



Responses to novel stimuli of free-ranging small mammals along a gradient of human disturbance

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ABSTRACT

Understanding how animals adjust to human presence and disturbance is critical for conservation. Behavioural plasticity is key to the expression of appropriate responses, and determines which individuals cope better in disturbed and altered environments. However, anthropogenic alterations are usually investigated within highly urbanised areas, leaving the effects of human disturbance in natural areas – where less innovation-prone animals are presumed to find refuge – relatively uninvestigated. Here we exploited a gradient of human presence and disturbance that included different levels of protection within a National Park to examine neophobia and innovation of free-living small mammals ($N = 158$ observations from repeated experimental trials). We investigated: 1) how wood mice (*Apodemus sylvaticus*) respond to novel structures; 2) their propensity to express novel behaviour (i.e. innovation) in a foraging context; and 3) response pattern consistency across these different types of novel stimuli. Findings indicate spatial sorting for responses to novelty along the gradient of human disturbance. Mice living in the buffer zone displayed higher avoidance towards novel objects compared to conspecifics living in both strictly protected and non-protected areas. Foraging innovation propensity, instead, scaled positively with the degree of human presence and disturbance. Together, results suggest that even low levels of human disturbance are linked to differences in neophobia and innovation, albeit the response patterns appear context-dependent. Understanding such complex behavioural adjustments provides valuable insights for future conservation efforts, including more effective management strategies to reduce disturbance to wildlife by human activities, and to assess the actual effectiveness of protected areas and protection regimes.

1. Introduction

Human activities are causing unprecedented damages to habitats worldwide — from overharvesting and the introduction of invasive species to land use and climate changes (e.g. Vitousek et al., 1997; Wong and Candolin, 2015). These human-induced rapid environmental changes (HIREC, Sih et al., 2011) result in a dramatic loss of biodiversity, as wildlife struggles to cope with higher rates of change compared to those experienced in its evolutionary past (e.g. Barnosky et al., 2011; Ceballos et al., 2015; Grimm et al., 2008; Sih et al., 2010; Torres-Romero et al., 2024).

Protected areas are intended to shield natural ecosystems from most direct anthropogenic pressures (e.g. resource exploitation, land use change, or pollution), thereby safeguarding biodiversity components

and functions and mitigating the impacts of human activities on nature (e.g. Maxwell et al., 2020; Cerini et al., 2025). However, biodiversity hotspots are being encroached by expanding human settlements, and human-wildlife spatial overlap is expected to increase to more than 50% by 2070 (e.g. Cincotta et al., 2000; Ma et al., 2024). While humans are increasingly concentrating in cities (e.g. Gao and O'Neill, 2020; Seto et al., 2012), their presence and impact unavoidably extend to remote or protected areas leaving virtually no habitat in really pristine conditions (e.g. Carter et al., 2012; Cincotta et al., 2000; Grogguz et al., 2026; Ma et al., 2024; Morant et al., 2025; Procko et al., 2023; Zanette and Clinchy, 2019). This is worrying because protected areas are supposed to be the refuges of animals that do not manage to adjust to more human-dense habitats (e.g. Fardell et al., 2020; Fischer et al., 2015; Haigh et al., 2017).

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The ability to coexist with humans and tolerate their presence and disturbance is thus becoming essential for more and more animals (e.g. [Mirante et al., 2024](#); [Samia et al., 2015](#)), and the study of individual differences in the capacity to adjust to human disturbances is increasingly recognised as key for bridging the gap between ethology and conservation (e.g. [Anthony and Blumstein, 2000](#); [Berger-Tal et al., 2016](#); [Fardell et al., 2020](#); [Jeltsch et al., 2025](#); [Cardilini et al., 2026](#); [Mazza and Carere, 2024](#); [Mazza and Šlipogor, 2024](#); [Merrick and Koprowski, 2017](#)).

Behavioural flexibility enables animals to react to changes in the environment (e.g. [Shettleworth, 2009](#); [Tebbich and Teschke, 2014](#)). Cognitive processes mediate two important pathways to behavioural flexibility, namely (i) applying existing behaviour to new situations, and (ii) acquiring new behavioural patterns (e.g. [Reader and Laland, 2003](#); [Tebbich and Teschke, 2014](#)). In combination, these abilities constitute a “first line of defence” against environmental alterations (e.g. [Duckworth, 2009](#); [Sih et al., 2010](#)), as they are particularly useful for the discovery of novel resources and the subsequent acquisition of new behavioural patterns to exploit them (e.g. [Tebbich and Teschke, 2014](#)). Behavioural and cognitive flexibility also determine reactions to changes in resource availability or tolerance to variation in community composition, including overwhelming presence of heterospecifics (e.g. [Čapkun-Huot et al., 2024](#); [Magory Cohen et al., 2020](#)). The tendency to encounter novel situations is in turn influenced by the propensity to approach and explore unfamiliar stimuli (e.g. [Tebbich and Teschke, 2014](#)).

Responses to novelty are ecologically-relevant behaviours that arise through a cognitive assessment of novel stimuli ([Greggor et al., 2015](#)). Novelty can elicit both aversion (neophobia) and attraction (neophilia), and these responses are usually considered as a continuum (e.g. [Greenberg, 2003](#)), although in many bird species they are governed by independent motivations (e.g. [Greenberg, 2003](#); [Greenberg and Mettke-Hofmann, 2001](#); [Mettke-Hofmann, 2014](#); [Mettke-Hofmann et al., 2002](#)). Variation in responses to novelty can also mediate the expression of innovative behaviours in several contexts, including foraging and dietary innovations, defined as the propensity to eat unfamiliar food and incorporate novel food items into the diet (e.g. [Thomas et al., 2004](#); [Webster and Lefebvre, 2001](#)). Therefore, depending on their propensity to respond to novel stimuli, individuals within a population may vary in their potential to occupy areas with different levels of human activity, presence, and disturbance.

The majority of studies investigating responses to human disturbance takes place within highly-populated urban habitats (e.g. [Damas-Moreira et al., 2024](#); [Ellington et al., 2024](#); [Lazzaroni et al., 2024](#); [Mazza et al., 2020](#); [Morton et al., 2023](#), but see e.g. [Morant et al., 2025](#); [Perona et al., 2019](#)). Rural habitats are usually considered as a sort of control where “natural” conditions are assumed, i.e. that anthropogenic influences resemble those animals experienced in their evolutionary past (e.g. [Dammhahn et al., 2020](#); [Ditchkoff et al., 2006](#)). To the best of our knowledge, few studies investigated responses to human disturbance at the opposite end of the spectrum, namely in areas that should offer higher levels of protection (e.g. strictly protected areas) to individuals with lower tolerance to human disturbance (e.g. [Carzon et al., 2024](#); [Martin and Réale, 2008](#)).

Here, we examined the responses to novelty of small mammals in relation to their distribution across a gradient of human disturbance. Small mammals represent >60% of species of wild land mammals (e.g. [Greenspoon et al., 2023](#)), and play a crucial role in terrestrial trophic dynamics. Most are non-commensal and non-synanthropic, i.e. they have no incentive to live in close proximity to humans (e.g. [Deacon and Mac Nally, 1998](#); [Delibes-Mateos et al., 2011](#)). Studying within-species differences in small mammals' responses to novel stimuli in the context of human activity and disturbance may then provide the first building blocks for targeted conservation measures. Additionally, current research strongly focuses on species with high dispersal abilities, namely birds and large mammals (e.g. [Mirante et al., 2024](#); [Samia et al., 2015](#)), leaving a gap concerning the determinants and constraints of

successful coping with human disturbance of species both more cryptic and physically more confined to specific locations, on which selection could potentially be stronger ([Baxter-Gilbert et al., 2019](#)). Our study species was the wood mouse (*Apodemus sylvaticus*), an omnivorous small rodent distributed throughout most regions of Europe, in both natural and human-altered habitats (e.g. [Arnan et al., 2014](#); [Bauduin et al., 2013](#); [Michaux et al., 2003](#); [Montgomery and Montgomery, 1990](#); [Montgomery, 1999](#)).

