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Chemosensory behavioural responses to prey and conspecific chemical stimuli in *Elaphe quatuorlineata* (Bonnaterre, 1790)

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Abstract. Skin lipids and other semiochemicals of the integument of snakes act as chemical signals and have various functions, but the behavioural responses to semiochemicals are rarely studied. In this study, we isolated the scent of the Four-lined Snake (*Elaphe quatuorlineata*) both from a living individual and from shed skin. We then examined the tongue-flicking responses of these snakes to determine if isolated lipid extractions of snake skin could be recognized by conspecifics. We detected that the snakes flicked their tongues more frequently when exposed to the scent of prey and shed skin extract than to a control with no scent. We also examined the influence of ontogeny, with adult female snakes exhibiting higher relative tongue flick rates than subadult females. *Elaphe quatuorlineata* is protected and listed as Near Threatened by the IUCN, and these snakes are difficult to detect for biomonitoring purposes due to their elusive lifestyle. The use of semiochemicals that elicit behavioural responses could facilitate field searches, improve knowledge of the species' biology and behaviour, and contribute to its conservation.

Keywords. Chemical communication, sexual cues, dietary cues, pheromones, behaviour, snakes, protected species

Introduction

Squamate reptiles use chemical cues for a variety of behaviours, including exploration, prey and predator detection, optimal foraging, mate choice, mate searching, tracking, courtship behaviour, and other aspects of their social behaviour (Halpern and Kubie, 1983; Schwenk, 1995; Clark, 2007; Mason and Parker, 2010; Wyatt, 2014; Kutsuma et al., 2018; Teshera and Clark, 2021; Jellen et al., 2023). Organisms can also produce species-specific chemical signals or pheromones (see Wyatt, 2014), which are found in the skin, glands, or faeces. These are molecules that have evolved as signals between conspecifics and trigger a specific behavioural response or developmental process (Karlson and Lüscher, 1959). In squamate reptiles, some chemicals in the skin, faeces, and glandular secretions are used for intraspecific communication, but due to the wide variety of conspecific responses, these chemicals are generally considered "semiochemicals" rather than pheromones (Wyatt, 2014).

In snakes, semiochemicals are mainly components of skin lipids (Mason et al., 1989) and are not produced by glands. When a snake moves over the substrate, semiochemicals are deposited together with skin lipids and leave a chemical trail. Conspecifics that encounter this trail can perceive the semiochemicals with their Jacobson's organ during "tongue-flicking" (Halpern and Kubie, 1983; LeMaster et al., 2001; Houck, 2009), which also provides directional information (Halpern, 1992; Schwenk, 1995). Chemical trails in snakes are thought to be used for aggregation, locating potential mates, and locating winter hibernacula in species that hibernate communally (Ford, 1986).

Previous studies have shown that snakeskin semiochemicals are primarily non-volatile compounds consisting of long-chain (C25–37) saturated mono- and di-unsaturated methyl ketones (Mason et al., 1987, 1989, 1990; Murata et al., 1991; LeMaster and Mason, 2002). This has been analysed quite extensively in a few American and Australian species, with much less known about the skin chemicals of European species (but see Andonov et al., 2020, 2023). A comprehensive study that analysed skin secretions from 13 Old-World snake species using two extraction methods identified 88 compounds (predominantly alkanes) with potential roles in water permeability, defence, and communication (Andonov, 2023). In addition, there are some studies suggesting that airborne compounds may

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also be present in snakes and play an important role in their chemical communication (Shine and Mason, 2001; Aldridge et al., 2005).

The Four-lined Snake, *Elaphe quatuorlineata*, is a large (up to 250 cm in total length), non-venomous European colubrid (Fig. 1). It inhabits Mediterranean biotopes, usually with ample vegetation, such as meadows with broad hedgerows, maquis vegetation and dry stone-walls, edges of open deciduous forests and scrubby areas around swamps and lakes (Speybroeck et al., 2016). *Elaphe quatuorlineata* has a fragmented distribution, occurring in mainland Italy south of Tuscany and along the eastern Adriatic coast, including many Mediterranean islands, in most parts of Greece with many Aegean and Ionian islands, and in extreme southwestern Bulgaria (Kornilios et al., 2014; Sillero et al., 2014). It is usually found at elevations below 900 m but can occur at up to 1400 m in the southern part of its range (Speybroeck et al., 2016). It is classified as a near threatened species by the IUCN (Crnobrnja-Isailović et al., 2009) and protected by the European Union's Habitat Directive and the Bern Convention.

