness. Please refer to Fig. 1 for a roadmap of our hypotheses and accompanying predictions.

Materials and methods

Study area

We conducted the experiments in Zhuolan township, Miaoli County (24.311°, 120.826°) of northwestern Taiwan (Fig. S1). This region has low elevation (< 1000 m) and comprises a modified landscape with agricultural fields, namely, orchards, and human settlements, as well as a secondary forest and a shrubland habitat.

Based on preliminary surveys, we determined that this area has a high leopard cat activity (INB, unpublished data). Other small carnivores that inhabit the area include ferret badger (*Melogale moschata*), masked palm civet (*Paguma larvata*), small Indian civet (*Viverricula indica*), and crab-eating mongoose (*Herpestes urva*), though none of these species typically predate on rodents (Qi 2008; Hunter and Barrett 2011). There are also the introduced domestic dog (*Canis lupus familiaris*) and domestic cat, which both occur as free-ranging and pets. The rodent species observed in this area include the lesser rice field rat (*Rattus losea*) and the striped field mouse (*Apodemus agrarius*). Both *R. losea* and *A. agrarius* are predated upon by leopard cats and domestic cats (Chuang 2012).

Predator odor

We used odor cues from the native leopard cat, introduced domestic cat and exotic bobcat. All odor samples were obtained from healthy, captive individuals. Leopard cat fecal samples were collected from two individuals housed at Pingtung Rescue Center for Endangered Wild Animals at National Pingtung University of Science and Technology and one individual from Taipei Zoo. Domestic cat fecal samples were obtained from three pet cats. Donor individuals

A)

Experiment 1: GUD (Indirect vs. direct cues of predation risk)
Dataset: GUD

H1: GUD will be higher at stations with predator odors

- P1: GUD will be highest at stations with leopard cat odors

H2: GUD will be higher at stations in exposed microhabitat

Experiment 1 & 2: Behavioral responses
Dataset: Camera trap (specific behaviors)

H3: Predator odors will elicit antipredator behaviors, e.g. increased vigilance, decreased foraging

- P3: Foraging activity will be reduced at stations with predator odors

H4: There will be inter-specific differences in behavioral responses of prey species

- P4: The smaller species will demonstrate more boldness

B)

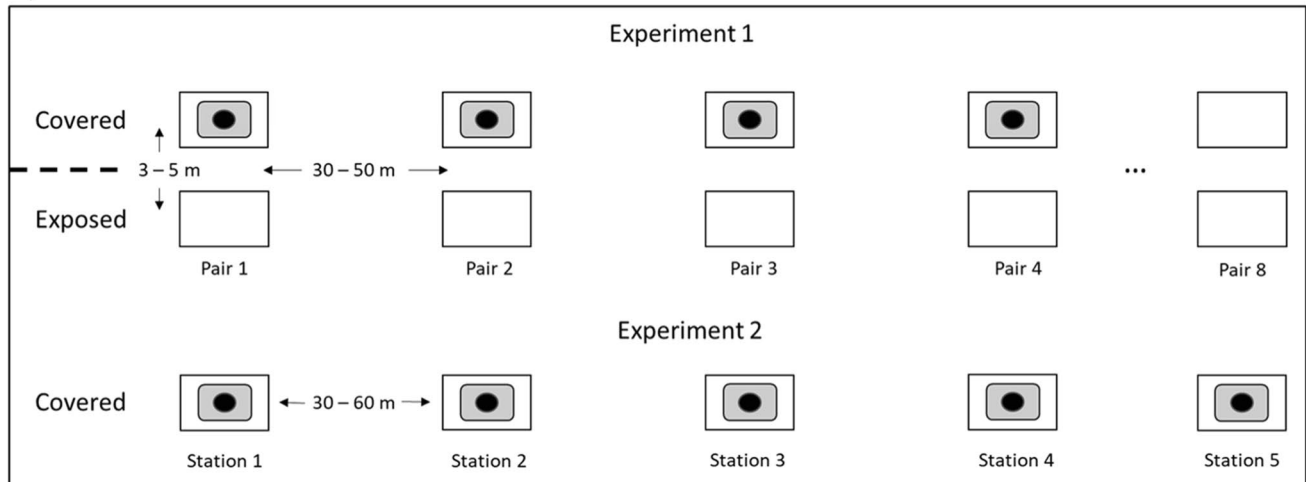


Fig. 1 Hypotheses and schematic of experimental design. **A** Roadmap of specific hypotheses and accompanying predictions for each experimental setup/dataset. H refers to hypothesis, and P refers to prediction. **B** Schematic of the experimental design of foraging stations for experiments 1 and 2. The schematic illustrates the design at one site; we used three sites in both experiments. A rectangular box represents a foraging station; camera traps are indicated by the camera icon. “Covered” and “Exposed” refer to microhabitat type; boxes parallel to “Covered” represent stations set in covered microhabitat,

and boxes parallel to “Exposed” represent stations set in exposed microhabitat. In experiment 1, at each site, we deployed 16 stations comprised of eight pairs; the distance between a pair of stations (one covered, one exposed) was 3–5 m, and the distance to the next pair was 30–50 m. Camera traps were not always at the first four covered stations. In experiment 2, at each site, we deployed five stations in covered microhabitat set at intervals of 30–60 m apart; each station was equipped with a camera trap

from both cat species were considered healthy and fed with high-protein diets. Fresh feces of both types of cats were retrieved, placed in airtight, resealable plastic bags, and stored in a freezer at $-20\text{ }^{\circ}\text{C}$ for no longer than 1 month before the experiment. At the time of the experiment, the feces were thawed, crushed, pooled together, and diluted to a mixture consisting of 30 g feces and 150 mL distilled water for both the leopard cat and domestic cat treatments. Similar ratios for fecal solutions have been used in other predation risk studies (Kovacs et al. 2012; Cremona et al.