In order to better understand the role of novelty responses in relation to human disturbance, we asked: (a) do free-ranging wood mice display behavioural differences along a gradient of mild human activity and frequentation? (b) Is there spatial sorting of wood mice across this gradient according to their responses to novelty? (c) Are responses to novelty expressed consistently across types of novelty, i.e. in relation to novel structures or food? To address these questions, we exploited a gradient of human presence and disturbance that included areas with different levels of protection within a National Park, as well as green areas and small human settlements outside the Park. In a preliminary step we habituated free-ranging mice to visit testing stations, and consume familiar food in fixed locations with different levels of human frequentation and activity. We then quantified *in situ* the behavioural responses to replicated novel structures and food resources. We also examined if responses to novelty were consistent across novelty types, and whether they were driven by disturbance being perceived as a source of risk as opposed to a loss of available resources.

We hypothesised that if mild habitat alterations and human frequentation are perceived as disturbance, then behavioural/cognitive trait expression will shift. If mice react to this disturbance as a source of risk, we predicted decreased neophobia and increased innovation propensity in the most protected areas of the Park, where human presence is sporadic and activities are restricted, compared to areas with lower or no protection, where human activities are allowed, in line with hypotheses suggesting higher innovation in animals that can afford to invest in such new behaviours (e.g. [Kummer and Goodall, 1985](#); [Reader and Laland, 2003](#)). Conversely, if small mammals respond to the presence of humans and their activities as to a loss of available resources, we predicted increased neophobia and decreased innovation propensity in the most protected areas of the Park compared to areas with lower or no protection, where the disturbance/loss of available resources and the consequent necessity for innovative behaviour is highest (e.g. [Laland and Reader, 1999](#); [Reader and Laland, 2003](#)).

2. Methods

2.1. Study sites

The study was conducted across a gradient of human presence and disturbance that extended from Sila National Park (39°07'53.6"N 16°38'21.1"E) to the non-protected areas surrounding it. The Sila National Park was established in 1997, extending the protection of a previous park founded in 1968. The Sila National Park now encompasses 73,695 ha of mountain forests and highlands. The Park is structured according to the UNESCO Man and the Biosphere (MAB) zonation design (e.g. [Dyer and Holland, 1988](#)), with a core area (protected since 1968 as part of the old Calabrian National Park) that constitutes a strictly protected integral reserve (e.g. [Baliva et al., 2024](#)), a buffer zone where only activities compatible with the conservation objectives can take place, and an external transition area which is not protected, but where sustainable resource management practices are promoted and developed.

We positioned 7 testing stations (described below) within the core area of the park, 5 in the buffer zone, and 6 outside the park, for a total of 18 stations. Slight differences in the final number of testing stations per area are due to theft of some stations and difficulty of replacing them with short notice. Simultaneous deployment of multiple testing stations per zone minimized biases arising from unequal participation rates, such as a single individual visiting in one area type while multiple individuals

visited in another. Testing stations were placed at a minimum distance of 1.5 km, to prevent the same animal from visiting different stations within the same night.

Human presence and disturbance could be considered as a whole group of factors, including proximity and consequent stressful situations, possible presence of dogs, and indirect effects such as predator and food abundance and distribution (e.g. [Laundré et al., 2010](#); [Martin and Réale, 2008](#); [Zanette and Clinchy, 2019](#)). Since human frequentation and activity were found to be highly correlated with these other factors ([Martin and Réale, 2008](#)), we decided to focus on the protection level granted to the location of each testing station as a proxy for human presence and activity. The core area of the Park allows limited access to humans, and only activities such as hiking. The buffer zone is a wider area around the core, where activities such as sustainable wood and mushroom harvesting are allowed, and where a few dwellings and touristic structures (e.g. restaurants and bars) are active, mostly during the weekends. Finally, the sites outside the park were not under any protection, and thus open to all human activities (although sustainable practices are promoted, see above) but still relatively low in terms of human density; here the testing stations were located in the green areas surrounding small settlements in the Park vicinity. Areas inside the Park have higher hiking path coverage compared to non-protected areas outside the park ([Table A1](#) in the Appendix). The non-protected area outside the Park has a higher proportion of sealed surface ([Table A1](#) in the Appendix), i.e. the coverage of natural soil with artificial impervious surface (e.g. buildings and paved roads), which is a proxy of the degree of urbanisation, human population density, disturbance by humans and pets, noise and light pollution (e.g. [Buchholz et al., 2018](#); [Seress et al., 2014](#)). In terms of natural predators, areas inside the park had similar bird communities and species richness ([Chiatante et al., submitted](#); [Table A1](#) in the Appendix), and cameratrap registered the presence of mammalian predators in all areas. All sites provided suitable habitats for

small mammals, and their presence in each location was confirmed through camera trap monitoring during a pilot phase. The study took place between August and October 2023, a time where both mice and human presence (due to tourism) is highest, making it the most relevant time to assess responses to novelty under different levels of human disturbance.

2.2. Experimental procedure

We investigated wood mice's object neophobia and foraging innovation propensity by presenting a battery of tests to free-ranging animals, directly in their natural environment, and without interference from researchers. We used specific testing stations where the tests could be conducted on a voluntary participation basis, monitored by motion-activated wildlife camera traps (Coolife 16MP 1080P HD). A testing station consisted of a wooden structure ($16.5 \times 16.5 \times 41$ cm) with a Plexiglas ceiling, open at both ends ([Fig. 1](#)). The camera trap was fixed to one end, and the other was used as entrance for the animals. Two round holes (5 cm Ø) in the vicinity of the camera trap served as additional exits. Testing stations were placed in suitable spots in each site, and camouflaged with branches and leaves, so as to blend in with the surroundings, and overall providing a perceivably safe setting for small mammals to spend some time engaged in the tests ([Mazza et al., 2025](#)).

Testing stations were left in place for approximately 6 weeks before the start of the experiments ([Fig. A2](#) in the Appendix), and regularly provided with oat flakes, so that the animals could discover and familiarise with the testing stations, and learn to visit them regularly ([Mazza et al., 2025](#)). Besides ensuring visits during the experimental phase, this “pre-baiting period” allowed us to maximise the efficiency of the data collection, and to disentangle the responses to novel stimuli provided in the testing station from the responses to the testing station itself (e.g. [Kimball and Lattin, 2024](#); [Mazza et al., 2025](#)).



Fig. 1. Experimental set-up (modified from [Mazza et al. \(2025\)](#)). A testing station is shown partially concealed on site (A), viewed from the camera-trap perspective during example videos (B), and from above (C). On the right the different stimuli provided in the experiments: novel foods (upper) quinoa, linseed, tofu, and almonds, and the plastic toys used as novel objects (lower).

At the start of the experiment, the camera traps were activated, the stations were provided with oatflakes, and no alteration was made to the conditions they experienced in the previous weeks, thereby providing a baseline for the animals' behaviour in a familiar environment in presence of familiar stimuli (e.g. Kimball and Lattin, 2024). This initial phase lasted 2 nights. Oatflakes were refilled and cameratraps checked every 24 h (Fig. A2 in the Appendix).

We then started to present the novel stimuli varying in size, shape, colour, and texture (Fig. A2 in the Appendix). We presented two novel objects over the first two nights (one every 24 h). Afterwards, we removed objects and oatflakes, and provided two different kinds of novel food over two more successive nights (one every 24 h). The presentation of the stimuli was alternated, so that adjacent testing stations contained different stimuli. After an interval of 2 weeks, we repeated this procedure with new objects and foods (Fig. A2 in the Appendix). The use of eight different stimuli allowed us to decrease the likelihood that responses were affected by stochastic unmeasured variables, such as an aggressive interaction with a conspecific immediately before entering the testing station (e.g. Kimball and Lattin, 2024). We rebaited the testing stations with the new stimuli and checked the cameras every morning between 9:00 and 13:00. Since the animals were neither trapped nor individually marked, in this study we only considered the first visit to each station each night (i.e. for each stimulus type), thereby ensuring that was indeed the first time the animal encountered the respective stimulus.

Overall, we considered 158 video observations: 33 observations during the habituation phase (14 in the strictly protected area, 9 in the buffer, and 10 in the non-protected area), 62 observations during the Novel Object phase (25 in the strictly protected area, 17 in the buffer, and 20 in the non-protected area), and 63 observations during the Novel Food phase (27 in the strictly protected area, 17 in the buffer, and 19 in the non-protected area). Restricting these observations to the very first visit of a mouse in each testing station is a highly conservative approach. While reducing the sample size, it also ensures that animals could not habituate in any way to the specific stimuli, thereby avoiding confounds due to repeated presentations or experiences, even within the same night.

