



Glyphosate-based herbicide increases the number of foraging trips but does not affect the homing of *Bombus terrestris*

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Abstract – The intensification of pesticide use is believed to be one of the main causes of the global decline in pollinators. The ability to forage resources effectively and return to the colony is crucial for individual eusocial bees and their colonies, and some pesticides are known to disturb this ability. Our study investigated the effects of the most widely used type of pesticide, glyphosate-based herbicides (GBHs), on the foraging and homing ability of the buff-tailed bumblebee, *Bombus terrestris* (L.) (Hymenoptera: Apidae). We conducted two experiments in which we exposed bees to field-realistic doses of GBH at colony and/or individual levels and observed their foraging activity and the homing ability of displaced bees. We found that 24-h colony-level GBH exposure increased the number of bumblebees' foraging bouts, but it did not affect the duration of bouts or the homing ability. Regarding the homing rate, there was a marginally significant interaction between acute individual-level treatment and release distance from the colony. Even though the negligible impacts of short-term GBH exposure on homing ability are encouraging, the greater number of (possibly unnecessary) foraging bouts after colony-level GBH exposure might be costly for bumblebees.

Bumblebee / Navigation / Pollinator / Pesticide exposure / RFID

1. INTRODUCTION

Insect pollinators are important for terrestrial biodiversity and agriculture, with 78–94% of flowering plants needing or benefiting from such pollinators and more than a third of crops depending on them (Klein et al. 2007; Ollerton et al. 2011). Insect pollinators are mainly bees, including a few managed species such as *Apis mellifera* (L.) (Hymenoptera: Apidae) and *Bombus terrestris* (L.) (Hymenoptera: Apidae), but they also include flies, butterflies, beetles, and thrips. The global decline in the abundance and diversity of insect pollinators (Zattara and Aizen

2021) calls for studies on the causes of this pollination crisis. The Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services has claimed that the increasing use of pesticides is one of the main reasons for the decline in pollinators (Potts et al. 2016). Pesticides can be classified into three main groups: insecticides, fungicides, and herbicides. Insecticides are used to control insect pests and are thus considered the highest risk for pollinators. In recent years, research on the consequences of pesticides for pollinators has focused on neonicotinoids (Lundin et al. 2015), which are known to have adverse effects on the health of pollinators (Laycock et al. 2014; Singla et al. 2021; Tsvetkov et al. 2017; Whitehorn et al. 2012; Woodcock et al. 2017) and the foraging and homing behaviors of honeybees (Matsumoto 2013; Stanley et al. 2016). However, the

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most common pesticides worldwide are herbicides, which account for approximately 60% of all used pesticides (Duke and Dayan 2018). Herbicides prevent the growth of unwanted vegetation in agriculture, horticulture, silviculture, and the management of urban environments. The most utilized active ingredient in herbicides is glyphosate (Benbrook 2016) with over 750 commercial products called glyphosate-based herbicides (GBHs) (Guyton et al. 2015). The action of glyphosate is based on the inhibition of the 5-enolpyruvylshikimate-3-phosphate (EPSP)-synthesizing enzyme in the shikimate pathway (Helander et al. 2012). The EPSP synthase enzyme is found only in green plants and many microbes (Leino et al. 2021). Therefore, glyphosate has been assumed to be safe for animals (Amrhein et al. 1980; Duke and Powles 2008). Nevertheless, recent studies have shown that glyphosate and GBHs might have harmful, nonlethal effects on nontarget organisms, including pollinators. The negative effects of glyphosate and/or GBHs on pollinators range from disrupting sensory and cognitive abilities (Farina et al. 2019; Helander et al. 2023a; Kaakinen et al. 2024; Vázquez et al. 2020) to delaying larval development (Odemer et al. 2020; Vázquez et al. 2018; Weidenmüller et al. 2022) and changing feeding and appetitive behaviors (Faita et al. 2020; Herbert et al. 2014; Mengoni Goñalons and Farina 2018). Glyphosate has also been found to disrupt honeybees' navigation ability by extending homing flights and affecting flight trajectories (Balbuena et al. 2015). Navigation is essential for efficient foraging; eusocial bees need to find high-quality feeding sites, handle flowers, and find their way back to the colony (Klein et al. 2017). Bees are known to use different sources of information to navigate, such as the position of the sun (Dovey et al. 2013; El Jundi et al. 2014; Wehner et al. 1994), patterns of polarized light (Dovey et al. 2013; El Jundi et al. 2014; Wehner et al. 1994), fine magnetic-field variations (Wajnberg et al. 2010), and visual scenes and landmarks (Collett et al. 2013; Goulson and Stout 2001). The ability to navigate across large distances from a central nest site is a cognitively demanding task, and an increasing

amount of time spent foraging and/or deteriorated homing ability can potentially result in colony failure (Bryden et al. 2013).