2014, 2015). The same homogenous mixture for a predator odor was applied to all the assigned stations during the experiment. For the bobcat odor treatment, we used urine samples purchased from PredatorPee® Inc. (Maine Outdoor Solutions, Maine, USA). The use of “natural” olfactory cues, such as fecal or urine samples, has been found to be more sufficient in simulating predator presence compared to the use of a single, synthesized volatile molecule (Apfelbach et al. 2015; Jones et al. 2016). Moreover, the application of predator urine and/or feces has induced antipredator

behaviors in prey species in other experiments (Apfelbach et al. 2015; Eccard et al. 2017). Bobcats were chosen as the exotic predator because they are of a similar size to leopard cats and domestic cats, and they also predate on rodents (Hunter and Barrett 2015). Therefore, applying the odor of bobcats made it possible for a comparative approach testing the risk cues of a native, introduced, and exotic predator.

Experiments

All the experiments were conducted during the new moon phase of the months February and April in 2020. This timeframe was selected to control for varying degrees of luminosity. Illumination is another indirect cue of predation risk and has been found to influence prey behavior (Prugh and Golden 2014); moonlight can inhibit the foraging activity of rodents (Orrock et al. 2004; Farnworth et al. 2019). There was no precipitation during any testing night. We established three sites in the study area (Fig. S1); each was at least 500 m distance apart to maintain the spatial independence of rodent populations. Each site comprised a similar habitat and was inhabited by *R. losea* and *A. agrarius*.

Experiment 1: enclosed foraging stations

Two experimental components (GUD and behavioral responses) were included in experiment 1.

GUD (indirect vs. direct cues of predation risk) We performed a GUD experiment to investigate the foraging behavioral responses of rodents in different microhabitat conditions coupled with different predator odors from February 20 to February 26 2020. At each site, we deployed 16 experimental food patches (hereafter stations) in transects with eight stations placed under vegetation cover (shrubs, grasses, small trees) and eight stations exposed (1 m from vegetation). Please see Fig. S2 for pictures of foraging stations in each microhabitat type. The 16 foraging stations were divided into eight “pairs” at each site; a pair comprised one covered station and one exposed station set 3–5 m apart. Please see Fig. 1B for a schematic of our experimental design. The transects of “pairs” of stations were at intervals of 30–50 m (Fig. 1B). In this experiment, microhabitat type was defined as either with vegetative cover (covered) or without (exposed). The vegetative ground cover of the “covered” and “exposed” stations were measured to be 50–90% and less than 10%, respectively. These measurements were taken using a 1 m² quadrant at the time of the experiment.

Each food station consisted of a transparent plastic container (28 × 19 × 14 cm, 5 L) containing 10.0 g of millet seeds mixed thoroughly in 800 g of an extra-fine sand substrate. All containers were covered by a clear plastic lid to

prevent non-target species entry, which is a common design of GUD experimental apparatus (Bytheway et al. 2013; Cremona et al. 2014; Crego et al. 2018). On every container, we drilled a hole (44 mm diameter) at both ends to allow access to the target rodent species. During the experimental period, insects were not observed to affect the seeds in the containers. To prevent small birds from exploiting the seeds in the containers, we affixed rubber tubes (40 mm diameter, 44 mm length) to the holes at each end. This modification did not deter the rodents from entering the containers.

This experiment consisted of two rounds of two consecutive nights of testing. There was a two-night interval of no testing between the two rounds to make sure any lingering odors from the predator cue treatments had sufficiently dissipated. During both rounds on the first night, predator odors were not applied to the foraging stations. Therefore, the first night provided a baseline of rodent foraging activity and permitted before- and after-predator treatment comparisons. On the second day of testing (during both rounds), at least 1 h before dusk, predator odor treatments were applied to the foraging stations. We employed a stratified sampling design to ensure that at each site a given foraging station was not assigned the same odor during both rounds. The odor apparatus consisted of a tag made of a highly absorbent cotton material affixed to a wooden stake (25.4 cm long). Depending on the assigned odor type, tags were soaked in a leopard cat fecal mixture, a domestic cat fecal mixture, bobcat urine, or distilled water for the non-odor control. At each station, the odor apparatus was placed adjacent to the foraging container.

One week prior to the experiment, food stations were introduced to the sites, and the rodents could forage freely without any of the predator odor cues. During the experimental period, in the morning after each night of testing, we checked all the stations for animal visitation based on footprints and/or feces and foraging activity. The contents in the containers were sieved and the remaining amount of millet seeds were weighed (± 0.1 g) using an electronic scale to determine a GUD measurement. The contents of the food containers were replaced, refilling the seeds to 10.0 g.

Behavioral responses at enclosed foraging stations The following experimental setup was performed in tandem with the GUD experimental component. The purpose of this experimental component was to measure the fine-scale behaviors of individual species that visited and foraged from the enclosed stations, investigate responses to predator odors, and test for interspecific behavioral variation. Due to logistical constraints, accessibility, and concerns about theft, we set up camera traps at four covered (but not exposed) stations at each site (overall 12 stations for the three sites). We also predicted that there would be more activity at covered stations, which was a requirement for the camera trap

component of the study. The number of cameras used at each site was to also facilitate a full representation of odor types (non-odor control, leopard cat odor, domestic cat odor, and bobcat odor). We used a total of 12 KeepGuard KG 780 trail cameras (KEEPWAY Industrial Co., Kowloon, Hong Kong). Each camera was affixed to a tree at a height for an optimal field of view of the foraging station apparatus (1–1.5 m distance). The cameras were set to take 60-s videos with a 1-s interval between potential animal triggers and with the sensors set to high. The cameras were active for the full duration of the day (24 h) during the testing period.