In a recent publication by Andonov et al. (2023), 48 compounds were detected in the skin secretion mixture of *E. quatuorlineata*. However, no study to date has investigated or documented the species' responses to these chemical stimuli. In our study, we describe for the first time the behavioural response to semiochemicals in *E. quatuorlineata* by analysing the responses to different chemical stimuli by measuring tongue flicking behaviour.

Material and Methods

Test subjects. We procured eight captive *E. quatuorlineata* (three adult females, three subadult females, two subadult males; Table 1). These individuals were captive born, except for one adult female, found in 2019 in Ljubljana, the capital city of Slovenia. This location is outside of the natural range of *E. quatuorlineata*, and the animal was most likely transported there as an incidental "blind passenger" from the Adriatic coast; its exact origin is unknown. We did not include adult males because we limited our experiments to available captive animals.

In their captive setting, the three adult snakes were housed together in a 150 × 80 × 60 cm terrarium with an overhead heating lamp connected to a thermostat to simulate the day and night cycle. The subadults were housed together in a 120 × 50 × 45 cm terrarium with an identical heating system. Both terraria were equipped with a substrate composed of soil and leaf litter, sticks, pieces of bark, and a water dish. The snakes were fed every 14 days with frozen and thawed mice or rats, occasionally also with quail chicks.

Figure 1. Adult Four-lined Snake, *Elaphe quatuorlineata*, in its natural habitat, Dragonja, Slovenia. Photo by Davorin Tome.

All snakes hibernated between the end of November and the end of February at temperatures of 6–8 °C, with a gradual cooling period before and a gradual warming period after hibernation to mimic natural conditions (Mršić, 1997). Hibernation, cooling, and warming periods were simulated with a refrigerator, connected to a thermostat. Two adult females (AD-F-2 and AD-F-3) are siblings from the same clutch and unrelated to the third adult (AD-F-1). All subadults are descendants of AD-F-1, which was gravid when it was found in Ljubljana. The last oviposition of any adult female took place in 2019 or earlier, more than three years before the behavioural experiments of this study were conducted.

Sample collection. Skin lipids were collected in May 2021 using two different methods, (1) directly from a live individual and (2) from shed skin. We extracted skin lipids from a captive adult female that had never been in contact with the individuals used in the experiments, to avoid possible behavioural abnormalities in response to her own scent. We obtained skin lipids by dipping a cotton swab in hexane and rubbing it on the dorsal and lateral surfaces of the snake, avoiding contact with the cloaca and surrounding area to exclude chemicals that may be present in the faeces. Swabs were immediately wrapped in sterile aluminium foil to prevent contamination and stored at –8˚C.

To create an extract from freshly shed skins, we removed the head and cloacal sections and weighted the skin. To extract the odour sample, we followed the method of Baedke et al. (2019) and soaked the skin (3.21 g) in 200 ml of GC-grade hexane (Riedel-de Haën) for 24 h. Whole skin extract was concentrated by evaporating the solvent using a rotary vacuum evaporator (Buchi) to the final sample volume of 20 ml. Extract was kept in glass vials with polyethylene-lined screw caps in a freezer at –20°C.

Table 1. *Elaphe quatuorlineata* used in chemosensory behavioural experiments. ID numbers include a notation to identify adult (AD) and juvenile (JUV) male (M) or female (F) individuals. Age is given in years, and total length (TTL) in cm.

ID	Sex	Age	TTL	Origin
AD-F-1	F	> 6	143	Found in Ljubljana
AD-F-2	F	6	115	Born in captivity
AD-F-3	F	6	112	Born in captivity
JUV-M-1	M	2.5	88	Born in captivity
JUV-M-2	M	2.5	97	Born in captivity
JUV-F-1	F	2.5	92	Born in captivity
JUV-F-2	F	2.5	94	Born in captivity
JUV-F-3	F	2.5	89	Born in captivity

