



OPEN Increasing canopy cover elevates vehicle collision risk for barbastelle bats (*Barbastella barbastellus*) at roads

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Roads can form barriers to movement and act as mortality sinks for bats. However, understanding flight behaviour over roads has been limited by reliance on human observers to characterise flight patterns. Moreover, both species-specific behaviour and the local environment may alter bat-road interactions. Using paired near-infrared cameras with 3-D tracking analysis, we reconstructed the flight trajectories of barbastelle bats (*Barbastella barbastellus*) at nine road sites in West Sussex, England. Of the 400 flight paths, 56% occurred at heights that placed bats at risk of vehicle collision, and this risk increased as bats flew closer to canopy cover. Increasing canopy cover was associated with bats flying along rather than across roads, and with faster flight speeds (by 0.14 ms^{-1} per 10% increase in canopy cover). Flight behaviour was not influenced by traffic density. These findings suggest that hop-overs, in which trees are planted to provide continuous canopy cover, may create an ecological trap by encouraging *B. barbastellus* to cross roads at unsafe heights. Our results also highlight the value of 3-D tracking to understand bat behaviour, an approach that could be applied to predict better the impact of road developments on bats and evaluate the effectiveness of mitigation in reducing collision risk.

Keywords *Barbastella barbastellus*, 3-D tracking, Road ecology, Hop-overs, Collision risk, Flight behaviour

The road network is expanding rapidly across the world, with an expected increase from 45 to 70 million paved lane-kilometres between 2010 and 2050¹. In Europe, almost a quarter of all land area is within 500 m of the nearest paved road or railway² and in the USA only 18% of the landscape is more than 1 km from a road³. There is widespread evidence for the negative effects of roads on biodiversity. Roads represent one of the major causes of habitat fragmentation, loss of landscape connectivity, genetic differentiation, and mortality for wildlife populations^{4–6}. Moreover, the influence of roads at the landscape-scale (i.e., the road effect-zone) can extend many kilometres beyond the immediate boundaries of the road network^{7–9}.

Bats possess several life-history traits which make them vulnerable to various threats, including roads. These traits, which are often associated with much larger species, include a low fecundity, long life span, and large home range^{10,11}. Due to their low reproductive rate, bat populations are limited in their ability to respond to mortality threats¹¹, whilst the use of multiple geographically separated locations for foraging, mating, hibernating, and breeding increases their encounters with roads. Many bat species fly at heights that bring them into the path of vehicles, particularly when commuting between roosts and foraging sites. Consequently, roads have been identified as being one of the major threats to bat conservation, serving as mortality sinks and acting as a potential barrier to flight between roosts and foraging sites^{12–14}. Bat fatalities from vehicle collisions on roads have been well documented^{15–25}, revealing a notable bias towards low-flying species, males, and juveniles¹³. For instance, observations in Poland over a four-year period recorded between 0.3 and 6.8 bat casualties per kilometre per year, with the highest rates found where roads were bordered by trees¹⁹. However, these figures likely underestimate true mortality due to limited searcher efficiency²⁶ and rapid carcass removal by scavengers²⁷. After adjusting for some of these biases, Russell et al.²² estimated that roadkill may account for up to 5% of a local *Myotis lucifugus* population in North America annually. Such levels of additive mortality, particularly when sustained over time, may have serious implications for the viability of slow-reproducing bat species.

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The barbastelle bat (*Barbastella barbastellus*; Schreber, 1774) is an elusive bat species that is currently classified as 'Vulnerable' in both Great Britain²⁸ and Europe²⁹. It primarily roosts in mature, unmanaged woodlands, where dead and veteran trees provide the crevices and loose bark it requires for shelter³⁰. *Barbastella barbastellus* is a long-distance forager, typically traveling 1–10 km from roosts and foraging in broadleaved woodland, riparian vegetation, and along forest edges^{31,32}. These long-distance nightly movement means it is likely to encounter roads frequently. As an edge-adapted species, it also uses linear landscape features such as tree-lined roads for commuting and foraging^{33–35}. However, it is difficult to assess the full extent of the risk that roads pose to the viability of *B. barbastellus*, owing to a lack of data on its population size. Nonetheless, the relatively high proportion of casualties recorded in numerous studies¹³ suggests that roads may represent a significant threat, especially given the rarity of the species and its limited reproductive output. Previous research indicates that *B. barbastellus* will cross motorways with heavy traffic during roost switching and, unlike other woodland species such as *Myotis bechsteinii*, is less reliant on underpasses for passage³⁶. *Barbastella barbastellus* is adapted for foraging in open spaces and capable of both low- and high-altitude flight, which may contribute to the high number of casualties that have been reported. It has been suggested that the lack of road avoidance behaviour could increase their mortality risk if they fly at an inadequate height to avoid larger vehicles such as trucks³⁶.

Whilst species-specific behaviour has a significant effect on the collision risk posed to bats on roads¹³, there are several other factors that may have an influence. These have the potential to alter bat behaviour, affecting the height, speed, and duration of time spent over roads by bats, as well as dictating the degree of avoidance behaviour. For example, Russell et al.²² reported that fewer individuals of the species *Myotis sodalis* crossed a major highway when canopy cover was lacking, but they crossed lower and closer to traffic when it was present. Similarly, Bennett and Zurcher³⁷ found that if trees were absent or there were gaps greater than two metres along commuting routes, bats were more likely to turn around. This change in behaviour can significantly impact the risk of mortality, particularly when it is considered in the context of high-quality habitat for bats²⁴.

Understanding how bats navigate along commuting routes is critical, especially considering how environmental features like tree cover affect their movement. Several studies have therefore aimed to characterise the flight height of bats over roads. These are usually based on human observations, sometimes employing surrounding objects as reference points^{22,37–39}. However, both thermal and near-infrared cameras are increasingly being used to provide insights into bat behaviour, particularly in the ecological consultancy sector. For instance, Claireau et al.⁴⁰ used a novel approach, combining the use of reference points with 2-D bat flight trajectory reconstructions, to infer height and assess the impact of a bat overpass installation. However, recent advances in tracking analysis and software availability have made the extraction of 3-D animal trajectories from videos much more accessible^{41–43}. This technology has been driven in part by the need to better understand the impact of wind energy developments on bats^{44,45}, and can provide accurate information on flight height, speed, and direction.

By employing near-infrared cameras in combination with 3-D tracking approaches, alongside acoustic recordings for species-level identification, this study digitally reconstructed the flight trajectories of *B. barbastellus* over roads. Building on the observations by Russell et al.²², which found that bats crossed a highway at greater heights in areas with increased canopy cover, we hypothesised that more canopy cover and a greater canopy height would lead to higher flight elevations and lower collision risk. Additionally, given that bats may perceive moving traffic as a threat^{12,38}, we expected increased traffic density to result in bats flying higher and more directly over roads to minimise risk. Lastly, owing to the increased predation risk associated with open spaces⁴⁶, we hypothesised that flight speed would be higher at road sites with less canopy cover. These hypotheses, grounded in broader bat ecology research, have not been explicitly tested in *B. barbastellus*, but align with the species' known reliance on cluttered habitats and its sensitivity to anthropogenic disturbances.