During each round, stations with camera traps at each of the three sites were assigned different predator odors ($n=3$ for each odor type during one round). This design enabled each site to have two replicates of each odor type ($n=6$ for each odor type after both rounds). After each night of testing, the camera traps were checked for observations and, when necessary, memory cards and batteries were replaced.

Experiment 2: lidless foraging stations

Behavioral responses at lidless foraging stations We further investigated the effect of predator odors on the fine-scale behaviors of different rodent species with a secondary experiment involving lidless foraging stations. An aim was to test if the larger rodent species, *R. losea*, would be more inclined to visit and forage from the lidless food stations, since it was found to be a more cautious species in a laboratory study (Best et al. 2020). We performed this experiment from April 19 to April 25 2020. At each of the three sites (same as experiment 1), we set up five experimental food patches with camera traps (a total of 15 stations). We used the 12 preexisting locations for stations that had been equipped with camera traps in experiment 1, with an additional camera deployed at another covered station at each respective site. Therefore, for this experiment, we only used stations under vegetation cover since our aims were to focus on identifying the species visiting the food stations and the associated behaviors observed via camera trap monitoring. Additionally, assessing the effect of microhabitat on rodent foraging behavior was not an objective for this experiment. At each site, the stations were set at intervals of 30–60 m (Fig. 1B). The lidless stations consisted of transparent containers (25.8 × 16.3 × 6 cm, 1.5 L) without lids and containing 10.0 g of millet seeds mixed thoroughly in 800 g of sand (the same contents as experiment 1).

With the exception of the type of foraging container (with vs. without a lid) and number of foraging stations deployed at each site, we kept all key parameters of this experiment the same as experiment 1 (camera model and settings; predator odor treatment apparatus and application procedure;

temporal design: two rounds of two consecutive testing nights separated by a two-night interval; stratified sampling design: each station was not assigned the same odor type twice, each site featured all odor groups). The sample size (number of stations) for control, leopard cat, domestic cat, and bobcat odor types was 7, 8, 8, and 7, respectively.

The following morning after each night of testing we checked all the stations for animal visitation and foraging activity. Because we could not prevent non-target species, such as birds, from exploiting the seeds in the containers due to lack of lids and seed removal was not a main objective of this experiment, we did not take GUD measurements as they may have been invalid. If we observed traces of rodent activity at a station, we replaced the contents recharging the millet seeds to 10.0 g. When necessary, memory cards and batteries were replaced in the camera traps.

Camera trap video data analysis

The videos from the camera traps were analyzed manually. It was not possible to analyze the video data completely blind because predator odor treatments were apparent, e.g., the odor apparatus with the control treatment compared to the odor apparatus with the bobcat treatment. However, the observer was unable to distinguish between the leopard cat and domestic cat treatments. From the camera trap video footage of both experiments 1 and 2, the two rodent species *A. agrarius* and *R. losea*, were confirmed to visit the stations and forage. Both species were also recorded visiting and foraging at the same stations on the same night. These two species were easily distinguishable due to the size disparity, as well as the distinct stripe along the back of *A. agrarius* individuals (see Fig. S3 for pictures of each species). *Rattus losea* is up to five times the size of *A. agrarius* (*R. losea*: 115.9 ± 6.5 g (\pm SE), *A. agrarius*: 28.0 ± 1.4 g) (Qi 2008; Best et al. 2020). No other small mammal species foraged from the stations equipped with cameras. The behaviors measured and included in the scope of the main text were *locomotion*, *investigation*, *vigilance*, *foraging*, and *total time in view* (Table 1). We also measured other count variables (i.e., number of occurrences), but due to possible differences in population density (e.g., more foraging events of a species may be due to their higher population density instead of behavioral variation), they were removed from the main text (see Supplementary Material, Table S1, for all behaviors scored and Tables S6–S9 for results). For each behavior, the cumulative time spent performing a specific behavior in the field of view of the camera was calculated from all videos for each species at each station, as well as the total time a species spent in view at a station, which was the sum of all the specific duration-based behaviors. We were then able to calculate the proportion of time a species spent performing each of these behaviors. The use of proportional variables helped minimize the variation

Table 1 Behaviors measured from camera trap videos in experiments 1 and 2

Behavior	Unit measured	Definition
Locomotion	Proportion of total time	Proportion of time in view spent walking quickly, running, climbing, or jumping
Investigation	Proportion of total time	Proportion of time in view spent investigating the food tray apparatus and odor apparatus (treatment trial); including sniffing and biting
Vigilance	Proportion of total time	Proportion of time in view spent vigilant, e.g., alert, motionless, and head scanning
Foraging	Proportion of total time	Proportion of time in view spent foraging; searching for and/or consuming seeds in the food tray
Total time in view	Duration (s)	Total time a species was in view at a station (cumulative duration calculated for each species at each station)

Seconds (s); proportion of total time was calculated by dividing durations (total) of each specific behavior by the total time in view for each species, *A. agrarius* and *R. losea*, at each station. Behavioral responses were adapted from Carthey and Banks (2018) and Best et al. (2020). Please see Supplementary Material (Table S1) for a full list of behavioral responses measured

between stations influenced by population density. *Rattus losea* is much larger than *A. agrarius*, more territorial, and can have larger home ranges (Wang and Wang 2001; Qi 2008; Best et al. 2020); therefore, it may have a lower population density within a designated area.

The behaviors *vigilance* and *foraging* provided species-level information on variation in boldness, and the behaviors *locomotion* and *investigation* pertained to activity and exploration (Mella et al. 2015; Patrick et al. 2017; Carthey and Banks 2018; Montiglio et al. 2018). Please see Supplementary Material for links for videos and stills of behaviors (Figs. S4 and S5).

