Scientific Reports

https://doi.org/10.1038/s41598-026-41952-y

Article in Press

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Received: 5 November 2025

Accepted: 23 February 2026

Published online: 17 March 2026

Cite this article as: Stryjek R., Parsons M.H., Bebas P. *et al.* Buffering effects of shelter and palatable foods mitigate fear responses in foraging wild mice. *Sci Rep* (2026). https://doi.org/10.1038/s41598-026-41952-y

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# Buffering effects of shelter and palatable foods mitigate fear responses in foraging wild mice

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**Short title:** Experimental factors may influence fear responses

**Abstract**

Animal responses to fear cues are shaped by competing motivations such as hunger, access to mates and safety. In our previous work, wild mice (*Apodemus* spp.) showed little reaction to non-native predator scents. To test if native predator scents would elicit stronger reactions, we deployed fully enclosed laboratory chambers alongside a highly palatable food and olfactory cues from native foxes and cats and three types of controls, an herbivore scent (deer) and two procedural controls of wet and dry scent probes (the substrate on which we presented the scents) in the field. Despite using ontogenetically and evolutionarily relevant predator scents, mice showed no overt fear responses at any time, and only trivial behavioral differences between treatments. However, response variance was markedly higher for wet and dry controls compared to those exposed to animal-derived scents, suggesting a relatively greater perception of safety in chambers without scents. Collectively, these findings indicate that increased motivation for food and shelter during winter months buffered measurable responses to native predator scents. We conclude that the interpretation of risk sensitive behavior under natural conditions must account for ecological context, including shelter and food resources embedded within experimental assays, as well as seasonal tradeoffs associated with foraging decisions.

**Keywords:** approach-avoidance conflict, aversive and appetitive drives, dual motivation drives, free-ranging rodents, risk-reward trade-offs

## Introduction

Olfaction and fear detection systems[1,2] are commonly studied experimentally in both field and laboratory settings. However, experimental paradigms often yield conflicting results, particularly when laboratory findings are compared to those from free-ranging animals in natural environments[3-6 7]. In laboratory conditions, predator scents typically elicit increased vigilance, freezing or a startle responses in mice[8,9], whereas the same cues may not provoke significant reactions in the field[7]. Conversely, some scents that are ineffective in the laboratory may induce responses in the field. The underlying causes for these discrepancies remain unclear[7,10], though it is generally accepted that behavioral variability is greater in field studies[11,12].



Due to these disparities, researchers increasingly integrate both approaches to improve precision and clarity[13,14]. These differences often stem from the laboratory's elimination of nuisance variables, which reduces contextual relevance. In natural environments, fear responses are influenced by multiple competing motivations[15], many of which (e.g., nutritional status, diurnal patterns, seasons, group structure, learning and experience (for a review see[9])), may not be present in laboratory tests[16,17]. To maximize this opportunity, researchers have begun to better understand and predict which factors in the field are causing the disparity in outcomes. The principal cause of these differences may relate to the practice of

isolating and eliminating nuisance variables in the laboratory, which comes at the cost of losing contextual relevance.

Because wild animals live in environments that trigger conflicting motivational drives, the relative strength of each drive helps determine their responses to fear cues. Wild rodents, for example, are simultaneously influenced by numerous conflicting drives, such as hunger and thirst (a positive valence) weighed against the risk of predator exposure (negative valence), or mating drive versus territorial defense. In order to assess the potential risks and trade-offs, animals, driven by an exploratory drive (see[18]), investigate their environment to develop robust assessments. Such 'dual-motivation drives' can lead to approach-avoidance conflicts, where the same goal-stimulus acts both as an attractant and a repellent[19]. In rodents, resolution of these conflicts involves the hippocampus (HPC) and related neural structures, at least within rodents studied in the laboratory[20-22].

