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Biomass burning smoke pollution stimulates painted lady butterflies (*Vanessa cardui* L.) to increase flight speed☆

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A R T I C L E I N F O

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A B S T R A C T

Smoke from biomass burning significantly degrades air quality due to high concentrations of particulate matter ($PM_{2.5}$) and trace gases. While the ecological and health impacts of smoke pollution are well documented, its effects on insect migration remain poorly understood. In this study, we conducted two experiments to investigate the flight performance of *Vanessa cardui* butterflies under varying smoke conditions and identify the mechanisms influencing their behaviour. Butterflies were tethered to flight mills (TFMs) for 6 h, during which flight speed, distance, and duration were recorded across clean-air conditions and three levels of $PM_{2.5}$ concentrations. Statistical analysis revealed that flight speed increases significantly as smoke concentration increases, although the increased range decreases. At a mean $PM_{2.5}$ concentration of 120 μg m^{-3}, flight speed increased by 52 % compared to clean-air conditions. To determine whether particulate matter was driving this response, individuals were exposed to smoke with and without particulates. In smoke with particulates retained, butterflies exhibited nearly double the flight speed compared to filtered smoke, indicating that particulates play a key role in altering flight behaviour. Scanning electron microscopy revealed significant deposition of smoke particulates on the antennae and abdomen, suggesting a sensory or physical response triggering accelerated flight. We interpret these findings as evidence that *Vanessa cardui* accelerates flight in smoky environments as an escape response. This study highlights the remarkable sensitivity of butterflies to smoke pollution and provides novel insights into the ecological consequences of biomass burning, particularly its potential impacts on insect behaviour and migration dynamics.

1. Introduction

Landscape fires are crucial disturbance agents in terrestrial ecosystems and are commonly used by humans for landscape management (Baillie and Bayne, 2019; Cascio, 2018; He et al., 2014; van der Werf et al., 2010). The African continent has long been referred to as 'the fire continent' because of its frequent and extensive annual landscape fires (Strydom and Savage, 2016), and on average over 200 million hectares burn annually in Africa, accounting for approximately 70 % of the global burned area (Andela and Van Der Werf, 2014; Wei et al., 2020). In the Sub-Saharan Africa (SSA) region, fires are extensively employed for land management practices such as crop expansion, grazing management, invasive species removal, and to change soil properties (Kahiu and Hanan, 2018; Le Page et al., 2010). Certain fire occurrences can be linked to warmer environmental conditions (Dupuy et al., 2020; He et al., 2014; Richardson et al., 2022). For instance, the Northern Sub-Saharan African region experiences intense biomass burning during the dry season (November–April) (Ichoku et al., 2016). Beyond Africa, fire-prone areas have expanded, including southern Europe and the northern and Mediterranean mountain ranges. In the European Union (EU) Mediterranean member states, forest fires are alarmingly frequent, ranging from 30,000 to 60,000 annually, devastating over 10 million

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hectares of land in the past 25 years (Gonçalves and Sousa, 2017; Schmuck et al., 2011). Climate change is increasing the frequency and intensity of landscape fires, which will intensify as global heating increases (Andela and Van Der Werf, 2014; Jones et al., 2022).

Smoke is released by landscape fires, and contains high concentrations of carbon dioxide (CO_2), monoxide (CO), methane (CH_4), nitrogen oxides (NO_x), sulfur dioxide (SO_2), hydrocarbons, and other organic chemicals, as well as significant amounts of particulate matter (PM) (Caamano-Isorna et al., 2011; Cristofanelli et al., 2009; Dhammapala et al., 2007; Kaiser et al., 2012; Li et al., 2019; Ravindra et al., 2019). Among these particulate emissions, carbonaceous aerosols are particularly prominent, including black carbon (BC) - primarily formed during flaming combustion and composed mainly of elemental carbon (EC), as well as organic carbon (OC) (Bond et al., 2013; Rathod et al., 2021; Titos et al., 2017; Vakkari et al., 2018; Zhang et al., 2013). Incomplete combustion of organic material also generates toxic organic compounds such as polycyclic aromatic hydrocarbons (PAHs) and phenolic compounds (Colom-Díaz et al., 2017; Yang et al., 2012; Zhang et al., 2022). In addition to these primary pollutants, secondary aerosols are formed post-emission through the atmospheric oxidation of volatile organic compounds (VOCs), which are also released during biomass burning (Kelly et al., 2018; Lim et al., 2019; Tasoglou et al., 2017; Vakkari et al., 2018). Other components such as water-soluble potassium (K^+) and particle-bound mercury are also associated with biomass-derived particulates (Tripathi et al., 2024; Zhang et al., 2013). The respirable fraction of particulate matter ($PM_{2.5}$) is considered the smoke component of most concern to human health, and is able to affect air quality and human health even in areas far away from the fires themselves (Roberts and Wooster, 2021). Smoke from North African fires regularly spreads into to Europe and influences air quality over the Mediterranean basin as far as north Italy (Cristofanelli et al., 2009; Majdi et al., 2019). The regions where fire smoke affects air quality are important for many insect migrations (Pedgley et al., 1995), such as *Thaumetopoea pityocampa* (Pine processionary moth) (Bourougaaoui et al., 2021; Roques et al., 2014); *Oplostomus fuligineus* (Large Hive Beetle) (Abou-Shaara et al., 2021); and also the notable migrant *Vanessa cardui*, which migrates between Africa and Europe (Stefanescu et al., 2013; Talavera et al., 2023, 2018). However, the actual impact of this air pollution source on insect behaviour, especially on migration, remains poorly understood (Liu et al., 2021).

Flight ability is an essential part of migration for many insects. The particulates emitted from landscape fires significantly impact air quality at both local and regional scales (Garcia-Hurtado et al., 2014), which strongly reduces visibility and may affect insect movement. For example, the smoke created by a forest fire in British Columbia, Canada, darkened the sky so that grasshoppers significantly reduced their straight-line flying to only short distances (Hegedüs et al., 2007; Pahlow et al., 2005). Migratory insects play a crucial role in ecosystem functioning and services, yet the effects of smoke pollution resulting from burning activities are often inadequately understood. Some evidence has been presented by Liu et al. (2021) to show that smoke can negatively impact butterfly flight performance, but the smoke conditions used in that experiment were extremely high (up to 4000 μg m^{-3}), the flight duration of butterflies was limited to only 30 min, and the same butterflies were re-flown in multiple experimental runs. Whilst a link between flight performance and $PM_{2.5}$ concentration was demonstrated, we considered it beneficial to repeat the study with more realistic smoke concentrations and a focus on longer-term insect movement. We aim to investigate how migratory insects react to atmospheric conditions polluted by biomass smoke during their initial exposure and to determine whether the observed effects on flight behaviour are predominantly caused by particulate matter or gaseous components in the smoke.