Experimental protocol. During experiments with snakes, we did not observe any stress-related behaviour (Benn et al., 2019). Hexane is a standard solvent used in reptile experimentation (e.g., Andonov et al., 2023) and handling was by the author who keeps the animals, so handling stress was minimized due to familiarity. We used sterile cotton swabs (e.g., Amo et al., 2004; Blouin-Demers and Weatherhead, 2001) to present one of five different scent substances in tongue flick experiments: Control 1 – dipped in hexane; Control 2 ("pungent control") – dipped in commercially available s.Oliver For Him perfume, diluted with water in a 1:9 ratio to avoid excessively strong odours to interfere with the chemosensory system, which might lead to non-specific or adverse reactions (Clark, 2007); Prey – dipped in hexane and rubbed on a thawed mouse (one of the main prey items of *E. quatuorlineata*); Extraction 1 – dipped in hexane and rubbed on the skin of a live *E. quatuorlineata*; Extraction 2 – dipped in the skin extract. The order of stimulus presentation was randomized. Each snake was tested five times in total, once with each scent and only once per day. The snakes were not fed at least six or at most 14 days before the experiment.

The experimental terrarium was a 51 × 36 × 30 cm glass terrarium with a mesh lid. The video camera was fixed on a metal stand approximately 1 m above the centre of the experimental terrarium. The terrarium was located in an empty room away from the room where the snakes were kept. The room had a constant temperature of 21–22°C and was illuminated with natural light from a window. Before the experiment, snakes were kept in their housing terraria, which were equipped with a heater so that they could thermoregulate and reach their activity temperature.

Experiments were conducted in April and May 2022 from 8:30–12:30 h to avoid the effects of season and time of day on snake activity patterns. The experiment began by placing the snake in a clean experimental terrarium, closing the lid, and going out of the room for 15 min to allow the snake to acclimate. All experiments were conducted by the first author. After the 15-min acclimation period, the experimenter slowly entered the room, removed the lid and turned on the video camera. A cotton swab with a particular chemical stimulus was positioned in front of the snake's snout at a distance of approximately 2–3 cm. Throughout the experiment, the cotton swab was constantly and slowly repositioned to follow the snake as it moved. This allowed the swab to remain in the immediate vicinity of the snake's snout

continuously for 5 min. At the end of the experiment, the swab was removed, the video recorder was switched off, and the snake was returned to its original terrarium. Before the next experiment, the experimental terrarium was cleaned with acetone and dried.

Tongue-flick analysis. We reviewed the video footage and counted the snake's tongue flicks (TFs) using the Counter app on a mobile phone. Since reptiles flick their tongues more frequently when active (Van Damme and Castilla, 1996) and we found that there was inter-individual variability in the activity rate of our studied individuals, we decided to calculate the relative number of tongue flicks (e.g., Žagar et al., 2015). First, we determined the activity time of the snake in each experiment by analysing the videos and recording the time in seconds when snake was moving (activity) and not moving (non-activity). The relative number of TFs was calculated by dividing the total number of TFs by the time of activity in seconds. In this way, we can compensate for the differences between snakes that are differently active in different experiments (Van Damme and Castilla, 1996, Žagar et al., 2015).

The number of TFs per second was used as the dependent variable. First, we used a Shapiro-Wilkins Test and a Levene's Test for Equality of Variance, which showed that the dataset was not normally distributed. We therefore transformed the data using a logarithmic transformation and also ensured the normality of residuals. We used a General Linear Mixed model (Gaussian distribution) with Sex-Age and Treatment (chemical cue) as factors and including Individual as a random factor. We used Tukey post-hoc tests to compare differences between data subsets divided by age and by scent. Results include Chi-square values (χ^2), degrees of freedom (*df*), and *p*-values. All analyses and visualizations were carried out in Jamovi (Jamovi Project, 2022) using R package *jmv* in R (R Core Team, 2024).

Results

There were statistically significant differences in TFs between three sex-age groups ($\chi^2 = 8.0523$, $df = 2$, p = 0.018; Fig. 2A) and among different scent treatments ($\chi^2 = 27.7562$, $df = 4$, $p < 0.001$; Fig. 2B). Among the sex-age groups tested in our study, adult females exhibited the highest TFs, significantly higher than TFs of subadult females (Fig. 2A, Table 2). Comparing the different scent treatments, we found significantly higher TFs of snakes towards prey and *E. quatuorlineata* skin chemicals compared to the control but not compared to the pungent control (Fig. 2B, Table 2).