2.3. Novel Object Test

The Novel Object Test measured the behaviour of the animals confronted with a novel object (a toy car and a toy duck in the first test session, a toy smurf and a toy soldier in the second session, alternated so that adjacent testing stations contained different objects). The novel object was placed next to the station wall, beside the oat flakes. The test started once an animal entered the testing station and triggered the motion activated camera-trap. The following parameters were extracted from the videos: (i) latency to approach the object, defined as coming within 2 cm of it, with the head turned towards it. If the animal did not approach the novel object latency was coded as NA. If the camera triggered when the animal had already reached the object, the latency to approach was coded as 0; (ii) latency to start foraging on the familiar oatflakes. If the animal did not consume the food, latency was coded as NA; (iii) overall duration of approaches to the object (defined as i). If the animal was in the testing station but did not approach the novel object in any way, the duration of interaction was coded as 0; (iv) number of vigilance events, defined as cessation of feeding or object approach with head up and inspection of the surroundings (e.g. Lima and Bednekoff, 1999).

2.4. Foraging innovation assessment

We investigated wood mice innovation propensity in a dietary context by offering different novel foods (quinoa and linseed in the first test session, tofu and crushed almonds in the second session, alternated so that adjacent testing stations contained different food types), which

are not available to rodents in these areas. The test started once an animal entered the testing station and triggered the motion-activated camera-trap. The following parameters were extracted from the videos: (i) latency to approach the food, defined as coming within 2 cm of it, with the head turned towards it. If the camera triggered when the animal had already reached the food, the latency to approach was coded as 0; (ii) latency to start foraging, defined as putting the food into the mouth. If the animal did not consume the food, the latency to start foraging was coded as NA; (iii) overall duration of foraging (defined as ii) in relation to the duration of the visit. If the animal was in the testing station but did not consume the novel food, the duration of foraging was coded as 0; (iv) number of vigilance events, defined as cessation of feeding with head up and inspection of the surroundings (e.g. Lima and Bednekoff, 1999).

2.5. Video analysis

Videos obtained from the camera-traps were analysed to extract the behavioural variables listed above. We used the software BORIS (Friard and Gamba, 2016). All videos were analysed by the same coder (VM), but a second coder (GS) analysed a random subsample of 16 observations (10%) to ensure the accuracy, objectivity, and robustness of the approach. We calculated inter-observer reliability among the two observers (after Stanton et al., 2024) using Spearman's correlations for latency to approach the novel stimulus ($r_s = 0.93$), latency to start foraging ($r_s = 0.96$), overall duration of interaction with the novel stimulus in relation to the duration of the visit ($r_s = 0.88$), and number of vigilance events ($r_s = 0.82$).

2.6. Statistical analyses

We tested whether behavioural responses to novel objects and foods differed under different levels of protection, and thereby human presence and disturbance. We investigated latency to approach the novel object, latency to start foraging in presence of the novel object, duration of approaches to the novel object, and rate of vigilance events. We fitted (generalised) linear mixed models ((G)LMMs) by restricted maximum likelihood, including testing station ID as a random factor to account for potential site-specific effects. This was done because we were not aiming to investigate differences between replicates in the same protection zone, but rather to control for variation stemming from unmeasured local characteristics (e.g. microhabitat conditions, local environmental features, or other site-level effects) and the non-independence of observations collected at the same location. Protection zone (strictly protected, buffer, non-protected), and test session (1st vs 2nd round) were included as fixed factors in all models. The duration of the visit was included as an offset in the models regarding vigilance events and the duration of approaches to the novel object, to account for the variation in the time animals spent in the testing stations. Testing phase (habituation with only familiar food vs presence of novel object) was added to the models concerning the latency to start foraging and the vigilance events as control and comparison. Stimulus presentation order (1–4) and type of object (toy duck, car, smurf, soldier) were initially included as fixed factors, and excluded from all models based on their lack of explanatory importance using stepwise backward model selection based on log-likelihood ratio tests comparing nested models (e.g. Zuur, 2009).

We investigated mice propensity to innovate in a dietary context by fitting (generalised) linear models ((G)LMMs) by restricted maximum likelihood, with latency to approach the food, latency to consume the food, proportion of time spent consuming the food, and rate of vigilance behaviour as dependent variables. Testing station ID was added as a random factor in each model to account for potential site-specific effects. Our objective was not to test for differences among sampling locations within the same protection zone, but rather to control for variation stemming from unmeasured local characteristics (e.g. microhabitat conditions, local environmental features, and other site-level effects)

and the non-independence of observations collected at the same location. Protection zone (strictly protected, buffer, non-protected), testing phase (habituation with only familiar food vs presence of novel food), and test session (1st vs 2nd round) were included as fixed factors in all models. The duration of the visit was included as an offset in the models regarding vigilance events, to account for the variation in the time animals spent in the testing stations. Stimulus presentation order (1–4) and type of food (linseed, quinoa, tofu, almonds) were initially included as fixed factors, and excluded from all models based on their lack of explanatory importance (e.g. Zuur, 2009).

Latencies were log-transformed to meet the normality assumption. We ensured that there was no strong collinearity between model predictor variables (i.e., an $R^2 > 0.70$) before analyses. Visual inspection of residual plots did not reveal any obvious deviations from homoscedasticity or normality. The accepted significance level was $\alpha \leq 0.05$. All data analyses were conducted with R version 3.2.3 (R Core Team, 2015). We used the R packages *lme4* (Bates et al., 2015) and *MuMIn* (Barton and Barton, 2015).

2.7. Ethical note

Behavioural observations of wild wood mice were conducted according to guidelines obtained from the Italian Institute for Environmental Protection and Research, and with a permit from the Sila National Park (protocol nr. 22082023 for PNRR research activities). Experiments were performed on a voluntary-participation basis (i.e. the mice were free to choose to engage with the tests), without contact or

interference from researchers (no trapping or handling), and in accordance with all applicable international, national and/or institutional guidelines for the use of animals, including the ASAB/ABS guidelines for the Use of Animals in Research (ASAB Ethical Committee/ABS Animal Care Committee, 2025). Testing stations were positioned in suitable, sheltered areas. During data collection, daily checks to the cameratraps were made with a slow approach to reduce the risk of disturbing nearby animals, and thereby affecting their natural behaviour. In all our field recordings, we never observed mice being disturbed away from the station by an approaching researcher.

3. Results

All mice responded to the presence of a novel object in the testing station by increasing the latency to start foraging on the oatflakes compared to when there was no object in the testing station ($\beta = 0.32 \pm 0.07$, $z = 4.74$, $P < 0.001$; Fig. 2 and Table A2 in the Appendix). Mice living in the buffer zone had higher latencies to approach the object ($\beta = 0.62 \pm 0.13$, $z = 4.63$, $P < 0.001$; Fig. 2 and Table A2 in the Appendix), higher latencies to start feeding close to the object ($\beta = 0.18 \pm 0.08$, $z = 2.17$, $P = 0.030$; Fig. 2 and Table A2 in the Appendix), and shorter durations of interaction with it ($\beta = -1.18 \pm 0.34$, $z = -3.50$, $P < 0.001$; Fig. 2 and Table A2 in the Appendix) compared to conspecifics living in both the strictly protected and non-protected areas.

