



# Free-Roaming and Captive Cats Prefer Silver Vine to Catnip for Self-Anointing

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## Abstract

Chemical cues that appear potent in controlled laboratory bioassays do not necessarily function as effective behavioural cues under natural conditions, where animals can freely approach or ignore stimuli. How chemical detectability translates into voluntary behavioural engagement, therefore, remains an important unresolved question. Plant-derived semiochemicals provide a tractable system for examining this issue because the same compounds can be presented either as intact natural sources or as purified chemicals. Domestic cats (*Felis silvestris catus*) show a characteristic self-anointing response to iridoid-producing plants, including catnip (*Nepeta cataria*) and silver vine (*Actinidia polygama*), both widely regarded as cat-attractants. Here, we tested whether these plants differ in their ability to induce voluntary engagement under free-choice conditions. Free-roaming cats rarely showed self-anointing behaviour (face-rubbing and rolling) toward intact catnip plants, but consistently engaged with silver vine. The same bias toward silver vine was observed in captive cats presented simultaneously with plant extracts. Chemical analyses confirmed that catnip contained abundant bioactive nepetalactone, indicating that weak responsiveness was not explained by a lack of bioactive compounds. These findings demonstrate that chemical abundance and laboratory bioactivity do not necessarily predict behavioural reliability under natural encounter conditions. Instead, whether a cue consistently elicits voluntary engagement may determine its ecological effectiveness as a behavioural cue.

**Keywords** Self-anointing · Catnip · Silver vine · Free-roaming cats · Chemical ecology · Iridoids

## Introduction

Controlled bioassays are widely used to demonstrate the bioactivity of chemical cues. However, bioactivity measured under standardised experimental exposure does not necessarily establish ecological function. In natural environments, animals can freely approach, investigate, or ignore a stimulus. Consequently, cues that appear potent under laboratory conditions may fail to elicit behaviour reliably when animals are free to respond (Vet and Dicke 1992).

This discrepancy may arise because real-world stimuli differ from experimental presentations in both form and delivery. For example, intact plants release odours as dynamic plumes whose emission rates and composition vary with environmental conditions and plant damage (Cai et al. 2022). Thus, chemical abundance or laboratory potency does not necessarily predict behavioural outcomes under free-choice conditions. This raises a broader ecological question: under what conditions does chemical detectability translate into reliable behavioural activation in natural environments?

Plant-derived semiochemicals provide a useful framework for examining the gap between laboratory bioactivity and voluntary engagement, because the same compounds can be presented as intact natural sources, plant extracts, or synthetic chemicals under comparable free-choice conditions. Domestic cats (*Felis silvestris catus*) provide a particularly tractable system for testing this idea because they exhibit a conspicuous self-anointing response to iridoid-producing plants, including catnip (*Nepeta cataria*) and

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silver vine (*Actinidia polygama*) (Meinwald 1954; Obara et al. 2024; Sakan et al. 1959a, 1959b, 1969; Uenoyama et al. 2021). These iridoids, such as *cis-trans* nepetalactone and *cis-trans* nepetalactol, are volatile plant-derived compounds that also possess mosquito-repellent properties. During rubbing and rolling, they are transferred onto the cat's fur, linking this behaviour to antiparasitic defence (Uenoyama et al. 2021). Cats can respond to these compounds even without naso-oral contact with the stimulus, supporting the idea that they are initially detected through the olfactory system. Similar responses have been reported in other felids, suggesting that sensitivity to these compounds may be widely conserved across the Felidae family (Bol et al. 2017; Hill et al. 1976; Uenoyama et al. 2021).

Despite the widespread view that catnip and silver vine are both reliable “cat-attractant” plants, most existing evidence derives from assays using dried plant material or experimental designs that facilitate contact. Under such conditions, a larger proportion of cats respond to dried silver vine than to dried catnip (Bol et al. 2017, 2022). This pattern is paradoxical because, under comparable analytical conditions, catnip releases approximately 40-fold more total iridoids (predominantly *cis-trans* nepetalactone) than silver vine, which emits a smaller quantity but as a chemically complex blend dominated by *cis-trans* nepetalactol together with numerous minor iridoids (Obara et al. 2024; Uenoyama et al. 2022). When tested individually, *cis-trans* nepetalactone and *cis-trans* nepetalactol induce more prolonged rubbing and rolling than the minor iridoids (Uenoyama et al. 2021). Nevertheless, bioassays using synthetic mixtures suggest that the chemically diverse blend of silver vine can compensate for its lower total dose (Uenoyama et al. 2022), raising the possibility that chemical complexity, rather than quantity alone, determines behavioural effectiveness.

A key question therefore remains: do these differences between catnip and silver vine persist when cats encounter fresh, intact plants under free-choice conditions? In naturalistic settings, behavioural reliability, rather than potency measured under constrained exposure, determines whether a cue translates into voluntary self-anointing. Direct comparisons using fresh plants are also uncommon because the two species rarely co-occur naturally. Catnip is widely cultivated as a garden herb in Europe and North America, whereas silver vine typically occurs in forested or mountainous habitats in East Asia (Asakura and Hoshino 2016). This geographic separation limits opportunities to test whether intact plants differ in their ability to induce voluntary engagement under shared environmental conditions.

Here, we tested whether fresh catnip and silver vine differ in behavioural reliability when cats can freely approach or disengage. To do so, we combined four complementary experiments spanning three assay types: (i) outdoor

free-roaming encounter assays with intact plant-derived stimuli, (ii) an outdoor extract assay using catnip- and silver vine-treated sides of the same brick, (iii) a simultaneous dual-stimulus assay with catnip and silver vine extracts in captive purebred cats kept under unconstrained housing conditions and with no known prior exposure to silver vine or catnip, and (iv) individual laboratory assays testing purified nepetalactone isomers. These experiments were not identical choice designs, but together they allowed us to compare voluntary engagement with plant-derived stimuli across naturalistic and controlled contexts. We predicted that silver vine would elicit voluntary self-anointing more reliably than catnip under these conditions, despite catnip containing larger quantities of bioactive nepetalactone. By distinguishing chemical abundance and laboratory bioactivity from behavioural reliability, this study examines the possibility that chemically potent plant-derived cues do not always elicit voluntary behaviour reliably when animals are free to engage or disengage.

## Materials and Methods

### Stimuli Used for Behavioural Assays

**Plants** Catnip stimuli were obtained from a single cultivated patch consisting of multiple catnip plants grown from commercially obtained seeds in an outdoor garden in Morioka, Iwate Prefecture, Japan (39°72' north latitude, 141°13' east longitude). Silver vine branches with leaves attached (hereafter, silver vine material) were freshly harvested from a wild population in Morioka.