Discussion

Tested *E. quatuorlineata* showed pronounced tongue-flicking behaviour when exposed to various scent treatments, including prey scent and semiochemical extractions from the skin of the same species. While we recognize that our sample size is small (three females and five subadults), we detected high responses to prey and potential semiochemicals extracted from shed skin, followed by the extract obtained from the swab of a live individual. Moreover, we showed that adult females exhibited higher relative tongue flicks than subadults, a result similar to what was found in previous studies (e.g., Aldridge et al., 2005). It is important to note that we did not include adult males, so a male-female comparison with males was not possible. Due to the behavioural variability observed in females, this is an interesting area for future studies.

Statistical analyses revealed a significant increase in relative tongue flicks towards prey and *E. quatuorlineata* skin extracts compared to control stimuli, indicating an increased interest in this specific stimulus. This was expected, since many snake species rely strongly on scent for foraging and hunting (Burghardt and Danny, 1983). However, these responses were not significantly higher than the responses to the perfume control. This apparent lack of an ability to discriminate against artificial scents is unexpected and may be due to the small sample size. Further studies are needed to clarify this result.

Table 2. Significance values for pairwise comparisons using Tukey's post-hoc tests on the significant factors in the general linear mixed model, Sex-Age and Treatment. The significance of *p*-values (*p*) is provided using asterisks for values ≤ 0.05 (*), ≤ 0.01 (**), and ≤ 0.001 (***).

Sex-Age		***p***
FJUV	FAD	0.013*
MJUV	FAD	0.350
MJUV	FJUV	0.481
Treatment		
Pungent control	Control	0.360
Prey	Control	< 0.001***
Extraction 1	Control	0.002**
Extraction 2	Control	< 0.001***
Prey	Pungent control	0.165
Extraction 1	Pungent control	0.346
Extraction 2	Pungent control	0.065
Extraction 1	Prey	0.995
Extraction 2	Prey	0.995
Extraction 2	Extraction 1	0.936