Statistical analysis

GUD (indirect vs. direct cues of predation risk)

An objective of experiment 1 was to compare foraging activity via GUD in different microhabitat types. Therefore, if there was an activity and seeds were removed at only one food station within a pair (exposed and covered), the measurement of the corresponding station was also included in the analysis; the same rodent individual could forage from either station within a pair due to the close range (3–5 m apart). Another objective was to assess foraging behavior under different contexts: with or without predator odor. If there was a foraging activity at a given station on one testing night but not the other within a round, both measurements were included in the analysis. Including both measurements would determine the effect of the predator odors (difference between the first trial without predator odor and the second trial with odor). If there was no foraging activity for either corresponding station during either testing night within a round, the station measurements were excluded from the analysis. Therefore, after combining both rounds the GUD sample size for control, leopard cat, domestic cat, and bobcat odor types was 20, 20, 22, and 20, respectively. We did not attempt to determine separate GUD measurements for each target prey species. Therefore, the GUD measurements

included in this analysis are representative of rodent communities, more specifically, the species *A. agrarius* and *R. losea*.

To test for the effects of perceived risk on the GUD of rodents, we used a linear mixed model (LMM). The fixed effects included in the model were *trial* (pre-treatment/no odor vs. treatment/odor), *odor type* (non-odor control vs. leopard cat vs. domestic cat vs. bobcat), and *microhabitat type* (exposed vs. covered). The random effect in the model was station ID nested within a site. The nested design was incorporated into the model to account for the block experimental design of our study and minimize spatial autocorrelation. Due to our limited sample size, we only included the interaction between trial and odor type, which was most pertinent to our research objectives. More specifically, the interaction between trial and odor type would indicate an effect of the predator odor on GUD, since predator odor treatments were only applied on the second night of testing in each round.

Behavioral responses

For all variables based on the camera trap datasets, if there was no activity during both trials at a station within a round, the measurements were excluded from the analysis. The behavioral variables *locomotion*, *investigation*, *vigilance*, and *foraging* were tested with an LMM. Due to the modest sample size of the datasets from both experiments 1 and 2, we combined the three predator odor types (leopard cat, domestic cat, and bobcat) and compared them with the non-odor control group (hereafter referred to as *odor*). Additionally, in experiment, 1 the sample size was very small for specific *odor type* × *species* combinations ($n=2$ for *R. losea* × domestic cat odor). We also excluded three-way interactions between trial, odor, and species from our official models due to the modest sample size. Therefore, the final LMMs included the fixed effects *trial*, *odor* (predator odors vs. control), *species* (*A. agrarius* vs. *R. losea*), and the two-way interaction between trial and odor. Similar to the GUD

analysis, the interaction between trial and odor would indicate an effect of the predator odors on specific behaviors. For random effects, station ID was nested in a site in our models.

To assess potential effects of specific odor types and the three-way interaction between trial, odor (or odor type), and species while also taking into account the small sample size of specific odor type and *R. losea* combinations for experiment 1, we performed the following exploratory analyses: 1) LMMs with trial, odor, species, trial × odor interaction, and trial × odor × species interaction as fixed effects using the dataset from the enclosed foraging stations (experiment 1, Table S2); 2) LMMs with trial, odor type, species, trial × odor type interaction, and trial × odor type × species interaction as fixed effects using the dataset from the lidless foraging stations (experiment 2, Table S2); 3) LMMs with trial, odor type, trial × odor type interaction as fixed effects using the *A. agrarius* dataset from enclosed foraging stations (experiment 1, Table S3). For random effects in all the models, station ID was nested in a site. Considering the modest sample size and qualitatively similar conclusions between the simpler LMMs (trial, odor, species, trial × odor) and the more complex LMMs from the exploratory analyses (Tables S2 and S3), we decided to present the results from the former in the main text.

For all mixed model analyses, we used estimated means with pairwise comparisons incorporating least significant difference for post hoc analysis of main effects and interactions. We calculated marginal and conditional *R* squared values for each LMM using the packages “lme4” (Bates et al. 2015) and “r2glmm” (Jaeger 2017) from the statistical software R Studio v. 4.1.3 (R Development Core Team 2022). Please see Supplementary Material (Table S5) for the *R* squared results, as well as variance estimates of the random effects. The normality of all response variables was confirmed based on the residuals of the models. For all of the statistical analyses, significance was considered at $\alpha = 0.05$. All the statistical analyses, except for the *R* squared tests, were performed with SPSS v.26.0 (IBM, Armonk, USA).

Results

Experiment 1: enclosed foraging stations

GUD (indirect vs direct cues of predation risk)

Of the 192 foraging opportunities we examined (48 stations × 2 nights × 2 rounds), there was a foraging activity in 118 (61.5%). The GUD values were considerably higher at the exposed stations compared to the covered ($F_{1,148} = 56.954$, $p < 0.001$) irrespective of predator odor type ($p > 0.05$, Table 2, Fig. 2). On average, the rodents removed 77.4% of the seeds at the covered stations, whereas only 19.0% of the seeds were removed at the exposed stations.