**Catnip and Silver Vine Extracts** The leaves were frozen in liquid nitrogen within 2 h of harvesting, and subsequently manually ground into a fine powder. The powder (400 g) was extracted with 4 L of *n*-hexane (FUJIFILM Wako Pure Chemical Corp., Osaka, Japan; reagent grade, ≥96.0% purity) at room temperature for 2 days. After removal of residues using filter paper (Advantec qualitative No. 2; Toyo Roshi Kaisha Ltd., Tokyo, Japan), the solvent was removed using a rotary evaporator (N-1200A; EYELA, Tokyo, Japan). The extracts were dissolved in *n*-hexane to a concentration equivalent to 1 g of fresh leaves per ml and stored at 4 °C until use.

**Iridoids** *Cis-trans* nepetalactone and *cis-trans* nepetalactol were synthesised as previously reported (Uenoyama et al. 2021). *Trans-cis* nepetalactone and *cis-cis* nepetalactone were obtained as pure materials from catnip leaves using the following procedure. Catnip leaves (120 g) harvested from the same garden used for behavioural assays in July

2023 were steam-distilled. The resulting oil (145.6 mg) was applied to a column (1.4 × 4.5 cm) packed with 7 g neutral silica gel, and eluted with 1:1.5 dichloromethane/pentane (v/v) followed by 1:1 dichloromethane/pentane. The fractions containing the desired nepetalactone isomers were evaporated to dryness, yielding the pure *trans*–*cis* nepetalactone and *cis*–*cis* nepetalactone. Compound identities were determined by comparison of the <sup>1</sup>H NMR spectrum with reported spectra (Liblikas et al. 2005).

### Experiment I. Outdoor Free-Roaming Encounter Assays with Intact Plant-Derived Stimuli

All procedures involving animals followed local and national animal ethics guidelines and were approved by the animal research committee of Iwate University (A202124, A202441). An overview of all behavioural experiments conducted in this study is provided in Table 1. In Experiment I, freshly harvested silver vine branches with leaves attached (silver vine material) were presented on 10 presentation nights (Fig. 1). On one Experiment I presentation night only, freshly harvested catnip material was additionally presented together with the silver vine material, as shown in Fig. 2a. All stimuli were presented on the ground at the same fixed location approximately 1 m from the cultivated catnip plant.

### Experiment II. Outdoor Extract Assays Using Catnip- and Silver Vine-Treated Sides of the Same Brick

In this experiment, paired stimuli were presented on a brick (14 cm × 7 cm × 3.5 cm; DCM Co., Ltd., Tokyo, Japan) placed at the same fixed location. This experiment comprised two stimulus conditions: Experiment IIa, in which the brick was treated with catnip extract on one side and silver vine extract on the opposite side (each equivalent to 1 g of fresh leaves; preparation methods are described above) on 10 presentation nights; and Experiment IIb, in which the

brick was treated with catnip extract on one side and either 2 mg of *cis*–*trans* nepetalactone or *cis*–*trans* nepetalactol on the opposite side on two presentation nights.

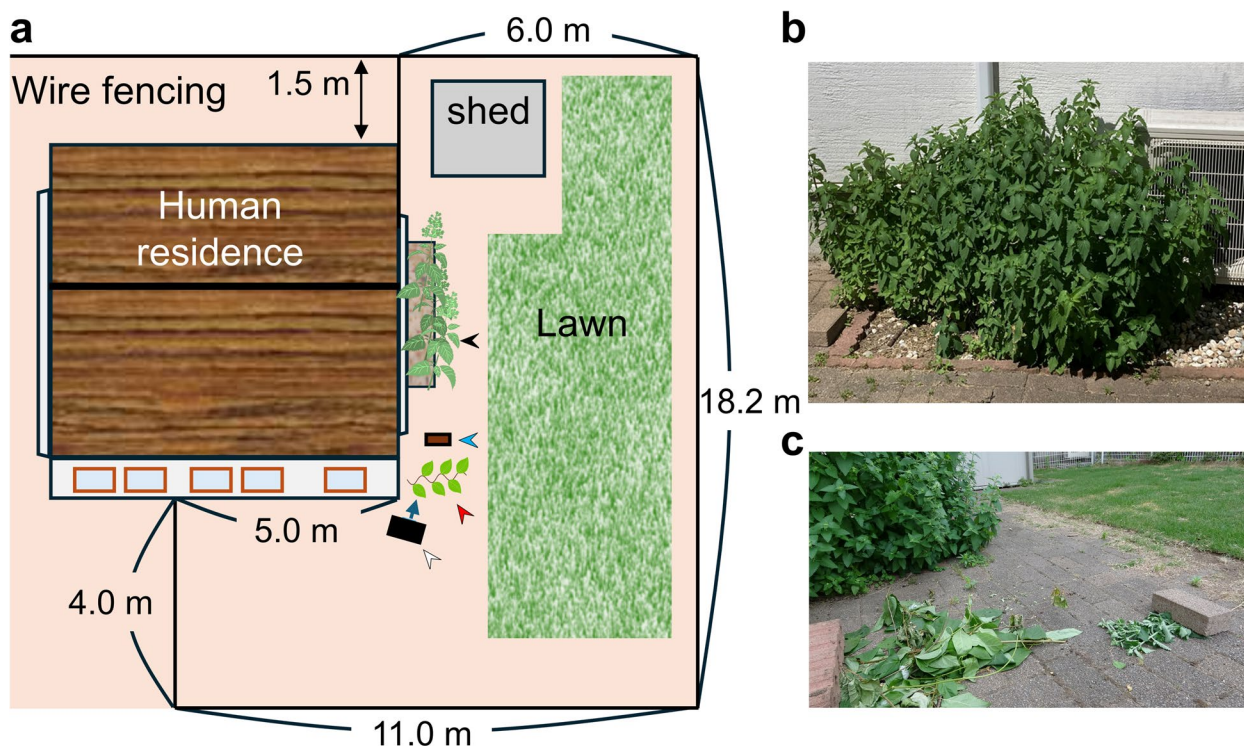
### Common Procedures for Experiments I and II

A total of 22 stimulus presentation events were conducted on free-roaming cats in the same garden where the catnip plant was cultivated. Although the garden was enclosed by wire fencing (height 1.2 m) and was adjacent to a human residence, free-roaming cats could freely enter and leave the garden by climbing over or passing under the fence. Stimuli were placed at 6:00 p.m. and left in place until 5:00 a.m. the following morning; each stimulus presentation event was conducted on a single date/night only. Field assays were conducted from June to September, and no trials were performed on rainy days. The order of stimulus presentation and the number of presentation events for each stimulus condition are summarised in Table 2. Because these assays were designed to compare voluntary responses to ecologically relevant stimuli, stimulus amounts were determined based on the measured iridoid content of each material and on doses that reliably elicited responses in previous behavioural assays (Uenoyama et al. 2022, 2021) rather than by matching absolute mass across conditions.