The negative effects of insecticides on beneficial insect pollinators are generally well understood as these chemicals are specifically designed to target insect pests. For instance, neonicotinoids are neuroactive pesticides that bind to nicotinic acetylcholine receptors (nAChRs) in the insect nervous system (Manjon et al. 2018; Simon-Delso et al. 2015). However, the exact mechanisms behind the effects of glyphosate and GBH on pollinators and other insects have remained unanswered. One potential explanation for glyphosate's negative impact is its effect on the gut microbiota (Blot et al. 2019; Helander et al. 2023a; Motta et al. 2018; Motta and Moran 2023). In addition to protecting bumblebees from parasites and pollutants (Koch and Schmid-Hempel 2011; Rothman et al. 2019), gut microbiota may affect cognitive functions such as memory (Li et al. 2021). Some bumblebee gut microbiota bacteria are known to be sensitive to glyphosate while others have been classified potentially resistant (Helander, Jeevanavar, et al., 2023a).

In this study, we investigated the effect of GBH (Roundup Flex) on bumblebees' foraging activity and homing ability by conducting two experiments with buff-tailed bumblebees (*B. terrestris*), which are important managed pollinators. Individuals of *B. terrestris* are central-place foragers that regularly forage 2 km from their colony (Walther-Hellwig and Frankl 2000) and can return to it from long distances (up to 9.8 km), mainly by using familiar landmarks and landscape features for navigation (Brebner et al. 2021; Goulson and Stout 2001). In the first experiment (called "foraging activity"), we compared the number and duration of foraging bouts between bees from colonies that were exposed to sub-lethal levels of GBH for 24 h and bees from untreated control colonies. We hypothesized that the bumblebees in the GBH-treated colonies would have a reduced number of foraging bouts and prolonged foraging time compared to those from the control colonies. In the second experiment (called "homing ability"),

we displaced individual bumblebees from their colonies, released them at certain distances (500 m and 1000 m), and observed their homing rate and homing time. Prior to displacement, the bumblebees were subjected to 24-h and/or single acute oral exposure to GBH, or they were fed with sugar water to serve as controls. We hypothesized that the bees with both acute and 24-h GBH exposure would perform worse than the control bees—that is, they would exhibit more homing failures and homing would take more time. In addition, we weighed colonies before and after the experiments to examine the colony-specific influence of 24-h GBH exposure. We predicted that the GBH-exposed colonies would be lighter at the end of the experiment compared to the control colonies due to longer foraging bouts, fewer gathered resources, and lost bumblebees that did not return home.

2. METHODS

2.1. Preparations

We conducted the two experiments in the Botanic Garden of University of Turku on the island of Ruissalo in southwestern Finland (N 60°26'00", E 22°10'23") in June and July 2023, using a total of 10 colonies of commercial buff-tailed bumblebees (*B. terrestris*) from Koppert B. V. Ruissalo is an elongated island (23.1 km²) that includes forest strips, meadows, open fields of different sizes, buildings, and roads. The two experiments were performed with different individual bees originating from the same colonies; the bees underwent the same procedure for the first days of the experiments. The timetable of both experiments is shown in Fig. 1. We always observed two colonies—GBH treatment and control—simultaneously (five paired replicates in total). Before the experiments (day 0), we transferred the bumblebee colonies in two-chamber wooden nest boxes (29 × 30 × 9 cm) connected to a wooden flight arena (60 × 45 × 25 cm) with a transparent top. We placed a mass feeder with a 40% sugar water solution into the flight arena to encourage foraging bumblebees to enter the

arena. Then, we marked 10–15 foraging bumblebees per colony (140 in total from 10 colonies) with tiny (1.5 mm³) radio frequency identification (RFID) tags (Microsensys mic3Q1.6), and we released them back into the colony. Each tag contained a unique identification number. When the tagged bee came within reach of the reader placed on top of the entrance, the tag received an electromagnetic signal from the reader and transmitted its identification number. The reader stored this information on its external memory together with the date and time. On the first day of the experiment (day 1), we weighed the nest boxes with the colony inside and placed them in a greenhouse. To let foraging bumblebees move between the colony and the external environment, we attached a transparent tunnel to the nest boxes that went through the wall of the greenhouse. Because the two colonies in each replicate were close to each other (3.5 m), we painted their entrances with different colors (green and silver) to ease their identification. Bumblebees were allowed to forage and familiarize themselves with the outside environment for 1 day (24 h). On day 2, we randomly assigned one of the colonies in the paired replicate to the 24-h GBH treatment and the other to the control treatment. The colonies assigned to the GBH treatment received a gravity feeder containing 30 mL of 60% sugar water with 10 mg/L of Roundup Flex (Bayer Agriculture BV, Belgium, registration number 3072; glyphosate concentration 480 g/L as glyphosate potassium salt CAS: 3,864,194–0), while the control colonies received a similar gravity feeder with only sugar water. The use of the gravity feeder allowed us to expose the entire colony simultaneously and observe possible colony-level effects afterwards. In previous studies conducted on honeybees, the concentration of glyphosate ranged between 2.5 and 10 mg/L (Balbuena et al. 2015; Herbert et al. 2014; Weidenmüller et al. 2022). As we used bumblebees, which face additional exposure routes (direct exposure of queens and exposure to soil residues) and may be exposed to larger amounts of pesticides than honeybees (Gradish et al. 2019), we chose to use 10 mg/L of glyphosate. This amount can be considered

