Insectes Sociaux (2025) 72:437–449
https://doi.org/10.1007/s00040-025-01022-4

Insectes Sociaux

RESEARCH ARTICLE

Exposure to diesel exhaust particles impairs takeoff but not subsequent homing and foraging behavior of workers of the buff-tailed bumblebee *Bombus terrestris*

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Received: 15 November 2024 / Revised: 17 January 2025 / Accepted: 19 January 2025 / Published online: 12 February 2025

Abstract

The loss of insect diversity and biomass has been documented in many terrestrial ecosystems. Drivers of this insect decline include climate change, habitat degradation, and pollution. Exposure to airborne particulate matter, such as diesel exhaust particles, may be harmful, especially for insects around urban or industrial areas. Ecotoxicological experiments have shown that chronic oral uptake of diesel exhaust particles can result in higher mortality and changes in the gut microbiome in bumblebees. However, how such effects manifest under natural conditions is still largely unknown, especially effects on foraging activity. Here, we exposed workers of the bumblebee *Bombus terrestris* to diesel exhaust particles in the field at distances of 380 m and 1100 m from their colony. We measured the time until bumblebees took off, the duration of their homing flight after a one-time exposure, and subsequent foraging activity over 1.5 days, recording the number and duration of the foraging flights in comparison to untreated bumblebees. The treated bumblebees needed significantly longer to start their homing flight, caused by some workers that were even unable to take off vertically from the exposure box and performing extensive grooming behavior. Homing flight duration and the subsequent foraging activity did not differ between treated and control workers. It remains unclear why bumblebees struggled to take off after exposure to diesel exhaust particles. This observation needs further investigation to elucidate whether this behavior is induced by particulate matter in general or related to specific physico-chemical properties of the particles inducing a physiological effect.

Keywords Air pollution · Particulate matter · Insect decline · Pollinator · Homing flight

Introduction

The global decline in biodiversity and its ecological consequences have shifted into the focus of research, policy, and society. Preserving biodiversity with a wide variety of life forms and the associated individual traits and interactions contributes to maintaining the stable functioning of ecosystems (Cardinale et al. 2012, Loreau et al. 2001). Insects provide an array of ecosystem services, such as pollination, nutrient cycling, or decomposition of organic matter (Cardoso et al. 2020, Noriega et al. 2018). Hence, the ongoing loss of insect biomass and diversity observed in many regions worldwide (Cowie et al. 2022, Hallmann et al. 2017, Wagner et al. 2020) threatens the stability and resilience of ecosystems. The loss of insect biodiversity is, besides biological impacts, primarily driven by anthropogenic factors like climate change as well as habitat destruction and environmental pollution due to intensive agriculture and proceeding urbanization (Cameron and Sadd 2020, Ganivet 2020, Müller et al. 2023, Sánchez-Bayo and Wyckhuys 2019, Uhler et al. 2021, Wagner 2020). Research on the effects of environmental pollution on insects focused mainly on pesticides and fertilizers as they are extensively applied in agriculture (Sánchez-Bayo

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and Wyckhuys 2019). The recurrent use of fertilizer leads to floral homogenization and, consequently, to a simplification of associated insect biodiversity (Cameron and Sadd 2020, Sánchez-Bayo and Wyckhuys 2019). Pesticides have various negative impacts on insects depending on the dose applied. Even in non-target species such as bees and bumblebees, high doses may increase mortality, while sublethal doses can impair neurological functions responsible for memory, navigation, and motor function (Cameron and Sadd 2020, Stanley et al. 2016, Tison et al. 2017, Tosi et al. 2017), as well as the immune system (Czerwinski and Sadd 2017).

Especially in urban areas, an important contributor to environmental pollution is airborne particulate matter. It is mainly generated and emitted into the atmosphere by domestic heating, industry, and traffic (Dimitriou and Kassomenos 2014, Jandacka and Durcanska 2019). These air pollutants vary in their composition and size depending on their origin. Particles from road traffic make up around 20% of all airborne particulate matter in Western Europe and are separated into non-exhaust and exhaust particles (Hopke et al. 2020). The incomplete combustion of fuels leads to the production of a non-volatile and quantitatively large proportion of exhaust airborne particulate matter. The exhaust airborne particulate matter from diesel engines consists of elementary carbon. Due to the surface properties, it mainly binds organic components and polycyclic aromatic hydrocarbons in small amounts, as well as metals and other trace elements (Hüftlein et al. 2023, Sánchez-Piñero et al. 2022, Viteri et al. 2021, Wichmann 2007). Because of their small size of ≤ 10 or ≤ 2.5 µm (PM_{10} and $PM_{2.5}$, respectively), particles are inhaled easily and thus represent a serious health problem for humans. The harmful properties of diesel exhaust particles are associated with the large proportion of polycyclic aromatic hydrocarbons they contain and their carcinogenic, mutagenic, and immunosuppressant effects on mammals, including humans (Kim et al. 2013, Pant et al. 2017, Sánchez-Piñero et al. 2022, Viteri et al. 2021). Once taken up, reactive metabolites of the polycyclic aromatic hydrocarbons can bind to cellular proteins and DNA, which disrupts the biochemistry of the cells and consequently leads to their damage (Lee et al. 2002). There is less scientific evidence regarding the potentially debilitating effects of polycyclic aromatic hydrocarbons or diesel exhaust particles on invertebrates. However, for most of the invertebrate species that have been studied to date extended exposure to polycyclic aromatic hydrocarbons resulted in adverse effects, including insects, mussels, or annelids. The exposure typically leads to oxidative stress, resulting in a suppressed immune function, significant DNA damage, and increased mortality (Ball and Truskewycz 2013). Because insects are a very diverse group, the impact of polycyclic aromatic hydrocarbons on the metabolism can be manifold. Especially physically demanding and cognitive activities, such as flying or finding food, might be impaired under oxidative stress.