To experimentally assess competing stimuli among free-ranging rodents, researchers often use highly-palatable baits[9] or specially engineered foods[23] to attract subjects into an experimental area. Typically, such baits are many times more attractive and energy-dense than natural food sources, creating unnaturally strong motivation. When laboratory-style chambers or enclosures are used to study response to experimental scents, the inherent attraction of the chamber—especially under extreme weather conditions—must also be considered. Chambers can thus have a positive valence by

offering shelter from adverse weather and by containing attractive food baits[15,24-27].

To better understand the effects of motivational context, we adapted laboratory-style chambers for field use[9,28,29 9,29]. Previous studies showed that free-ranging prey were highly-attracted to experimental field chambers and readily participated in olfactory risk assessment[29]. Unexpectedly, two rodent species we have investigated, *Apodemus agrarius* and *Apodemus flavicollis*, spent more time in chambers containing predator scents. This likely reflects fear inspection, where animals paradoxically approach predator scents in order to assess risk[30,31]. These outcomes may be driven by the presence of highly-palatable food, by low predator density in this area (RS, personal observations), and by shelter provided by the enclosed chambers[29].

Given the many uncontrolled contextual factors, we refrain from concluding that *Apodemus* spp. are unresponsive to predator scents. Indeed, these results could have been obtained simply because scents from non-native predators were less risky than those scents derived from native animals[7,32,33]. For instance, marsupials have shown stronger aversive responses to dingo scents, which share several thousand years of evolutionary history, as compared to domestic dog (*Canis lupus familiaris*), or novel coyote scent (*Canis latrans*). Whereas native predators scents from the pine marten (*Martes martes*[33]), elicit a fear response in endemic red

squirrels (*Sciurus vulgaris*), but not invasive gray squirrels (*Sciurus carolinensis*[33]). For a review see Apfelbach et al[7].

To address the possibility that previous findings were due to a historical mismatch, e.g., lack of coevolutionary experience[32], in predator prey coevolution, we used scents from sympatric predators to enhance the likelihood of a fear response [7]. Here we hypothesized that that *A. agrarius* and *A. flavicollis* would spend less time in test chambers (Figure 1) with native predator scents than a control chamber and would show stronger behavioral responses to these scents than to herbivore or controls.



## Methods

### *Study site*

Data were collected during winter, from 16 January to 25 March 2023 using procedures adapted from [29] to transition laboratory style studies into welfare-friendly field contexts[17,34]. Prior to the experimental period, the apparatus was pre-baited for 1.5 months. Observations took place in a peri-urban area near Warsaw, Poland, on privately-owned land adjacent to forest and meadows (52°20′20.00″N; 21°03′30.00″E; altitude: 80 m), with landowner permission. Temperatures ranged from –8°C to 20°C.

### *Subjects and scent preparation*

Two species, striped field mice (*A. agrarius*) and yellow-necked mice (*A. flavicollis*) regularly visited the experimental chambers. The two co-occurring species are closely related to *Mus musculus,* a common

laboratory model[35,36]. Notably *A. flavicollis* exhibits diverse defensive responses to predator odors[37]. Previous trapping in the vicinity indicated population sizes ranging from several dozen to hundreds per species depending on season and home range (R Stryjek, pers. observations).

Native predator scents were obtained from 2-3 healthy, unneutered, adult, male red foxes (*Vulpes vulpes* from the Stowarzyszenie Leśne Przytulisko Wildlife Rehabilitation Center in Skrzynice Drugie, Poland). We also collected scents from domestic cats (*Felis catus*; two healthy, intact, indoor males aged 4.5 and 5 years). Control scents were collected from 2-3 adult, unneutered Roe deer (*Capreolus capreolus*) at the same facility. We constructed standardized 'scent probes' so that we could avoid having smeared or evaporated scents in the test area. These were made from 10 cm-long, 12 mm-diameter birch sticks placed 4 cm from food bowls. To maximize aromatic pungency, scent probes were treated with a mixture of 3-5 g of fresh feces moistened with urine and/or feces from foxes or cats. Deer feces (mixed with hay and presumed urine) served as animal control from a non-predator. All scents were unfrozen, unfiltered, and used within a few hours to 14 days from collection and stored at 2°C. Additional controls included dry probes (no scent or liquid) and moist probes (saturated with 10 ml tap water).