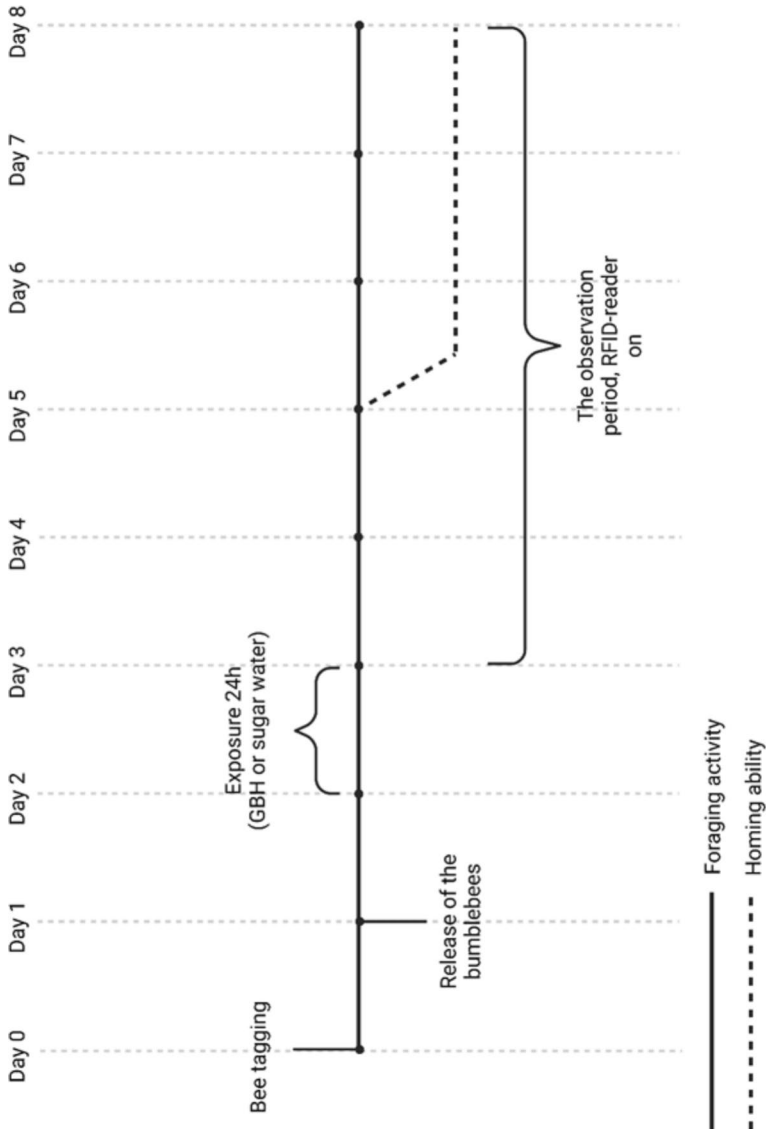


Figure 1. Timetable of the foraging activity and homing ability experiments conducted with paired colonies of *Bombus terrestris*. Each pair consisted of a control colony and a colony under 24-h glyphosate-based herbicide (GBH) exposure. Both colonies followed similar procedures until day 5, when the homing ability experiment began and involved new foraging bumblebees captured from the same colonies and individually exposed to GBH. Figure created with BioRender.com.

a field-realistic dose because nectar in recently GBH-treated flowers may contain up to 31.3 mg/kg of glyphosate residues (Thompson et al. 2014). The gravity feeders were placed inside the nest boxes; in all the colonies, the bumblebees had emptied them by the next day.