Eusocial pollinators such as honeybees and bumblebees are central place foragers and stay in the area of their colony and brood they care for. As a result, their reproductive success depends on the success in foraging and the quantity and quality of the resources in the landscape surrounding the nest (Osborne et al. 2008). Additionally, the pollution level around the nest influences pollinators (Gradish et al. 2019). Traditionally, researchers used honeybees for the assessment of ecotoxicological effects of substances on pollinators. However, honeybees and bumblebees differ in their life history, behavior, and morphology, affecting susceptibility and exposure to pollutants (Gradish et al. 2019). Solitary foraging in spring and autumn may result in high exposure to bumblebee queens. Many bumblebee species build their nest underground, exposing the colony, including the brood, to residues of pollutants in the soil (Gradish et al. 2019). The use of bumblebees for the assessment of potentially harmful substances helps to predict the impact of these substances on some of the other important wild bee species (Gradish et al. 2019). The buff-tailed bumblebee *Bombus terrestris* (Linnaeus, 1758) is common and widespread in Central and Western Europe, especially in urban areas (Goulson et al. 2008), and is commercially bred for greenhouse pollination. These aspects make it a suitable, if not necessary, test organism to study the effects of diesel exhaust particle exposure. The diesel exhaust particles can be taken up by bumblebees orally via pollen and nectar (Leita et al. 1996, Hüftlein et al. 2023, Seidenath et al. 2023, Seidenath et al. 2024) and may additionally stick to their cuticle, hairs, and wings (Balestra et al. 1992, Negri et al. 2015). Such diesel exhaust particle deposits on the body surface may impede the flight activity of bumblebees, similar to the painted lady *Vanessa cardui* showing decreased speed, flight distance, and stamina after exposure to combustion-generated airborne particulate matter (Liu et al. 2021).

Although social insects have emerged as model organisms and bioindicators to study the effects of anthropogenic pollution because of their ecological dominance and importance (Cameron & Sadd 2020, Chapman and Bourke 2001, Leita et al. 1996), only a few publications have examined the effects of diesel exhaust particles on pollinators so far. Exposure to high doses of diesel exhaust impairs associative learning abilities, memory, and tolerance to additional abiotic stress in honeybees at the individual level but also reduces colony fitness (Reitmayer et al. 2019, Reitmayer et al. 2022). We have shown increased mortality of bumblebee workers when fed with high doses of diesel exhaust particles over several days (Hüftlein et al. 2023) and a shift in the gut microbiome and transcriptome after sublethal exposure (Seidenath et al. 2023) while colony development was not affected negatively under laboratory conditions

(Seidenath et al. 2024). In addition, pollinators can be affected indirectly. Pollution with diesel exhaust leads to the rapid degradation of floral volatiles, which hinders the perception of flowers and reduces the foraging efficiency and, thus, the pollination performance of honeybees (Girling et al. 2013, Lusebrink et al. 2015, Ryalls et al. 2022).

To test if we find similar effects of airborne particulate matter in a wild bee, we exposed *Bombus terrestris* workers to diesel exhaust particles in a field experiment and tracked their flight activity. We collected workers from their colony and released them at two different distances from the nest after a one-time exposure to diesel exhaust particles. We monitored the behaviour after release and the time a worker needed to return to its colony, i.e. the homing flight. We also observed the subsequent flight activity, i.e. duration and number of foraging flights. Since diesel exhaust particles may stick to the body surface of the bumblebees, we expect that treated bumblebees initially start auto-grooming and wiping off the particles and thus need more time to start vertically from the exposure boxes compared to the untreated bumblebees of the control group. Additionally, it is conceivable that exposed bumblebees perform additional cleaning stops during the flight, have an impaired spatial orientation, a lowered motivation doing foraging flights, or are negatively affected by the harmful properties of the particles. We, therefore, expect that bumblebees treated with diesel exhaust particles need more time to fly back to their colony and assume that fewer individuals will find their way home. Finally, we expected an impaired foraging activity of the bumblebees and hypothesized that bumblebees treated with diesel exhaust particles do foraging flights less frequently and for longer than the bumblebees of the control group.

Material and methods

Bumblebee husbandry

At the beginning of August 2021, we ordered a *Bombus terrestris* colony from Biobest® (Biobest Group NV, Belgium) with an estimated 50 individuals. We kept this colony in a ventilated box (21 × 13 × 17 cm) in a climate chamber under controlled conditions (26 °C, 70% humidity) with an inverted day and night rhythm of 12:12 h of light–dark cycles. We provided the colony with ad libitum sugar water (50% Apiinivert®, Südzucker AG, Mannheim, Germany) and pollen (Imker Pur, Osnabrück, Germany). After eleven days in the climate chamber, we placed the colony in a meadow on the campus of the University of Bayreuth and left it there for 13 days to acclimatize. During this period, the workers were allowed to forage under natural conditions and get acquainted with the new environment. In addition to the meadow where we placed the colony, the Ecological Botanical Garden of the University of Bayreuth, immediately adjacent to the campus area, guaranteed the food supply of the colony.

Experimental procedure

After the acclimatization period, we conducted the field experiments on three days within one week in the early September 2021 (2nd to 8th September). The air temperature on these days ranged between 9.9 °C at night and 21.8 °C maximum during the day with slightly cloudy to sunny weather. Over the three days, we tagged 80 bumblebees when leaving the colony with an individual square tag for identification (see: individual identification and transport). We randomly assigned the bumblebees to either a diesel exhaust particle exposure treatment ($N = 40$) or no treatment (control group) ($N = 40$). Then, we transported half of the exposed and half of the control group to 380 m ($N = 2 \times 20$) and the other two halves 1100 m away ($N = 2 \times 20$) from the colony. There, we released the workers and automatically tracked the foraging and flight activity of the bumblebees for 1.5 days via video camera (time of release: approx. 2:30 p.m.–11:59 p.m. the following day). We defined the homing flight duration of a worker as the period between the takeoff and the first observation by the video recording device. After the first return to the colony of each bumblebee, we observed flight activity for 1.5 days. We measured the foraging duration as the time between leaving and returning to the colony. Moreover, the number of foraging flights was counted. Flights of bumblebees that either did not return to their colony or only returned the next day and thus spent the night outdoors were not included in the measurements of the foraging activity.