Table 2 GUD of seeds by rodents in response to trial, odor type, and microhabitat, and their interactions. Significance is indicated in bold

Effect	<i>F</i>	<i>df</i>	<i>P</i>
Trial	0.863	1	0.355
Odor type	1.140	3	0.335
Microhabitat	56.954	1	< 0.001
Trial × odor type	0.770	3	0.513

Original GUD values from experiment 1 were used for this analysis, $n = 164$; odor type (treatment trial: non-odor control = 20, leopard cat = 20, domestic cat = 22, bobcat = 20); residual $df = 155$, K (number of parameters) = 11. Please refer to Table S4 in SI 1 for R^2 values and variance estimates of random effects in LMM

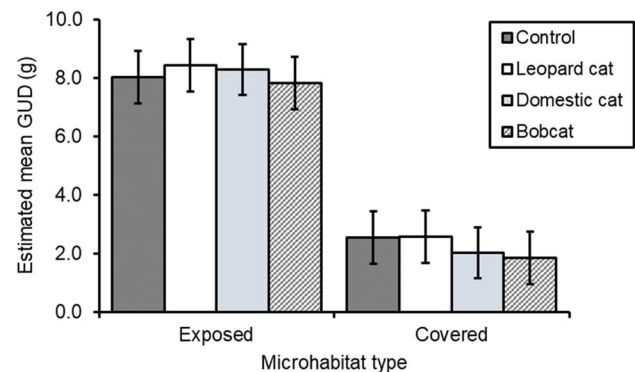


Fig. 2 Estimated mean giving up density (GUD) (out of 10.0 g) by rodents compared between predator odor type and microhabitat type. Error bars represent the standard error of the mean. Means were taken from only the treatment trial (when predator odors were applied). There were no significant differences between any predator odor type for either microhabitat type, based on post hoc analysis (all $p > 0.05$). Rodent GUD was significantly different between microhabitat type (Table 2)

Behavioral responses at enclosed foraging stations

We examined 48 foraging observations based on 12 stations (with cameras) for two rounds of two testing nights. *Apodemus agrarius* visited and foraged in 36 (75.0%) of the observations, whereas *R. losea* in only 15 (31.3%). The mean total time in view per station for *A. agrarius* and *R. losea* was 1069.7 ± 165.0 (\pm SE) and 499.8 ± 155.1 s, respectively.

Based on the dataset of enclosed foraging stations (experiment 1), there was no significant interaction between trial and odor for any behaviors, nor were there significant effects of trial or odor (all $p > 0.05$, Table 3). We found interspecific differences for the behaviors *investigation*, *vigilance*, and *foraging* (*investigation*: $F_{1,59} = 5.301$, $p = 0.025$; *vigilance*: $F_{1,59} = 6.432$, $p = 0.014$; *foraging*: $F_{1,59} = 8.993$, $p = 0.004$, Table 3). *Apodemus agrarius* spent more time foraging compared to *R. losea*, whereas *R. losea*

Table 3 Mean behavioral response variables of rodents compared between trial, odor, and species, and the interaction of trial and odor. Significance is indicated in bold

Variable	Experiment 1 ^{a,b,c}				Experiment 2 ^{a,d,e,f}			
	Effect	F	df	P	Effect	F	df	P
Locomotion	Trial	2.173	1	0.147	Trial	0.003	1	0.955
	Odor	0.547	1	0.462	Odor	0.077	1	0.782
	Species	0.113	1	0.738	Species	0.688	1	0.409
	Trial × odor	3.770	1	0.058	Trial × odor	0.653	1	0.422
Investig	Trial	0.019	1	0.892	Trial	0.000	1	0.993
	Odor	0.915	1	0.343	Odor	0.013	1	0.911
	Species	5.301	1	0.025	Species	7.231	1	0.009
	Trial × odor	0.003	1	0.960	Trial × odor	0.786	1	0.378
Vigilance	Trial	0.001	1	0.977	Trial	0.148	1	0.702
	Odor	0.474	1	0.494	Odor	0.452	1	0.504
	Species	6.432	1	0.014	Species	5.524	1	0.021
	Trial × odor	0.392	1	0.533	Trial × odor	0.028	1	0.868
Foraging	Trial	0.141	1	0.709	Trial	0.468	1	0.497
	Odor	0.167	1	0.684	Odor	2.444	1	0.125
	Species	8.993	1	0.004	Species	21.000	1	<0.001
	Trial × odor	0.301	1	0.586	Trial × odor	0.000	1	0.993

Investig, investigation. *Different datasets were used for experiment 1 (enclosed foraging stations) and experiment 2 (lidless foraging stations). Datasets include measures from both pre-treatment and treatment trials. ^a Subset of dataset, *n* = 64; ^b odor (treatment trial: non-odor control = 9, predator odors = 23); predator odors were combined due to limited sample size. ^c Residual *df* = 59 for all variables of experiment 1, *K* (number of parameters) = 7 for all variables for experiment 1. ^d Subset of dataset, *n* = 80. ^e Odor (treatment trial: non-odor control = 9, predator odors = 31); predator odors were combined due to limited sample size. ^f Residual *df* = 75 for all variables of experiment 2, *K* (number of parameters) = 7 for all variables for experiment 2. Please refer to Table S5 in SI 1 for *R*² values and variance estimates of random effects in LMMs

spent more time investigating the apparatus and being vigilant compared to *A. agrarius* (Fig. 3).

Experiment 2: lidless foraging stations

Behavioral responses at lidless foraging stations

In this experiment, there were 60 foraging opportunities (15 stations × 2 nights × 2 rounds). Our analysis found that there was

a foraging activity from *A. agrarius* and *R. losea* in 42 (70.0%) and 27 (45.0%) of the opportunities, respectively. The average total time in view per station for *A. agrarius* and *R. losea* was 2590.2 (*SE* = 283.0) and 945.0 (*SE* = 169.7) s, respectively.