2.2. Foraging activity

On day 3, after a 24-h exposure period, we turned on the RFID tracking device. The bumblebees were allowed to enter and exit the colonies freely to forage for 5 days (days 3–8). The tracking device was connected to two entrance readers that were placed on top of the hives' entrances. All the arrivals and departures of the tagged bees were stored in the memory of the device with a time stamp, which enabled us to count the number of bouts that a single bee made during the observation period and estimate the duration of its foraging trips. After 5 days of free flying (day 8), we transferred the colonies indoors during nighttime when most of the bumblebees were back in the colonies. We weighed the colonies again, euthanized the bumblebees with CO₂, and placed them in a freezer. The data provided by the Microsensys tracking device consisted of a time stamp of the departure or arrival of the bee. First, we counted the number of bouts and the foraging time spent outside the colony of each tagged bee. For further analysis, we removed all the bouts where the time interval between departure and arrival was under 2 min to discard false bouts (e.g., guardian bees walking under the reader without leaving the colony) (Free 1955). We also removed all bouts that were longer than 8 h because some marked bees did not return by night. Drifting (i.e., entering the nonnatal colony by accident) is common for commercial *B. terrestris* (Lefebvre and Pierre 2007; MacKenzie et al. 2021; Zanette et al. 2014); in our experiment, 41% of the marked foraging bees visited a nonnatal colony at least once. Because colony-level treatment (GBH, control) did not affect the proportion of drifters (GLMM: $\chi^2=0.3471$, $df=1$, $p=0.56$), we handled visitations in the nonnatal colonies as normal visitations.

2.3. Homing ability

On day 5, we chose 8–12 nontagged foragers from both colonies in each paired replicate (Fig. 1)—a total of 112 bees. These bees had been observed entering the colony from outside, indicating that they had been foraging and could recognize landmarks around their colony. We marked the bees with RFID tags and recorded their original colony. These bees had already been exposed for 24 h to either sugar solution or sublethal levels of GBH solution (10 mg/L) for a 24-h period on day 2 in the first experiment (Fig. 1). For the newly marked bees, we conducted an acute exposure treatment by giving them either 7 μ L of plain 60% sugar water or 7 μ L of 60% sugar water with 5.28 g/L of glyphosate ($n=56$ bees per treatment originating from both the GBH-exposed and control colonies). The advantage of this exposure method compared to the gravity feeder was that it ensured the same dose of glyphosate for each treated bee. The concentration of this single acute dose given to half of the foragers was over 500 times stronger than the earlier colony-level exposure. Bumblebees may be exposed to such a high amount of GBH during the application of herbicides in the field (Gradish et al. 2019). As bumblebees may visit up to thousands of flowers a day, the given amount of active ingredient (~37 μ g) can still be considered a field-realistic dose. Next, we randomly selected two release sites for each paired replicate (GBH treatment and control) that were either 500 m or 1000 m from the colonies placed in the greenhouse. As the study area consisted of large open fields and dense forest, the actual release site was the closest open area to the randomly selected point (Fig. 2). We transported the marked and exposed (GBH, control) bees to the release sites in transfer boxes; half of the bees to the closer site (500 m) and the other half to the farther site (1000 m). We opened the transfer boxes one by one and let the bumblebees leave the release site. To prevent the bees from following each other, we waited until the previous treatment group of bees had left the release site before opening the next transfer box. Because the bees had been fed either with sugar water or sugar water with GBH just before releasing them, we expected



Figure 2. The release sites (yellow dots) of the homing ability experiment conducted on *Bombus terrestris*. The radii of the inner and outer circles are 500 m and 1000 m, respectively.

them to be motivated to return to the colony. The bees had 2.5 days to return to their colonies (Goulson and Stout 2001) until the colonies in the greenhouse were removed and replaced with a new pair of colonies. If a bumblebee did not return to its colony in a given time period, it was considered lost. If a bumblebee returned to the wrong (non-natal) colony during the designated 2.5-day period, it was still classified as “returned” because of the well-documented phenomenon of drifting between commercial *B. terrestris* colonies (Lefebvre and Pierre 2007; MacKenzie et al. 2021; Zanette et al. 2014), a phenomenon also consistently observed in our experiment (Table I).

2.4. Statistical analysis

2.4.1. Foraging activity

All the statistical analyses were performed using R version 4.3.2 (R Core Team 2023) applying a significance threshold of $p < 0.05$. We used linear mixed-effects models (LMMs) (lme4::lmer) (Bates et al. 2015) to examine whether the number and duration of the foraging bouts differed between the two treatments (GBH-exposed for 24 h and control colonies). We also included date as a continuous explanatory variable to investigate a possible temporal

Table 1 Summary data regarding the foraging activity and homing ability experiments, as well as *Bombus terrestris* colony growth. Back-transformed least square mean and standard error (SE) with sample sizes (*n*). *P* value indicates the significant differences between treatments (n.s. = not significant, **p* < 0.05)