Individual identification and transport

To label individual bumblebees, we created AprilTags 3 (type 36h11) with 2D barcodes using the code for generating tag families from APRIL Robotics Laboratory (Edwin 2019) based on the work of Krogius et al. (2019). The 2D barcodes (4 × 4 mm) consist of a 36-bit code, which can generate a total of up to 587 unique identification numbers. The 2D barcodes were printed on white plastic film (1 mm, laser-Fol PETP 275 opak, creativ papier, Neuenhaus, Germany) and additionally provided with the associated identification number with a maximum of three digits in a font size of 5 pt to allow a direct readout by observers. We cut out the tags manually to a dimension of approximately 5 × 6 mm (Fig. 1).

For tagging, we transferred each bumblebee to an individual live capture jar (22 × 63 mm) and placed it on ice for 10–20 min until immobilization. Then, each bumblebee was carefully fixed between fingers and working surface to attach the individual tag to the thorax with a small drop of

Fig. 1 Image of a single frame with a top view of the arena from one of the videos recorded. Shown is a tagged bumblebee that recently entered and a stone in the center of the arena that served as a barrier for the bumblebees to prevent them from crossing the arena too fast on foot or even in flight

odorless superglue (UHU® GmbH & Co. KG, Germany) placed between the first yellow and black stripe on the mesonotum. During this process, we ensured that the lower edge of the tag was slightly above the first pair of wings and did not cover the tegulae. Like this, the tags do not impair the wing movement. Depending on the size of the bumblebees, the upper part of the tag reached over the head but not over the total length of the antennae. At the end of the procedure, we visually inspected each bumblebee to ensure normal wing and head movement. All bumblebees failing the process of tagging were excluded and replaced. After tagging, we individually transferred the bumblebees into transport cages, in which they remained until the exposure to the treatment and their release. The transport cages consisted of a Nicot®-Queen cage (Nicotplast SAS, Maisod, France) attached to a 10 ml plastic syringe, which we filled with one ml of sugar water. During this period, the bumblebees were able to recover from the previous process and ingest sucrose solution ad libitum.

Colony observation

To protect the colony and the video recording device (see below) from bad weather conditions and other external influences, we put the colony box into a gray, untransparent plastic box with a hinged lid and ventilation holes on the sides (60 × 40 × 33.5 cm, Auer-Packaging, Amerang, Germany; Fig. 2). The bumblebees were able to leave and enter the colony by crossing a transparent and flexible PVC tube (inner diameter 1.6 cm) that served as a passage between the colony and the outside environment (Fig. 2).

All bumblebees leaving or entering the colonies had to pass through an arena (8.54 × 2.5 × 8.54 cm) located inside the plastic box between the colonies and the outer flight hole (Fig. 2). The arena consisted of a white plastic base and a transparent plexiglass cover. Above the arena, we installed a tower (12.2 × 26.9 × 12.2 cm), which carried the video recording device required to track the flight activity of the bumblebees during the experiment. To identify the bumblebee individuals and their exact homing flight duration, we used a Raspberry Pi HQ Camera V1.0 2018 (12.3 megapixel, Raspberry Pi Trading Ltd. Cambridge, England) and a Raspberry Pi single-board computer (Raspberry Pi Model 3B, Raspberry Pi Trading Ltd.) to record short videos when a bumblebee passed the arena (for an overview of the camera settings see Table 1 in Appendix). We fixed the camera and single-board computer centrally above the arena at the

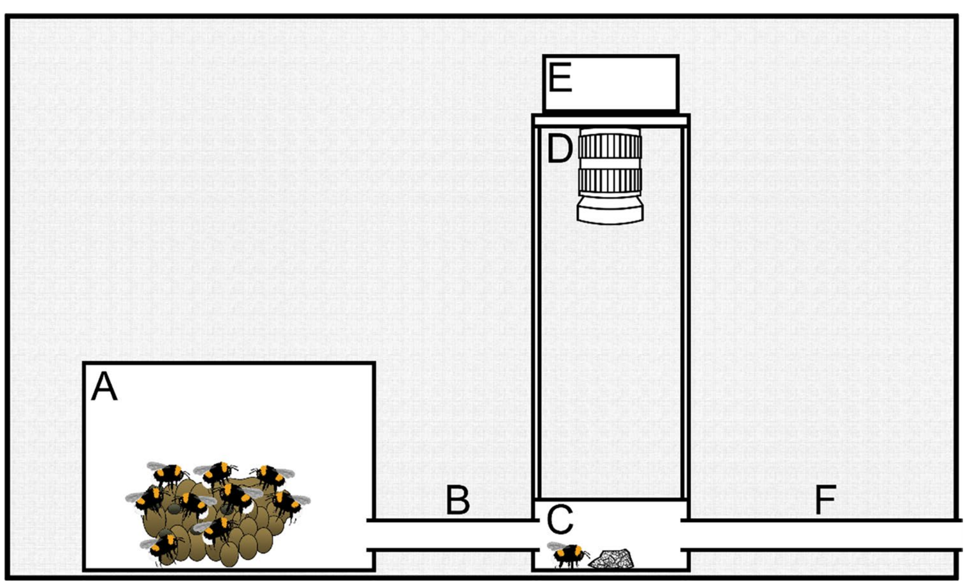

Fig. 2 Schematic of bee filming setup inside Euro container: **A** bumblebee colony, **B** tube connecting colony and **C** filming arena containing stone to hinder fast passage of arena, **D** HD-Camera, **E** Raspberry Pi computer for movement detection and recording of videos, **F** exit tube

highest point of the tower (Fig. 2). We 3D-printed the arena and the tower (for detailed information on the dimensions, see Figs. 6 and 7). We controlled the camera via a web-based interface (Melchior and Tidey 2013). As soon as the camera detected any motion in the frame, it started to record a video while the movement lasted. We stored the data as mp4 video files on an SD card for later analyses. With an LED light strip (length: 48.8 cm, 14 LEDs) attached about 4 cm above each arena at the respective outer edges of the tower, we ensured constant lighting even during twilight (Fig. 2). In addition, we placed a small stone (approx. 2 × 1.5 × 2 cm) in the center of the arena (Fig. 1) to serve as a small barrier for the bumblebees. It prevented them from crossing the arena too fast on foot or even in flight and thus improved the automatic detection of barcodes or manual reinspection of video material and identification of individual bumblebees.