*Molecular species identification*

*A. agrarius* is readily distinguishable by a dorsal black stripe, whereas *A. flavicollis* lack such prominent features and is often phenotypically similar to *A. sylvaticus*, especially in southern Europe[38,39]). No *A. sylvaticus* were observed in video recordings. However, to confirm identification, tail samples from 18 putative *A. flavicollis* were collected in the vicinity of the recording chambers (December 2021 to June 2023) and analyzed by PCR. All 18 samples were verified as *A. flavicollis*. Additionally, five mice (three *A. flavicollis* and two *A. agrarius)* were tested for *Toxoplasma gondii* by PCR detection of parasite DNA in the brain and cardiac muscle, as this parasite is known to decreasing the level of fear from predator odor[40-42]. The results were negative, indicating a low probability of *T. gondii* occurrence in the examined populations.

*Animals and Test chambers*

All animals were presumed adults based on season (winter) and body size. Both sexes were observed, though we could not reliably determine them from the overhead view. Individual mice were, however, distinguished by body dimensions, coat pattern variation, and unique traits such as scars or tail morphology.

Artificial chambers are readily frequented by urban wildlife. These chambers enabled controlled delivery of olfactory cues and behavioral monitoring. Further, despite being artificial, they provide a haven from predators and harsh weather conditions. They are frequently visited

because they serve as a windbreak and are warmer inside than outside, thus their attraction remains in the absence of food or other attractants. Scent presentations followed a Latin Square Design for each chamber, ensuring that only one predator scent was present per chamber at a time, and controlling for stimulus presentation order and carryover effects.

Test chambers (Figure 1) consisted of wooden boxes (35 × 40 cm base and 70 cm height) constructed from 12 mm waterproof plywood and coated with odorless acrylic paint (Luxens, Leroy Merlin, France). Each chamber was fitted with a 7 cm diameter, 50 cm long plastic entry/exit sewer pipe (Certus, Cieszyn, Poland). Two test chambers were positioned 20 cm apart, and were accessible at all times, enabling free-ranging mice to visit at their discretion. Continuous behavioral monitoring was achieved using three infrared cameras (Easycam EC-116-SCH; Naples, FL, United States) linked to a digital video recorder with motion detection (Easycam EC-7804 T; Naples, FL, United States), enabling round the clock data collection.



Chambers were baited daily after dusk coinciding with peak nocturnal rodent activity. Ten grams of chocolate-nut cream (Nutella;[43,44]) were evenly spread on a 70 mm Petri dish placed centrally in each chamber, every day. To eliminate residual odors, floors of each chamber were covered with 1 cm of rinsed sand and replaced after each change in treatment. Entrance/exits to pipes were cleaned every 2-4 days with unscented liquid

soap Biały Jeleń (Pollena, Ostrzeszów, Poland) to remove potential scent markings.

*Behaviors recorded*

Behavioral responses to the olfactory exposure were intended to detect overt and subtle antipredator responses and scent inspection; they were quantified as follows: *Visits (discrete):* the number of times animals were captured on video entering the chamber; *Time Spent Inside Chamber (duration):* total time in seconds spent by each animal inside the chamber for each visit; *Flight (discrete):* the number of times an animal exhibited a rapid retreat response; *Freeze (discrete):* the number of occurrences of a sudden immobility. *Withdrawal (discrete):* instances when an animal slowly or systematically backed away from the predator cue, whether engaging in vigilance or not; *Foraging Effort (duration): Total time* (in seconds) spent by animals engaging with, or consuming, food in the bowl; and *Interactions (discrete), and time with probe (duration):* the *number of instances* (raw number) and *total time* (in seconds) during which animals actively interacted (e.g., overt touching or sniffing) with the scent probe.