	Control			Glyphosate-based herbicide			
	Mean	SE	<i>n</i>	Mean	SE	<i>n</i>	<i>p</i>
Foraging activity							
Drifting %	0.43	± 0.091	13/30	0.37	± 0.06	20/55	n.s.
No. bouts per bee	9.12	± 4.21	30	17.6	± 7.78	55	*
Average time spent on bouts per bee	44.70 min	± 7.43 min	30	35.52 min	± 4.71 min	55	n.s.
Homing ability							
Proportion of bees returned (24-h exposure)	46.11%	± 7.54%	56	34.28%	± 7.23%	56	n.s.
Proportion of bees returned (acute exposure)	32.63%	± 7.04%	56	47.94%	± 7.60%	56	n.s.
Time taken to return per bee (24-h exposure)	10 h 32 min	± 4 h 44 min	26	8 h 22 min	± 3 h 52 min	20	n.s.
Time taken to return per bee (acute exposure)	12 h 29 min	± 5 h 46 min	19	7 h 4 min	± 3 h 9 min	27	n.s.
Colony growth							
Weight difference	-0.45%	± 0.52	5	-1.02%	± 0.75	5	n.s.

trend in foraging activity during the experiment, particularly concerning the duration of foraging bouts. The paired replicate and bee's identification number were used as random factors to consider multiple observations from the same bees. Both the response variables were log transformed to improve the fit of the model residuals. For both models, we determined the significance of the fixed explanatory variables using *F* tests with the type III Kenward-Roger's method for adjusting the denominator degrees of freedom (`lmerTest::anova`). We visually verified the model assumptions from the residual plots.

2.4.2. Homing ability

We investigated the effects of GBH exposure and release distance on the homing rate and homing time of dislocated bumblebees. The homing rate was defined as the binary outcome of whether an individual bumblebee returned to the colony, while the homing

time was measured as the duration in minutes required to return. The study included acute exposure (GBH-treated and control bees), 24-h exposure (GBH-treated and control colonies), and release distances (500 m and 1000 m) as fixed categorical explanatory variables. We also analyzed all possible two-way and three-way interactions among these variables. Date was included as a continuous explanatory variable, and paired replicate was included as a random effect. For homing rate, we used a generalized linear mixed-effects model with a binomial distribution and a logit-link function (`glmmTMB::glmmTMB`) (Magnusson et al. 2017); for homing time (log transformed), we used an LMM. For the binomial model, we determined the significance of the fixed explanatory variables with the type II Wald's χ^2 test (`car::Anova`, Fox and Weisberg 2019); for the LMM, see the description above. We validated the binomial model by visually examining the residual plots and checking the model dispersion, which was close to 1 (0.97) (`DHARMA::testDispersion`) (Hartig 2018).

2.4.3. Colony growth

As colonies may differ in initial weight, we assessed the significance of the proportional weight change between the GBH-exposed and control colonies during the experiments with a two-tailed *t* test (stats::t.test). The proportional weight difference was calculated between the beginning (day 1) and end of the experiment (day 8) for each colony. We checked that the data were normally distributed (stats::Shapiro.test).

3. RESULTS

In the foraging activity experiment, a total of 30 bees out of 70 in the control colonies and 55 bees out of 70 in the GBH-treated colonies were identified by the RFID tracking device during the observation period. The 24-h colony-level GBH exposure affected the number of bouts that bees made during the 5-day measuring cycle (LMM: $df = 1$, $ddf = 77.5$, $F = 6.39$, $p = 0.01$), with bumblebees from the GBH-treated colonies completing 93.5% more bouts than those from the control colonies (Fig. 3a, Table I). Neither colony-level GBH exposure (LMM: $df = 1$, $ddf = 75.9$, $F = 1.75$, $p = 0.19$) nor date (LMM: $df = 1$, $ddf = 10.6$, $F = 0.65$, $p = 0.44$) affected the duration of the foraging bouts (Table I).

In the homing ability experiment, 24-h colony-level exposure and date had no effect on the homing rate on their own or through interactions (Table II). However, there was a marginally statistically significant interaction between acute individual-level exposure and release distance (Table II). GBH-treated bees released at a distance of 500 m from their colonies tended to have a higher homing rate than control bees, while the homing rates of these two groups were identical when they were released at a distance of 1000 m from their colonies (Fig. 3b). Regarding homing time, none of the explanatory variables considered (acute exposure, 24-h exposure, release distance, and date) was significant (Table II).

Weight change did not differ between the GBH-exposed and control colonies ($t = -0.62$, $df = 8$, $p = 0.55$; on average, the weight loss was

0.47% and 1.0% for the control and GBH-treated colonies, respectively; Table I).

4. DISCUSSION

In this study, we evaluated the effects of field-realistic concentrations of the herbicide Roundup on the foraging activity and homing ability of bumblebees. We found that GBH had no significant effect on the duration of foraging bouts, but it did affect the number of bouts; the bumblebees in the GBH-treated colonies made 93.5% more foraging bouts than the bees in the control colonies. Pesticides have been reported to disturb the navigation of eusocial bees (Balbuena et al. 2015; Fischer et al. 2014; Matsumoto 2013; Stanley et al. 2016). In contrast, the results of this study show that neither acute individual-level nor 24-h colony-level exposure to GBH affected homing ability in terms of the homing rate or homing time of the displaced bumblebees. The interaction between acute treatment and release distance approached statistical significance ($p = 0.066$), suggesting a potential trend worthy of further exploration. The 24-h colony-level exposure did not affect the colonies' weight change, which was extremely small; the GBH-treated colonies lost 1.0% of their weight, whereas the control colonies lost 0.45% of their weight.