2. Methodology

2.1. Subjects

Adult *Vanessa cardui* was chosen as the test species as it is one of the best-known insect migrants between Africa and Europe (Stefanescu et al., 2017; Talavera and Vila, 2017; Talavera et al., 2023), forming the largest population of migrant butterflies regularly arriving in the UK each year. Adults of *Vanessa cardui* used in these experiments were bred by *Gribblybugs LLP*, a UK entomological supplier. The butterflies emerged from pupae in a controlled greenhouse, so each individual has a similar lifespan (five weeks) and body size (mean wingspan = 61.5 ± 6 mm). The one hundred and twenty butterflies were ordered in four batches of forty each. Each batch corresponded to one experiment and was delivered three days before commencement. The gender of each batch of butterflies is randomized, with the proportion of male and female being approximately 6:4. After arrival, they were fed with honey water (at a ratio of 9:1) and placed in the refrigerator in individual containers to keep them inactive and prevent their wings from getting damaged.

2.2. Experimental setup

All experiments were conducted between September and November 2020 in the King's Wildfire Testing (Combustion) Chamber at Rothamsted Research, Harpenden, UK, see Fig. 1, coinciding with the autumn migration period of *Vanessa cardui* (Stefanescu et al., 2017). One side of the chamber, oriented northwest (296°), was open to the external environment but covered with a transparent tarpaulin. This design allowed natural light to enter directly while protecting the interior from adverse environmental factors such as rain and wind.

Within the combustion chamber, two additional enclosures were constructed using a frame covered with transparent plastic sheeting: one designated for smoke conditions and the other for ambient clean-air (control) conditions. Both enclosures were positioned near to the open side of the chamber to allow natural light to enter. Individual butterflies were attached to TFM instruments, allowing them to evaluate their flight duration and distance within a defined period (Jones et al., 2016; Minter et al., 2018). For a detailed diagram of the TFM setup, refer to Liu et al. (2021). Each enclosure was equipped with four TFMs, enabling the simultaneous flight of four butterflies. To minimize potential mutual influence, white paper visual barriers separated the TFMs.

Particulate sensors (Plantower PMS5003) and PurpleAir PA-II SD air quality sensors were positioned at the centre of each enclosure to monitor the $PM_{2.5}$ concentrations experienced by the butterflies throughout each experiment. Three axial fans were installed in each enclosure -two on the sides and one at the bottom - to ensure uniform particle distribution and airflow. The speed and positioning of fans was carefully adjusted gently mixed the smoke without creating turbulence that could interfere with butterfly flight performance. Different smoke environments were established by setting distinct $PM_{2.5}$ concentration targets within the smoke enclosure. Smoke concentrations within the enclosures were regulated using a solenoid control system linked to particulate sensors. When smoke levels exceeded the preset threshold on the control panel, excess smoke was vented outside, maintaining the concentration within the target levels set for different smoke conditions. For example, the high smoke (HS) condition was set to maintain $PM_{2.5}$ concentrations at approximately 900 μg/m^3. Although the control system worked to stabilize concentrations, a slight delay in the feedback loop resulted in minor fluctuations around the set points. As a result, the actual $PM_{2.5}$ concentration in the high smoke (HS) condition was 887.87 ± 33.27 μg m^{-3}. Continuous burning of incense sticks ensured a steady supply of fresh smoke rather than recirculated "aged" smoke, with a small amount continuously extracted by an extractor fan. A photosynthetically active radiation (PAR) light sensor (SQ-100X) was placed on the top of the TFM to record the sunlight intensity (wavelengths

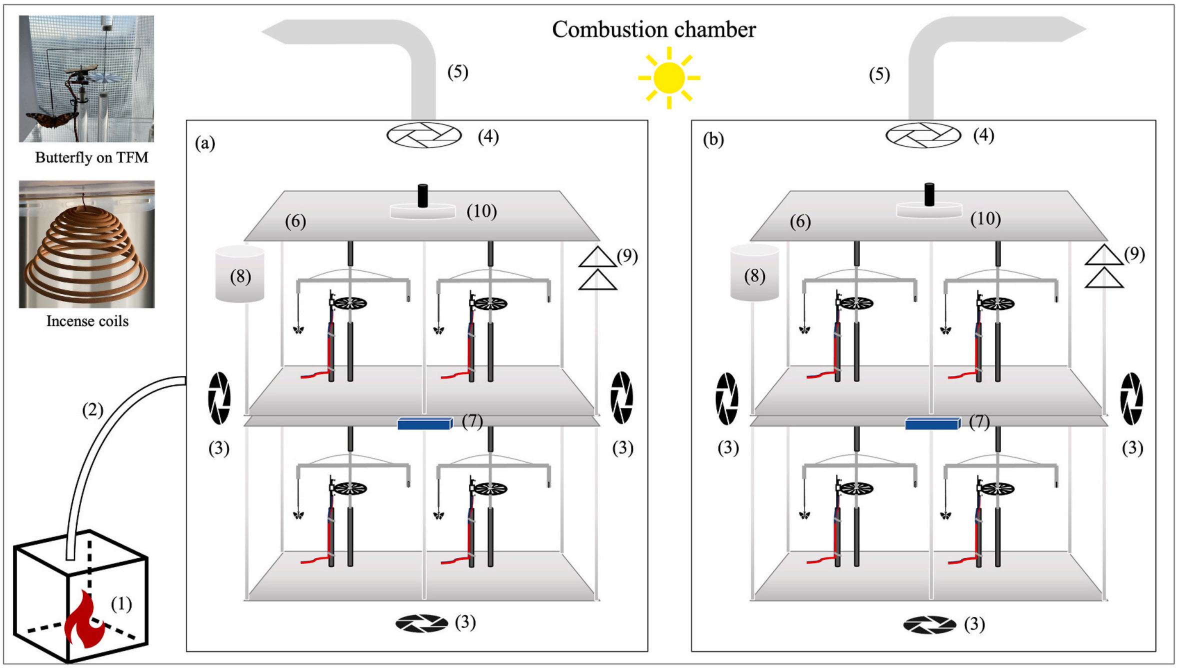

Fig. 1. A diagram of the experimental setup. Individuals were put in (a) smoke enclosure or (b) the control enclosure. Smoke was released from burning incense coils in a smoke box (1) and transported to the smoke enclosure via a tube (2). Three axial fans (3) were placed in right, left, and underneath the enclosure to promote air circulation, exhaust fan (4) and extract duct was used to remove excess smoke. The TFM equipment (6) was used to record the butterfly flight performance. A particulate sensor (7) and PurpleAir PA-II SD air quality sensor (8) were used to record $PM_{2.5}$ concentration. A temperature-humidity sensor (9) and light intensity sensor (10) recorded the environmental factors.