Methods

Study sites

The study was conducted at nine sites in southern England between August and September 2020 (Fig. 1). These sites were selected for their proximity to two woodlands (The Mens and Ebernoe Common), which host well-documented maternity colonies of *B. barbastellus*. Both woodlands are designated Special Areas of Conservation (SACs), with the presence of *B. barbastellus* being cited as either the primary or qualifying feature. Given the extensive radio-tracking data available for these colonies, earlier studies had identified the locations of previously used roost trees, flightlines, and foraging areas^{47,48}. Each study location was within 4 km of an occupied woodland and was positioned where previously known flightlines intersected roads, or where crossing points were predicted based on linear feature (i.e., treelines, unmanaged hedgerows) configuration leading from occupied woodlands. Preliminary surveys using acoustic bat detectors were conducted at each study location to verify the local and substantial presence of *B. barbastellus*. All sites were located on two-lane B-roads, with a mean width of 6.97 m (SD = 1.00 m), on straight sections where vehicles were allowed to drive up to 60 mph (96 kmph). Several features were avoided: (1) streetlights and urban areas, (2) motorways, and (3) water bodies other than small streams. A single road section at each site was surveyed for either three ($n = 5$) or four ($n = 4$) nights, with the aim of completing all surveys at a site within a 10-day period to optimise data collection whilst considering logistical and weather constraints. Surveys were only undertaken when the conditions complied with best practice guidelines for bat surveys in the UK (sunset temperature ≥ 10 °C, no rain or strong wind)⁴⁹.

Survey design

Road sections were filmed using one Canon XA11 and one XA20 camera (Canon, Japan), both capable of near-infrared recording, from 30 min after sunset until sunrise. All video was captured at 50 frames per second at 1920 × 1080 pixel resolution. Cameras were mounted on tripods and positioned on either side of the road, at a mean distance of 0.46 m (range: 0.28–0.77 m) from the road edge and at a mean height of 0.65 m (range: 0.60–0.80 m) (Fig. 2).

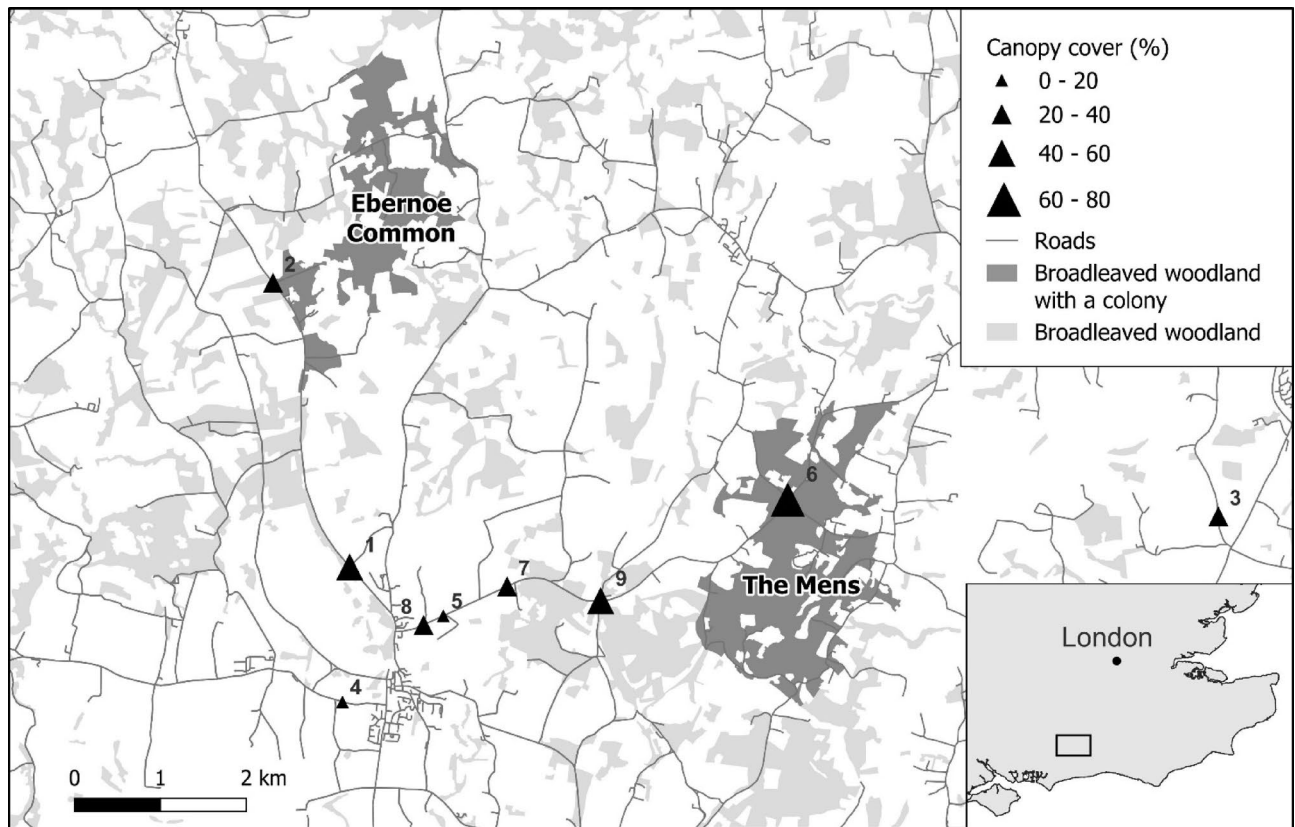


Fig. 1. Location of the nine study sites in relation to woodlands occupied by known *B. barbastellus* colonies in the county of West Sussex, England. Canopy cover represents the percentage cover within a 20 m buffer around the centre of each site. Site ID numbers are shown next to each site marker. Map created using QGIS (v3.6.3-Noosa; <https://www.qgis.org/>).

Each camera was paired with a primary light source; an infrared illuminator (LIR-IC88, 850 nm, IRLAB, Shenzhen, China) that had a range of 180 m and a lighting angle of 40°. These were placed approximately 5–10 m behind each camera to maximise the area lit and minimise any “blind spots” directly in front of the cameras. In addition, having the primary light sources placed in these positions helped minimise over-exposure of vegetation immediately in front of the cameras. In practice, bats were only clearly visible at distances up to approximately 50 m using these illuminators, therefore this was the maximum distance considered when deploying acoustic detectors. Secondary lighting (96 LEDs IR illuminator array, 850 nm, KKmoon, Shenzhen, China) was added along both sides of the road to improve illumination via uplighting. Six secondary lights were placed at “stations” between 25 and 50 m at each site (Fig. 2). Lighting was not added at shorter distances as the primary lighting provided sufficient illumination. Due to limitations in field-of-view caused by roadside vegetation, camera angles, and lighting coverage, this study focused on flight behaviour directly above the road surface, rather than over surrounding vegetation or roadside structures.