The behaviour of cats entering the camera's field of view near the stimuli was recorded using a trail camera (Sanwa Supply Inc., Okayama, Japan) placed on the ground. To minimise disturbance, human presence near the stimuli was avoided during the experimental trials. If an individual appeared, responded, left the area, and later returned and responded again on the same day, each visit was counted as an independent event. For clarity, repeated visits were treated as separate events only for descriptive reporting of encounter frequency; all inferential statistics were conducted at the individual level to avoid pseudoreplication (see Statistical analysis). Because the plant species (plants and

**Table 1** Overview of the experiments conducted in this study

Experiment	Subjects	Stimuli	Assay context	Comparison type	Main purpose	Number of presentations
I	Free-roaming cats	Intact catnip plant, fresh catnip material, fresh silver vine material	Outdoor, natural encounter	Free-choice encounter assay	To assess voluntary responses to intact plant-derived stimuli under outdoor conditions	10
II	Free-roaming cats	Catnip extract and silver vine extract on opposite sides of the same brick; catnip extract vs synthetic iridoids in some presentations	Outdoor, natural encounter	Close-proximity paired comparison	To compare responses to catnip- and silver vine-derived extracts under outdoor conditions	12
III	Captive purebred cats	Catnip extract vs silver vine extract on paired filter papers	Indoor, usual group-living environment	Simultaneous dual-stimulus assay	To test whether the bias toward silver vine is also observed in a larger captive cohort	22
IV	Laboratory cats	<i>trans</i> – <i>cis</i> nepetalactone, <i>cis</i> – <i>cis</i> nepetalactone, control, and catnip extract	Indoor, individual cage assay	Compound vs control assay	To assess the behavioural activity of additional nepetalactone isomers	<i>trans</i> – <i>cis</i> : 14 <i>cis</i> – <i>trans</i> : 12



**Fig. 1** Schematic of the garden used for behavioural assays with free-roaming cats. **a** The garden (129.2 m<sup>2</sup>) was enclosed by wire fencing (1.2 m high) and adjacent to a human residence; however, free-roaming cats could enter and leave the garden by climbing over or passing under the fence. Depending on the experiments, one of the following stimuli was placed on the ground near a growing catnip plant (black arrow): freshly harvested silver vine branches with leaves attached (red arrow; Experiment I in Table 1), a brick impregnated with cat-

nip extract and silver vine extract (Experiment IIa), or a brick treated with catnip extract and a synthetic iridoid (*cis-trans* nepetalactone or *cis-trans* nepetalactol; blue arrow; Experiment IIb). A trail camera (white arrow) recorded the behaviour of cats entering its field of view; the arrow attached to the camera icon indicates the camera's viewing direction. **b** A growing catnip plant. **c** Freshly harvested silver vine and catnip materials placed near the growing catnip plant

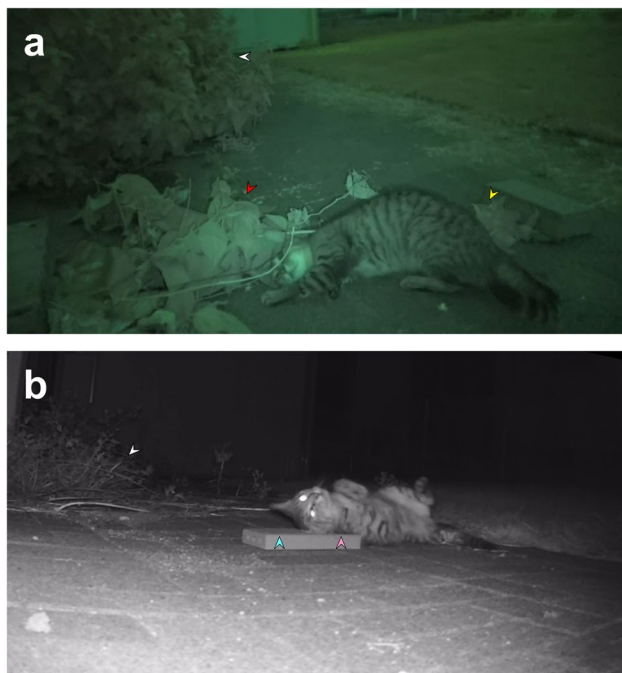
nip extract and silver vine extract (Experiment IIa), or a brick treated with catnip extract and a synthetic iridoid (*cis-trans* nepetalactone or *cis-trans* nepetalactol; blue arrow; Experiment IIb). A trail camera (white arrow) recorded the behaviour of cats entering its field of view; the arrow attached to the camera icon indicates the camera's viewing direction. **b** A growing catnip plant. **c** Freshly harvested silver vine and catnip materials placed near the growing catnip plant

materials) and extract types were visually distinguishable based on external appearance and colouration, behavioural scoring could not be performed under blinded conditions. Across all of the free-roaming assays, a total of six cats were recorded visiting the site. The precise age of the free-roaming cats was unknown, but based on observations, all six appeared to be adults. Based on external genital characteristics, three of the six cats were identified as males and one as a female, whereas the sex of the remaining two cats could not be determined. Free-roaming individuals were distinguished across visits based on stable external features visible in the videos (e.g., coat colour/pattern, hair length, body size, tail length and shape, and distinctive markings). Individual identity assignments were made consistently across recordings, and only visits for which the individual could be confidently identified were used for individual-level analyses. To minimise observer bias, rubbing/rolling was scored from video recordings using pre-defined behavioural criteria and a binary endpoint (presence/absence) by two observers (M.M. and R.U.).

### Experiment III. Simultaneous Dual-Stimulus Assay in Captive Purebred Cats

Twenty-two purebred cats housed at two zoological facilities in Japan were tested (Facility A: 9 cats, aged 5–9 years; Facility B: 13 cats, aged 3–16 years; Table 1). Behavioural tests were conducted with the permission and oversight of each facility. The breed, sex, and age of each cat are shown in Table 3. The captive assay was intentionally conducted in the cats' usual group-living environment rather than in individual cages. This design was chosen to preserve the animals' normal behavioural context and to assess whether they would voluntarily approach, investigate, or ignore the stimuli under conditions that differed as little as possible from their everyday state. According to husbandry records and caregiver reports at both facilities, the cats had not previously been given silver vine or catnip before the present study. Thus, to the best of our knowledge, this assay represented the first presentation of these plant-derived stimuli to this cohort.