All mice responded to the presence of a novel food in the testing station by delaying both the approach ($\beta = 0.18 \pm 0.06$, $z = 2.82$, $P = 0.005$; Fig. 3 and Table A3 in the Appendix) and the start of the

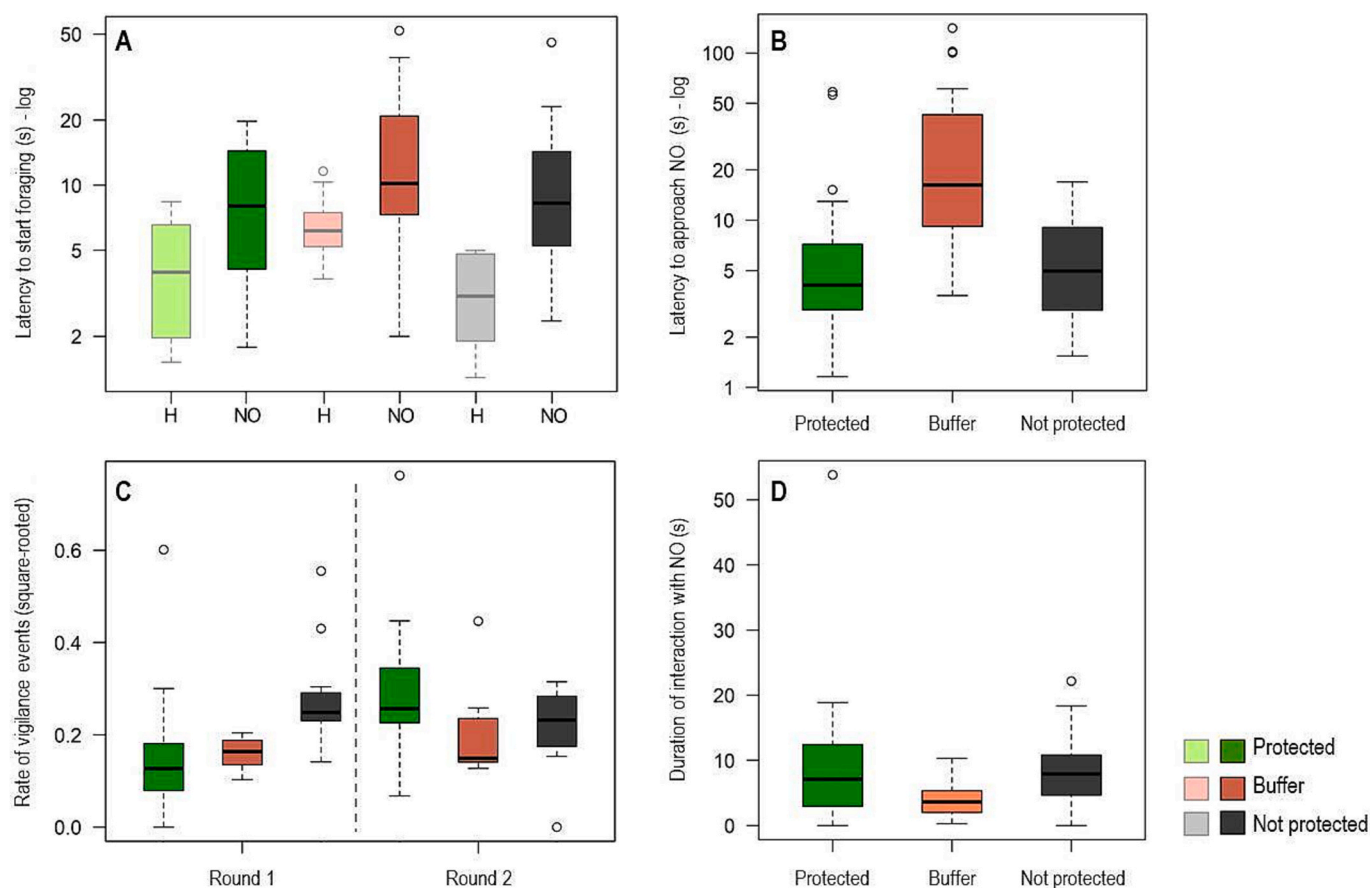


Fig. 2. Behavioural responses of free-ranging wood mice (*Apodemus sylvaticus*) to the presence of a novel object in habitats belonging to the strictly protected area in a National Park, the buffer zone, and non-protected areas outside the National Park, for a total of 33 observations during the Habituation (H) phase and 62 observations during the Novel Object (NO) phase. A: Latency to start foraging on familiar food in the presence (darker shade) vs absence (lighter shade) of the novel object. B: Latency to approach the novel object. C: Rate of vigilance events displayed in presence of the novel object during first and second round of testing. D: Duration of the approach to the novel object. Error bars represent the 95% confidence interval.

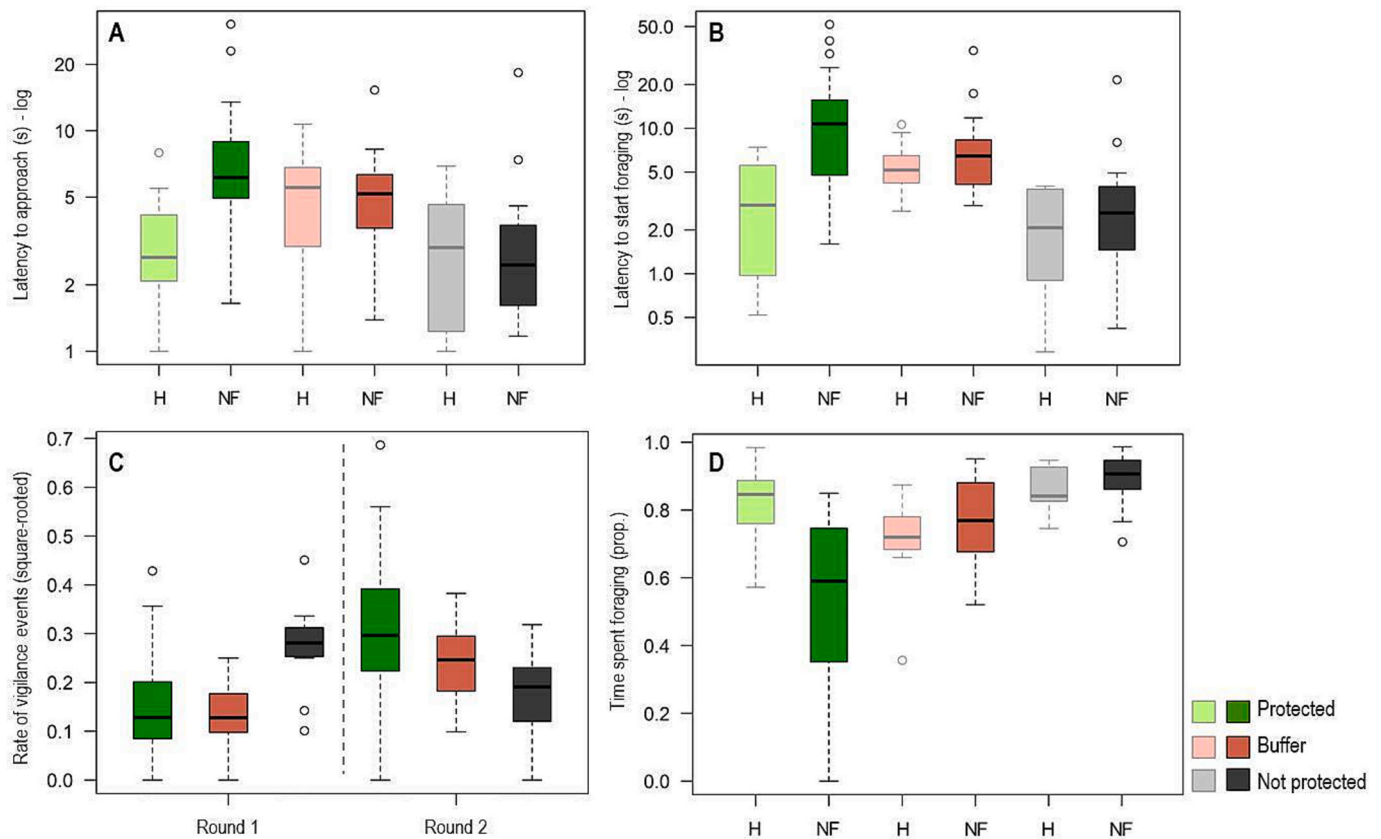


Fig. 3. Behavioural responses of free-ranging wood mice (*Apodemus sylvaticus*) to novel food in habitats belonging to the strictly protected areas in a National Park, buffer zone of the National Park, and non-protected areas outside the National Park, for a total of 33 observations during the Habituation (H) phase and 63 observations during the Novel Food (NF) phase. A: Latency to approach the novel (darker shade) vs the familiar (lighter shade) food. B: Latency to start foraging on novel (darker shade) vs familiar (lighter shade) food. C: Rate of vigilance events displayed in presence of the novel food during first and second round of testing. D: Time spent foraging on novel (darker shade) vs familiar (lighter shade) food. Error bars represent the 95% confidence interval.

consumption ($\beta = 0.25 \pm 0.06$, $z = 4.07$, $P < 0.001$; Fig. 3 and Table A3 in the Appendix) of the novel food compared to the familiar food. Mice living outside the protected area displayed shorter latencies to approach the novel food ($\beta = -0.24 \pm 0.07$, $z = -3.46$, $P = 0.001$; Fig. 3 and Table A3 in the Appendix), and to start eating it ($\beta = -0.35 \pm 0.07$, $z = -4.96$, $P < 0.001$; Fig. 3 and Table A3 in the Appendix) compared to conspecifics living inside it. Mice living in more disturbed areas also foraged longer on novel food compared to conspecifics in more protected areas (Buffer: $\beta = 0.13 \pm 0.05$, $z = 2.83$, $P = 0.005$; Non-protected: $\beta = 0.25 \pm 0.05$, $z = 5.48$, $P < 0.001$; Fig. 3 and Table A3 in the Appendix).