Acoustic data were collected at study sites to facilitate species-specific identification of bats recorded on video cameras. These data were gathered at survey points along the 50 m section of road at each site using full-spectrum Song Meter SM2BAT static detectors with SMX-U1 omni-directional microphones (Wildlife Acoustics, Maynard, Massachusetts, USA). One detector was placed by each camera, with further detectors placed at stations 10 m apart along either side of the road (up to a maximum of 50 m), staggered by 5 m on opposite sides of the road (Fig. 2a). Microphones were placed approximately 1.5 m off the ground on 5 m tall metal poles at each station, and orientated horizontally towards the road. Reflective markers were spaced at 1 m intervals along the poles to serve as additional reference points for the extrinsic calibration. Where it was not possible to deploy a detector at the specified distance due to an intersecting road ($n=3$ sites), it was either placed at the next nearest point or removed. Detector numbers deployed therefore ranged between 10 and 12 per site. Detectors were programmed to record from sunset until sunrise, using the following settings: sampling rate = 364 kHz; trigger level = 18 SNR; trig window = 2.0 s; gain = 12 dB; high-pass filter = 4 kHz; low-pass filter = OFF. All sound files were manually checked for *B. barbastellus* calls using Kaleidoscope version 5.3.9 (Wildlife Acoustics, Maynard, Massachusetts, USA), with reference to parameters in Russ⁵⁰.

For a detailed breakdown of the equipment used and their respective costs, please refer to (Supplementary Table S1).

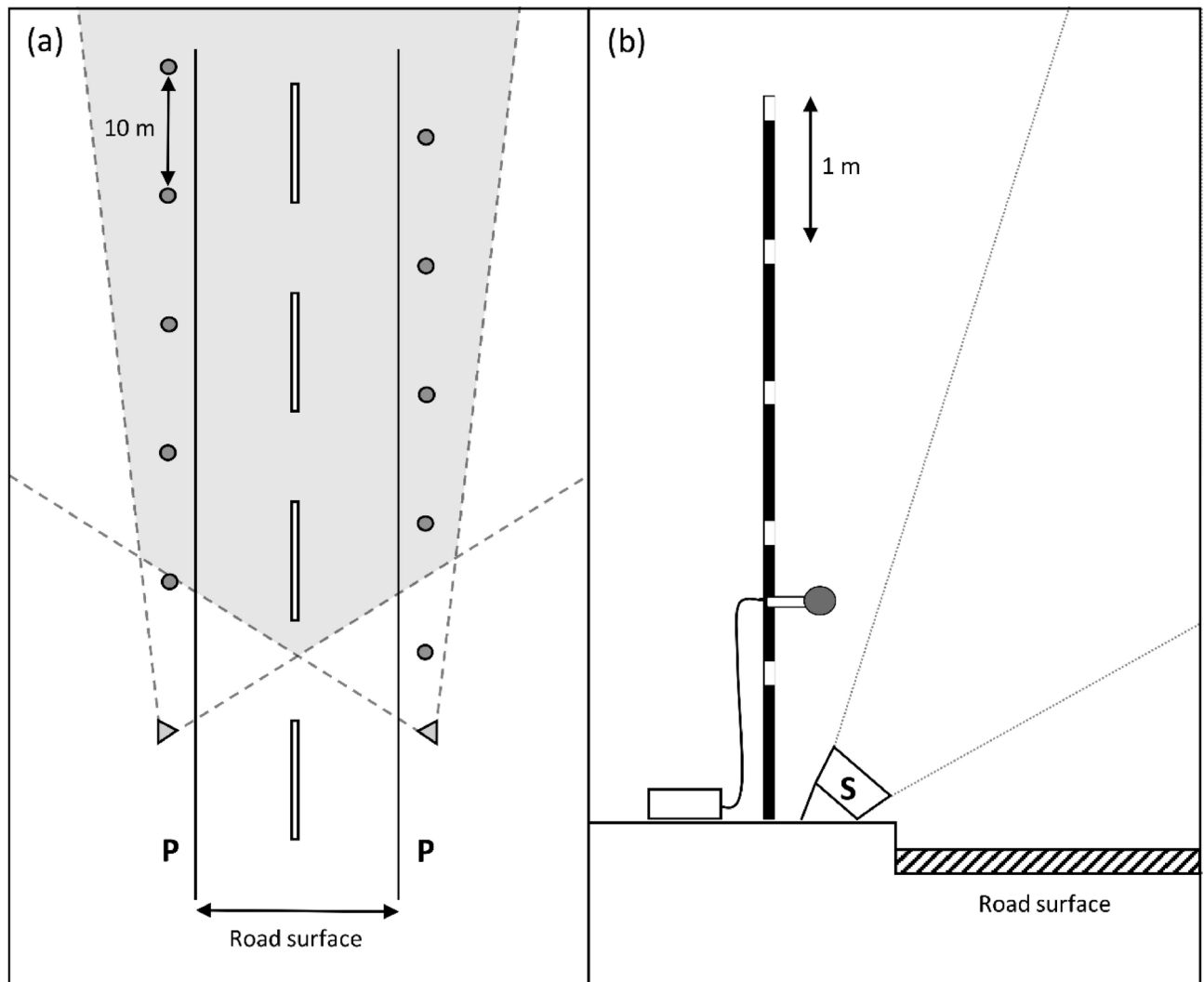


Fig. 2. Overview of the 3-D tracking and acoustic survey set-up used to monitor bat flight behaviour over roads. **(a)** Top-down view of the field set-up. The small dashed lines represent the field of view (67.8° horizontally) of individual cameras, with the shaded area illustrating the combined field of view captured by both cameras. The large dashed lines represent the centre lane markings of the carriageway. Triangle = camera, circle = station, P = primary infrared light source. **(b)** An overview of the station set-up, consisting of a SM2BAT static detector with a SMX-U1 omni-directional microphone attached to a 5 m pole. A secondary infrared light source (S) was included at stations between 25–50 m.

Camera calibration and video processing

Position measurements were recorded during each survey to calibrate the cameras in 3-D space, facilitating the reconstruction of bat flight trajectories. The distances between the cameras and their respective heights were measured using a laser measuring device (Tacklife HD40, Take Tools Cp., Shenzhen, China; accuracy ± 1.5 mm, range 40 m). The inclination angle of each camera and the mean slope of the road were recorded using a digital inclinometer (Neoteck LCD Digital Angle Finder, Neoteck Technology Ltd., Kowloon, Hong Kong; accuracy $\pm 0.1^\circ$). The slope was calculated by averaging inclination measurements taken every 10 m along the 50 m section of road being surveyed. This value was used to offset the camera inclination and ensure that height values from the flight trajectory reconstructions were referenced to the road surface.

Videos from the left and right cameras were synchronised by clapping loudly in view of both cameras during recording, providing both audio and visual markers. Video processing was performed using Shotcut version 22.12.21 (Melytech LLC, Oceanside, California, USA). *Barbastella barbastellus* presence over roads was determined by matching time points from acoustic detectors to the corresponding video segments, which were then processed to analyse flight trajectories.

The intrinsic calibration parameters of the cameras were calculated using ThruTracker version 2.0.5⁴³, a software package for automated two- and three-dimensional animal tracking. Subsequently, for each survey night, the cameras' 3-D positions and orientations were calibrated using background points from synchronised video footage with DLTdv8 version 8.1.8⁵¹. These points were exported and used in combination with the

position measurements (i.e., camera inclinations, distances between cameras) and intrinsic camera parameters to calculate the direct linear transformation (DLT) coefficients, using a modified version of the easyWand software tool⁴¹ in MATLAB R2023a version 9.14 (MathWorks, USA). Further details on the camera calibration process are provided in Supplementary Note S1.