Controlled production of diesel exhaust particles

We collected diesel exhaust particles from a four-cylinder diesel engine (OM 651, Daimler AG, Stuttgart, Germany) during a reaping cycle of transient and stationary operating points, resembling an inner-city driving scenario with stop-and-go intervals. We operated the engine on a test bench with a water-cooled eddy-current brake, as previously described in Zöllner (2019). We collected diesel exhaust particle samples with an electrostatic precipitator (OekoTube Inside, Mels-Plons, Switzerland). We applied a fast response differential mobility particulate spectrometer DMS500 (Combustion, Cambridge, England) to measure sub-micron particle size distributions of raw exhaust samples. Solid particles showed a median diameter between 52.1 ± 1.8 nm and 101.9 ± 1.7 nm, depending on engine load and speed during the inner-city cycle.

We characterized diesel exhaust particle composition by thermogravimetric analysis (TGA, STA 449 F5 Jupiter, Netzsch-Gerätebau GmbH, Selb, Germany). A fraction of 72.2 ± 1.1% of the diesel exhaust particle mass was attributed to elemental carbon, 23.2 ± 0.9% w/w to organic fractions, and 4.6 ± 0.7% w/w to inorganic matter. Quantification of polycyclic aromatic hydrocarbons revealed concentrations of 444 ppm for pyrene, 220 ppm for phenanthrene, and 107 ppm for fluoranthene. We analyzed the elemental composition of the diesel exhaust particle samples by Inductively Coupled Plasma Optical Emission Spectrometry (ICP-OES, Optima 7300 DV, PerkinElmer Inc., Waltham, United States of America) and interpreted it according to Zöllner (2019). It showed fractions of calcium (1.63% w/w), zinc (0.53% w/w), and phosphorus (0.50% w/w) that can be traced back to diesel fuel and lubrication oil. Copper (1.03% w/w), aluminum (0.02% w/w), and iron (0.02% w/w) can be attributed to abrasion of piston rings, cylinder head, and engine block material, respectively. In addition, we found small amounts of boron (0.13% w/w), magnesium (0.10% w/w), molybdenum (0.03% w/w), natrium (0.02% w/w) and sulphur (0.17% w/w).

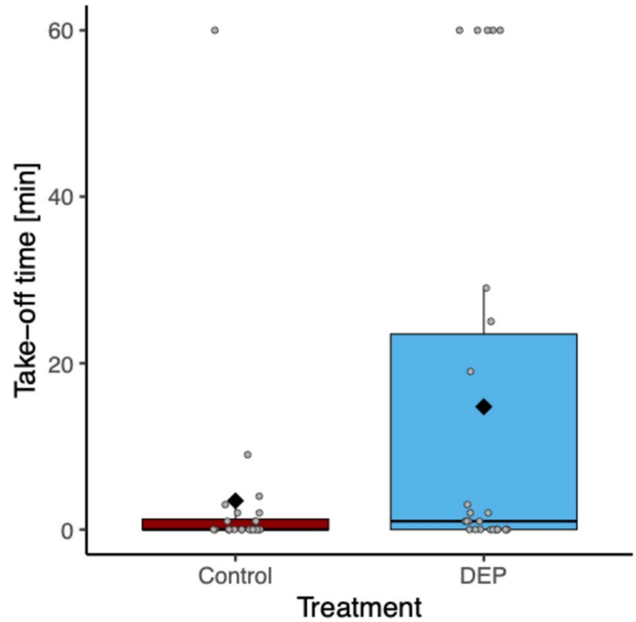

Fig. 3 Comparison of the bumblebee takeoff times (Control $n = 39$, diesel exhaust particle exposed $n = 37$) in minutes. The diesel exhaust particle exposed bumblebees needed significantly longer to take off vertically out of the exposure boxes than the bumblebees of the control group (Kruskal–Wallis rank-sum test: $X^2 = 8.85$, $df = 1$, $p = 0.003$). Shown are boxplots with median and the first and third quartiles (Q1-Q3). The mean values are represented by the large diamond shape in each box. Small dots represent individual data points

Diesel exhaust particle exposure and behavioral observations

The exposure to the treatment with diesel exhaust particles (DEP) and the subsequent release of the bumblebees occurred at two different locations at distances of either 380 or 1100 m southeast of the colonies. Consequently, there were four different treatment-distance combinations: Control_380m, DEP_380m, Control_1100m, and DEP_1100m. At the two exposure sites, the bumblebees were simultaneously transferred to individual square plastic boxes with a volume of 200 ml (approx. 7.5 × 5 × 7.5 cm) in a randomized order and locked in for exactly three minutes. The boxes with the diesel exhaust particle treatment contained 1.5 mg ± 0.1 mg (mean ± SD) diesel exhaust particles, while the control did not contain any particles. Inside the boxes, the diesel exhaust particles are whirled up due to the wing movement of the bumblebees, resulting in a distribution of the particles and subsequent contamination of the bumblebees' body surface. After three minutes, the boxes were opened, and the bumblebees were able to take off.

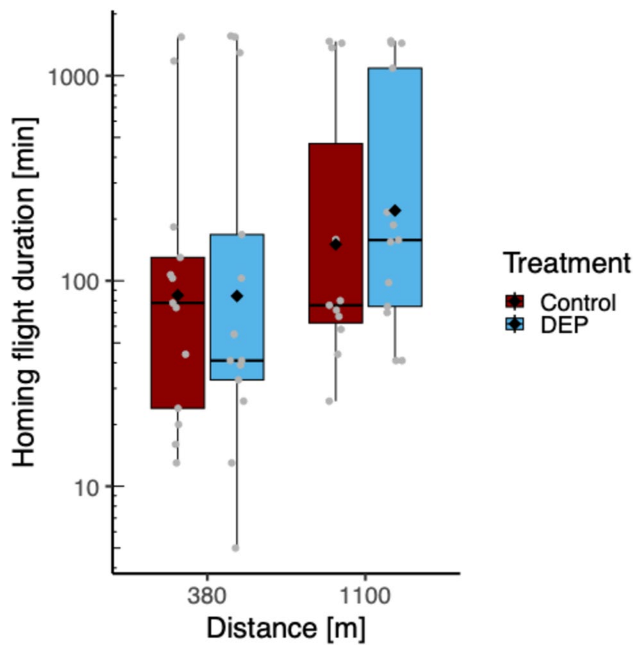

Fig. 4 Comparison of homing flight duration (Control_380m ($n=19$), Control_1100m ($n=20$), DEP_380m ($n=16$), DEP_1100m ($n=20$), $N=75$) depending on the treatment and distance combination. The line in each box represents the median. Shown are boxplots with median and the first and third quartiles (Q1-Q3). The mean values are represented by the large diamond shape in each box. Small dots represent individual data points

Exposure and release took place in the afternoon from 2:45 p.m. to 4:45 p.m. We measured the time each bumblebee needed to leave the exposure box. If a worker did not manage to leave the box within one hour, we released it exactly after 60 min on the meadow next to the box. As all those workers immediately took off and flew away, we included them in our further analysis.