400–700 nm), aiming at checking whether the light intensity in the two enclosures was similar. A temperature & humidity sensor (BME280) was positioned on the right side of the TFM. An extractor fan was activated to remove all smoke in the two enclosures and maintain consistent airflow through each enclosure once the experiment was complete. Replacement air entered either through the smoke inlet for the smoke enclosure or via a small opening at the base of the control enclosure. All sensors were integrated with an Arduino controller, an open-source electronics platform, which recorded data at 5-s intervals.

2.3. *Experimental design*

Two one-way factorial experiments were conducted to examine the effects of smoke pollution from biomass burning on the flight behaviour of *Vanessa cardui*. Experiment A assessed the flight performance of butterflies under smoke and clean-air conditions, while Experiment B investigated which components of smoke (trace gases or particulates) might influence their behaviour. In both experiments, butterflies were placed in the TFM for 6 h, as a pilot study demonstrated that *Vanessa cardui* could sustain continuous flight for approximately 6 h or longer in the TFM. Key flight metrics, including total flight distance (m), average flight speed ($m \cdot s^{-1}$), maximum flight speed ($m \cdot s^{-1}$), flight duration (minutes), and percentage of flight duration (%), were recorded for butterflies in both enclosures for subsequent analysis. Additionally, scanning electron microscopy (SEM) analysis was performed on a subset of the butterflies after exposure to smoke to determine if particulate matter had adhered to their bodies.

2.3.1. *Experiment A: investigating flight performance of Vanessa cardui in smoke and clean-air conditions*

The objective of this experiment was to investigate the flight behaviour of butterflies under varying smoke concentrations—low (LS), medium (MS), and high (HS) smoke levels—based on $PM_{2.5}$ concentrations in the smoke enclosure, compared to clean-air conditions in the control enclosure. Three sets of comparative experiments were conducted, each consisting of four replicates. In each replicate, four butterflies were tested simultaneously under smoke and control conditions.

The $PM_{2.5}$ concentrations were used as a metric to assess the severity of the smoke conditions experienced by butterflies. This parameter is easy to measure accurately with low-cost, laser-based sensors that respond quickly to concentration change. $PM_{2.5}$ is the primary health-impacting component of landscape fire smoke and influences atmospheric opacity (Nguyen et al., 2021; Roberts and Wooster, 2021). LS, MS, and HS conditions were set at $PM_{2.5}$ concentrations of 150 $\mu g\ m^{-3}$, 450 $\mu g\ m^{-3}$, and 900 $\mu g\ m^{-3}$, respectively. These levels reflect typical fluctuations during biomass burning events, which can range from low (e.g. 10 $\mu g\ m^{-3}$) to extreme (e.g. 1000 $\mu g\ m^{-3}$), such as during the 2015 fire episode in Palangkaraya, Indonesia, where concentrations likely exceeded 2000 $\mu g\ m^{-3}$ (Wooster et al., 2018). *Vanessa cardui* migrates within 150–1200 m altitudes during large-scale movements (Stefanescu et al., 2013). The WACCM global chemistry model predicts absolute maximum $PM_{2.5}$ concentrations in Africa from the surface to 1200 m altitude to fall within this range during the fire season (NCAR, 2020).

Smoke was generated by burning unscented incense coils in a sealed box, producing consistent smoke for 6 h. The smoke was delivered to the smoke enclosure through a tube, which was exposed to ambient conditions to minimize heat transfer and avoid altering the temperature inside the smoke enclosure. This approach effectively simulates the chemical composition of biomass smoke, as supported by previous studies (Cheng et al., 2015; Jetter et al., 2002; Song et al., 2023). Fresh air was supplied to the box via a pump, and solenoid-controlled pumps regulated smoke delivery to the enclosure and vented excess smoke through a filter. An Arduino controller linked to a $PM_{2.5}$ sensor (Plantower PMS5003) ensured target concentrations were maintained. Temperature, humidity, and light intensity were consistent across smoke and control enclosures (details in Supplementary Materials).

2.3.2. Experiment B: investigating flight performance of Vanessa cardui in smoke conditions with and without particles

The aim here was to investigate whether particulates or trace gases in the smoke affect butterfly flight performance. Therefore, we compared the flight performance of *Vanessa cardui* in HS conditions with particulates (smoke enclosure) and without particulates, where particles were filtered out, leaving only trace gases (control enclosure). Experiment B included four replicates, with four butterflies in both conditions per replicate.

Smoke conditions were generated using a pump with two pipes connected to the smoke box. One pipe transported unfiltered smoke directly to the smoke enclosure, while the other directed gaseous emissions (with 99.99+% of particles ≥0.1 μm filtered out) to the control enclosure. The primary trace gases present in the smoke - CO_2, CO and CH_4 (Andreae and Merlet, 2001; Lee and Wang, 2004; Yang et al., 2012; Yokelson et al., 2011) - were measured using a Los Gatos Research (LGR) Ultraportable Greenhouse Gas Analyser during experiment B. Two tubes connected to the analyser allowed the measurement of gas concentrations in both enclosures, which were found to be very similar during the experiment.

2.4. Post-exposure examination using scanning electron microscopy (SEM)

SEM was used to observe the distribution and quantity of particulate matter (PM_1/$PM_{2.5}$/PM_{10}) adhered to butterfly body parts after exposure to various smoke conditions (control, LS, MS, and HS conditions). The forewing, hindwing, antenna, head, eye, and abdomen were analysed.