Flight trajectory reconstruction

The reconstruction of flight trajectories was performed using ThruTracker version 2.0.5⁴³. Initially, extracted video clips from both the left and right camera were processed to obtain 2-D flight tracks. Pairs of 2-D tracks, along with the unique DLT coefficients generated for each survey, were then processed to obtain 3-D flight trajectories (note that 3-D trajectories could not be reconstructed if data were obtained from only one camera). We used MATLAB to visualise the reconstructed bat flight trajectories, as well as extract data on the average height, speed, and angle of individual tracks (see Supplementary Fig. S1 for distributions of flight characteristics). The angle of each flight trajectory relative to the road was classified as either 'following' (0–45°) or 'crossing' (45–90°) the road. We chose this binary classification for our analysis, as a discernible shift in bat behaviour was observed beyond 45° (Supplementary Fig. S2). For a comprehensive overview of the steps involved in reconstructing flight trajectories, including data collection and processing, please refer to (Fig. 3 and Supplementary Note S2).

Local vegetation characterisation

We characterised the local vegetation around each flight trajectory in QGIS (v3.6.3-Noosa; <https://www.qgis.org/>) software⁵². A canopy height model (CHM) was created using one-metre resolution LiDAR data collected between 2019 and 2021 by the UK Environment Agency (open source survey data; <https://environment.data.gov.uk/survey/>), by subtracting the digital terrain model (DTM) from the first return digital surface model (FZ DSM). Raster pixels were reclassified to generate the final CHM, where only pixels > 3 m were retained, to exclude ground level vegetation. This ensured that the model captured a range of tree canopies, including those of mature and young trees⁵³. Subsequently, a 20 m buffer was added around each flight trajectory, as this represented the approximate sonar range of echolocating *B. barbastellus* bats⁵⁴. The maximum and mean canopy height was calculated over each of the buffered trajectories. Canopy cover was determined by calculating the proportion of the buffered trajectories covered by the CHM. Distance to canopy cover was calculated as the mean distance between all points along a trajectory and the nearest straight-line distance to canopy cover. See Supplementary Fig. S3 for vegetation distributions across sites.

Collision risk and traffic density

Bat passes were categorised based on the collision risk posed to them, determined by the mean height of their flight track. Following the approach of Berthinussen and Altringham³⁹, and considering the maximum vehicle height in the UK is 4.9 m, bats were categorised as being at an 'unsafe' height if their flight was below 5 m and 'safe' if it was above 5 m. Although a single height threshold was used in the analysis, we acknowledge that different vehicle types pose varying risks. In interpreting the results, we therefore considered flights below 2 m as potentially at risk of collision with all vehicles, including cars, SUVs, and motorbikes, whilst flights between 2 m and 5 m were considered primarily at risk from larger vehicles such as lorries and trucks. To determine whether traffic density influenced bat behaviour, we analysed the camera footage to count the number of vehicle passes within several time intervals preceding a bat pass. Traffic density was calculated for the time windows of 10 s, 30 s, 1 min, 2 min, 4 min, and 8 min.

Lighting variables were excluded from the analysis due to practical challenges in quantification. All of the roads were unlit but we recognise that light emission from headlights may modify the response of bats to the presence of vehicles. Because vehicles frequently alternated between high and low beams, and the road curvature at different sites resulted in varying areas of light exposure, complicating the derivation of appropriate light-exposure variables, we were not able to separate out the individual effects of lighting from other stimuli (such as noise) associated with the presence of vehicles.

Data collection took place during a non-lockdown period of the COVID-19 pandemic, with traffic flow in the area (Petworth, West Sussex) reduced by approximately 17.5% between 8pm and 6am across the study period, in comparison to the preceding four years⁵⁵.

Data analysis

We tested three key hypotheses relating to how environmental and traffic variables (Table 1) influence bat flight behaviour across roads. First, to assess whether increasing canopy cover, distance to canopy cover, canopy height, and traffic density were associated with higher flight heights and subsequently reduced collision risk (hypothesis 1), we modelled (1) mean flight height and (2) the proportion of flight trajectories at risk. Second, to test whether increasing traffic density caused bats to cross roads more directly (hypothesis 2), we modelled (3) flight orientation. Third, to test whether bats flew faster over road sections with less canopy cover (hypothesis 3), we modelled (4) flight speed.

We conducted initial exploratory analyses using Mann-Whitney U tests to assess whether bat flight heights differed between nights at each site. As we expected minimal variation in flight behaviour between nights and had limited sampling nights per site, excluding 'night' from further analyses would help reduce model complexity. Differences were only observed at one site, where flight trajectories were consistently higher than at other sites; therefore, 'night' was not included in subsequent analyses.

Prior to model fitting, we also assessed collinearity among all predictors (Table 1) using Spearman's rank correlations. Canopy cover and distance to canopy cover were highly correlated ($r = -0.92$), so only the variable associated with the lower AICc was retained in each model. In addition, to determine appropriate time windows