During treatment periods (days), 1 ml of a mixture of cat, fox, or herbivore control (roe deer) urine and feces was applied to scent probes, 4 cm from food bowls (Figure 1). In the second chamber, 1 ml of tap water served as a 'wet' control. Scents were alternated randomly between chambers, always ensuring one ‘safe’ chamber and one with either a predatory or herbivore

scent, thus providing subjects with a choice between food + scent or food + control. Each scent, including the wet control, was presented five times in five blocks, with each exposure lasting one day. A dry scent probe was introduced for two days between each treatment day to prevent area effects that could reduce chamber affects and prematurely end the study, as occurred during trials undertaken in[23].

*Statistics*

One outlier (mouse asleep in a non-treated chamber) was excluded. Due to non-normality and heterogeneity of variance, non-parametric tests were used. Kruskal-Wallis tests assessed overall differences across treatment groups, followed by Dunn's post-hoc comparisons with a Bonferroni adjustment added to account for multiple comparisons. For targeted two-group comparisons, Mann-Whitney U tests were conducted. Distributions of four dependent variables (*time in chamber, time at the scent probe*, *interactions with the scent probe* and *time at the bowl* (foraging effort), were compared across three independent variables (*treatment*, *chamber* and *species)*. Epsilon-squared ($\varepsilon^2$) was computed as a non-parametric effect size for the Kruskal-Wallis test, using the formula $\varepsilon^2 = (H - k + 1) / (n - 1)$, where H is the test statistic, k is the number of groups, and n is total sample size. Cohen's d was calculated for targeted pairwise comparisons based on Mann–Whitney U outcomes, using group means and pooled standard deviations as a standardized effect size. Chamber visitation rates (*number of visits* to each chamber) were analyzed with a t-test. Pearson chi-square

test compared missed camera triggers between species on entry and exit to assess time spent in the chambers by species. Levene's tests (with Holm-Bonferroni correction) assessed variance equality with scent groups aggregated into three categories *predator (cat, fox)*, *herbivore (deer)*, and *non-animal (dry, water)* categories. All analyses were performed with IBM SPSS Statistics (version 29.0, Armonk, NY, USA), except for the Levine's test which was calculated separately by R with the jamovi interface (The jamovi project, version 2.3.28).

## Results

*Visits and overt responses by wild animals*

Animals visited chambers 912 times (650 *A. flavicollis*, 262 A. *agrarius*; 435 visits to chamber 1, 477 to chamber 2). Treatment had no effect on visitation rate to the chambers ($F_{4,67} = 0.96$; $P = 0.436$). There were 115 missed camera triggers, whereby animals were seen in the video, but were not recorded entering the chamber. These missed triggers came predominantly from *A. flavicollis* (100 instances) with very few from *A. agrarius* (15 instances) ($\chi^2$ (4, 797)=15.811, $P < 0.001$), and were equally distributed between entry and exit events. No withdrawals, flights, or freeze behaviors were observed during any treatment. Extended sleep episodes inside chambers occurred only during control treatments. Extended sleep episodes inside chambers were anecdotally observed during control treatments but did not occur during scent treatments. This event did not occur in our previous trials and thus was not included in analyses. Overall,

variation in time spent inside chambers was high with animals averaging 324.6 ± 470.7 s per visit. *A. flavicollis* spent 359.7 ± 366.4 s and *A. agrarius* 308.8 ± 510.2 s per visit ($F_{1,714} = 2.003$; P = 0.157). Time spent by *A. flavicollis* was more variable than *A. agrarius* (Figure 2a).

Only the time in the chamber varied among treatments (Table 1). Pairwise comparisons indicated minor differences: time spent differed between deer and fox treatments, cat and fox, water control and dry control, and dry control and fox. However, these differences were trivial (Figure 2). There was a modest chamber effect, animals spending 8.4% more time in chamber 1 than chamber 2. Species effects were prominent across all variables except number of approaches, but these effects were also trivial or inconsequential (see effect sizes, Table 1).