Prior to SEM analysis, butterfly specimens were frozen at −20 °C for 48–72 h and transferred to a desiccator. Specimens were dissected to remove wings, head, antennae, and abdomen then mounted on SEM stubs. Wings and antennae were fixed on sticky carbon tape and covered with additional carbon, while the head and abdomen were glued using silver paint. All samples were gold-coated and imaged using a JEOL 6360LV SEM (3.0 nm resolution, 20 mm observation distance) at Rothamsted Research's Bioimaging Facility. Three random areas (100 × 90 μm^2) per body part were selected, and images were captured at 1500 × magnification to observe PM_1, $PM_{2.5}$, and PM_{10}.

2.5. Statistical analysis

Data from each butterfly mounted on the TFM were analysed at 5-s intervals using a MATLAB (version R2019a) script to calculate flight variables, including total flight distance (m), average speed ($m.s^{-1}$), maximum speed ($m.s^{-1}$), and time spent flying (minutes). Descriptive statistics, including the mean and standard deviation (SD), were computed to assess the overall flight performance of the butterflies. Univariate Analysis of Variance (ANOVA) was employed to evaluate whether significant differences existed in the average flight speeds among the three control groups in Experiment A. Normality of the data was assessed using the Shapiro-Wilk test (Hanusz and Tarasińska, 2015). As the average flight speeds in the 'smoke with particulates' and 'smoke without particulates' conditions from Experiment B did not follow a normal distribution ($P = 0.016$), a Mann-Whitney U test—a non-parametric alternative to the T-test for independent samples—was conducted to determine if significant differences existed between these two conditions.

3. Results

3.1. Incense coils successfully created three smoke conditions

As described in Section 2.3.1, three stable smoke conditions with different $PM_{2.5}$ concentrations were created in the smoke enclosure, with means ± standard deviation of 120.42 ± 10.42 μg m^{-3}, 371.24 ± 31.54 μg m^{-3} and 887.87 ± 33.27 μg m^{-3} for LS, MS, and HS respectively. These levels reflect realistic concentrations found in regions affected by biomass burning. The mean $PM_{2.5}$ concentration in the control was 9 μg m^{-3}, equivalent to the annual mean $PM_{2.5}$ concentration recorded at urban background monitoring sites in the (UK Department For EnvironmentFood & Rural Affairs, 2023). Although a filter was used to remove particles in the "smoke without particulates" condition, some particles entered the chamber, resulting in higher concentrations than the control condition. Analysis of variance confirmed that $PM_{2.5}$ concentrations across the five smoke conditions were significantly different (ANOVA, P value < 0.001).

3.2. Flight speed increased in smoke conditions

The 6-h flight speed data from the control enclosure in each subexperiment of Experiment A were divided into 36 10-min intervals. The mean flight speed for each group showed a decreasing trend over time under clean-air conditions. However, these mean values included periods of both flight and rest, as the butterflies were free to alternate between flying and stopping on the TFMs at will. Analysis of the percentage of time butterflies spent flying versus resting within each 10-min interval revealed that resting periods increased over time, contributing to the observed decline in overall mean flight speed. When resting periods were excluded, the analysis showed that butterflies maintained a relatively constant flight speed during active flight, with minimal variation over time.

An ANOVA test was conducted to compare mean flight speeds across the three control groups, with the null hypothesis (H_0) positing no significant difference and the alternative hypothesis (H_1) suggesting differences. The test found no significant differences among the groups ($P = 0.33$). Consequently, the flight performance data from the control groups were pooled for further analysis. Under clean-air conditions, butterflies exhibited a mean total flight distance of 3984 m, an average flight speed of 0.24 m s^{-1}, a maximum flight speed of 0.65 m s^{-1}, and a total flight duration of 200 min.

Flight data from LS, MS, and HS smoke conditions (Fig. 2a) were analysed using the same methodology as the control data. Butterfly flight performance under these smoke conditions displayed a similar temporal decline to that observed under clean-air conditions. Additionally, the percentage of time spent flying versus resting in each 10-min interval followed a comparable trend to that in the control enclosure.

When resting periods were excluded from the analysis, flight speed exhibited an upward trend across all smoke conditions. As shown in Fig. 2b, flight speed increased over time in LS, MS, and HS conditions.

To explore the relationship between flight speed and time, mean values from each boxplot in Fig. 2b were extracted, and a linear best-fit analysis was conducted (Fig. 3). Unlike the slight decline in flight speed observed under control conditions, smoke conditions displayed a clear upward trend over 6 h, particularly in LS and MS scenarios. The data also revealed periodic variations, with flight speed alternating between acceleration and deceleration. Under HS conditions, the trend was nonlinear, with flight speed increasing during the first 2 h before decreasing over the following 4 h.

Butterflies in smoke conditions covered greater total flight distances compared to the control, increasing by 26 %, 27 %, and 23 % in LS, MS, and HS conditions, respectively. This increase was primarily driven by higher flight speeds, with average speeds improving by 52 %, 44 %, and 36 % and maximum speeds increasing by 45 %, 29 %, and 8 %, respectively. However, flight duration decreased by 13 % and 7 % in LS and MS conditions, while it remained similar to control conditions under HS conditions.