Filter papers (5 × 10 cm, Advantec No. 526; Toyo Roshi Kaisha Ltd.) were impregnated with either catnip leaf



**Fig. 2** Representative self-anointing responses of free-roaming cats. **a** A free-roaming cat (Cat A) exhibiting rubbing and rolling toward freshly harvested silver vine material. **b** The same cat exhibiting rubbing and rolling toward a spot of silver vine extract applied to a brick. White, red, and yellow arrows indicate the growing catnip plants, silver vine material, and catnip material, respectively. Light blue and pink arrows indicate the catnip-treated side, and the silver vine extract-treated side of the brick, respectively

extract or silver vine leaf extract (each equivalent to 100 mg of fresh leaves). For each presentation, a pair of filter papers (catnip vs. silver vine; 15 cm apart) was placed simultaneously at multiple locations within the room in a randomised left–right order. Digital video cameras (Handycam HDR-CX680; Sony, Tokyo, Japan) were positioned in front of the papers to record the cats' behaviour. Videos were later scored to attribute rubbing and/or rolling behaviours to individuals. Because the catnip and silver vine extracts were visually distinguishable based on their colouration, behavioural scoring could not be performed under blinded conditions.

### Gas Chromatography/Mass Spectrometry (GC/MS) Analysis

One microliter of leaf extract (equivalent to 0.1 g of fresh leaves per ml in *n*-hexane) was injected into a QP-2010 Ultra GC/MS (Shimadzu Corp., Kyoto, Japan) at an injector temperature of 250 °C using an AOC-20i/s autosampler (Shimadzu Corp.) in splitless mode. The compounds in samples were separated on a DB-WAX column (60 m × 0.25 mm internal diameter, 0.25 μm film thickness; Agilent Technologies, Inc., Santa Clara, CA, USA) with helium carrier gas at a constant flow rate of 1.5 ml/min. The GC oven temperature

was maintained at 40 °C for 2 min, increased to 250 °C at a rate of 4 °C/min, and held at 250 °C for 10 min. The mass spectrometer was operated in electron ionization (EI) mode at 70 eV with an ion-source temperature of 200 °C, and mass spectra were acquired in full-scan mode over an *m/z* range of 35–500. Shimadzu GCMSsolution software (version 4.53; Shimadzu Corp.) was used to process the raw data. Peak identities in the total ion chromatograms were assigned by comparison of retention times and EI mass spectra with those of NMR-verified iridoid standards. Quantification was performed from extracted ion chromatograms for characteristic fragment ions of each compound (*m/z* 135 for *cis*–*trans* nepetalactol, *m/z* 81 for *cis*–*trans* nepetalactone, *m/z* 95 for iridomyrmecin, *m/z* 81 for isoiridomyrmecin, *m/z* 81 for dihydronepetalactone, and *m/z* 113 for isodihyronepetalactone). Peak areas were quantified using calibration curves constructed from authentic standards. Calibration curves for *cis*–*trans* nepetalactol were generated using standard solutions at 1.1, 2.2, 8.4, 34.2, 136.8, and 546.0 μg/mL, whereas those for the other iridoids were generated at 0.18, 0.36, 1.4, 5.7, 22.8, and 91.0 μg/mL. The limit of detection (LOD) and lower limit of quantification (LLOQ) were defined as signal-to-noise ratios of  $\geq 6$  and  $\geq 10$ , respectively.

### Experiment IV. Individual Laboratory Assays of *trans*–*cis* and *cis*–*cis* Nepetalactone

Sixteen healthy, mixed-breed domestic cats (ages 5–16 years; eight intact males, four intact females, and four spayed females) were used for the behavioural assay (Table 1). The cats were kept as laboratory cats at Iwate University, as described previously (Uenoyama et al. 2023). The sex and age of each cat are shown in Table 4.

Solutions of *trans*–*cis* nepetalactone and *cis*–*cis* nepetalactone were prepared at a concentration of 5 mg/ml in ethanol (reagent grade, 99.5% purity, FUJIFILM Wako Pure Chemical Corp.). Twenty-microliter aliquots of each solution (corresponding to 100 μg of each isomer) and 20 μl of ethanol were pipetted onto separate Petri dishes (9 cm diameter; Sansyo Co., Ltd., Tokyo, Japan), whose inner surfaces were abraded with 100-grit sandpaper to facilitate spreading of the compounds.

Fourteen cats were tested with *trans*–*cis* nepetalactone, and twelve cats were tested with *cis*–*cis* nepetalactone. Each cat was placed individually into test cages (93 cm × 63 cm × 59 cm) for the assay. Immediately before each assay, a dish containing a nepetalactone isomer and a control dish were placed 30 cm apart on the floor of the cage using double-sided tape, and the lids were removed. The position of the dishes (left or right) was randomised. Cat behaviour was recorded using a digital video camera (Handycam HDR-CX680; Sony, Tokyo, Japan) positioned in front of the cage.

**Table 2** Individual-level rubbing and rolling response of free-roaming cats to catnip- and silver vine-derived stimuli in outdoor experiments

Presentation event	Date	Experiment	Stimuli	Cat A	Cat B	Cat C	Cat D	Cat E	Cat F
1	13-Jun-24	I	CP, SM	SM	SM	-	-	-	-
2	18-Jun-24	I	CP, SM	-	-	-	-	-	-
3	19-Jun-24	I	CP, SM	-	-	-	-	-	-
4	20-Jun-24	I	CP, SM	SM	-	-	-	-	-
5	21-Jun-24	I	CP, SM, CM	SM×2	SM	SM	-	-	-
6	22-Jun-24	Ila	CP, CE, SE	-	-	A	SE, CE	-	-
7	23-Jun-24	Ilb	CP, CE, NN	-	A	A	-	-	-
8	25-Jun-24	Ila	CP, CE, SE	-	SE	-	-	-	-
9	27-Jun-24	Ilb	CP, CE, NL	-	NL	NL×2	-	-	-
10	13-Jul-24	Ila	CP, CE, SE	-	SE	SE, CE	-	-	-
11	14-Jul-24	Ila	CP, CE, SE	-	-	A	-	-	-
12	3-Aug-24	I	CP, SM	-	-	-	SM	-	A
13	4-Aug-24	I	CP, SM	-	-	-	-	-	-
14	5-Aug-24	I	CP, SM	-	SM×2	SM	SM	SM	-
15	6-Aug-24	I	CP, SM	-	SM	SM	SM×2	SM	-
16	9-Aug-24	I	CP, SM	SM	SM	SM	-	A	-
17	9-Sep-24	Ila	CP, CE, SE	SE	-	-	SE	-	-
18	10-Sep-24	Ila	CP, CE, SE	SE×2	-	-	-	-	-
19	11-Sep-24	Ila	CP, CE, SE	SE	-	-	-	-	-
20	12-Sep-24	Ila	CP, CE, SE	-	SE	-	-	-	-
21	13-Sep-24	Ila	CP, CE, SE	SE	-	-	-	-	-
22	16-Sep-24	Ila	CP, CE, SE	SE, CE	-	-	-	-	-