Both in the novel object and novel food test phases, mice changed their rates of vigilance across testing rounds, with animals in the protected areas increasing vigilance rates from the first to the second round of testing, and mice in the non-protected area decreasing vigilance rates (Figs. 2–3 and Tables A2 and A3 in the Appendix).

4. Discussion

Based on two behavioural assays for novel object response and foraging innovation propensity, we found evidence of non-random spatial sorting of wood mice in response to human disturbance based on their behavioural characteristics. Mice living in the buffer zone waited for longer before approaching the novel objects, delayed the foraging in presence of novel objects, and spent less time inspecting them, indicating a stronger novelty avoidance compared to conspecifics living in both strictly protected and non-protected areas. In contrast, mice living in more disturbed areas were faster to approach and consume novel foods compared to conspecifics living inside the protected

area, displaying a higher propensity for dietary innovation. Together, these findings suggest that even low levels of human disturbance are linked to differences in responses to novelty and innovation propensity, albeit the response patterns appear context-dependent. In line with our general hypothesis, we found shifts in behavioural/cognitive trait expression along a gradient of mild human frequentation, suggesting an adjustment to human disturbance. However, our specific predictions were only partially confirmed. While we expected decreased neophobia and higher innovation with increasing human disturbance—assuming mice responded to it as to a loss in resource availability—this was evident only in the novel food context. In the context of novel object responses, mice showed a pattern more consistent with our alternative expectation of increased novelty aversion in areas of higher perceived risk. Overall, findings suggest that human disturbance elicits behavioural responses to novelty relative to both risk perception and resource availability.

4.1. Patterns of response to structures and food

The animals in this study showed different response patterns to novel objects and food. On the one hand, this contrasts with the idea that there could be an underlying dimension to novelty responses, in which reactions to a particular type of novelty are extended to novelty in general (e.g. Crane et al., 2020; Greggor et al., 2015). However, this pattern is consistent with previous studies with other small mammal species in which at least two axes of variation in responses to novelty were found, with responses to food configured separately from others. For example, in captive striped field mice (*Apodemus agrarius*) and common voles (*Microtus arvalis*), responses to novel objects and spaces were underlain

by the same factors, while novel food appeared to be perceived and reacted to in a markedly different manner (Mazza et al., 2021). Behavioural responses to novel food thus appear to form a separate dimension from other types of novelty in small mammals, perhaps indicating responses to potential unknown dangers in the first case and to potential resources in the other (e.g. Šlipogor et al., 2016), and supporting the idea that different selective pressures act on these axes separately (e.g. Greenberg and Mettke-Hofmann, 2001; Mettke-Hofmann, 2014; Mettke-Hofmann et al., 2002). An alternative – or complementary – explanation is that mice in the more disturbed sites were in poorer body condition and therefore more attracted by the novel food but showing different responses to novel objects, which were not resource-related. While we do not have information on body condition for the mice in this study (it would have required trapping and handling), a previous multi-year study along a rural-urban gradient showed that body condition did not affect dietary innovation propensity (Mazza et al., in prep.).

The only aspect in which we found a consistent pattern across contexts was in relation to vigilance behaviour, where mice in the non-protected area exhibited a higher rate of vigilance in the first round compared to conspecifics and then decreased vigilance in the second round, while mice in the protected area exhibited the opposite pattern. Since vigilance was the more general parameter we measured here, this could be an overall response to the test situation itself rather than the specific stimulus provided (structure or food). Thus, mice in the protected area responded more strongly to the repeated encounter with novel stimuli in their familiar environment, whereas mice in the non-protected area habituated to them (e.g. Blumstein, 2016; Ordiz et al., 2019; Uchida and Blumstein, 2021). This is an indication that living in more human-disturbed area may expose wood mice to frequent encounters with novel stimuli which may facilitate habituation processes, whereas in protected areas novel stimuli could be a novelty in itself, i.e. a situation the animals were less familiar with and which elicited increasing rates of vigilance (e.g. Blumstein, 2016). Similar patterns of individualised responses of habituation and sensitization to human disturbance were reported in a long-term study on other non-commensal rodents, such as marmots (Uchida and Blumstein, 2021). Our short-term study (focused on novelty rather than habituation) aligns with this pattern, although a combination of prolonged novelty exposure and behavioural monitoring is needed to understand whether and how these patterns hold through time (e.g. Blumstein, 2016; Uchida and Blumstein, 2021) and how they generalise to other species. While the focus of the present study was to assess responses to novel stimuli, which entails that each stimulus is experienced just once by an animal, we could not follow up with an investigation of habituation patterns because of the lack of individual identification of the mice. Future studies examining habituation curves are needed to illuminate whether and how initial reactions develop over the course of repeated presentations of the same stimuli, and whether a similar pattern of sensitization vs habituation emerges in other taxa (e.g. Price et al., 2025). We acknowledge that in this study the sample size is relatively contained, and that future studies may improve this aspect by aiming for a higher number of sites per area. At the same time, restricting our observations to just the first interaction between an animal and a specific stimulus is an extremely conservative approach, which ensures that what we recorded are indeed responses to novel stimuli, without confounds from habituation via repeated visits. We could thus minimise the confounds that can be introduced when cognitive aspects are only partially considered in field studies and conservation assessments (e.g. Greggor et al., 2020).

4.2. Responses to a novel object

Positive responses to novelty are expected when animals live in human-disturbed habitats such as urban settlements, where they are constantly faced with novel stimuli of all kinds, including structures and objects (e.g. rubbish in the park, nesting material or opportunities),

spaces (e.g., habitat configurations, plant composition), and food resources (e.g. presence of human waste, or different prey communities). In this study, however, we found no difference between the responses to novel objects of wood mice living in strictly protected areas and non-protected areas. This is in line with a few previous studies on other species, including other small mammals and birds, reporting highly conserved neophobia in animals living in human-disturbed habitats, even when a decrease in neophobia could potentially be beneficial when linked to higher disturbance tolerance (e.g. Bókony et al., 2012; Echeverría and Vassallo, 2008; Mazza et al., 2021). Living in non-protected areas, where human activity and disturbance is higher, did not appear to alter the pressures shaping responses to novel structures. The dangerous niche hypothesis posits that increased neophobia is adaptive when novel stimuli are likely dangerous, e.g. if traps or a high level of predation risk characterize an individual's environment (e.g. Bókony et al., 2012; Greenberg, 2003; Greenberg and Mettke-Hofmann, 2001). Since neophobia is likely evolved to protect individuals from potential harm in unknown situations (e.g. Greenberg, 2003), maintaining comparatively high life-preserving fear of novel stimuli might be the most appropriate response for a taxon in which fitness is strongly determined by the survival component.