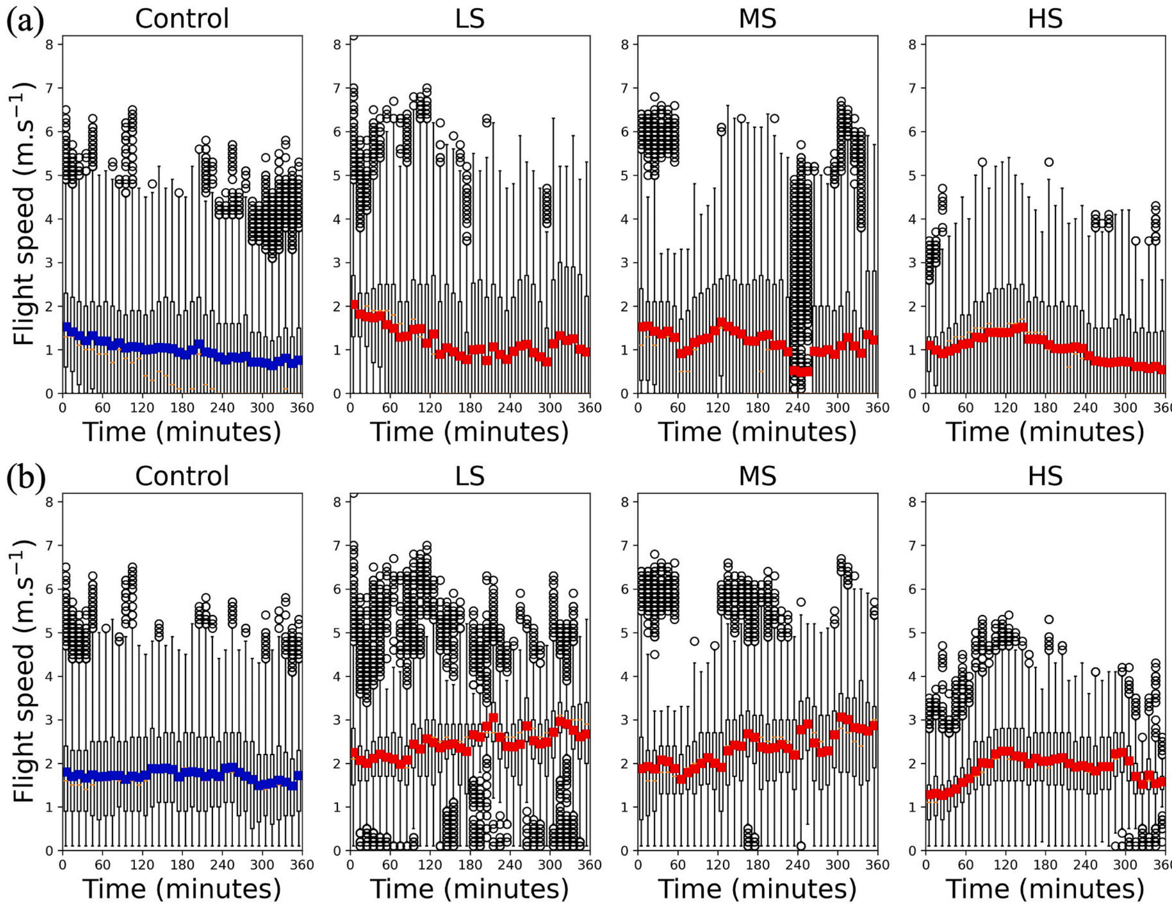

Fig. 2. Boxplots showing the flight speed of butterflies from different smoke conditions (red) and control conditions (blue) separated into 36 10-min segments, collected from Experiment A. (a) includes all data, whilst (b) excludes that from any period when a butterfly stopped flying altogether. The higher and lower bars of the plots are the maximum and minimum values, respectively. The rectangle illustrates the first quartile, the median, and the third quartile (bottom to top). The red square is the mean, and the black circles are outliers. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

3.3. Flight performance comparison between smoke conditions with and without particulates

To further investigate the effects of smoke constituents on butterfly flight behaviour, *Vanessa cardui* were exposed to smoke conditions with and without particles in Experiment B. Flight data were analysed using the same methods as previous experiments. Flight speed decreased over 6 h in both smoke conditions, accompanied by an increase in resting periods over time. Butterflies exposed to "smoke with particulates" condition exhibited longer resting periods than those in the "smoke without particulates" condition. After excluding resting periods, flight speed in the "smoke without particulates" condition showed a slight decrease over time, while butterflies in the "smoke with particulates" condition displayed an initial rapid increase in flight speed during the first 1.8 h, followed by a sharp decline, as shown in the subsequent analysis (Fig. 4).

Flight performance metrics revealed a 35 % longer flight distance in the "smoke with particulates" condition (4924 m) compared to the "smoke without particulates" condition (3643 m). Similarly, average flight speed nearly doubled from 0.16 m s^{-1} in the "smoke without particulates" condition to 0.30 m s^{-1} in the "smoke with particulates" condition. However, flight duration was 20 % shorter in the "smoke with particulates" condition (211 min) compared to the "smoke without particulates" condition (263 min). A Mann-Whitney *U* test confirmed that average flight speeds significantly different between the two groups ($P = 0.043$, $n = 16$). These findings suggest that particles in the smoke are the primary factor driving the increased flight speed observed in the "smoke with particulates" condition.

3.4. Scanning electron microscopy of butterfly bodies

Imagery collected from the scanning electron microscope (SEM) analysis showed some particulates with diameters between 1 μm and 10 μm observable on the antennae and abdomen of butterflies exposed to smoke conditions. No visible particulates were observed on other body parts, including the eyes, forewings, and hindwings. Where present, particulates were not homogeneously distributed (Fig. 5). Additionally, no significant increase in particulates was observed with increasing smoke concentrations (from LS to HS conditions).

4. Discussion

4.1. Burning incense coils generated different $PM_{2.5}$ concentrations that simulated real landscape fire smoke exposure

Although the $PM_{2.5}$ concentrations observed in the experiments were slightly lower than the preset values, they represent levels that butterflies might encounter in real-world conditions. Studies on vegetation fires in Africa have reported $PM_{2.5}$ concentrations ranging from 30 μg m^{-3} to 1620 μg m^{-3} during the dry season (early June-early August) (Korontzi, 2005; Ofosu et al., 2013). These studies also recorded excess CO_2 concentrations emitted by fires between 2 ppm and 1043 ppm, CO