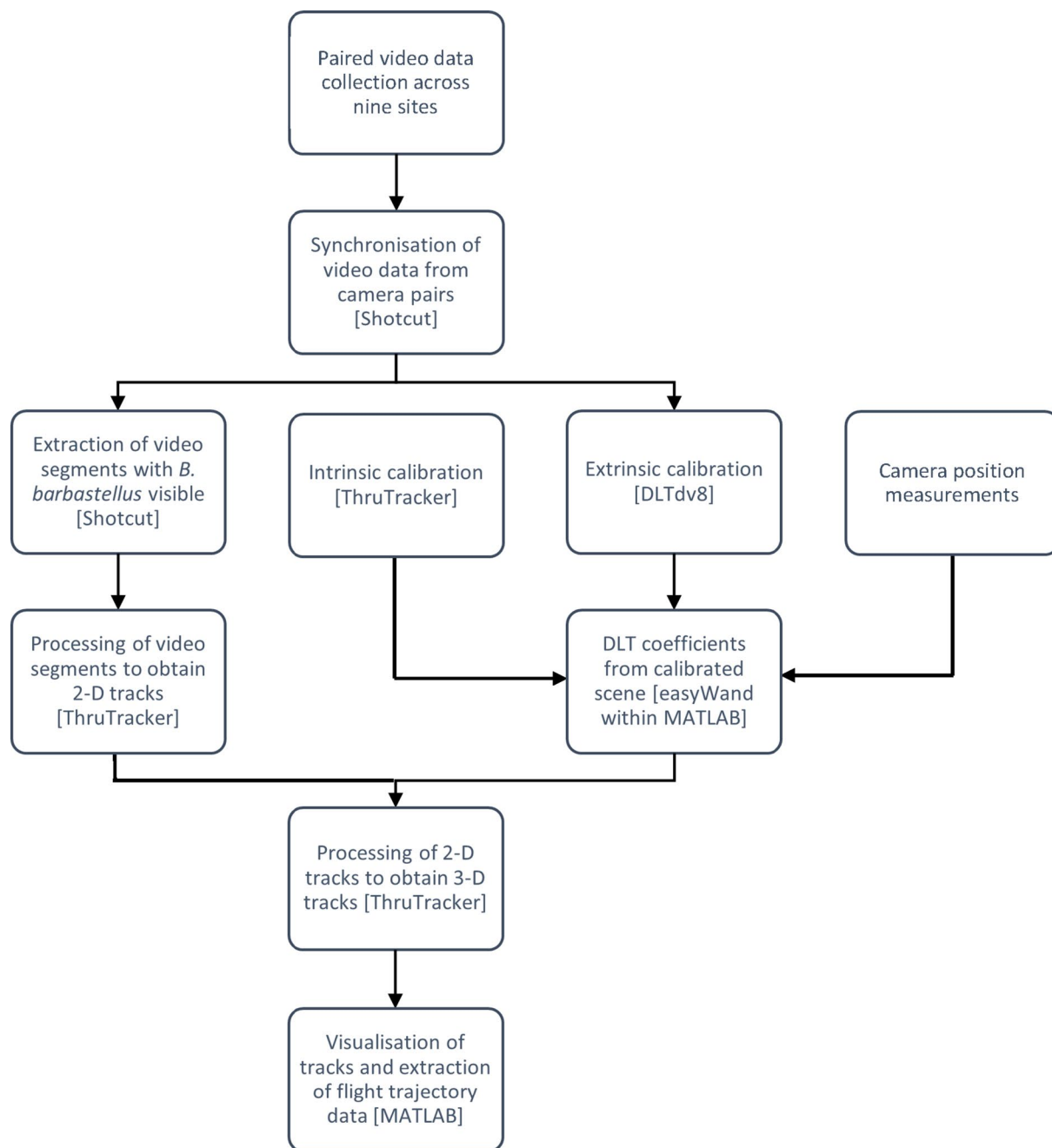


Fig. 3. Research methodology flowchart outlining the steps for collecting and processing video data to obtain 3-D flight trajectories. If relevant to the step, the software package used is indicated in square brackets.

Predictor	Description
Canopy cover	Percentage canopy cover (vegetation > 3 m in height) within a 20 m buffer surrounding each flight trajectory.
Mean canopy height	Mean height (m) of canopy within a 20 m buffer surrounding each flight trajectory.
Maximum canopy height	Maximum height (m) of any canopy recorded within a 20 m buffer surrounding each flight trajectory.
Distance to canopy cover	Mean distance (m) to canopy cover for all points along a trajectory. Only considers horizontal distance, not vertical height. A single point represents the 3-D location triangulated from a pair of synchronised frames.
Traffic density	Number of vehicle passes within a specified time window preceding a bat pass.

Table 1. Description of predictors used in the modelling of flight height, collision risk, speed, and orientation.

for traffic density, we first ran univariate analyses and retained the time window associated with the lowest AICc for each response variable.

We constructed separate candidate model sets for each response variable: (1) mean flight height, (2) proportion of flight trajectories at risk, (3) flight speed, and (4) flight orientation. Hypothesis-driven models were implemented using either linear mixed-effects models (LMMs) or generalised linear mixed-effects models (GLMMs) via the 'lme4' package⁵⁶. Site ID was included as a random effect in all models to account for the non-independence of flight trajectories recorded within sites.

Base model structures were as follows:

1. Mean flight height (hypothesis 1): Modelled using a LMM with a log-transformed response variable to meet normality assumptions.

$$\begin{aligned} \text{Log}(\text{Mean flight height}_{ij}) &= \beta_0 + \beta_1 \cdot \text{Distance to canopy cover}_{ij} + \beta_2 \cdot \\ &\text{Canopy height}_{ij} + \beta_3 \cdot \text{Traffic density}_{ij} + u_j + \varepsilon_{ij} \end{aligned}$$

2. Proportion of flight trajectories at risk (hypothesis 1): Modelled using a GLMM with a binomial error structure, where 0 = not at risk and 1 = at risk.

$$\begin{aligned} \text{Logit}(\text{Risk}_{ij}) &= \beta_0 + \beta_1 \cdot \text{Canopy cover}_{ij} + \beta_2 \cdot \text{Canopy height}_{ij} + \beta_3 \cdot \\ &\text{Traffic density}_{ij} + u_j + \varepsilon_{ij} \end{aligned}$$

3. Flight orientation (hypothesis 2): Modelled using a GLMM with a binomial error structure, where 0 = following and 1 = crossing the road.

$$\text{Logit}(\text{Orientation}_{ij}) = \beta_0 + \beta_1 \cdot \text{Traffic density}_{ij} + u_j + \varepsilon_{ij}$$

4. Flight speed (hypothesis 3): Modelled using a LMM.

$$\text{Flight speed}_{ij} = \beta_0 + \beta_1 \cdot \text{Canopy cover}_{ij} + u_j + \varepsilon_{ij}$$

In all models, i denotes individual flight trajectories, j denotes site, u_j is the random intercept for site, and ε_{ij} is the residual error.

To explore additional effects beyond those hypothesised, we used forward selection to test the remaining candidate predictors (Table 1) and interaction terms one at a time, retaining only those that improved model fit based on AICc. Specifically, we tested for an interaction between the selected canopy predictor (canopy cover or distance to canopy cover) and mean canopy height, where applicable. No other interactions were considered due to moderate collinearity among predictors and to limit model complexity, given that most predictors represented aspects of canopy structure. All retained predictors were checked for multicollinearity using variance inflation factors (VIF), with $\text{VIF} > 3$ used as a threshold for exclusion⁵⁷. This approach allowed us to evaluate whether additional variables improved model performance without removing theoretically justified predictors, consistent with the recommendations of Burnham and Anderson⁵⁸.

We assessed model residuals for normality and heteroscedasticity using the *testResiduals* function from the 'DHARMA' package⁵⁹. To visualise spatial flight behaviour, kernel density plots were generated using all positional points obtained from flight trajectories. All analyses were conducted in RStudio using R version 3.6.1⁶⁰, and figures were produced using the 'ggplot2' package⁶¹.

Results

Of the 35 surveyed nights, flight trajectories were obtained and analysed for a subset of 19 nights (Supplementary Table S2) due to the extensive data processing requirements. These nights were randomly selected from each site, ensuring a representative sample of flight trajectories across all sites for further analysis. A total of 400 flight trajectories were subsequently reconstructed from approximately 1268 *B. barbastellus* passes (as multiple detectors would simultaneously record a pass it was not always possible to discern if it was the same bat, hence an approximation) recorded over the 19 nights (see Supplementary Videos S1 for videos displaying 3-D reconstructed flight trajectories). An average of 45 flight trajectories were successfully obtained for each site (range: 3–136, $\text{SD} = 39.31$). Trajectories were reconstructed from 23,554 frames (totalling 7 min 51 s), with an average track length of 59 frames, corresponding to a flight duration of 1.2 s.

Using base model structures derived from *a priori* hypotheses, followed by forward stepwise selection, we identified distinct sets of predictors for each behavioural response variable (Table 2). These results highlight the varying influence of vegetation structure and traffic conditions on *B. barbastellus* flight height, collision risk, orientation, and speed.