Notably, a consistent trend was observed across all dependent variables, with variance being substantially greater for controls compared to treatment scents (Figure 2a-2e). Levine's Test confirmed that the variance in the number of approaches to the scented probe was significantly higher for the control scent (M = 1.98; SD = 1.31) and herbivore scent (M = 2.01; SD=0.90); F(1, 801) = 5.47, $p = 0.04$. For the same variable, the variance for predator scent (M = 2.20; SD = 1.54) exceeded that for herbivore scent (M = 2.01; SD = 0.90); F(1, 168) = 7.39, $P = 0.021$.

*Time to consume food.*

The Mann-Whitney test indicated no significant differences in the time spent consuming food between chambers containing animal-derived scents and those with water-based control (U = 323, P = 0.363). Each scent (fox, cat, deer) was presented five times, with the alternate chamber always containing a water-based control. To assess relative attractiveness, we recorded the frequency with which food was consumed first from each chamber i.e., how many times a certain type of scent was preferred over water. The results were as follows: deer vs. water, 3:2; fox vs. water 3:2; and for cat vs. water, 2:3. Binomial tests (P >0.05) confirmed that these proportions did not differ significantly from a 50:50 distribution. Therefore, the outcomes confirmed no significant preference for either of the animal-derived scents or for the water-based control.



**Discussion**

No significant effects of ecologically and evolutionarily familiar predator or non-predator scents were detected on the behavior of two species of wild mouse in laboratory-inspired activity chambers under field conditions. This finding aligns with previous research which reported only modest behavioral responses to novel predator scents in a similar field assay [29]. In the current study, even after attempting to amplify fear responses using native predator scents [45], behavioral changes were not evident. Any potential response could only be inferred after careful examination of the variance—which happened to be a magnitude higher in raw number for predator scents than water or other controls. Despite the expectation that

small, vulnerable, rodents should exhibit heightened wariness toward a broader range of predator scents[46], neither native, nor non-native predator scents elicited measurable changes in mouse behavior.

Despite the absence of overt fear responses, we anticipated that, at the very least, altered palatability might elicit changes [47]. Given the strong, pungent signature of the scents (to our nose) and how they remained fresh and noxious under cold ambient conditions. However, the combination of highly palatable bait and provision of shelter during winter was likely sufficient to override any olfactory risk cues presented within the chambers.

Subtle differences emerged between responses to non-native (as observed in our first study) and native predator scents (in the present study). Specifically, the earlier study documented clear scent inspection, a subtle indicator of fear. We were perplexed as to why non-native scents would have caused this subtle response, but not native scents. The discrepancy may be attributed to the novelty of the non-native scents, which could have triggered exploratory or inquisitive behavior, whereas the native predators, being familiar, were potentially ignored due to the perceived safety of their surroundings.

Also perplexing, in the current study, both predator and herbivore scent treatments elicited indistinguishable responses. Although no treatment effect was apparent when comparing median values, a more detailed examination of the data distribution revealed that variance across all

independent variables was markedly higher among the three procedural controls---including the herbivore scent control. It is important to consider the impact of widely-differing variances, as this can help avoid Simpson's paradox, where underlying trends may be obscured by aggregated means [48,49]. Therefore, rather than concluding an absence of response to risk cues, we report that any effects were so negligible as to be undetectable by statistical tests, with Levene's test supporting the observed differences in variance between animal-derived scents and non-animal controls.

The elevated variance observed among animal scent treatments, as opposed to the wet or dry controls, may suggest that animals were indeed responding to animal-derived scents. For instance, only during wet and dry control conditions did animals remain inside the chamber for more than 15 minutes, occasionally for up to an hour. Previous research has proposed that noxious elements emitted from animal scents could induce avoidance behaviors because such cues are associated with parasites or pathogens[47,50-52]. Although deer feces are not inherently noxious, they are still capable of transmitting pathogens[53,54]. Additionally, herbivore scents may be avoided by prey species because their scents may attract predators[51].