In the foraging activity experiment, which was based on 24-h colony-level GBH exposure, the number of foraging bouts almost doubled in the GBH-treated bees that were let to fly freely for 5 days. As GBH exposure did not affect the duration of foraging bouts, our results suggest that the GBH-treated bees were more active than the control bees. Increased foraging activity is typically considered a positive response because more active bees can forage more resources and support the colony growth and survival, especially during less favorable seasons. However, we did not check whether the GBH-treated bumblebees were better pollinators and whether they returned to the colony carrying more nectar or pollen than the control bees. In a previous study based on a similar setup with neonicotinoids, Stanley et al. (2016) found that bees exposed

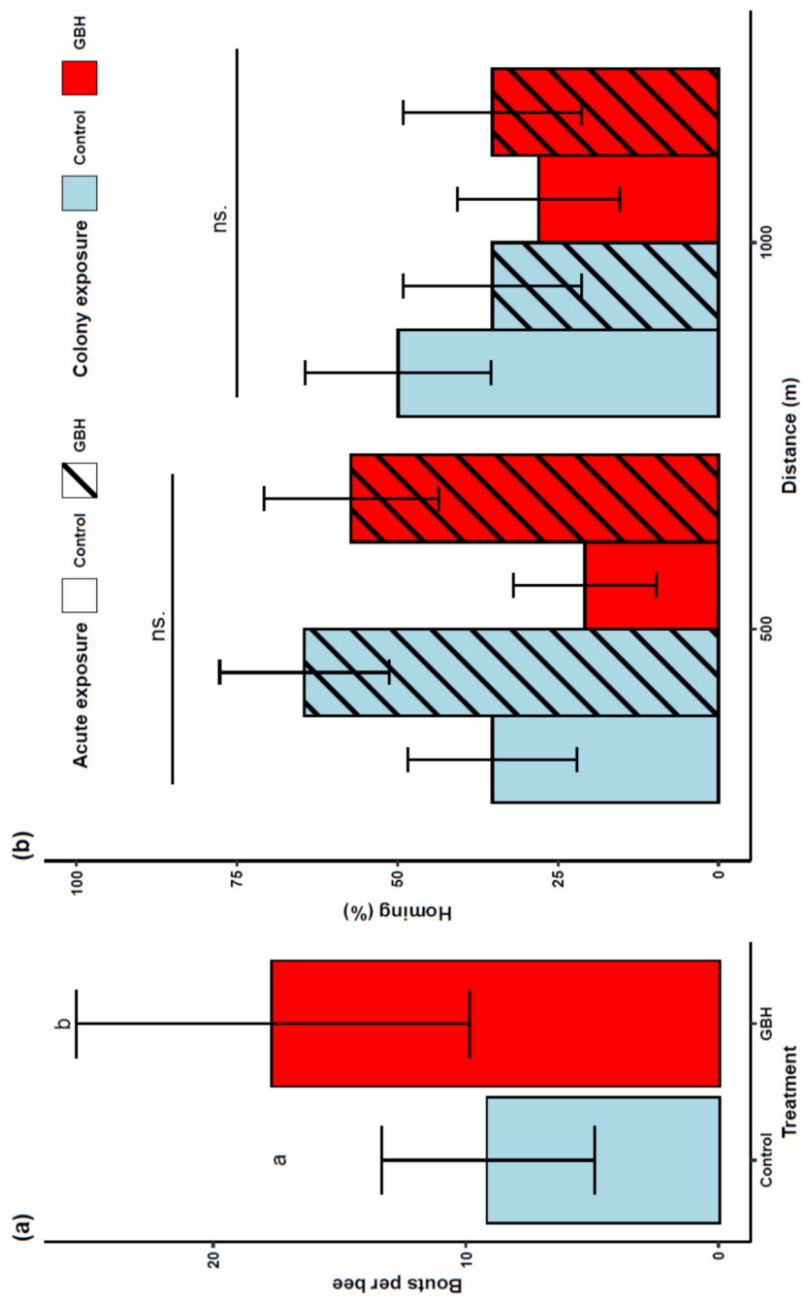


Figure 3 Number of foraging bouts per bumblebee from the control colonies and colonies exposed to glyphosate-based herbicide (GBH) during the foraging activity experiment (a). Homing rate (%) of displaced bumblebees (500 m and 1000 m) with 24-h and acute GBH exposure in the homing ability experiment (b). The figures show back-transformed least square means (\pm SE). The bars with different letters indicate significant differences ($p < 0.05$).