Abbreviations: *CP* intact catnip plant, *SM* silver vine material, *CM* catnip material, *CE* catnip extract, *SE* silver vine extract, *NN* *cis-trans* nepetalactone, *NL* *cis-trans* nepetalactol

Entries indicate the stimulus that elicited rubbing and/or rolling behavior during each presentation nights

Experiment numbers correspond to those defined in Table 1

“×2” denotes two rubbing/rolling responses by the same individual within a single night

“A” indicates that the cat appeared within the camera’s field of view but did not exhibit rubbing or rolling behavior

“-” indicates that the cat did not appear during the presentation event

To minimise observer bias, the presence or absence of rubbing and/or rolling toward each dish was scored from video recordings blinded to treatment identity.

After each assay, when the cats had shown no further interest in the stimuli for at least 10 min, a Petri dish impregnated with 100 µl of catnip extract (1 g fresh leaves per ml; corresponding to 100 mg of leaves) was presented as a positive control to confirm that the individual was capable of exhibiting rubbing and/or rolling behaviour.

## Statistical Analysis

At the individual level, a cat was scored as a positive responder to a stimulus if it exhibited rubbing and/or rolling behaviour at least once under that stimulus condition; otherwise it was scored as a negative responder. For analyses based on repeated observations across visits, visit-level responses were first converted to binary indicators (response present=1, absent=0) for each stimulus, and individual-level responses were then obtained by aggregating visit-level data using the maximum value across visits for each individual and stimulus. Because repeated visits by

the same individual are not independent and could inflate the effective sample size if treated as separate observations, inferential statistics were performed at the individual level (responded vs did not respond), whereas visit counts are reported descriptively. Paired differences in behavioural responses (presence or absence of rubbing and/or rolling) were analysed separately for the following comparisons: catnip versus silver vine, catnip extract versus silver vine extract, and *trans-cis* and *cis-cis* nepetalactone versus catnip extract. For each comparison, responses were evaluated using a two-sided McNemar’s test with a mid-P correction, based on a 2×2 contingency table of individual responses. The mid-P value was calculated from the exact two-sided binomial test by subtracting half the probability of the observed discordant cell count, thereby reducing the conservativeness of exact tests for small sample sizes (Fagerland et al. 2013; Pembury Smith and Ruxton 2020). For each comparison, the test evaluated whether the number of discordant individuals responding only to one stimulus differed from the number responding only to the other. All analyses were performed in R (version 4.5.2; R Foundation for Statistical Computing, Vienna, Austria) using RStudio

**Table 3** Individual characteristics and behavioural responses of captive purebred cats to catnip and silver vine extracts

Cat_id	Breed	Origin of breed	Sex	Age (years)	Rubbing and/or rolling toward catnip extract	Rubbing and/or rolling toward silver vine extract
1	American Shorthair	USA	M	9		✓
2	Exotic Shorthair	USA	M	8		✓
3	Munchkin	USA	M	9		✓
4	Scottish Fold	UK	M	9		✓
5	Exotic Shorthair	USA	M	8		✓
6	Maine Coon	USA	M	9		✓
7	Exotic Shorthair	USA	M	7		✓
8	Exotic Shorthair	USA	F	7		✓
9	Minuet	USA	F	5		✓
10	Scottish Fold	UK	F	8		✓
11	Persian	Iran	M	16	✓	
12	Russian Blue	Russia	F	11	✓	
13	Exotic Shorthair	USA	M	8		✓
14	Exotic Shorthair	USA	M	6		✓
15	Exotic Shorthair	USA	M	9		✓
16	American Shorthair	USA	M	8		✓
17	Bengal	USA	M	8	✓	✓
18	Exotic Shorthair	USA	M	8		✓
19	American Shorthair	USA	F	9		✓
20	Maine Coon	USA	M	3	✓	✓
21	Scottish Fold	UK	F	13		
22	Persian	Iran	M	15		

Abbreviations: *M* male, *F* female

The country of origin for each breed was obtained from the website of The International Cat Association ((TICA) 2026)

(version 2026.01.0+403). The R script used to reproduce the McNemar's tests from the supplementary datasets (electronic supplementary material, Tables S1–S3) is provided as electronic supplementary material, code S1.

## Results

### Responses of Free-Roaming Cats to Catnip and Silver Vine

In the initial outdoor free-choice encounter assays in which freshly harvested silver vine material was presented near a cultivated catnip plant (Experiment I in Table 1), 23 visits by six free-roaming cats were recorded across 10 presentation nights. Five of the six cats were recorded on multiple occasions across multiple presentation days. They exhibited rubbing and/or rolling behaviour toward silver vine material during 21 of the 22 visits in which they appeared (Fig. 2a and Table 2; electronic supplementary material, Movie S1 and Table S1). However, no such behaviour was observed toward either the catnip plant or catnip material. The remaining cat appeared only once and did not respond to any of the stimuli. At the individual level, a significantly

higher proportion of free-roaming cats responded to silver vine material than to catnip (defined as a response to either the live plant or freshly harvested material) (Discordant pairs: silver vine yes/catnip no=5; catnip yes/silver vine no=0. mid-P McNemar's test,  $p=0.031$ ;  $n=6$ ).

In the subsequent assays using a brick impregnated with catnip and silver vine extracts (Experiment IIa in Table 1), four of the six free-roaming cats appeared on camera, yielding 14 visits across ten presentation days between June and September (Fig. 2b and Table 2; electronic supplementary material, Table S1). Three cats (Cats A, C, and D) showed rubbing and/or rolling behaviour toward both extracts, whereas one cat (Cat B) responded only to the silver vine extract. Among the three cats that responded to both extracts, two showed more frequent responses toward the silver vine-treated side than toward the catnip-treated side of the brick (Cat A: silver vine side only in 5/6 visits; Cat D: silver vine side only in 1/2 visits). No cat responded exclusively to the catnip-treated side without also responding to the silver vine-treated side.