Drawing on the outcomes of our two related studies, we propose that the benefits conferred by the experimental chambers—namely as shelter and extremely palatable food—was more influential than the aversive effects of

predators or herbivore scents. This finding underscores a broader challenge in interpreting field assays when the experimental setup is itself attractive to the study species. Future research should consider reducing the attractiveness of baits, for example by comparing them to the nutritional baseline available in the natural environment, and minimizing the appeal of the test apparatus, to better assess risk perception in wild populations. When comparing laboratory and field results, it is essential to recognize the extent to which contextual information shaped behavioral outcomes, often weighing the impact of fear cues from allopatric and sympatric predators.

## Declarations

*Funding*

The research was partially funded by the University of Warsaw project BOB-IDUB-622-256/2025 awarded to PB with in-kind assistance from the Centre for Urban Ecological Solutions, LLC.



*Conflicts of interest/Competing interests*

All authors declare they have no conflicts of interest

*Availability of data and material*

All data will be made freely upon request. The corresponding author, Michael Parsons, will be responsible for handling all data requests. Additionally, the data can be found in Open Science Framework within two weeks of publication.

*Ethics Statement*

The study was designed and carried out in compliance with the ARRIVE guidelines (Kilkenny et al. 2010) and carried out on private land with permission of its owners, and all procedures were conducted in accordance with the Polish Animal Protection Act (21 August, 1997). For the molecular part of the study, Certified staff members of University of Warsaw and the Polish Academy of Sciences collected tissue for genetic testing to identify species and detect the possible presence of *T. gondii*. This work was conducted within the Faculty of Biology at the University of Warsaw, registered as number 0031 in the Polish Ministry of Science's roster of institutions authorized for rodent studies. All animals were euthanized with an overdose of the inhalational anesthetic Forane (isoflurane; AbbVie Inc., North Chicago, IL, USA). Under the Act on the Protection of Animals Used for Scientific or Educational Purposes, enacted on January 15, 2015 (Article 2, point 6), euthanizing mice for organ or tissue use does not necessitate approval from an ethics committee.



The observational part of the study was based on the surveillance of free-ranging animals that were free to enter or ignore experimental chambers with food and video cameras, This activity falls under the scope of the Act of 15 January 2015 (Article 1, paragraph 2, point 5) on the Protection of Animals Used for Scientific or Educational Purposes, which serves as the primary legal framework for animal research in Poland. According to this Act—available upon request—its provisions do not apply to procedures that, in line with veterinary

medical standards, do not inflict pain, suffering, distress, or lasting harm on animals beyond the level caused by a standard needle prick.

*Authors' contributions*

RS and MP designed the experiment and wrote the first version of the manuscript. RS conducted the study. MC and KS scored videos. RS, MP, PB, MF, YK, MC, KS, and DTB participated in the writing and editing of the manuscript. All authors contributed to the article and approved the submitted version.

**Acknowledgements**

We thank Lena Grusiecka from the Wildlife Rehabilitation Center ‘Stowarzyszenie Leśne

Przytulisko’ (Skrzynice Drugie, Poland) for permission, and assistance, in the collection of fox

and deer scents.

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Table 1. Kruskal-Wallis tests by treatment, chamber and species. Effect sizes for overall treatment by Epsilon-squared ($\varepsilon^2$) and Cohen's r was used for two-group comparison

| **Variable** | ***N*** | **test statistic** | ***df*** | **sig.** | |
|---|---|---|---|---|---|
| *By Treatment* | | | | | Effect size |
| Time in chamber (s) | 797 | 9.66 | 4 | **0.047** | $\varepsilon^2 = 0.007$ |
| # Approaches | 906 | 2.89 | 4 | 0.576 | |
| Time interaction (s) | 906 | 7.07 | 4 | 0.132 | |
| Time at bowl (s) | 905 | 8.65 | 4 | 0.070 | |
| *By chamber* | | | | | |
| Time inside each | 797 | 72077.5 | — | **0.034** | $r = 0.075$ |
| # Approaches | 906 | 96523.5 | — | 0.120 | |
| Time interaction (s) | 906 | 96253.5 | — | 0.115 | |
| Time at bowl (s) | 905 | 96889.5 | — | 0.186 | |
| | | | — | | |
| *By Species* | | | — | | |
| Time in chamber (s) | 797 | 58505 | — | **0.002** | $r = 0.111$ |
| # Approaches | 906 | 89385.5 | — | 0.138 | |
| Time interactions (s) | 906 | 96139.5 | — | **<0.001** | $r = 0.112$ |
| Time at bowl (s) | 905 | 70097 | — | **<0.001** | $r = 0.132$ |