Table II Results of the GLMM and LMM analyzing the effects of 24-h exposure, acute exposure, release distance, and date, as well as their interactions, on the homing rate and homing time of *Bombus terrestris*. Df indicates the degrees of freedom in the numerator; ddf refers to the degrees of freedom in the denominator

	Homing rate			Homing time			
	χ^2	df	p	F-value	df	ddf	p
24-h exposure (10 mg/L, 0 mg/L)	1.396	1	0.237	0.0531	1	34.755	0.819
Acute exposure (37 μ g, 0 mg)	2.418	1	0.120	0.859	1	35.326	0.360
Release distance (500 m, 1000 m)	0.5726	1	0.449	0.132	1	34.325	0.719
Date	0.991	1	0.320	2.453	1	3.439	0.204
24-h exposure \times acute exposure	0.682	1	0.410	1.731	1	36.276	0.197
24-h exposure \times distance	0.0054	1	0.942	0.0002	1	34.188	0.990
Acute exposure \times distance	3.376	1	0.066	0.181	1	34.743	0.673
24-h exposure \times acute exposure \times distance	0.0928	1	0.761	0.823	1	35.061	0.370

to pesticides were worse pollinators because they returned to the colony with less pollen than control bees. Glyphosate impairs the learning ability of bumblebees (Helander, Lehtonen, et al. 2023b; Kaakinen et al. 2024), potentially exacerbating the challenge of resource gathering. Therefore, it is possible that individual foragers exposed to GBH need to undertake additional foraging trips to gather enough resources to fulfill the needs of the colony, which could explain the greater number of foraging bouts observed in the present study. Foraging is extremely energy-consuming for bumblebees, and increasing foraging activity in terms of additional or prolonged foraging bouts due to pesticide exposure might indirectly affect the longevity of foraging individuals (Heinrich 1975; T. J. Wolf et al. 1999) and weaken colonies in the long term (Cartar and Dill 1991; Heinrich 1975; Holldobler and Wilson 2009).

A previous study based on a similar sample size to ours found that a greater proportion of bumblebees exposed to neonicotinoid pesticides were able to find their way back to the hive compared to control bumblebees (Stanley et al. 2016). Even though our homing ability experiment did not show a clear effect of GBH exposure on homing rate, we detected a weak interaction between acute treatment and release distance, where a higher proportion of the GBH-exposed bumblebees released closer

to home (500 m) successfully returned to their colony compared to the untreated control bees. This trend is similar to that reported by Stanley et al. (2016), who proposed that the reason for the greater homing rate of pesticide-exposed bumblebees might be hormesis—a biphasic dose response where low exposure to a stressor can stimulate biological processes (Cutler and Rix 2015)—or pesticide’s brain-accelerating effect, where pesticides cause acceleration in bees’ brain regions involved in navigation (Stanley et al. 2016). This brain-accelerating effect might also be the reason for increased activity seen in the foraging activity experiment.

The authors further presumed that differences among treatments might be due to behavioral changes. For example, pesticide-exposed bees might spend more time outside exploring the environment, making them more aware of surrounding landmarks (Stanley et al. 2016). In our study, the bumblebees from GBH-exposed colonies spent more time foraging as indicated by an increase in foraging-bout frequency, while the neonicotinoid-exposed bees of Stanley et al. (2016) extended their foraging-bout duration.

In the present study, homing rates in the homing ability experiment differed greatly from those reported in a previous study (Goulson and Stout 2001), where 90% of nontreated bumblebees returned to the colony from a distance of 1.1 km. In our study, only 36% of nontreated

(control) bees returned from a distance of 500 m, and 50% returned from a distance of 1000 m. There are at least two potential explanations for the lower homing rate of control foragers in the present study compared to that of Goulson and Stout (2001). First, the biotic and abiotic environments of the two studies might have affected their results. Our study area was in the Botanic Garden in Ruissalo, where a high abundance of suitable flowering plants may have shortened the foraging range. Even though *B. terrestris* is known to forage more than two kilometers from the colony (Walther-Hellwig and Frankl 2000), several studies (Darvill et al. 2004; Knight et al. 2005; S. Wolf and Moritz 2008) have indicated that the normal foraging distance for bumblebees is less than one kilometer, if plenty of resources are present. Therefore, it is possible that the foraging trips of our bees were relatively short and that the bees were unable to identify and use landmarks for orienteering. This hypothesis is supported by the data from similar experiments done in the same area during the following summer, where the homing rate of bees also remained relatively low, with fewer than 50% of bees returning from a distance of 1000 m (Kaakinen et al., unpubl.). The second plausible explanation for the lower homing rate observed in our study is the difference in observation periods between the two studies. In Goulson and Stout (2001), bumblebees had up to 10 days to return to the colony, while in our experiment, the observation period was limited to 2.5 days. This raises the question whether a longer observation period might have been needed. However, in the study by Stanley et al. (2016), bees returned to the hive approximately in one hour from a distance of 1000 m. Additionally, although our formal observation period was 2.5 days, the RFID devices remained active beyond this period, and no bees were detected returning after 2.5 days. It is also important to notice that the aim of our study was not to examine the homing of bumblebees per se but to compare the homing abilities of GBH-exposed and untreated bees. We acknowledge that due to the lower homing rates than expected, future studies would be necessary to confirm our findings.