In the final assays using a brick treated with catnip extract and synthetic iridoid standards (Experiment IIb in Table 1), three of the six free-roaming cats appeared on camera, yielding six visits across two presentation days in

**Table 4** Individual-level rubbing and rolling response of laboratory cats to *trans-cis* and *cis-cis* nepetalactone

Cat_id	Sex	Age (years)	<i>trans-cis</i> nepetalactone (n=14)	<i>cis-cis</i> nepetalactone (n=12)	Catnip extract (n=16)
1	SF	14	✓	-	✓
2	IM	10		-	✓
3	IM	5	✓	-	✓
4	IF	7	✓	-	✓
5	IM	5	✓	-	✓
6	IF	16	✓	✓	✓
7	IF	15	-	-	✓
8	IF	5	✓	✓	✓
9	SF	13		✓	✓
10	SF	12	✓	-	✓
11	IM	5	✓	✓	✓
12	IM	5	-	-	✓
13	IM	6	✓		✓
14	IM	5	-		✓
15	SF	7	✓		✓
16	IM	7	✓		✓

Abbreviations: *IM* intact male, *IF* intact female, *SF* spayed female

"✓" indicates that the cat exhibited rubbing and/or rolling behaviour  
 "-" indicates that the cat did not exhibit rubbing and/or rolling behaviour

Blank cells indicate that the cat was not included in the specific assay

June (electronic supplementary material, Table S1). Two cats (Cats B and C) showed rubbing and/or rolling behaviour toward *cis-trans* nepetalactol, a major bioactive compound in silver vine, whereas no cat responded to *cis-trans* nepetalactone, a predominant iridoid in catnip. Across all presentation days and stimuli, no rubbing or rolling behaviour was observed toward the nearby growing catnip plant or freshly harvested catnip material.

### Responses of Captive Purebred Cats to Catnip and Silver Vine Extracts

Because the outdoor observations involved only a small number of identifiable free-roaming cats from a single site, we next asked whether the lower probability of response to catnip than to silver vine would also be observed in a larger and more diverse domestic cat population under similarly free-choice conditions. We therefore presented catnip and silver vine extracts within the usual living environment of 22 captive purebred cats representing nine breeds originating from the USA, the UK, Russia, and Iran, such that whether to approach, investigate, or ignore the stimuli was left entirely to the cats themselves (Experiment III in Table 1). The cats remained in their usual group-living environment during testing and had no known prior exposure to silver vine or catnip. When catnip and silver vine extracts were

presented simultaneously, rubbing and/or rolling behaviour was observed in only three cats toward the catnip extract, in one cat toward both extracts, and in 15 cats toward only the silver vine extract (Table 3; electronic supplementary material, Movie S2 and Table S2). The remaining three cats sniffed the papers but did not show rubbing and/or rolling behaviour. At the individual level, a significantly higher proportion of cats responded to the silver vine extract than to the catnip extract (discordant pairs: silver vine extract yes/catnip extract no=15; catnip extract yes/silver vine extract no=3; mid-P McNemar's test,  $p=0.004$ ;  $n=22$ ).

### Chemical Analysis of Catnip Extract

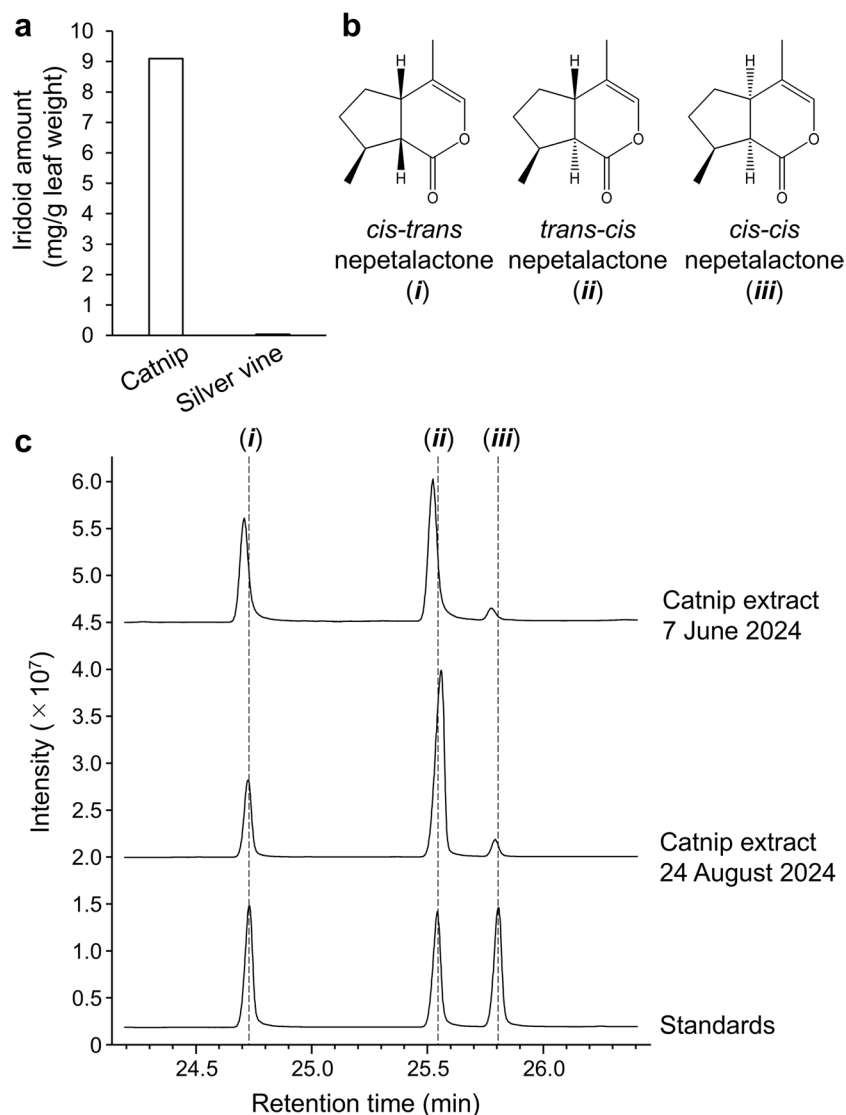
Given the infrequent responsiveness to catnip and catnip-derived stimuli compared with silver vine, we examined the quantity and chemical composition of the catnip extract. GC/MS analysis revealed the presence of *cis-trans* nepetalactone at 9.1 mg per g of fresh leaves (Fig. 3a, b). By contrast, the total amount of bioactive iridoids (*cis-trans* nepetalactol, isoiridomyrmecin, and dihydronepetalactone) in the silver vine leaf extract used in this study was 53.4 µg per g of fresh leaves, which was approximately 170-fold lower than that in catnip (Fig. 3a).