Statistical analysis

We recorded a total of 56,708 individual video files during all test days. Four bumblebees (one bumblebee of the control group and three diesel exhaust particles treated bumblebees) were excluded from the statistical analysis because they lost their tags inside the transport boxes or escaped after tagging but before treatment. When examining the exact homing flight duration of the bumblebees, we had to exclude one individual treated with diesel exhaust particles and released at a 380 m distance from the analyses. Although this bumblebee returned to the colony on the day of the treatment, we could not determine the exact homing flight duration. We evaluated the videos manually using the online available 'SMPlayer' (Version 21.1.0, by Ricardo Villalba, open source). Within this process, we identified the bumblebees and the date and the time of arrival or departure from the colony.

All statistical analyses were conducted with R version 4.1.1 (R Core Team, 2021). We used Pearson's Chi-square test of independence to analyze the effect of the treatment, distance, and their interaction term on the bumblebees' ability to return to the colony. This ability we measured as the proportion of workers that found their way back to the colony. We analyzed the impact of the treatment with diesel exhaust particles on the start behavior and the homing flight duration by conducting Kruskal–Wallis rank sum tests, as the residuals were not normally distributed. The number and duration of the foraging flights were analyzed by fitting generalized linear models (GLMs) with treatment as a predictor. We checked model assumptions using model diagnostic test plots, i.e., qqplot and residual vs. predicted plot from the package *DHARMa* (Hartig 2022). For the GLMs we did F-statistics with the function *Anova*() from the package *car* (Fox & Weisberg 2019) to calculate p-values for differences between the two groups. We used the package ggplot2 (Villanueva and Chen 2019) for plotting the data.

Results

Overall, 67.11% (51 of 76 individuals) of the bumblebee workers found their way back to the colony within 1.5 days. The proportion of returnees was not affected by treatment (Pearson's Chi-squared test: $X^2=0.66$, $df=1$, $p=0.41$), distance (Pearson's Chi-squared test: $X^2=1.31$, $df=1$, $p=0.25$), or the treatment-distance combination (Pearson's Chi-squared test: $X^2=3.17$, $df=3$, $p=0.37$). However, the bumblebees from the diesel exhaust particle treatments needed significantly longer to take off from the exposure boxes (Kruskal–Wallis rank-sum test: $X^2=8.85$, $df=1$, $p<0.01$; Fig. 3).

Homing flight duration did not differ between treatments (Kruskal–Wallis rank-sum test: $X^2=0.16$, $df=1$, $p=0.69$), distance (Kruskal–Wallis rank-sum test: $X^2=3.33$, $df=1$, $p=0.07$), or treatment-distance combination (Kruskal–Wallis rank-sum test: $X^2=3.97$, $df=3$, $p=0.27$) (Fig. 4).

Foraging activity was not affected by treatment. Neither the number of foraging flights differed between treatments (GLM with Gaussian distribution: $F_{1,37}=0.72$, $p=0.40$) nor the mean duration of foraging flights (GLM with Gaussian distribution: $F_{1,30}=0.14$, $p=0.71$) (Fig. 5).