An alternative explanation for the similarity of responses between wood mice living in protected and non-protected areas is that differences in disturbance levels do not affect the animals' tolerance or approach to novel structures. However, this contrasts with the fact that wood mice living in the buffer zone showed higher avoidance tendencies compared to conspecifics living in the rest of the gradient. Here, mice showed the longest latencies to start feeding when a novel object was present in the testing station, they had the slowest approach and shortest exploration of the objects. These findings highlight the importance of considering gradients of variation, rather than comparing and contrasting only two extreme situations, lest some potentially important patterns are lost. Besides the pressures that could have maintained comparable levels of neophobia in small mammals living in such mildly disturbed habitats discussed above, it is possible that the discontinuous and unpredictable patterns of human activities (e.g. opening of restaurants and presence of hikers during weekends, holidays, summer) contributed to keeping novelty avoidance in mice in the buffer zone of the National Park at its highest (e.g. Morand-Ferron et al., 2019; Niemelä et al., 2013; Vardi and Berger-Tal, 2022). A possible interpretation for this pattern of responses is that environments with high levels of variation and unpredictability are expected to lessen behavioural flexibility (e.g. Niemelä et al., 2013). This occurs because excessive variability prevents animals from using information effectively and information processing cannot keep up with environmental variability, so the costs of cognition are not covered (e.g. Coppens et al., 2010; Mathot et al., 2012; Niemelä et al., 2013; Överli et al., 2007; Price et al., 2025; Tello-Ramos et al., 2019; Winfield et al., 2026). In this case, mice in the buffer zone may have responded to the unpredictability of human disturbance by little to no modulation of their novelty avoidance tendencies (e.g. Tebbich and Teschke, 2014). Alternatively, enhanced uncertainty in the buffer zone translated to higher perception of risk, from which stemmed enhanced caution and neophobia (e.g. Witterick et al., 2025; Zanette and Clinchy, 2019). A careful and thorough information acquisition strategy should be favoured when environmental conditions change frequently (e.g. Carvalho et al., 2013; Hall and Kramer, 2008), or the costs of neglecting some key environmental features exceed the benefits of gaining fast but incomplete information (e.g. Carere and Locurto, 2011; Guillelte et al., 2011; Sih and Del Giudice, 2012; Udino et al., 2016). Here, elevated levels of neophobia could reflect wood mice's risk-aversion in the face of potential, unknown dangers (e.g. Carere and Locurto, 2011; Guillelte et al., 2011; Šlipogor et al., 2022). The connections between behavioural flexibility, responses to novelty, and environmental harshness and instability are poorly investigated empirically (but see e.g. Kozlovsky et al., 2015; Morand-Ferron et al., 2019; Roth et al., 2010; Tebbich and Teschke, 2014; Vardi and Berger-

Tal, 2022), and so far yielded mixed findings. Wildlife reactions to human disturbance represent a promising complementary approach to extreme or urban environments to further illuminate how information reliability and information acquisition strategies may interact to shape animals' responses to environmental variation and novel stimuli (e.g. Mazza and Carere, 2024; Müller and Pillay, 2024).

4.3. Foraging innovation

Foraging innovation propensity scaled positively with the degree of human presence and disturbance within the gradient we examined. The more disturbed by human presence a site was, the more the wood mice living in it were prone to approach, try, and eat the novel foods we offered. The cognitive buffer hypothesis posits that advanced cognitive abilities, such as innovation and behavioural flexibility, allow animals to modify their behaviour in adaptive ways when confronted with challenges in their environment (e.g. Sol, 2009a, 2009b). One of the benefits of innovation is that it allows animals to discover and exploit a wide variety of resources, which can be particularly useful when resources are scarce or when individuals face novel environmental conditions they did not evolve in (e.g. Overington et al., 2011; Reader and MacDonald, 2003). Compared to the strictly protected core area of the National Park, both the buffer and the non-protected areas allow for some level of alterations. In the buffer zones forests are managed, which leads to changes in vegetation composition and consequently in food availability (e.g. Tomao et al., 2020; Venanzi et al., 2016). Outside the park human activities can cause both direct and indirect (e.g. through fragmentation) alterations in vegetation composition (both in terms of plants, seeds, and insects) and in the relative abundance of familiar food sources. As a result, familiar resources may be less and/or have a more patchy distribution in less protected areas compared to strictly protected areas, while novel, unfamiliar food sources could be more present. Therefore, wood mice should be more prone to consume the novel foods in less protected areas, where they are most benefitted from trying unfamiliar items, as this could lead to the discovery of new resources. While foraging (consumer) innovation and ecological/dietary generalism were initially assumed to be part of a suite of related behavioural traits, they operate on different scales: where diet breadth is based on broad categorizations of food types (e.g. leaves, insects, seeds, etc.), a foraging innovation is recorded when an animal eats a new type of seed, even though this falls broadly within its regular diet (e.g. Overington et al., 2011). Here it is important to note that while wood mice are considered omnivorous rodents (e.g. Montgomery and Montgomery, 1990), like all *Apodemus* they are non-commensal and non-synanthropic, i.e. they do not habitually consume, and are not supposed to be particularly attracted to human garbage and anthropogenic foods. Nonetheless, human presence and disturbance may shape a resource landscape that favours more innovative animals in areas where this presence is higher, compared to protected areas where humans do not directly alter forest composition and resource availability. Our findings are in line with previous studies on wood mice as well as other small mammals and birds, which report higher innovation propensity in general, and foraging innovation in particular, in human-disturbed, novel, or more complex environments (e.g. Mazza and Guenther, 2021; Mazza et al., 2025; Mettke-Hofmann et al., 2002; Sol et al., 2002), suggesting a ubiquitous response to human alteration of resource landscapes across taxa, as well as a key role for cognition and innovation in the successful coping with human disturbance and environmental alterations (e.g. Goumas et al., 2020; Greggor et al., 2014; Griffin et al., 2017; Mazza and Šlipogor, 2024; Mazza et al., 2025).

Innovation also entails costs – in this case mainly the risk of ingesting poisonous or toxic food. While wood mice are not the target of any management program, small mammals are, however, among the most common victims of rodenticides intended for other species (e.g. Brakes and Smith, 2005). These risks may not be worth the acquisition of an occasional new resource in protected, undisturbed habitats, but may be

necessary or more advantageous in more disturbed ones. Thus, innovative animals may keep their potential for new discovery high, but do so with a high level of fear and arousal, which protects them from potential, unknown dangers that are associated with novelty (e.g. Greenberg, 2003; Greenberg and Mettke-Hofmann, 2001). This could partly explain why we recorded different patterns of responses to novelty along the gradient of human disturbance we examined, and why mice living in the most disturbed habitats showed both conserved neophobia towards a potentially dangerous object (at least, comparable with conspecifics in the strictly protected areas) and high innovation propensity in a foraging context.

In addition to habitat alteration (e.g. forest management, fragmentation, wildfire, urbanisation), direct human presence may provide opportunities for wildlife to consume anthropogenic or novel food: humans directly feeding animals, feeding stations, waste bins, and food left behind from human gatherings (e.g. Belant, 1997; Demeny et al., 2019; Griffin and Ciuti, 2023; Hansen et al., 2020; Murray et al., 2015; Rimbach et al., 2023). At the same time, human activities can often disturb, alarm, and induce behavioural changes in animals (e.g. Blanc et al., 2006; Chow et al., 2024). Even “innocuous” activities such as dog-walking, hiking, or cycling were found to affect other small mammals' innovative performance (e.g. Chow et al., 2024). Such activities are reduced or forbidden in National Parks, and may happen in such a discontinuous way (both spatially and temporally, e.g. seasonal fluctuations) that neither tolerance to disturbance nor discovery of associated novel resources are possible or advantageous for the wood mice that live there. Spatial sorting for innovation propensity may in turn provide animals living in more disturbed areas with more opportunities to develop tolerance to disturbances, leading to a non-random distribution of wood mice along the gradient of protection, disturbance, and human presence we examined.

5. Implications for conservation

This study contributes to conservation science by demonstrating that behavioural responses to novel stimuli vary across a gradient of human presence and disturbance within and around a protected area. While most research on behavioural responses to anthropogenic change has focused on highly urbanised environments, our results show that even comparatively low levels of human activity are sufficient for differences in novelty responses and innovation propensity to emerge. Wood mice living in different protection zones differed in object neophobia and foraging innovation, suggesting that human presence and associated disturbance contribute to non-random spatial sorting of behavioural phenotypes according to the individuals' potential for dealing with novel stimuli, and tolerate the effects of human activities (e.g. Martin and Réale, 2008; Merrick and Koprowski, 2017). Protection regimes may thus influence not only where animals are present, but also the behavioural characteristics they express (e.g. Merrick and Koprowski, 2017; Morant et al., 2025), in line with previous work on the physiological and behavioural alterations caused by human disturbance (e.g. Blane and Jackson, 1994; Blumstein et al., 2005; Carney and Sydeman, 1999; Chow et al., 2024; Dyck and Baydack, 2004; Fowler, 1999; Lacy and Martins, 2003; Lott and McCoy, 1995; Martin and Réale, 2008; Oriol-Cotterill et al., 2015; Romero and Wikelski, 2002; Walker et al., 2005). Since small mammals represent a fundamental link in most terrestrial trophic dynamics, and there is evidence for their non-random sorting in relation to disturbance and human activities, it is worthwhile to invest in their protection, and the protection of their habitats. In particular, it may be worth to invest in extending the study of responses to human presence to the less charismatic species without which the presence of umbrella ones would not be possible either inside or outside of protected areas.