**Figure captions**

Fig. 1. Experimental setup used in the study A) Two wooden chambers deployed next to a forest and meadows. B) A photo of striped field mouse (*A. agrarius*). (C) A photo of a yellow-necked mouse (*A. flavicollis*). (D) Two *A. agrarius* field mice inside one of the experimental chambers. (E) Two yellow-necked mice feeding inside one of the chambers.

Fig 2. Boxplot of all dependent variables by two species of wild rodent striped field mouse (*A. agrarius*) and yellow-necked (*A. flavicollis*) mouse in a dual-motivation assay including native predator scents.

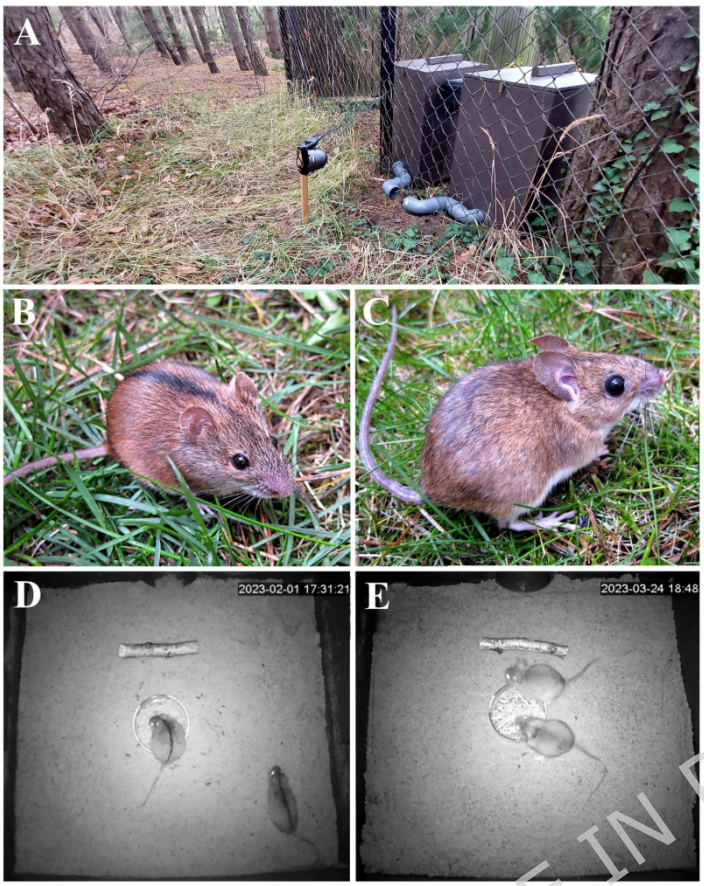


Figure 1. Experimental setup used in the study A) Two wooden chambers deployed next to a forest and meadows. B) A photo of a striped field mouse (*A. agrarius*). (C) A photo of a yellow-necked mouse (*A. flavicollis*). (D) Two *A. agrarius* field mice inside one of the experimental chambers. (E) Two yellow-necked mice feeding inside the one of the chambers.

Fig 2. Boxplot of all dependent variables by two species of wild rodent, striped field mouse (*A. agrarius*) and yellow-necked (*A. flavicollis*) mice in a dual-motivation assay including native predator scents. Box plots are presented for descriptive purposes to illustrate the similarity in data spread across treatments. Statistical comparisons were conducted using Kruskal-Wallis tests on ranked data. Note the number of outliers that increase the variation for all four non-scented controls, while animal scents have reduced variation.