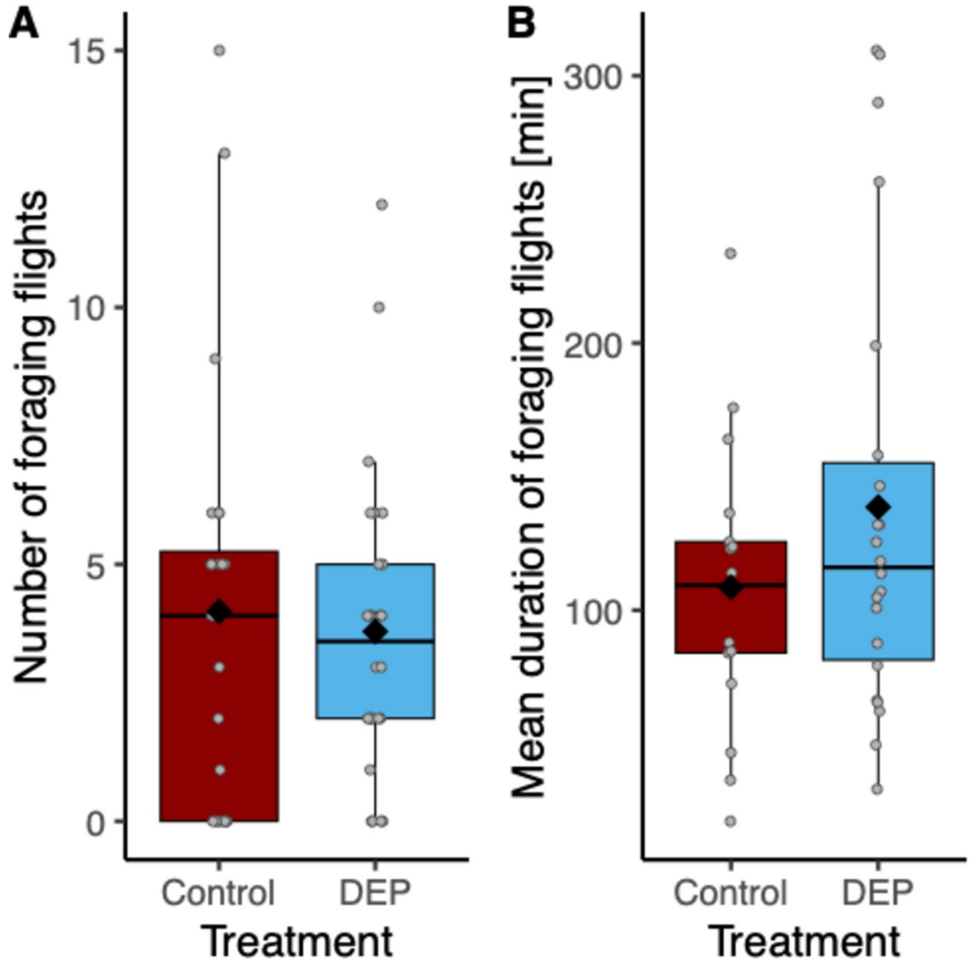

Fig. 5 Box plots showing the effect of the diesel exhaust particle exposure compared to the control group of **A** the average number of foraging flights and **B** the mean foraging flight duration for each bumblebee over 1.5 days. The line in each box represents the median. Shown are boxplots with median and the first and third quartiles (Q1–Q3). The mean values are represented by the large diamond shape in each box. Small dots represent individual data points

Discussion

In our study, we found that exposure to diesel exhaust particles increases the flight takeoff time of bumblebees after their release to perform a homing flight (Fig. 3). In contrast, the return flight to the colony was not affected by treatment (Fig. 4). Moreover, we did not see any differences in the subsequent foraging behavior (Fig. 5).

Our results show that the bumblebees exposed to diesel exhaust particles needed significantly more time to start vertically out of the exposure boxes than the untreated individuals (Fig. 3). One reason is that the treated bumblebees initially started wiping off the particles from their body surface. Hlavac (1975) described this process as auto-grooming. In this process, a set of setae (grooming structures) are arranged at a slant on legs or other movable body parts, which scrape against each other and along cuticular projections, wings, or mouth parts to transport particles from the body surface and sensory organs and eliminate them. The treated bumblebees of our experiment also distinctly showed this auto-grooming behavior, which explains the delayed takeoff start to some extent. However, we observed struggles in the diesel exhaust particle exposed bumblebees to fly vertically out of the box, causing a delayed start. We frequently observed diesel exhaust particle exposed bumblebees flying straight into the wall of the treatment box, incapable of overcoming the only 5 cm high rim to leave it. The struggle caused enormous delays in the flight takeoff time, forcing us to manually place the bumblebees outside the box after 60 min to measure the homing flight duration. The reasons for this behavior remain unclear. However, it could indicate underlying physiological malfunctions. For example, diesel exhaust particles might affect the sensory systems, especially on the antennae that carry different types of sensillae with functions in sensing chemical, thermal, mechanical, and water stimuli (Fialho et al. 2014, Rands et al. 2023). In addition, the visual perception of the bumblebees may be affected, which could impede the takeoff by failing to identify the walls of the box as a barrier and thus flying straight into them. Diesel exhaust particle deposition on mechanosensory hairs of the bumblebees may also impair the perception of electric fields, leading to motoric struggles to overcome the barrier (Sutton et al. 2016).

Contrary to our expectations, our results indicate that diesel exhaust particle exposure neither reduced the ability to return to the colony nor the homing flight duration (Fig. 4). In addition, the proportion of bumblebees that returned to the colonies did not depend on diesel exhaust particle exposure, flight distance, or their combination. We take this as evidence that a one-time exposure to diesel exhaust particles does not impair cognitive abilities and thus negatively affects spatial orientation and navigation. Besides visual landmarks (Ne'eman and Ne'eman 2017), the sun as a compass, and the polarization pattern of the sky (Wehner et al. 1996), bumblebees also rely on olfactory cues to navigate within their environment (Ne'eman and Ne'eman 2017). However, bumblebees cannot fully compensate for visual cues by other senses aiding in spatial orientation, as shown by experiments in complete darkness (Chittka et al. 1999). The observed problems in vertical takeoff by bumblebees exposed to diesel exhaust particles seem to be a short-term impairment from which the bumblebees recover rather rapidly, possibly due to the removal of the particles by grooming, as the longer homing flight is not affected.

In addition to the perception of sensory or olfactory impressions and their storage, the memory and retrieval of this information also play an important role in orientation. Previous studies show that sublethal doses or field-realistic levels of pesticides such as neonicotinoids negatively affect the learning behavior and short-term memory of honeybees (Tison et al. 2017) and bumblebees (Stanley et al 2015). Reitmayer et al. (2019) found that an acute exposure of diesel exhaust at high doses and over a long time (150–210 min; containing NO and NO_2) leads to impaired learning and memory of floral odors in honeybees. Thus, Reitmayer et al. (2019) suggested that treated bees need more repetitions to learn and accomplish the same task. As we did not see any difference in the ability to return to the colony between the treatments, our data suggest no cognitive impairment of the bumblebees in our experiment. The bumblebees seem to be able to remember the environment and landmarks they memorized during their foraging flights in the acclimatization period. In our experiment, bumblebees were exposed to diesel exhaust particles only once and for only three minutes, which might not have been enough to affect learning or memory (Dramstad et al. 2003; Goulson 2010). In addition, we exposed the bumblebees to particles filtered from diesel exhaust and not to genuine diesel exhaust, which contains other toxic volatile components such as NO and NO_2. It is also conceivable that diesel exhaust particles may have a less measurable effect on the memory processes of orientation than on the learning and memory of floral odors.

Most insects breathe through tracheae that connect the inner body to the air via spiracles. The spiracles serve as a mechanical barrier against environmental particles, which can be opened and closed actively (Chapman 1998, Hartung et al. 2004, Nikam and Khole 1989). Tan et al. (2018) found that caterpillars closed their spiracle valves for longer in poor air quality, which could decrease oxygen uptake and reduce metabolism. In our experiment, the treated bumblebees did not take longer to return to their colony than the control animals. We assume that the particle load was too low or the particle size too big to induce a closure of their spiracle valves. As we observed grooming behavior before the start in some workers, a large part of the particles may have been removed from the body surface. Therefore, we think that the oxygen intake and the metabolism were not or only slightly impaired in our setup.