Comparison of GC retention times and EI mass spectra with NMR-verified reference compounds further confirmed the presence of other geometric isomers of nepetalactone, *trans-cis* nepetalactone (iridoid ii in Fig. 3b) and *cis-cis* nepetalactone (iridoid iii), in addition to *cis-trans* nepetalactone (iridoid i). Thus, the catnip material used in the present study, despite eliciting low behavioural responsiveness, contained substantial amounts of the bioactive *cis-trans* nepetalactone as a major component, although other nepetalactone isomers were also detected. These results indicate that the weak behavioural responsiveness observed here cannot be explained simply by a lack of *cis-trans* nepetalactone from the catnip stimulus material.

### Bioactivity of Nepetalactone Isomers in Laboratory Cats

We finally examined whether the other geometric isomers of nepetalactone (*trans-cis* and *cis-cis*) also elicited such behaviour in laboratory cats (Experiment IV in Table 1). Rubbing and/or rolling was observed in eleven of the fourteen cats tested in response to 100 µg of *trans-cis* nepetalactone (Table 4; electronic supplementary material, Table S3), whereas only three of twelve cats responded to 100 µg of *cis-cis* nepetalactone. In both assays, all tested cats were confirmed to exhibit clear rubbing and/or rolling toward the catnip extract (equivalent to 100 mg fresh leaves). The proportion of cats responding to *cis-cis* nepetalactone was

**Fig. 3** Nepetalactone isomer composition in catnip extracts. **a** Iridoid amount (total of *cis-trans* nepetalactol, *cis-trans* nepetalactone, iridomyrmecin, isoiridomyrmecin, dihydronepetalactone, and isodihydronepetalactone) in extracts of catnip and silver vine leaves used in this study. **b** Chemical structures of nepetalactone isomers. **c** GC/MS total ion chromatograms of catnip extracts harvested on 7 June 2024 and on 24 August 2024, and authentic standards of the three nepetalactone isomers (Standards). Dashed lines indicate the retention times of each isomer. Supplementary Fig. S1 shows the mass spectra of iridoids i-iii



significantly lower than that responding to the catnip extract (Discordant pairs: *cis-cis* nepetalactone yes/catnip extract no=0; catnip extract yes/*cis-cis* nepetalactone no=9. mid-P McNemar's test,  $p=0.002$ ;  $n=12$ ). In contrast, the response rate to *trans-cis* nepetalactone did not differ significantly from that to the catnip extract (Discordant pairs: *trans-cis* nepetalactone yes/catnip extract no=0; catnip extract yes/*trans-cis* nepetalactone no=3. mid-P McNemar's test,  $p=0.125$ ;  $n=14$ ).

## Discussion

A central question in the field of chemical ecology is whether the detectability of a cue is sufficient for it to function as an effective behavioural cue. Many studies demonstrate that specific compounds can elicit behavioural responses under controlled laboratory exposure. However, in natural

environments, animals can freely approach, investigate, or ignore stimuli, and behavioural activation therefore depends not only on sensory detection but also on the probability that detection leads to voluntary engagement. A key strength of this study is that behavioural responses were evaluated under free-choice conditions without capturing, confining, or transferring cats to experimental cages. Instead, stimuli were presented within the usual environments of both free-roaming and captive purebred cats, allowing individuals to approach, investigate, or ignore them voluntarily. Even though catnip contained abundant bioactive iridoids and its major compound is known to induce self-anointing in laboratory assays, intact catnip rarely triggered this behaviour under free-choice conditions. In contrast, silver vine consistently elicited voluntary engagement across both free-roaming and captive populations. These findings suggest that behavioural reliability, the probability that detection leads to behavioural activation, may represent an important

ecological filter determining whether a chemical cue functions effectively.

Previous studies with captive cats reported higher response rates to silver vine than to catnip using dried materials (Bol et al. 2017, 2022). Our results show that this difference persists even when cats encounter fresh plant-derived stimuli under natural outdoor conditions. A similar bias toward silver vine was also observed in captive purebred cats of diverse breeds tested in unconstrained enclosures, indicating that the reduced effectiveness of catnip is not restricted to a single free-roaming population but reflects a broader behavioural pattern across domestic cats. Recent field observations reported in a preprint on European wildcats (*Felis silvestris silvestris*) also described more frequent interactions with silver vine than catnip, although the difference did not reach statistical significance (Linxweiler 2025). While preliminary, this observation is consistent with the pattern reported here. More broadly, these results suggest that the ecological effectiveness of a chemical cue depends not simply on chemical abundance or laboratory bioactivity, but on whether it reliably elicits voluntary engagement under free-choice conditions.

Our findings suggest that chemical abundance or potency demonstrated under laboratory conditions does not necessarily predict ecological effectiveness. Previous headspace analyses showed that intact catnip releases substantially greater quantities of iridoids than intact silver vine (Uenoyama et al. 2022), and catnip has long been regarded as a prototypical cat-attractant (Miller 1768; Tucker and Tucker 1988). Notably, the catnip extract used here contained more *cis-trans* nepetalactone than the catnip extract used in our previous study, in which catnip-derived material reliably elicited rubbing and/or rolling behaviour in laboratory cats (Uenoyama et al. 2022). Historical descriptions also indicate that domestic cats strongly interact with catnip, but also suggest that the response depends on plant condition. For example, Miller (1768) noted that cats were especially attracted to catmint when it was withered, and described rolling, tearing, and chewing behaviour toward the plant. These observations indicate that the lower behavioural reliability of intact catnip observed here is therefore unlikely to be explained simply by lower iridoid bioavailability. Instead, behavioural expression toward catnip may depend not only on the presence of bioactive iridoids, but also on stimulus state and presentation. In this context, our findings do not suggest that catnip lacks biological activity; rather, they indicate that under the present free-choice conditions, fresh intact catnip elicited voluntary self-anointing less reliably than silver vine.

The infrequency of responses to intact catnip plants in the garden contrasts with captive studies in which catnip-derived stimuli, including *cis-trans* nepetalactone and

catnip leaf extract, reliably elicited rubbing and rolling behaviour (Uenoyama et al. 2022). Notably, free-roaming cats that responded to the catnip extract did not consistently respond to the nearby intact catnip plant, suggesting that stimulus form and encounter context may influence behavioural expression. Moreover, repeated responses to silver vine-derived stimuli were observed across visits separated in time, indicating that responsiveness to silver vine was stable rather than transient. These observations support a genuine difference in the likelihood of voluntary engagement rather than simple sensory detection failure or temporary desensitization.