The two-way interaction between trial and odor was non-significant for all the behaviors (all *p* > 0.05, Table 3). Therefore, predator odor was not detected to have an effect on the behaviors tested in our models. Similar to the results from the enclosed foraging stations (experiment 1), the behaviors

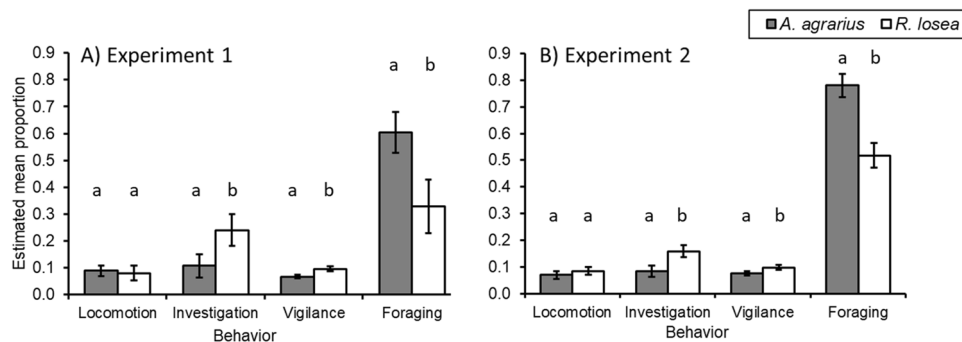


Fig. 3 Estimated mean proportion of time spent on the behavior locomotion, investigation, vigilance, and foraging compared between the species *A. agrarius* and *R. losea* for **A** experiment 1 (enclosed foraging stations) and **B** experiment 2 (lidless foraging stations). Error

bars represent the standard error of the mean. Estimated marginal means determined from LMMs (Table 3). Differences in letters (**a**, **b**) between each species indicate significant differences based on LMMs (Table 3)

investigation, *vigilance*, and *foraging* differed between the two species (*investigation*: $F_{1,75}=7.231$, $p=0.009$; *vigilance*: $F_{1,75}=5.524$, $p=0.021$; *foraging*: $F_{1,75}=21.000$, $p<0.001$, Table 3). *Apodemus agrarius* spent more time foraging when visiting the lidless foraging stations, and *R. losea* spent more time investigating and being vigilant (Fig. 3).

Discussion

Based on the results of our study, we did not detect any predator odor effects on rodent foraging efforts toward seed consumption and removal. Overall, the GUD values did not differ significantly between the predator odors, nor did the addition of the predator odors affect the amount of seeds remaining. Instead, microhabitat type was a strong predictor of rodent foraging activity. The rodents left considerably less seeds under vegetation cover compared to being exposed. Although our results do not support our first hypothesis, or specific prediction that rodents would respond to leopard cat odor, the significant effect of microhabitat on foraging activity supports our second hypothesis and is consistent with other studies. Many similarly designed studies targeting small mammals found that predator odors failed to influence prey foraging behavior, whereas microhabitat characteristics did (Pusenius and Ostfeld 2002; Orrock and Danielson 2004; Orrock et al. 2004; Verdolin 2006; Spencer et al. 2014). Spencer et al. (2014) found that the native spinifex hopping mouse (*Notomys alexis*) did not respond to fox (*Vulpes vulpes*) or cat predator odors, but that the rodent's foraging behavior was influenced by macro- and microhabitat. Comparably, Orrock et al. (2004) found that old field mice (*Peromyscus polionotus*) altered their foraging efforts in response to microhabitat features (reduced activity in exposed food patches compared to sheltered patches) but not to predator odors.

In the current study, the strong response to microhabitat as an indirect cue of predation risk may reflect avian predation pressure. For example, in Taiwan, the black-winged kite (*Elanus caeruleus*) consumes a high proportion of rodents with its diet comprising up to 90% of *R. losea* and *A. agrarius* (Severinghaus and Hsu 2015; Hong et al. 2019). This raptor species along with other rodent-consuming birds, the crested goshawk (*Accipiter trivirgatus*) and collared scops owl (*Otus lettia*), occupy low-elevation shrub lands and secondary forests (Severinghaus et al. 2012; Hong et al. 2019). These three species have also been observed in our study area (INB, unpublished data). Therefore, the exposed microhabitat at our sites may reflect a high risk from both avian and mammalian predators that consistently outweighs the rewards of exploiting food resources. Under vegetation cover, the rodents also have quick escape routes (Verdolin 2006; While and McArthur 2005; Searle et al. 2008), so if

they were to encounter a threat they could quickly flee into dense vegetation. Our results are consistent with the landscape of a fear framework (Laundré et al. 2001; Bleicher 2017) demonstrated by rodents perceiving exposed microhabitat to be high risk based on limited foraging activity in these food patches.

We predicted the rodents would respond to the odors of leopard cats due to their long shared evolutionary and ecological history. Field studies have found that rodents reduced their foraging activity in response to the odors of predators they recognize (Cremona et al. 2014; Carthey and Banks 2016). With respect to the other predator odors, domestic cat and bobcat, we expected that there would be a weaker effect compared to the leopard cat odor; however, our results suggested no difference between any of the odor type on GUD values. Our camera trap results confirmed that for both species, *A. agrarius* and *R. losea*, the application of predator odors on the second night of testing did not result in a significant increase in investigation or vigilant behavior, nor was there a decrease in foraging activity, thus rejecting our third hypothesis. Additionally, the addition of the odor apparatus did not induce increased investigation. Our results are in accordance with other field studies that in natural settings manipulated predator odors have been unsuccessful to elicit antipredator behaviors such as avoidance and reduced foraging activity, with no difference in effect between odors from native, introduced, or even unfamiliar predators (Orrock et al. 2004; Powell and Banks 2004; Verdolin 2006; Shapira et al. 2013; Stryjek et al. 2018). Predator odors have also been ineffective in inducing defensive behaviors in wild-caught rodents in laboratory conditions (Bramley and Waas 2001; Cremona et al. 2015; Jolly et al. 2018; Best et al. 2020). For many studies that have observed significant effects of predator odors, rodents were reared in captivity (Apfelbach et al. 2005; Hegab et al. 2014; Storsberg et al. 2018) and may have been subject to domestication. Domestication of rodents can result in reduced behavioral variation and adaptability, and subsequent elevated responses to foreign odorous stimuli (Price 1984; Barnett 2008).