The weight changes between the control and GBH-treated colonies did not differ significantly in our experiment, and the overall weight changes during our relatively short observation period were minimal. Research on the effects of glyphosate on the growth of eusocial bee colonies is sparse, but several studies have found that chronic exposure to glyphosate affects the larval development of honeybees (Dai et al. 2018; Odeemer et al. 2020; Vázquez et al. 2018). However, none of these studies show any effects at the colony level. Colony growth has been studied more with other pesticides, especially with neonicotinoid insecticides, and earlier studies have shown that neonicotinoid exposure reduces queen, worker, and drone production of bumblebees (Gill et al. 2012; Laycock et al. 2014; Rundlöf et al. 2015; Stanley et al. 2016; Whitehorn et al. 2012). Stanley et al. (2016), whose research questions and methods were similar to ours, did not find a difference between the size (number of bees) of control colonies and colonies exposed to the neonicotinoid insecticide thiamethoxam despite their longer observation period (45 days) compared to ours (8 days). Our hypothesis predicted that the exposed colonies would have been lighter at the end of the study due to glyphosate's negative impact on larval development, the loss of bumblebees, and the assumption that the exposed foraging bees would have been unable to gather as many resources as the foragers from the control hives. However, because the primary foci in our study were foraging activity and homing ability, we limited our observation period to 8 days. This duration may have been too short to detect any colony-level effects of GBH.

Our current study focuses only on short-term effects of glyphosate. European Food and Safety Authority (EFSA) recommends 10 days as a standard chronic assessment for pesticides safety for bees (Adriaanse et al. 2023), and previous studies have used even longer exposure periods to examine the chronic effects of various pesticides (Minnameyer et al. 2021; Richardson et al. 2024; Stanley et al. 2016). We chose to focus on the short-term effects of glyphosate exposure (24-h colony-level and single acute exposure) because glyphosate degrades relatively quickly

compared to other pesticides (Duke 2020). More importantly, the time window when pollinators can get exposed to glyphosate in arable land in our study area is short; glyphosate-resistant genetically modified (GM) crops are not cultivated within the European Union (including Finland) and GBHs are thus applied only before planting or after harvest.

Overall, our findings based on short-term exposures to glyphosate do not support the idea that glyphosate impairs the homing ability of bumblebees or affects the weight of their colonies. These findings are somewhat contrary to previous studies that have observed clear negative effects of glyphosate on eusocial bees' sensory and cognitive abilities (Farina et al. 2019; Helander et al. 2023b; Kaakinen et al. 2024), including the research of Balbuena et al. (2015), who found that a single episode of exposure to glyphosate delayed the return of foraging honeybees to the colony. However, the implications of increased foraging observed in the present study, particularly its impact on pollination efficiency, resource acquisition, and individual bee longevity, remain uncertain and warrant further investigation. While the minimal effects of GBH on homing ability are somewhat encouraging, the potential costs associated with the observed rise in foraging bouts following colony-level GBH exposure could have broader ecological consequences for bumblebees. It is plausible, that increasing foraging activity following GBH exposure, which has been earlier shown to reduce the learning performance of bees (Helander, Lehtonen, et al. 2023b; Herbert et al. 2014; Kaakinen et al. 2024), is not necessarily a positive outcome for bees in the long run.

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AUTHOR CONTRIBUTIONS

All authors contributed to the study conception and design. Material preparation, data collection, and analysis were performed by Kimmo Kaakinen. The first draft

of the manuscript was written by Kimmo Kaakinen and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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DATA AVAILABILITY

The dataset generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

DECLARATIONS

Ethics approval According to Finland's Ministry of Agriculture and Forestry, bumblebees are not classified as experimental animals; consequently, project authorization was not required (Act on the Use of Animals for Experimental Purposes 2006/62 §4). However, we considered ethical issues when designing our study. We tried to use bumblebees as effectively as possible to reduce the number of colonies in our experiments. We euthanized the bumblebees causing them as little pain as possible by stunning them with CO₂ gas and then placing them in a freezer.

Competing interests The authors declare no competing interests.

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