Why might intact catnip be less reliable under outdoor free-choice conditions? One possible explanation is that behavioural responses to catnip are modulated by the composition of its volatile blend. However, our results suggest that the weak responsiveness to intact catnip is not readily explained by a simple antagonistic interaction among nepetalactone isomers. Although *cis-trans* nepetalactone is bioactive (Bol et al. 2022; Sakurai et al. 1988; Uenoyama et al. 2022, 2021), intact catnip emits multiple nepetalactone isomers together with other volatiles. In insect chemical ecology, behavioural attraction often depends critically on precise isomer ratios and minor components (Ansebo et al. 2005; Lassance 2010; Xu et al. 2016), raising the possibility that non-*cis-trans* components modulate behaviour output. However, our additional cage assays showed that *trans-cis* and *cis-cis* nepetalactone elicited rubbing and/or rolling in at least some individuals, and subsequent presentation of catnip extract elicited clear responses in all tested cats after exposure to these isomers, despite containing all three nepetalactone isomers. These findings suggest that any blend-dependent effect is likely to be more complex than simple antagonism among nepetalactone isomers.

A more plausible explanation is that stimulus delivery differs fundamentally between intact plants and their extracts. Free-roaming cats that responded to catnip extract on bricks often did not respond to the nearby intact catnip plant, suggesting that the physical presentation of the stimulus influences whether cats transition from detection to voluntary self-anointing. Intact catnip plants release a relatively strong, continuous odour plume whose intensity and composition may fluctuate with microclimate and plant condition. In chemically mediated systems such as insect pheromone communication, excessively high signal concentrations can sometimes reduce behavioural attraction (Rosell et al. 2008). In mammals, concentration-dependent recruitment of additional receptor populations can alter perceived odour quality (Doty 2025; Gross-Isseroff and Lancet 1988; Zgarbová and Vrzal 2023). Although airborne concentrations were not quantified here, these considerations raise the possibility that odour intensity or plume structure

from intact catnip reduces the probability that initial investigation develops into sustained rubbing and rolling. This interpretation is also consistent with the widespread use of dried catnip in enrichment products, where lower emission may fall within a more effective behavioural range.

In contrast, silver vine appears to provide a particularly robust stimulus for self-anointing across both controlled and naturalistic contexts. Silver vine leaves release a chemically complex blend, including *cis-trans* nepetalactol, isoiridomyrmecin, dihydronepetalactone, and isodihyronepetalactone, together with numerous minor iridoids (Obara et al. 2024; Uenoyama et al. 2023). Mechanical damage caused by feline licking and chewing further increases the chemical complexity of silver vine and enhances both feline responsiveness and mosquito repellency (Uenoyama et al. 2022). Such damage-dependent amplification may help maintain stimulus salience during interaction, increasing the likelihood that initial investigation progresses to prolonged rubbing and rolling.

The low frequency of spontaneous interaction with intact catnip under outdoor free-choice conditions also raises the possibility that catnip may not represent the primary ecological context in which this behaviour evolved. One speculative hypothesis is that felid responsiveness originated in association with plants producing more chemically diverse or damage-responsive iridoid blends, such as silver vine or similar ancestral plants. This idea is consistent with the incorporation of licking and chewing into the behavioural sequence, because in silver vine mechanical damage increases iridoid diversity and enhances mosquito-repellent activity, whereas in catnip nepetalactone remains the dominant compound regardless of leaf damage (Uenoyama et al. 2022). If so, the behavioural response to catnip may reflect a broader sensory responsiveness to iridoid-producing plants rather than the primary route by which this behaviour evolved. However, this interpretation remains speculative and will require comparative ecological, behavioural, and genomic investigation.

Several limitations should be considered when interpreting the present study. The catnip stimuli were derived from a single cultivated patch, and the silver vine material was collected from a single wild population. These limited sources may constrain the generality of the findings. The sample size of free-roaming cats was modest and derived from a single site, and behavioural scoring could not be blind because the stimuli were visually distinguishable. In addition, the captive purebred cats were tested while freely moving within their usual group-living environment rather than in strict individual isolation. This design was intentional, because our aim was to preserve the cats' usual living conditions rather than recreate a conventional cage-based bioassay. Although responses were attributed to identified

individuals and multiple stimulus pairs were distributed within the room, we cannot exclude potential effects of social facilitation, local occupancy, or short-range competition for access. In the captive dual-stimulus assay, the two filter papers were placed 15 cm apart so that cats could readily encounter both odours during a single approach under similar local conditions; however, greater spatial separation would have increased independence between the two stimuli. Similarly, in the outdoor extract assay, catnip and silver vine extracts were presented on opposite sides of the same brick so that a free-roaming cat would be likely to encounter both stimuli within a single visit and under similar microenvironmental conditions. We therefore cannot exclude partial overlap of their odour plumes, and this assay should be interpreted as a close-proximity comparison of responses directed toward the two treated sides of the brick rather than as a fully spatially separated dual-choice test. Nonetheless, video analyses confirmed that cats directed their behaviour to specific sides of the brick, and we did not observe evidence that the nearby alternative stimulus suppressed behavioural responses. We also cannot exclude the possibility that prior experience with plant-associated volatile blends contributed to behavioural responses in the free-roaming cats, whose exposure histories were unknown. By contrast, the captive cohort had no known prior exposure to silver vine or catnip before the present assays. The captive assay should therefore be interpreted as an unconstrained test of voluntary engagement in a naturalistic social context rather than as a fully independent individual-choice assay. Nonetheless, the behavioural response of cats to silver vine and catnip was pronounced, and the same directional bias toward silver vine was independently observed in the captive cohort. Moreover, chemical analyses confirmed that the catnip used here contained abundant bioactive nepetalactone. Taken together, these lines of evidence support a difference in behavioural reliability under the present conditions, although the extent to which this reflects innate responsiveness, associative learning, or both remains to be determined.

In conclusion, our findings highlight a general principle of chemically mediated interactions: ecological effectiveness depends not only on the detectability or abundance of a cue, but also on how reliably it triggers voluntary behaviour when animals can freely engage or disengage. Thus, chemical potency demonstrated under controlled exposure does not necessarily translate into behavioural reliability under natural encounter conditions. Evaluating chemically mediated interactions under free-choice conditions may therefore provide an important bridge between laboratory bioassays and the ecological function of chemical cues.

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**Data Availability** The datasets supporting this article are included in the electronic supplementary material (Tables S1–S3), which contain the visit-level behavioural observations and the individual-level behavioural response data used for the statistical analyses reported in this study. The R script used to carry out the McNemar's tests from these datasets is also provided as electronic supplementary material (Code S1). A README file describing the datasets and analysis code is provided to assist users in reproducing the analyses.

## Declarations

**Competing interests** The authors declare no competing interests.

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