Another possibility for the lack of responses to the predator odors could be due to predator demographics and activity. Leopard cats and domestic cats were both observed in our study area, with a high activity for the former. Despite this high level of activity, leopard cats in Taiwan have large home ranges with little overlap, especially in their core areas, between individuals, and can travel several kilometers in a day (Chen et al. 2016). Therefore, rodents may be unable to efficiently assess predator density or likelihood of encounters with predators based on odors alone and may be more dependent on other cues of risk (e.g., microhabitat structure, visual stimuli) on basing their foraging strategies (Verdolin 2006; Moll et al. 2017; Gaynor et al. 2019).

In both experiments 1 and 2, *A. agrarius* visited more stations and spent more time in view compared to *R. losea*, which can likely be attributed to differences in population density. For example, *A. agrarius* has been found to be more abundant in low-elevation habitat based on capture rates in other parts of Taiwan (Ku and Lin 1980; Kuo et al. 2011; INB, unpublished data). In experiment 2, we expected that there would be more rodent activities due to the “lidless open” food tray design, which was indeed the case for both species. The “lidless open” design better reflected a natural food patch with lower foraging costs (Price and Banks 2017; Cozzoli et al. 2019), but non-target species (e.g., birds) were no longer prevented from accessing the seeds, which made GUD measurements inaccurate. However, we think it is unlikely that this exploitation made the stations less attractive and/or discouraged rodents from visiting and foraging, since the number of visitations, foraging bouts, and time spent foraging in view was greater for both species at lidless foraging stations (experiment 2) compared to enclosed foraging stations (experiment 1).

There were still consistencies in interspecific variation for the behavior investigation, vigilance, and foraging across both experiments, which support our fourth hypothesis and prediction. The behavior investigation, vigilance, and foraging can be considered proxies for exploration, defensiveness, and boldness, respectively (Dammhahn and Almeling 2012; Mella et al. 2015; Best et al. 2020). *Apodemus agrarius* spent less time vigilant and investigating the food stations and more time foraging relative to the total time spent at a station compared to *R. losea*, which may characterize fast exploration followed by exploitation of resources for the former species. The prioritization of exploitation of resources over thorough, slow-paced exploration in different contexts associated with risk is often linked with boldness, since vigilance is sacrificed to a much higher degree when foraging (Careau et al. 2009; Berger-Tal et al. 2014; Mella et al. 2015). Our results are consistent with Best et al. (2020), where the smaller mouse species (including *A. agrarius*) exhibited bolder behaviors, such as more time foraging and shorter latency to forage, compared to the larger rat species (including *R. losea*) in laboratory experimental trials manipulating risk. Additionally, Best et al. (2020) reported that *A. agrarius* spent the most time performing foraging-related behaviors compared to other species. This interspecific behavioral variation may be linked to differences in POL following a fast-slow continuum (Réale et al. 2007; Wolf et al. 2007; Montiglio et al. 2018; Royauté et al. 2018). Not only is *R. losea* larger than *A. agrarius*, the former also has a lower basal metabolic rate (BMR) and longer lifespan (Chen 2005; Qi 2008), which are traits often associated with POL. Though most empirical studies examining the association between POL and behavior have focused on the individual- or population-level of a single species (Cremona

et al. 2015; Mella et al. 2015; Dammhahn et al. 2018), the few that have tested for interspecific variation have been conducted in laboratory conditions (Careau et al. 2009; Best et al. 2020; von Merten et al. 2020). Therefore, the current study provides evidence of interspecific behavioral differences in natural settings exemplified by the smaller species, *A. agrarius*, likely demonstrating more boldness compared to the larger species *R. losea*. Moreover, *R. losea* was found to spend more time exhibiting vigilance and investigation, which may reflect slower exploration and higher degree of caution (Wolf et al. 2007; Careau et al. 2009). Thorough exploration may indicate reactive lifestyle strategies and be more predominant in species with larger body sizes, longer life spans, and lower BMR (Sih et al. 2004; Wolf et al. 2007; Careau et al. 2009).

An alternative explanation for the differences in time spent foraging between species could be a disparity in harvesting rate abilities, e.g., the larger rat species consumes an adequate amount of food faster than the smaller mouse species. However, when factoring in body weight, metabolism, and energetic requirements, the differences in harvesting rate between the two species, *A. agrarius* and *R. losea*, were negligible based on consumption rates from a laboratory experiment (INB, unpublished data). Therefore, in order for *R. losea* to consume a sufficient amount of food to meet its energetic needs, it would have to spend roughly the same amount of time foraging as *A. agrarius*. Another possibility for the differences between the species in their foraging behavior could be that the larger species perceived the experimental food patches as low quality and/or gave up more quickly due to the depleted food availability as a testing night progressed. However, the former seems unlikely since *R. losea* was observed to forage millet seeds intently in both another experiment (Best et al. 2020) and during the current study at certain stations. Additionally, experiment 1 was conducted during winter, so it could be expected that food availability in the rodents' habitat would be low. Despite the temporal difference of experiment 2 and potential higher natural food availability, the behavioral responses of *R. losea* were consistent with experiment 1. We also confirmed that the *R. losea* individuals that did forage from the food stations in the current study did not demonstrate a reduction in time foraging as the night progressed when the food supply became more diminished (IN Best, unpublished data). For *R. losea* to efficiently assess the quality of an experimental food patch, it would need to enter the foraging trays. However, *R. losea* did not enter as many foraging stations compared to *A. agrarius*.