The flight trajectories of *B. barbastellus* were at a median height of 4.75 m (IQR: 3.40 m; range: 1.51–16.93 m). Bats showed relatively little variation in their height within individual flight trajectories (coefficient of variation $< 10\%$ for 86% of tracks), varying on average by 0.78 m. Overall, 56% of flight trajectories were at a height that put bats at risk of collision with vehicles. However, only 1% of bat flights were vulnerable to collision with small vehicles (< 2 m tall, such as cars, SUVs, and motorbikes); whereas the majority (55%) of flight trajectories were at risk from larger vehicles (such as lorries, trucks, busses, and vans), which comprised approximately 11% of road traffic recorded in our video assessments. A high concentration of bats crossing at unsafe heights can be seen from the kernel density estimation (Fig. 4). This pattern is evident across most sites,

Predictor	Flight height			Collision risk			Orientation			Speed		
	Estimate	95% CI	P-value	Estimate	95% CI	P-value	Estimate	95% CI	P-value	Estimate	95% CI	P-value
Intercept	1.351	0.930, 1.761	<0.001	0.044	-0.599, 0.687	0.026	0.690	-2.636, 3.359	0.619	3.902	3.427, 4.328	<0.001
Distance to canopy cover	0.024	0.006, 0.480	0.011	–	–	–	-0.650	-1.225, -0.111	0.019	–	–	–
Canopy cover	–	–	–	0.047	0.014, 0.081	0.006	–	–	–	0.014	0.005, 0.025	0.028
Mean canopy height	0.004	-0.037, 0.045	0.864	0.157	-0.116, 0.431	0.259	0.388	-0.075, 0.947	0.118	–	–	–
Maximum canopy height	–	–	–	–	–	–	-0.283	-0.556, -0.022	0.033	–	–	–
Traffic density	0.011	-0.039, 0.063	0.673	-0.183	-0.460, 0.094	0.196	-0.279	-0.638, 0.062	0.118	–	–	–
Dist. canopy * Mean height	–	–	–	–	–	–	0.115	0.051, 0.183	<0.001	–	–	–
Canopy cover * Mean height	–	–	–	-0.008	-0.285, 0.269	0.074	–	–	–	–	–	–

Table 2. Results for the final models of *B. barbastellus* flight behaviour over roads, derived using forward stepwise selection from hypothesis-based model structures. The table presents estimates, 95% confidence intervals (CIs), and p-values for each of the four behavioural responses: flight height, collision risk, flight orientation, and flight speed. Flight height and speed were modelled using linear mixed models (LMMs), whilst collision risk and flight orientation were modelled using generalised linear mixed models (GLMMs) with a binomial error structure. Flight height was log-transformed prior to analysis to meet model assumptions. Significant results ($p \leq 0.05$) are indicated in bold. A dash (–) indicates that the predictor was not included in the final model. Within interaction terms, *Mean height* refers to mean canopy height, and *Dist. canopy* refers to distance to canopy cover.

except for site four, where bats were concentrated around a height of 7 m. At this site, a greater range of flight heights were recorded than in other locations, and heights varied significantly between the two nights of survey (night one median = 6.02 m; night two median = 8.27 m; $U = 720$, $p < 0.001$), but for both nights the median height was outside the zone of risk. For all other sites, there was no significant between-night difference in flight heights ($p > 0.05$).

An increasing distance to canopy cover was associated with an increase in the flight height of *B. barbastellus* over roads (estimate: 0.024, 95% CI: 0.006–0.048, $p = 0.011$), suggesting that bats gained height when further from vegetative structure. Similarly, greater canopy cover caused a significant increase in the collision risk for bats (Odds Ratio (OR): 1.048, 95% CI: 1.014–1.084, $p = 0.006$). This meant that for every 10% increase in canopy cover, the odds of a bat flying at a collision-risk height increased by 60% (Fig. 5a). No significant effects were found between *B. barbastellus* flight height or collision risk and any of the other predictors retained in the final models ($p > 0.05$).

Overall, we found that 69.5% of flight trajectories were crossing the road, whilst 30.5% were following the road. There was a significant interaction between the distance to canopy cover and the mean canopy height on the orientation of flight trajectories ($p < 0.001$). Specifically, as the distance from canopy cover increased, bats were more likely to cross directly over the road. However, this effect was modulated by mean canopy height: lower canopy heights reduced the likelihood of bats crossing the road directly, although this effect remained positive (Fig. 5c). In addition, bats were more likely to be crossing the road with decreasing maximum canopy height (OR: 0.754, 95% CI: 0.574–0.979, $p = 0.033$; Supplementary Fig. S4). The level of traffic preceding a bat pass had no significant effect on the orientation of flight trajectories.

Bats flew at a mean speed of 4.40 ± 0.91 m/s (range: 2.01–7.57 m/s) over roads. Compared to the low variability observed for flight height, bats showed substantial variation in their speed along flight trajectories (mean 1.62 m/s; coefficient of variation > 10% for 35% of tracks). Increased canopy cover was associated with a higher average speed for *B. barbastellus* (estimate: 0.014, 95% CI: 0.005–0.025, $p = 0.028$), with bats flying 0.14 m/s faster for every 10% increase in canopy cover (Fig. 5b).

Discussion

This study revealed that *B. barbastellus* alters its flight behaviour over roads in response to canopy structure, findings that have important implications for understanding vehicular collision risk and developing effective mitigation strategies. In addition, we successfully demonstrated the practical application of near-infrared cameras and 3-D visual tracking techniques to reconstruct the flight trajectories of bats over roads. This approach can be applied to obtain detailed frame-by-frame data on flight height, speed, and orientation, providing valuable insights into the movement patterns of individual bats. Consequently, our results show that *B. barbastellus* frequently flies at heights that place it at risk of vehicle collisions, with flight height decreasing in areas with greater canopy cover, and flight speed and orientation also being influenced by canopy presence.

This study was undertaken to provide a greater understanding of the flight behaviour of bats along roads, using commonly available videography equipment. The use of background points (including the focal bats themselves) to calibrate the cameras, rather than needing dedicated calibration objects to be introduced into each camera's view, provided an easy and safe method to study bats along roads. Though we used cameras capable of near-infrared recording in this study's set-up, thermal imaging cameras could be used and would give a better ability to distinguish bats from background noise (e.g., vegetation) and detect bats at greater distances. However, whilst the sites within this study generally offered at least a partial view above the canopy, giving us confidence that few bats were missed, both near-infrared and thermal imaging cameras have limitations in