For most bumblebee species flight distance depends on the size of their colonies and the food availability in their foraging area (Goulson 2010). The maximum reported foraging distances of *B. terrestris* vary from 312 m (Darvill et al. 2004) up to 10,000 m (Cresswell et al. 2000). *B. terrestris* forages around the nest in the smallest possible radius, as this seems to be the most efficient way to obtain food (Dramstad et al. 2003, Goulson 2010). However, they have been reported to navigate back to their colony from distances up to 9.8 km (Goulson and Stout 2001). Bumblebees systemically search for familiar landmarks to locate their nest. If displaced outside their familiar home and foraging range, bumblebees take longer to return and fewer find their colony than bumblebees displaced within their familiar foraging range (Goulson and Stout 2001). Our findings did not show a significant difference between the two distances, indicating that the longer distance (1100 m) lies within the foraging radius of the bumblebees. These results are surprising, as the bumblebees released further away had to cover a longer distance on their way back to the colony which should result in a prolonged homing flight duration. As we only observed a tendency to an increased homing flight duration and had varying times in both treatments, we conclude that many bumblebees do not fly straight back to their colony on the fastest route. Instead, they might go on foraging prior to their return which may mask the difference in distance from release resulting in no significant difference in homing flight duration between the two distances. Nonetheless, we attribute the trend of a slightly longer time to the fact that the bumblebees must cross a longer distance to return to their colony.

Finally, we did not find any effect of the diesel exhaust particle exposure on foraging behavior after returning home (Fig. 5). In contrast, other studies have shown that the foraging motivation is reduced by anthropogenic pollution such as pesticides (Lämsä et al. 2018, Muth and Leonard 2019). In bumblebees, a low dose of neonicotinoid insecticides leads to reduced foraging motivation and they are slower to initiate foraging and visit fewer flowers (Lämsä et al. 2018).

As we did not observe any effect, our results indicate that a single treatment with diesel exhaust particles with its harmful components might not unfold the same toxic effects, as they are known for many pesticides (Cassereau et al. 2017, Devillers 2002).

In summary, we were able to show that a single exposition with diesel exhaust particles has a negative effect on the start behavior of the bumblebee *B. terrestris* but not on the homing flight duration and success. However, as we used a semi-artificial set up in a limited time span, we must be careful in interpreting the total effect of diesel exhaust particles on the foraging behavior. In nature, bumblebees must cope with additional stressors apart from anthropogenic pollution, such as pathogens or rising temperatures (Holmstrup et al. 2010). Normally, these multiple stressors do not occur in isolation but rather have an interactive effect and may reinforce their own negative impacts synergistically (Goulson et al. 2015). Although field-realistic doses of diesel exhaust particles are not directly lethal to bumblebees in general, they might reduce the ability to manage additional stressors (Czerwinski and Sadd 2017, Reitmayer et al. 2019). The colony function of eusocial pollinators like bumblebees depends on the efficient performance of many individuals. Due to the large number of individuals, large colonies are able to buffer or compensate for some effects of stress (Bryden et al. 2013). However, in an urban environment with heavy traffic and long-term diesel exhaust particle exposure, the small and sublethal effects that are imperceptible at the individual level have the potential to add up at the colony level and can be particularly fatal for the dynamics and functioning of whole colonies (Bryden et al. 2013) or even entire ecosystems. Our findings add to the understanding of the potential role of particulate matter pollution in the global insect decline. We suggest that the observed struggle taking off needs further investigation because its cause remains unclear, and such behavior may indicate underlying physiological constraints.

Appendix

See Figs. 6 and 7; Table 1.