The objective of our exploratory analysis was to test for any differences between odor type on rodent behavioral responses from our camera trap datasets, as well as differential responses of species to the predator odors. The results (please see Tables S2 and S3) are largely consistent with those of the formal analysis presented in the main text. In

experiment 1, we were unable to find effects of the addition of predator odors (predator odor vs. control) on any of the behaviors on either species (Table S2). We also did not find significant differences between predator odor types for any of the behaviors for *A. agrarius* (Table S3). In experiment 2, we did not detect significant differences in predator odor type for the behaviors *locomotion*, *investigation*, and *foraging*. The only significant interaction detected was the three-way interaction (trial \times odor type \times species) for the behavior *vigilance* (Table S2). Based on the post hoc analysis, *R. losea* was more vigilant at stations assigned domestic cat and bobcat odors compared to *A. agrarius* during both the pre-treatment and treatment trials for the former odor type. Therefore, we think that in place of disparate responses to the different predator odors, a possible explanation for this finding could be that the individuals of *R. losea* that visited the aforementioned stations demonstrated more caution and may be less bold (Réale et al. 2007; Mella et al. 2015). However, to confirm this conclusion, further research investigating individual-level behavioral responses to risk would be required. The findings of the exploratory analysis further support our conclusions that the addition of predator odors failed to elicit marked changes in the behavior of the species *A. agrarius* and *R. losea*, which would reflect antipredator responses. We do, however, acknowledge that the interpretation of these results should be treated with some caution due to the limited sample size of the datasets and statistical power of the models.

Although our study provides several insightful findings, we do acknowledge limitations of the experimental design and analysis. We were unable to analyze the camera trap video data completely blind due to the marked differences in appearance between the odor treatment types, e.g., control vs. bobcat. However, we do not view this to be a serious issue comprised of observer bias, since we did not find significant differences between the treatments on rodent foraging behavior, thus, rejecting our first and third hypotheses and the accompanying predictions. Moreover, due to the lack of significant effects of any predator odor on rodent foraging behavior, we do not think the use of urine for the exotic predator, bobcat, versus the fecal solutions sourced from the leopard cats and domestic cats prompts serious implications; there was no difference between bobcat odor treatments and the other treatment types. Additionally, we were unable to obtain fecal samples from the bobcats for use in this study.

Another constraint of the experimental design of this study concerns the spatial distance between pairs of stations in experiment 1 and stations in experiment 2, which may have influenced the spatial independence of our experimental unit. Since we did not employ RFID chips in the rodents or use radio telemetry, we were limited to distinguishing between species but unable to track individual rodents or confirm that different individuals foraged at different

stations. However, GUD values and behavioral responses were consistent at the different stations, even those furthest apart within a given site, which likely exceeds the movement distance of *A. agrarius* (Yang and Zhuge 2006). Furthermore, the amount of food provisioned in each foraging station (10.0 g) more than satisfies the daily energetic requirements of both species of rodents, *A. agrarius* and *R. losea*, based on their respective body masses and BMRs (Degen et al. 1998; Wolff and Sherman 2008), which would minimize the need for the same individual to visit multiple stations. In addition, the experimental unit of a foraging station utilized in our datasets (GUD, behavioral responses) could incorporate the foraging decisions of a rodent; when an individual visited a station and proceeded to forage, a decision to explore and exploit the food patch was made (Brown 1988). If the same forager were to visit and exploit another food patch, some energetic costs would be incurred, as well as increased risk (Brown 1988; Lima and Bednekoff 1999).

We understand that it may have been beneficial to deploy camera traps at the exposed foraging stations during experiment 1 to further uncover any behavioral intricacies, especially between our target species. However, as mentioned in Materials and methods, it would not have always been possible to position cameras in this exposed microhabitat due to logistical constraints and serious theft concerns. Additionally, based on the results of our GUD data, we surmise that the sample size of the data from exposed foraging stations would be too limited for meaningful conclusions, especially predicated on inter-specific behavioral differences.

The findings of this study demonstrate the importance of incorporating new technologies into well-established experimental frameworks to better elucidate the intricacies of species behavior in natural environments. Such was the case by combining camera trap video observations with the GUD method to delve further into understanding species-specific behaviors in a risky context. Despite the lack of responses to the addition of predator odors, there were interspecific behavioral differences at the foraging stations between the two murid rodent species, *A. agrarius* and *R. losea*. These behavioral dissimilarities, which were uncovered with the use of camera traps, indicate that the smaller, “faster” species, *A. agrarius*, performed behaviors relating to fast exploration and boldness, whereas the larger, “slower” species, *R. losea*, favored slower, more thorough exploration and caution. These results are consistent with the growing body of research illustrating the linkage between POL and behavior, and highlight the importance of fine-scale monitoring of animal behavior in risk-related studies.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00265-022-03277-4>.

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Author contribution INB, CCK, and KCJP conceived and designed the study; INB collected the data and performed the experimentation; INB and PJLS analyzed the data; INB wrote and prepared the first draft of the manuscript. All the authors edited and revised the manuscript. CCK oversaw the study; All the authors read and approved the final version of the manuscript.

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Data availability All the data analyzed during this study are included in Supplementary Material [ESM 2_GUD dataset, ESM 3_Camera trap dataset_Experiment 1, ESM 4_Camera trap dataset_Experiment 2].

Declarations

Ethics approval All components of this study were approved by National Taiwan Normal University. Since the experimentation in this study was noninvasive and no live animal trapping was performed, we did not require an animal handling permit from the university. The experimental procedures adhered to the ethical standards of 1964 Declaration of Helsinki, and all researchers involved in this study abided to the legal requirements of animal welfare in Taiwan.

Conflict of interest The authors declare no competing interests.

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