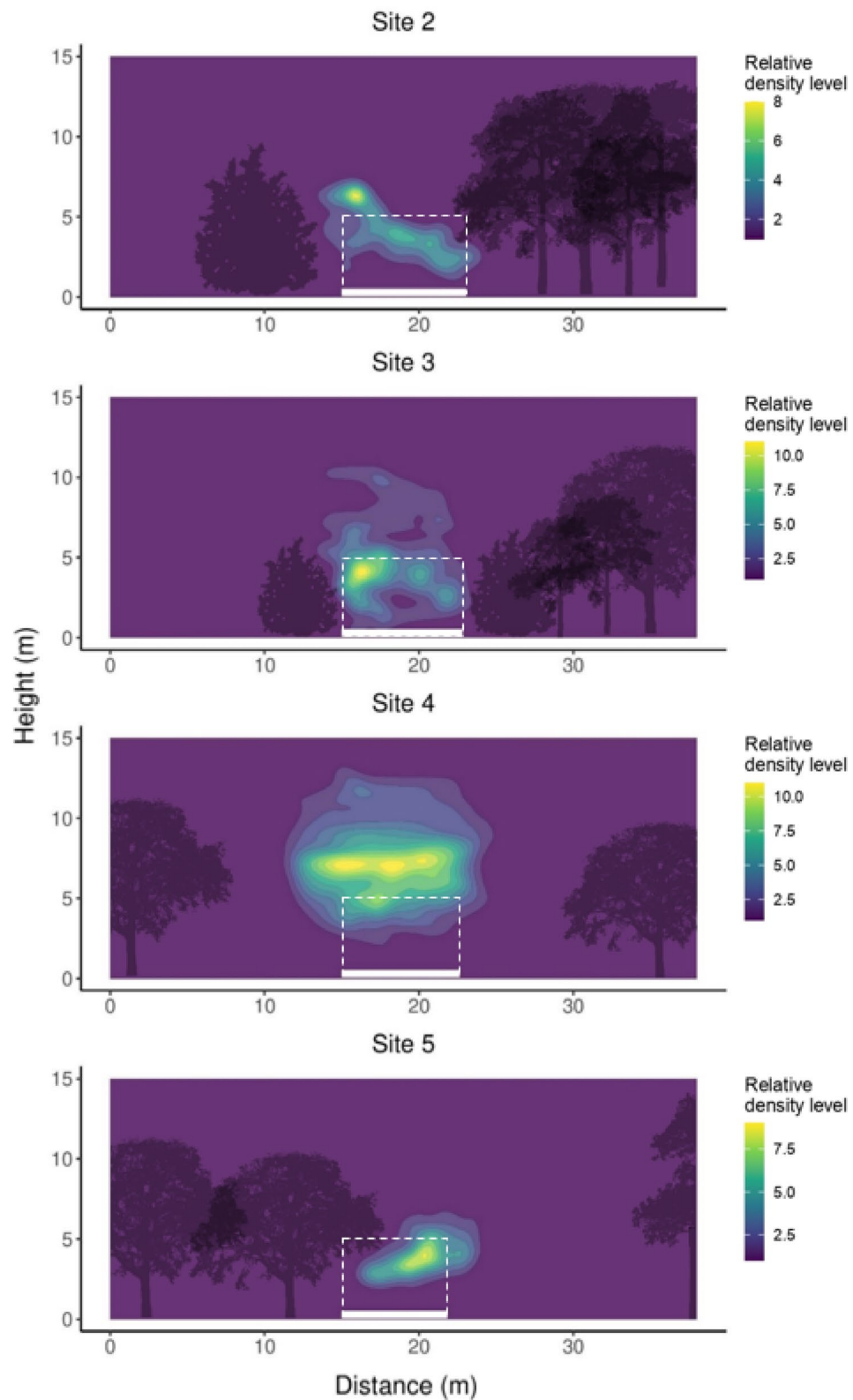


Fig. 4. Kernel density plots showing the spatial distribution of *B. barbastellus* flight trajectories over roads, including an approximate representation of the vegetation structure at each site. The colour gradient represents the relative density of flight activity within each site, with higher values including greater activity. Note that density levels are scaled independently per panel and should not be compared directly across sites. Solid white lines indicate the road surface, and dashed white lines represent the unsafe zone for bats. Site one is not shown due to low sample size.

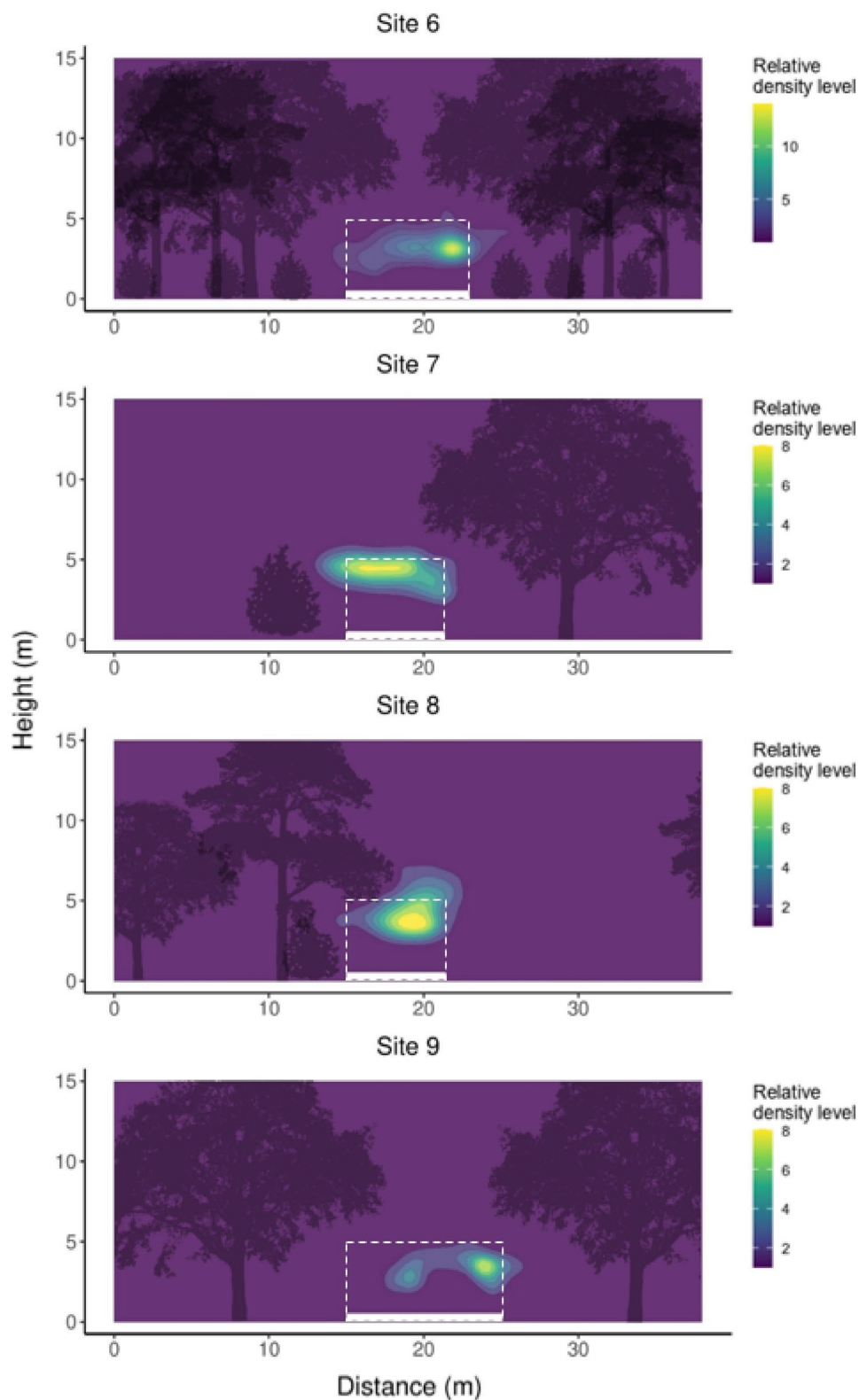


Fig. 4. (continued)

understanding flight behaviour of bats above canopies when canopy cover is high. Additionally, it is important to note that only 19 of the 35 nights were fully examined in detail due to technical limitations, and work is currently ongoing to streamline the method for more efficient future applications.