The effectiveness of protected areas is commonly evaluated using indicators such as species richness, abundance, occupancy, or habitat condition (e.g. Cerini et al., 2025). Wood mice are considered

generalists both in terms of habitat and diet (e.g. Arnan et al., 2014; Montgomery, 1999; Montgomery and Montgomery, 1990; Selås, 2016), and can be found even in some highly disturbed urbanised habitats (e.g. Baláz et al., 2026; Mitter et al., 2015; Rimbach et al., 2025). Consequently, their presence alone cannot be used as indicator of habitat quality or the degree of anthropogenic influence, as in the case of other, more sensitive species which drop out of excessively human-disturbed environments (e.g. Gerlach et al., 2013; Siddig et al., 2016). In contrast, wood mice's behavioural responses to novelty varied across the protection gradient despite continued occupancy throughout the study area. This suggests that behaviour and cognition can provide sensitive indicators of how wildlife experiences different management regimes and levels of human disturbance, serving as early-warning signs of distress that may reveal ecological effects that are not detectable through traditional population-level metrics alone (e.g. Anthony and Blumstein, 2000; Cerini et al., 2023; Fardell et al., 2020; McDougall et al., 2006). Such an approach would, for example, allow a direct and fast evaluation of the improvement in sustainability practices of transition zones through an assessment of similarity of behavioural responses to novel stimuli between transition zones and protected/buffer areas within the Parks – thereby improving land sharing practices (e.g. Berger-Tal and Saltz, 2016; Fardell et al., 2020; Gaynor et al., 2021; Hoffmann, 2021; Maxwell et al., 2020; Morant et al., 2025; Oriol-Cotterill et al., 2015).

This study also highlights the importance of considering multiple behavioural dimensions when assessing wildlife responses to anthropogenic change. Responses to novel objects and novel food followed different patterns across the disturbance gradient, indicating that behavioural and cognitive responses were context dependent. This finding cautions against treating behavioural flexibility or novelty responses as single, uniform traits and emphasizes the need for multidimensional approaches in conservation behavioural research. By revealing behavioural differentiation across protection regimes, even within a relatively low-disturbance conservation landscape, our results underline the strategic importance of expanding strictly protected zones and integral reserves by 2030, as envisaged in the European Biodiversity Strategy (European Commission, 2020). Upholding the principle of ecological primacy within strictly protected areas (e.g. Chiti and Piovesan, 2025) represents a necessary commitment to safeguarding the natural behavioural patterns and cognitive integrity of wildlife, providing the absolute refuge needed to maintain undisturbed behavioural dimensions that traditional, population-level metrics often fail to consider. Within the current debate surrounding the operational definition and ecological scope of strict reserves (e.g. Chiti and Piovesan, 2026), this study highlights that strict protection must transcend the conventional focus on species occurrence and habitat quality. Instead, our findings underscore that comprehensive ecological integrity inherently encompasses the preservation of unaltered behavioural and evolutionary processes. By demonstrating that low-intensity anthropogenic pressures induce significant behavioural and cognitive shifts even in highly resilient, generalist taxa, this research emphasizes that strict reserves are indispensable baselines for the effective management of protected areas. They represent control zones where natural ecosystems can function autonomously, free from the cryptic, non-lethal selective pressures and behavioural modifications imposed by human activities (e.g. Caro et al., 2026). Indeed, wide-scale literature corroborates that

non-lethal anthropogenic disturbance reshapes key behavioural dimensions, driving shifts towards, for example, altered nocturnality (e.g. Gaynor et al., 2018), modifying natural landscapes of foraging, fear and movement patterns (e.g. Doherty et al., 2021; Ripple and Beschta, 2006; Sordello et al., 2025), and inducing artificial selective pressures on wildlife risk-perception and habituation-mediated learning (e.g. Geffroy et al., 2015). Enforcing strict protection is therefore paramount to buffering these subtle yet pervasive evolutionary disruptions.

In conclusion, our findings suggest that protected areas may serve not only as refuges for species and habitats, but also as landscapes within which behavioural responses to human activities can be examined and conserved. Integrating behavioural measures into conservation monitoring may therefore improve our understanding of wildlife responses to environmental change and contribute to more comprehensive assessments of protected-area effectiveness.

Inclusion and diversity statement

Our study includes scientists based in the country where the study was conducted, and is composed of a mixed gender team who are residents of the local area in which the study was performed.

CRediT authorship contribution statement

Valeria Mazza: Writing – review & editing, Writing – original draft, Visualization, Validation, Resources, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Giorgia Scrivano:** Writing – review & editing, Methodology, Investigation. **Gianluca Piovesan:** Writing – review & editing, Resources, Methodology. **Alberto Garofalo:** Investigation. **Daniele Canestrelli:** Project administration, Funding acquisition, Conceptualization. **Claudio Carere:** Writing – review & editing, Validation, Supervision, Conceptualization.

Declaration of competing interest

The authors declare no conflict of interest.

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Appendix A

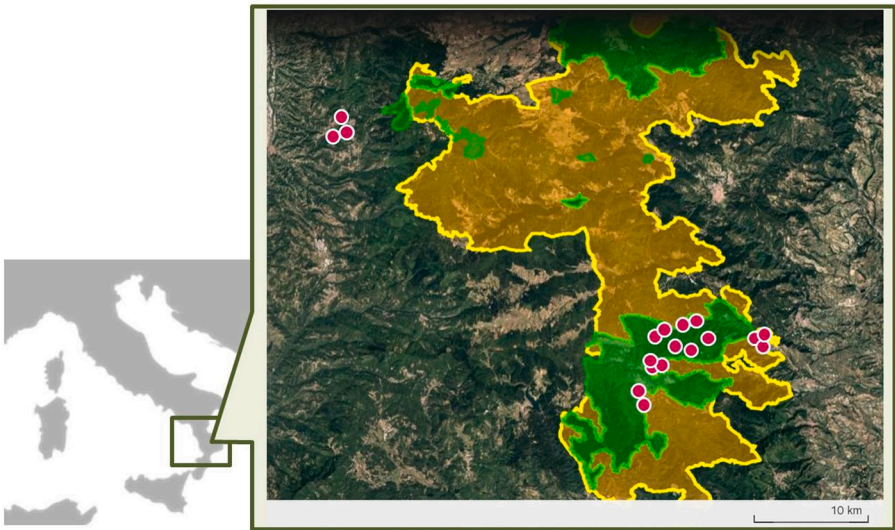


Fig. A1. Locations of the 18 testing stations positioned outside and inside Sila National Park (green: strictly protected, yellow: buffer zone). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

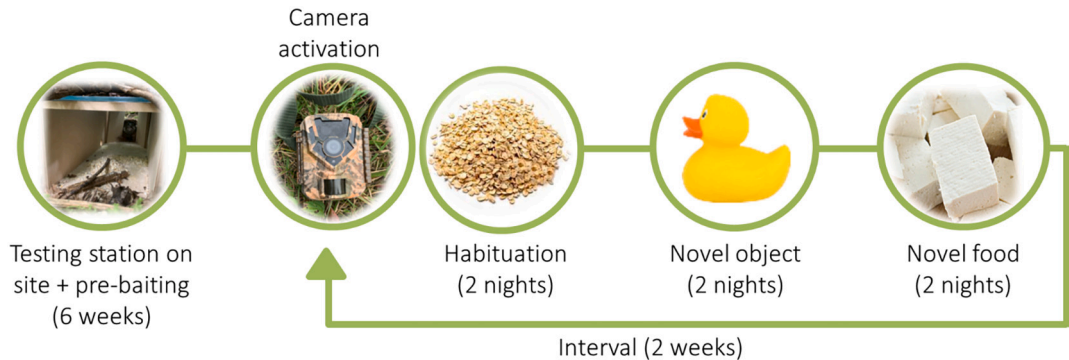


Fig. A2. Schematic timeline of the experimental procedure.