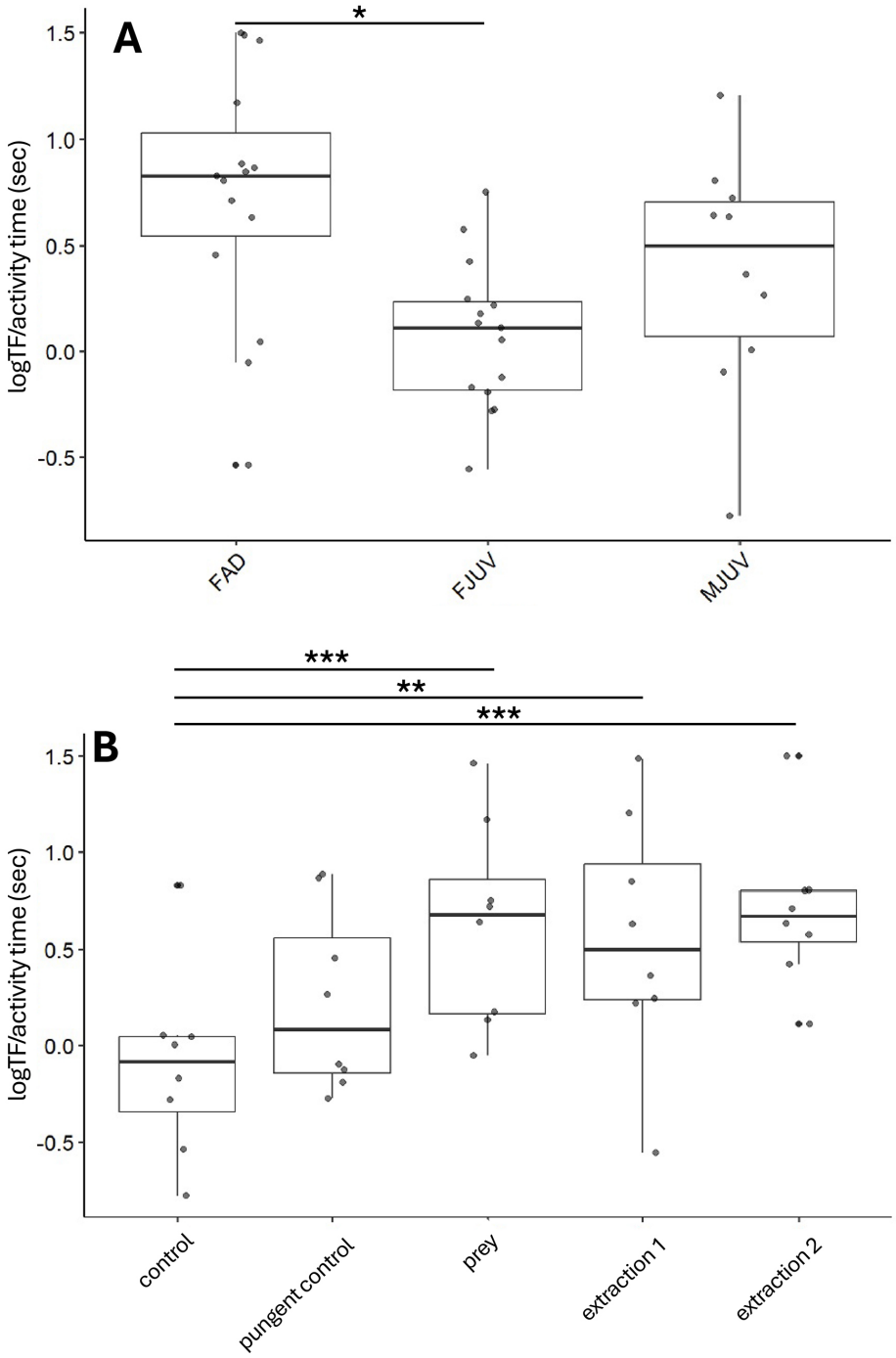

Figure 2. Log-transformed relative tongue flick frequency of *Elaphe quatuorlineata* from a chemosensory study, showing results for different (A) age-sex category and (B) scent treatments. Age-sex categories include female adults (FAD), female juveniles (FJUV), and male juveniles (MJUV). Scent treatments included a control with no scent (control); a control with perfume scent (pungent control); scent of a mouse, a potential prey (prey); skin semiochemicals obtained from a live specimen (extraction 1); and skin semiochemicals obtained from shed skin (extraction 2). Significant pairwise comparisons tested with Tukey post-hoc tests are labelled with a line and asterisks (*, $p \leq 0.05$; **, $p < 0.01$; ***, $p < 0.001$).

We detected slight differences in tongue-flicking responses to the snakeskin extracts, which were obtained by two different methods. Thus, it is possible that there was a difference in the semiochemical amount or concentration on the cotton swabs of these two test treatments, as reported by Andonov (2023), who did not detect any ketones in shed skin extracts while these were present in live animal extracts. However, the snakes still responded to these stimuli with high TFs compared to the control, suggesting that the concentration of semiochemicals obtained with this extraction method was still sufficient to elicit a clear behavioural response. Further investigation into the extraction efficiency and the threshold concentration necessary for behavioural activation is warranted to clarify these findings.

Overall, our main goal was to understand whether skin-extracted compounds elicited behavioural response in *E. quatuorlineata*. The use of lipid extracts from shed skins seems to elicit a response in adult females and subadults (males were not tested in our study). This result could be an important step towards the development of chemical-based monitoring of such an elusive and protected species. The next step would be to test whether these chemicals act as an attractant in a natural environment. If this is confirmed, special traps with lipid extracts could be developed and set up in study areas together with detection devices (such as automatic cameras; Walkup et al., 2022). Perhaps this elusive snake could be attracted and recorded for biodiversity monitoring purposes. Our results show promising potential for biomonitoring of *E. quatuorlineata* populations, but implementation is still some steps away.

Finally, certain limitations of our study must be acknowledged. Recommendations that could benefit further studies in this regard include: (i) increasing and balancing the sample size, both in terms of the number and sex of live animals and the number of skin samples; (ii) improving the methods of sampling skin semiochemicals by washing live snakes with hexane instead of skin sheds; (iii) consideration of the biology of the species in natural environments with possible seasonal effects during the breeding, pre- and post-hibernation periods; and (iv) application of a more sophisticated experimental design for the recognition tests that would also allow determination of the role and assessment of responses to individual compounds.

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