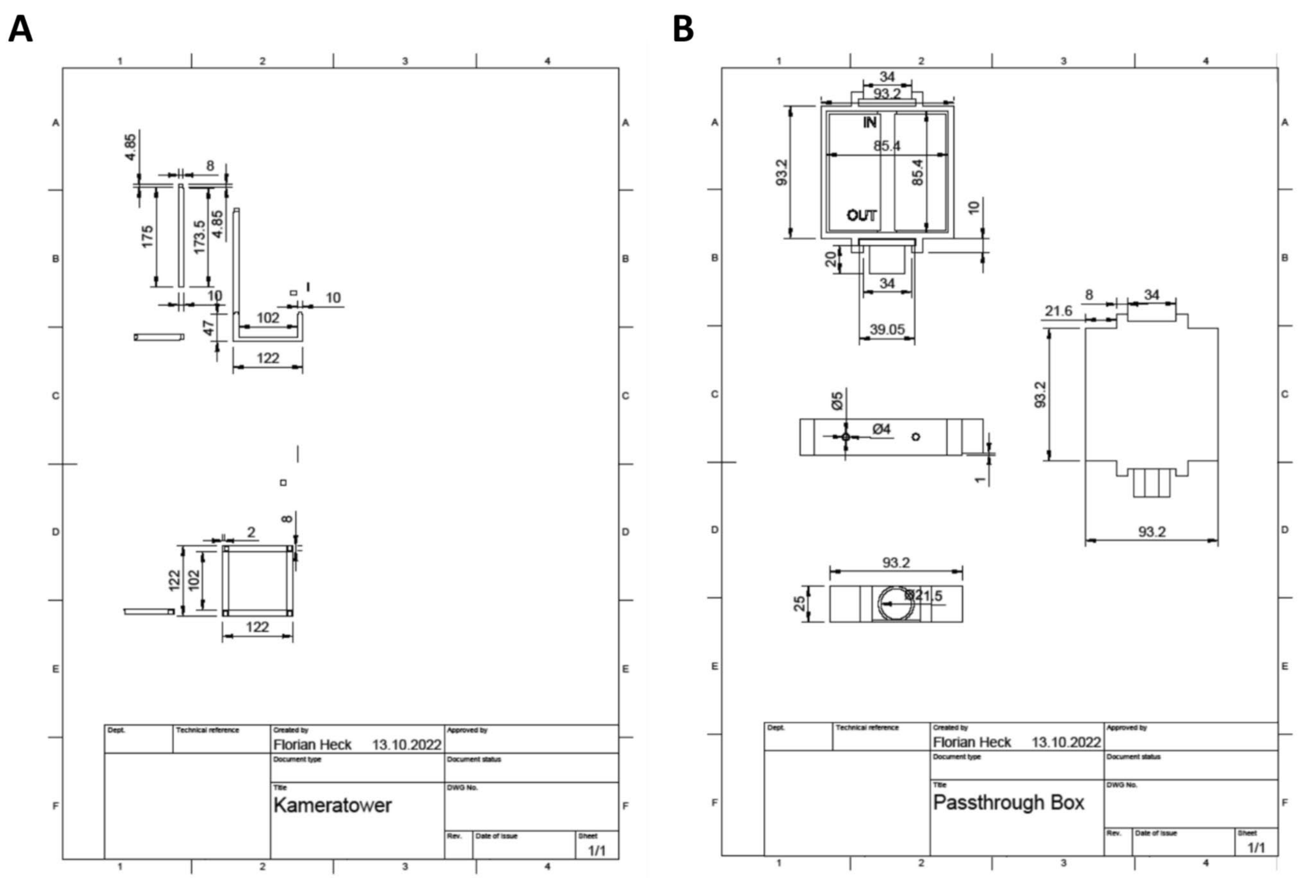

Fig. 6 Constructional drawings including the dimensions in millimeters of the individual components for the towers carrying the cameras (**A**) and the arenas (**B**) used for 3D print

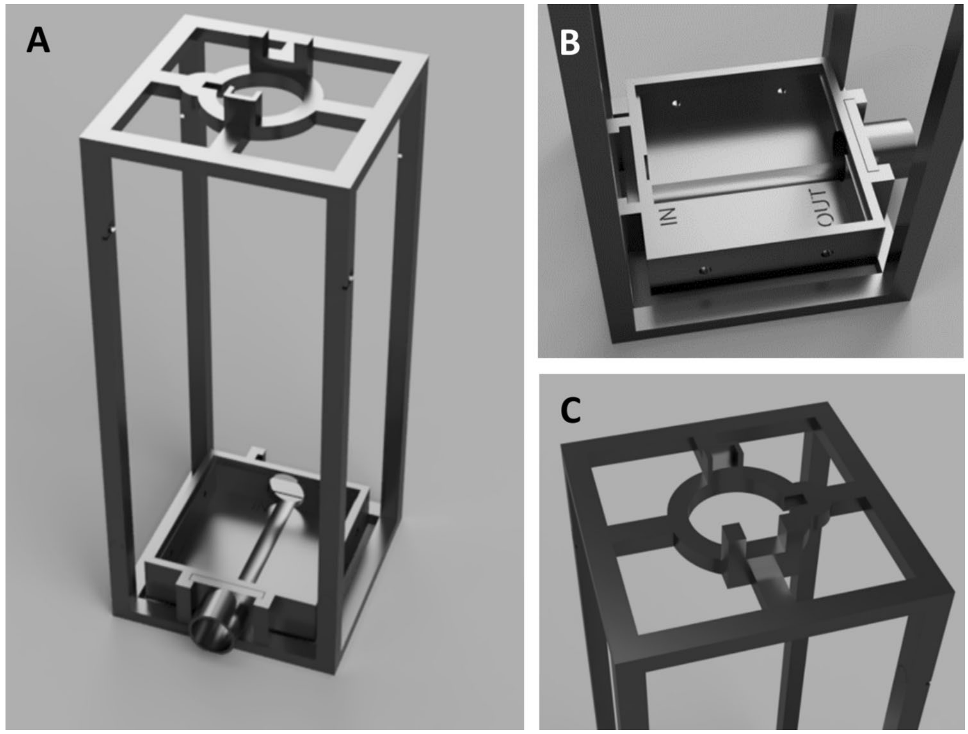

Fig. 7 3D-model of the tower including the arena, which served as a template for the 3D print in general view (**A**), top view of the arena (**B**) and the view of the top of the tower where the camera was attached

Table 1 Overview of the camera setting used in the experiment

Camera settings	First settings	Final settings	
Resolutions		Load preset Custom values: Video resolution Video fps FPS divider Image resolution	– 1296 × 972 pixel 25 recordig, 25 boxing 1 2592 × 1944 pixel
Timelapse-interval		3 s	
Video split		0 s	
Annotation		Text: OL/OR/UL/UR “daphnia1” & “daphnia2” Background	(Describes the Cam’s position) off
Annotation size		50	
Custom text colour		Disabled; y:u:v = 255:128:128	
Custom backgruond colour		Disabled; y:u:v = 0:128:128	
Buffer		0	
Sharpness		0	
Contrast	100	100	
Brightness	50	50	
Saturation		0	
ISO		0	
Metering mode	Average	Backlit	

Table 1 (continued)

Camera settings	First settings	Final settings	
Video stabilisation		Off	
Exposure compensation		0	
Exposure mode	Backlight	Auto	
White balance	Greyworld	Greyworld	
White balance gains	150	Gain_r 150; Gain_b 150	
Image effect		None	
Colour effect		Disabled; y:u:v = 0:128:128	
Image statistics		Off	
Rotation	270	Rotate_270	
Flip	Both	Both	
Sensor region		X:0; y:0 W: 65,536; h:65,536	
Shutter speed		80,000	
Image quality		10	
Preview quality		Quality: Width: Divider:	100 512 10
Raw layer		Off	
Video bitrate		17,000,000	
Minimise frag Init quantisation Encoding qp		MF: IQ: QP:	0 25 31
MP4 boxing mode		Background	
Watchdog		Interval: Errors:	3 s 3
Motion detect mode		External	
Log size lines		5000	

Author contributions DS, OO, MS, SP, CL and HF conceived the idea, designed the experiment, and wrote the manuscript. AM, TH, and DB produced and analyzed the particulate matter. DS and SP carried out the experiment. DS, SP and MS performed the data analysis. DS, SP, OO, MS, CL and HF interpreted the results. All authors read and approved of the final manuscript.

Funding Open Access funding enabled and organized by Projekt DEAL. This project was financed by the Bavarian State Ministry of the Environment and Consumer Protection as part of the project network BayOekotox. The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Data availability The data that support the findings of this study are available upon request.

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