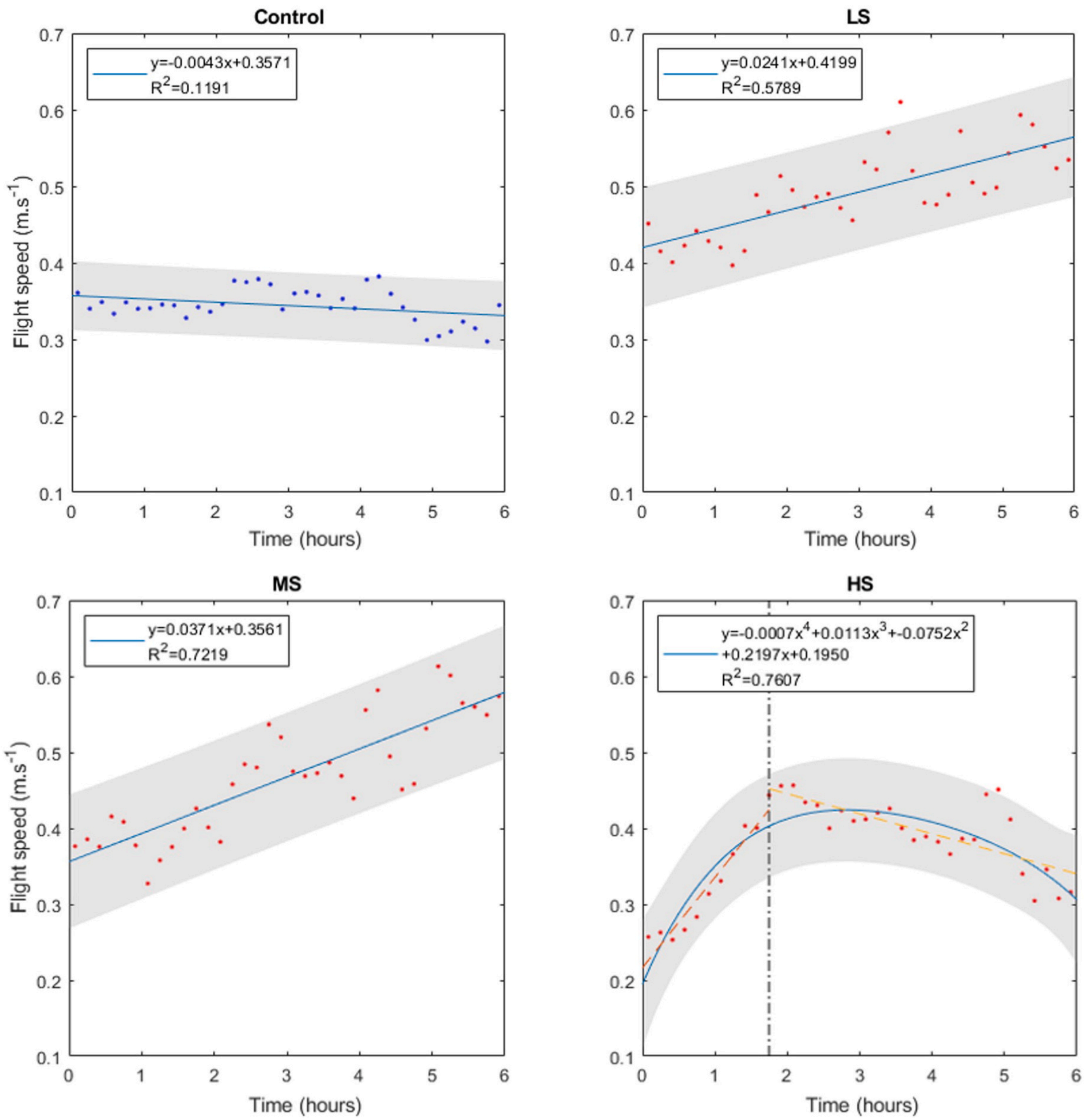

Fig. 3. Scatterplots of mean flight speed change over time extracted from data without the zero value flight speeds, as was the case with Fig. 2b in different smoke conditions (LS, MS, and HS) and control conditions. The blue line represents the least squares linear best-fit for control, LS, and MS conditions and non-linear best-fit for HS conditions, along with the 95 % confidence intervals on the slope (grey area). The equations for this are shown along with the coefficient of variation (r^2). The dashed line shows the flight speed variance thresholds, which divided the flight speed variance into two parts: an increasing trend and a decreasing trend. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

concentrations between 0.18 ppm and 92 ppm, and CH_4 concentrations between 0.026 ppm and 5.8 ppm (Korontzi et al., 2003; Ward et al., 1996). Roberts and Wooster (2021) state that some regions in central and western Africa experience $PM_{2.5}$ concentrations exceeding 250 μg m^{-3} due to landscape fire smoke, significantly impacting local populations. Climate change is projected to increase fire incidence in certain regions globally, heightening the risk of butterflies encountering smoke emissions during migration (Dupuy et al., 2020; Jones et al., 2022).

4.2. Smoke conditions change butterfly flight performance

The average flight speed of *Vanessa cardui* under clean-air conditions on TFM was 2.4 m s^{-1}, which is considerably lower than the 6 m s^{-1} reported for downwind flights during spring migration (Stefanescu et al., 2013). This discrepancy highlights the potential limitations of TFMs in replicating natural flight conditions, as TFMs may restrict natural wing flapping dynamics (Jones et al., 2016). Additionally, captive-bred butterflies may not fully replicate the migratory behaviour of their wild counterparts (Tenger-Trolander et al., 2019). Variability in flight performance between different batches of butterflies under control conditions may be due to the timing of breeding within the migration season, which typically spans from early August to early November, peaking between mid-September and mid-October (Stefanescu et al., 2017; Stefanescu et al., 2013). Individual differences arising from hatching in separate batches may also have contributed to variations in flight duration among control groups. Such variability has been observed in other species; for instance, *Euphydryas phaeton* (Baltimore checkerspot butterfly) exhibits significant differences in dispersal distance and habitat preferences due to individual variation (Garcia-Hurtado et al., 2014). Similarly, butterflies from different generations have shown distinct differences in flight performance and energy metabolism under standardized experimental conditions (Lebeau