Table A1

A) Information on study sites inside and outside Sila National Park, relative to the degree and capillarity of human presence and disturbance (expansion zones, site description, and rodent population) of each area (strictly protected, buffer, non-protected). The sealing index estimates the proportion of artificial impervious surface (i.e. coverage of natural soil with artificial impervious surface like buildings and paved roads) around each study site with radius of 1 km. Hiking path coverage expresses the linear length of unpaved, hiking paths within a 1 km radius of each site. Sealing indexes and path coverage were calculated with QGIS (v. 10/ESRI; <http://www.esri.com/>). B) Results of pairwise *t*-test of sealing index and hiking paths coverage for 18 testing stations across three study areas with different levels of protection (strictly protected, buffer, non-protected).

A)	Area			Non-protected
	Protected	Buffer		
Protection level	Integral	Intermediate		None
Allowed human activities	Hiking, biking	Harvesting (wood, mushrooms), cattle grazing, tourist infrastructure (bar, restaurant, hostlery)		All
Forest management	No	Yes		Yes
Mean (±SD) sealed surface % in 1 km buffer	0.04 ± 0.07	1.17 ± 1.07		15.8 ± 57.7
Mean (±SD) hiking paths coverage in 1 km buffer	6894.7 ± 4917.5	5826.0 ± 5580.9		21.8 ± 57.7
Avian species richness ^a	26	26		NA
Avian predator species richness ^a	2	2		NA

B)	Sealed surface			Hiking paths coverage		
	<i>t</i>	<i>df</i>	<i>P</i>	<i>t</i>	<i>df</i>	<i>P</i>
Zone protected vs buffer	0.259	17	0.972	−0.457	17	0.618

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Table A1 (continued)

B)	Sealed surface			Hiking paths coverage		
	<i>t</i>	<i>df</i>	<i>P</i>	<i>t</i>	<i>df</i>	<i>P</i>
Zone protected vs non-protected	3.748	17	0.005	−3.056	17	0.021
Zone buffer vs non-protected	3.342	17	0.012	−2.480	17	0.072

^a From Chiatante et al. (submitted).

Table A2

Behavioural responses of free-ranging wood mice (*Apodemus sylvaticus*) to the presence of a novel object, for a total of 33 observations during the Habituation phase and 62 observations during the Novel Object phase. Shown are the results of (generalised) linear mixed effects models ((G)LMMs) for latency to approach the novel object, latency to start foraging, duration of the approach to the novel object, and vigilance rates, in relation to level of protection of the surrounding area (strictly protected, buffer, non-protected), experimental phase (Habituation vs Novel Object), test session (1st vs 2nd round), and duration of the visit to the testing station. R_m reports the marginal R^2 value based on the fixed factors, R_c the conditional R^2 value including the testing station ID as a random factor. Reference levels are given in (). For statistically significant effects, *p* values are highlighted in bold.

Variable	Fixed factors	Estimate	SE	<i>z</i>	<i>P</i>	R_m	R_c
Latency to approach NO (log)	Intercept	0.91	0.20	4.55	<0.001	0.33	0.33
	Protection (buffer)	0.62	0.13	4.63	<0.001		
	Protection (none)	−0.03	0.13	−0.23	0.816		
	Round	−0.13	0.11	−1.19	0.236		
Latency to start foraging (log)	Intercept	0.36	0.12	3.00	0.003	0.27	0.28
	Phase (novel object)	0.32	0.07	4.74	<0.001		
	Protection (buffer)	0.18	0.08	2.17	0.030		
	Protection (none)	0.02	0.08	0.21	0.835		
Duration of NO interaction (sqrt)	Round	0.13	0.07	1.97	0.048	0.29	0.29
	Intercept	0.91	0.48	1.88	0.060		
	Protection (buffer)	−1.18	0.34	−3.50	<0.001		
	Protection (none)	0.59	0.33	1.82	0.069		
Vigilance rate (full model)	Round	0.18	0.28	0.65	0.516	0.40	0.69
	Intercept	0.52	0.39	1.32	0.186		
	Protection (strict)	−2.69	0.56	−4.82	<0.001		
	Protection (none)	1.58	0.55	2.86	0.004		
Vigilance rate (strictly protected)	Round	0.02	0.18	0.10	0.917	0.492	0.751
	Protection (strict) * round	1.70	0.27	6.29	<0.001		
	Protection (none) * round	−0.72	0.30	−2.38	0.017		
	Intercept	−2.17	0.42	−5.22	<0.001		
Vigilance rate (buffer)	Round	1.72	0.20	8.58	<0.001	0.00	0.334
	Intercept	0.48	0.38	1.24	0.214		
Vigilance rate (non-protected)	Round	0.03	0.19	0.18	0.856	0.20	0.611
	Intercept	2.09	0.38	5.47	<0.001		
	Round	−0.70	0.24	−2.87	0.004		

Table A3

Behavioural responses of free-ranging wood mice (*Apodemus sylvaticus*) to novel food, for a total of 33 observations during the Habituation phase and 63 observations during the Novel Food phase. Shown are the results of (generalised) linear mixed effects models ((G)LMMs) for latency to approach the food, latency to start foraging, duration of the foraging, and vigilance rates, in relation to level of protection of the surrounding area (strictly protected, buffer, non-protected), experimental phase (Habituation vs Novel Food), test session (1st vs 2nd round), and duration of the visit to the testing station. R_m reports the marginal R^2 value based on the fixed factors, R_c the conditional R^2 value including the testing station ID as a random factor. Reference levels are given in (). For statistically significant effects, *p* values are highlighted in bold.

Variable	Fixed factors	Estimate	SE	<i>z</i>	<i>P</i>	R_m	R_c
Latency to approach (log)	Intercept	0.59	0.11	5.45	<0.001	0.18	0.18
	Phase (novel food)	0.18	0.06	2.82	0.005		
	Protection (buffer)	−0.01	0.07	−0.20	0.844		
	Protection (none)	−0.24	0.07	−3.46	0.001		
Latency to start foraging (log)	Round	−0.02	0.06	−0.33	0.739	0.33	0.33
	Intercept	0.78	0.11	7.23	<0.001		
	Phase (novel food)	0.25	0.06	4.07	<0.001		
	Protection (buffer)	−0.01	0.07	−0.14	0.888		
Duration of foraging (prop.)	Protection (none)	−0.35	0.07	−4.96	<0.001	0.28	0.28
	Round	−0.04	0.06	−0.72	0.474		
	Intercept	0.71	0.07	10.02	<0.001		
	Phase (novel food)	−0.10	0.04	−2.38	0.018		
Vigilance rate (full model)	Protection (buffer)	0.13	0.05	2.83	0.005	0.35	0.69
	Protection (none)	0.25	0.05	5.45	<0.001		
	Round	−0.02	0.04	−0.41	0.684		
	Intercept	−0.79	0.45	−1.77	0.077		
	Protection (strict)	−0.69	0.58	−1.19	0.235		
	Protection (none)	3.02	0.62	4.88	<0.001		
	Round	0.98	0.20	4.89	<0.001		
	Protection (strict) * round	0.42	0.27	1.56	0.118		

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Table A3 (continued)

Variable	Fixed factors	Estimate	SE	z	P	R _m	R _c
Vigilance rate (strictly protected)	Protection (none) * round	−1.83	0.32	−5.66	<0.001	0.35	0.75
	Intercept	−1.49	0.41	−3.62	<0.001		
	Round	1.41	0.18	7.79	<0.001		
Vigilance rate (buffer)	Intercept	−0.80	0.41	−1.94	0.053	0.31	0.59
	Round	0.98	0.20	4.92	<0.001		
	Intercept	2.22	0.39	5.74	<0.001	0.28	0.56
Vigilance rate (non-protected)	Round	−0.82	0.25	−3.26	0.001		

Appendix B. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2026.112003>.

Data availability

The data that support the findings of this study are available in the Supporting Information of this article.

References

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