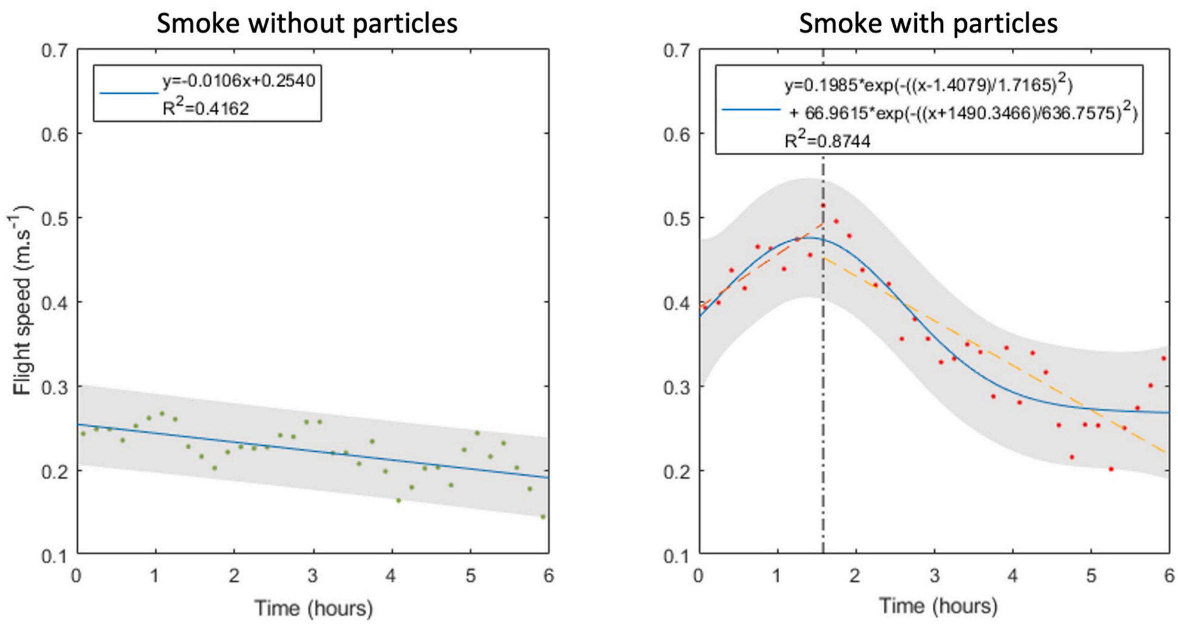

Fig. 4. Scatterplots of mean flight speed changes over time were extracted from data without the zero value flight speeds, The blue line represents the least squares linear best fit for 'smoke without particulates' conditions and the non-linear best fit for 'smoke with particulates' conditions, along with the 95 % confidence intervals on the slope (light blue area). The equations for these are shown along with the coefficient of variation (r^2). The dashed line showed the flight speed variance thresholds, which divided the flight speed variance into two parts: an increasing trend and a decreasing trend. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

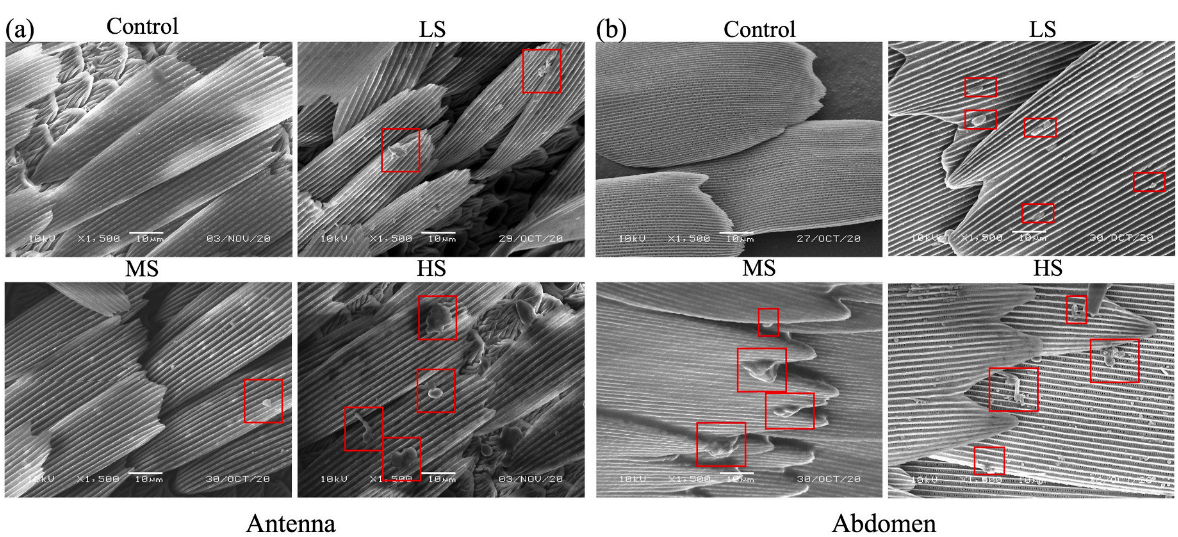

Fig. 5. Scanning electron microscopy images of (a) antenna and (b) abdomen in butterfly with ×1500 magnification to show the presence of $PM_1/PM_{2.5}/PM_{10}$ from (i) control condition; (ii) LS condition; (iii) MS condition; and (iv) HS condition. The red square shows the area where the particulates appeared. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

et al., 2016). The slight downward trend in flight speed under control conditions may reflect the depletion of energy reserves, as butterflies were fed before the experiment but lacked the opportunity to replenish these reserves during the trials.

Results from Experiment A demonstrate that butterflies exhibited higher flight speeds in smoke conditions, particularly in LS and MS conditions, suggesting that smoke exposure stimulates faster flight. This response may represent an attempt to escape unfavourable environments, as observed in other species. For example, the number of *Apis mellifera* (western honey bees) increases at the entrance of hives when it is affected by smoke and they flee quickly, which is a form of absconding behaviour (Gage et al., 2018; Tribe et al., 2017). Also, *Exyra semicrocea* (Pitcher plant mining moths) immediately vacate their host plants when exposed to smoke, taking an average of 6.5 s to leave (Lee et al., 2016). In dense smoke (HS), flight speed was significantly reduced compared to LS and MS, likely due to the negative effects of high particulate concentrations on flight performance, as observed in previous studies (Liu et al., 2021). These findings confirm that smoke is the primary factor influencing butterfly flight performance, rather than just energy depletion. The results suggest a concentration-dependent effect, where butterflies in lighter smoke conditions (LS and MS) sustain acceleration over extended periods, while denser smoke (HS) limits acceleration and flight duration. This highlights the critical role of smoke concentration in shaping butterfly flight behaviour.

Regarding flight duration, the reduction observed in smoke conditions may reflect increased energy consumption. Grasshoppers and seed bugs have been observed to reduce straight-line flight to short distances, and delay flight/migration behaviour when they were stuck in forest fire smoke conditions (Hegedüs et al., 2007; Johnson et al., 2005). In smoke conditions, total flight distance increased by approximately 25 % due to the significant increase in flight speed despite a slight decrease in flight duration. It highlights the interplay between flight speed and duration in determining overall flight performance under smoke exposure.

4.3. Particulates may be the main cause of the accelerated flight of butterfly

The results from Experiment B indicate that particulate matter is the primary factor driving the increased flight speed of butterflies. One possible explanation for this observation may be linked to effects on the energy conversion efficiency as identified in other species. For instance, when exposed to particulate matter, *Gonioctena quinquepunctata* (Leaf beetle) exhibited reduced mass and decreased efficiency in converting ingested food (Łukowski et al., 2018). Furthermore, Tan et al. (2018) demonstrated that larvae of *Bicyclus anynana* (Squinting bush brown) had a low survival rate, low weight mass, and long development period when exposed to smoke with a $PM_{2.5}$ concentration of 120 μg m^{-3}. In addition, *Heliconius ethilla* larvae fed on *Passiflora edulis* (passion fruit) leaves treated with Sedimentable Particulate Matter (SPM) exhibited reduced pupal weight and adult size, alongside increased mortality rates at higher SPM concentrations (Charpinel et al., 2024). These findings underscore the significant impacts of particulate matter on insects. It is plausible that the particulate matter in this study irritated the butterflies, prompting them to accelerate their flight as a behavioural response to escape the smoke-laden environment.

4.4. Particulates distributed on the antennae may be the main cause of changes in butterfly flight performance

Our findings revealed that particulates were not homogeneously distributed across the body of *Vanessa cardui* primarily located on the antennae and abdomen, with no visible accumulation on the eyes, hindwings, or forewings. A similar pattern was observed in *Musca domestica* (Housefly) exposed to ambient air pollution (Air Quality Index 100–150) for 12 h, where particulate matter was found to accumulate most densely on the antennae compared to other body parts such as the head, thorax, legs, and abdomen (Wang et al., 2023). This uneven distribution suggests that the wing-flapping motion during flight likely prevents particulate deposition on the wings, while the relatively stationary nature of the abdomen and antennae during flight allows for more particulate accumulation (Taylor, 2001).

The particulates accumulating on the antennae likely stimulated the butterflies and influenced their increased flight speeds. There is growing evidence that particulate matter can impair antennal sensitivity in insects. For example, PM exposure has been shown to reduce the olfactory sensitivity of houseflies, limiting their ability to detect odours (Wang et al., 2023). Similar effects have been reported in other insect taxa, including bees, wasps, moths, and various fly species (Skaldina et al., 2023; Wang et al., 2023), suggesting a widespread vulnerability of insect antennae to particulate pollution.

Insect antennae are complex sensory organs critical for flight performance (Donley, 2022; Gewecke, 1970; Sane, 2016; Sane et al., 2007). Donley et al. (2022) indicated that the antennae of *Vanessa cardui* consist of long, thin flagella covered with scales that sense a wide range of chemical stimuli. Smoke, as a chemical stimulus, may irritate the antennae, triggering altered flight behaviour. More specifically, smoke particulates adhering to the antennae may block access of pheromones to chemoreceptors, potentially disrupting normal sensory processes (Visscher et al., 1995).

The role of antennae in flight stability has been demonstrated in other species, such as *Manduca sexta* (hawk moth), where the antennal flagellum plays a critical role in maintaining balance and stability. Proper functioning of the antennal flagellum ensures accurate mechanosensory input and external stimulus response, which are essential for stable flight (Sane et al., 2007). Similarly, in *Triatoma infestans* (kissing bug), damaged or impaired antennae significantly alter movement patterns, leading to erratic changes in direction and impaired orientation toward thermal stimuli (Flores and Lazzari, 1996). These examples underscore the critical role of antennae in facilitating precise and stable movement.

Moreover, other chemical stimuli in smoke may also influence insect behaviour by interacting with sensory receptors on the antennae. For example, the antennae of jewel beetles can detect specific compounds emitted in smoke from burning wood, which serve as sensory cues to locate suitable habitats (Schütz et al., 1999). This highlights the possibility that both particulates and chemical compounds in smoke interact with the antennae of *Vanessa cardui*, driving specific behavioural responses such as increased flight acceleration.

4.5. Particulates may impact butterfly flight performance in other aspects

While the presence of particulates on the antennae of butterflies may influence their flight performance, it is unlikely to be the sole factor. Our study primarily examined the external distribution of particulates on butterfly surfaces, without investigating potential internal effects. It is well-documented that particulate matter ($PM_{2.5}$) significantly impacts on human respiratory systems, causing direct physiological effects (Thangavel et al., 2022; Xing et al., 2016). Furthermore, $PM_{2.5}$ exposure has been shown to induce inflammatory responses and endothelial dysfunction in the hearts of mice (Zhang et al., 2021, 2016). Therefore, particulate matter could enter the thoracic spiracles of insects, stimulating internal organs and subsequently affecting their flight performance.

In insects, air exchange occurs through diffusion via tracheoles directly into surrounding tissues, bypassing specialised respiratory systems. This makes them susceptible to chemical exposure in smoke, such as nitrogen oxides (NO_x) and sulfur dioxide (SO_2), which may stimulate physiological responses (Tan et al., 2018). Therefore, while the external accumulation of particulates on butterfly antennae represents one mechanism affecting flight performance, the combined effects of particulate and chemical stimulation on internal systems likely contribute to a more complex interplay influencing their behaviour.

5. Conclusion

This study is the first to demonstrate that butterflies increase their flight speed in stable smoke conditions with $PM_{2.5}$ concentrations that are realistic in natural environments. Notably, the extent of this increase diminishes as smoke concentrations rise. It also marks the first time *Vanessa cardui* has been studied on TFMs over an extended period, providing valuable insights into their flight performance under realistic environmental conditions, particularly during migration. Furthermore, this research is the first to differentiate between the effects of gaseous and particulate emissions from smoke on butterfly flight performance, suggesting that particulates are likely the primary driver of the observed alterations. To build on these findings, future studies should investigate which specific components of particulate matter are responsible for influencing insect physiology and behaviour.

However, TFMs may constrain natural flight behaviours, and real-world smoke effects are likely influenced by additional factors such as temperature, wind, and weather, which are critical to migration dynamics. With the increasing prevalence of landscape fires due to climate change and human activities, the ecological consequences for migratory species like butterflies could be significant. Future research should focus on how smoke impacts butterfly flight directions, migration patterns, and broader ecosystem dynamics to assess its ecological implications better.

CRediT authorship contribution statement

Yanan Liu: Writing – original draft. **Mark J. Grosvenor:** Writing – review & editing. **Martin J. Wooster:** Supervision. **Bruce Main:** Methodology. **Su Yan:** Software. **Robert Francis:** Writing – review & editing. **Eduri Venter:** Methodology.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.envpol.2025.126228.

Data availability

Data will be made available on request.

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