Just over half of *B. barbastellus* flight trajectories were at a height that put them at risk from collision with vehicles, with 56% of tracks recorded below 5 m (Figs. 4 and 5a). The mean flight heights observed in this study

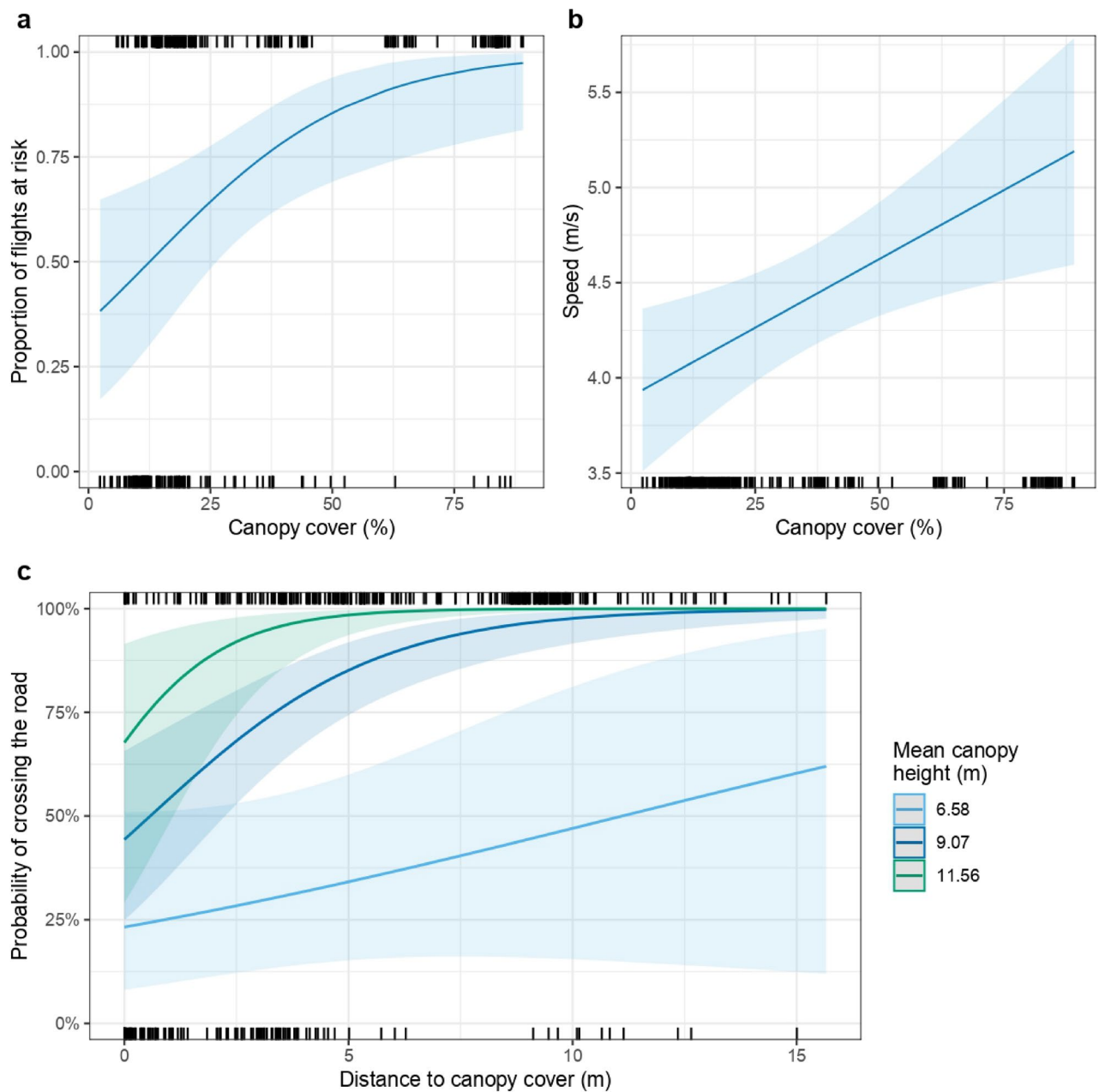


Fig. 5. Model predictions showing the effects of canopy composition on bat flight behaviour. **(a)** Relationship between increasing canopy cover and the proportion of flight trajectories at risk of collision with vehicles. Ticks represent data for bats flying at heights > 5 m (bottom) and < 5 m (top). **(b)** Relationship between increasing canopy cover and bat flight speed. Ticks on the x-axis represent sampled speed data. **(c)** Interaction between mean canopy height and distance to canopy cover on the probability of a flight trajectory crossing the road. Ticks represent data for flight trajectories that followed (bottom) or crossed (top) the road. Shaded areas in all plots represent 95% confidence intervals.

were higher than those reported for many other species, such as *Plecotus auritus*, *Myotis* spp., and *Pipistrellus* spp., in studies that relied on human observers^{22,37–39}. It is possible that these differences reflect the greater accuracy of the current method. For example, a 1 m discrepancy in the estimated flight height by human observers for a bat flying at 5 m represents a substantial 20% difference. Alternatively, species-specific differences in functional traits, such as body size, wing morphology, echolocation call structure, and roosting and foraging ecology, may result in greater collision risks for some species than those reported here for *B. barbastellus*¹². Additionally, road characteristics, including vehicle density and road width, may influence species' flight behaviour near roads.

It is important to note that, whilst we have focused on analysing the mean flight height of each individual trajectory, this approach does not fully capture the lower end of the flight height distribution where collision risk is greatest. Infrequent dips in flight height can have disproportionate consequences for mortality risk, and

future studies may benefit from incorporating centile-based metrics (e.g., 20th or 80th percentiles) to provide a more nuanced assessment of risk. It is also possible that even flights above 5 m may be unsafe owing to the creation of vacuum effects from fast-moving vehicles, which could draw bats to a lower height, potentially placing them in collision zones of following vehicles. Future application of our methodology to other species and road environments will help to clarify the relative importance of these factors in shaping bat flight behaviour and collision risk.

Canopy cover was associated with increased collision risk for *B. barbastellus* due to reduced flight height (Fig. 5a), contrary to our hypothesis that greater canopy cover would reduce collision risk. This suggests that *B. barbastellus* flies higher over roads lacking canopy cover, which opposes the general expectation that bats fly closer to the ground when crossing open spaces¹². Therefore, the implementation of hop-overs, in which trees are planted near road edges to provide continuous canopy cover⁶², may be an ineffective strategy for encouraging *B. barbastellus* to cross roads at a safer height. Roemer et al.⁶³ reached a similar conclusion, demonstrating that bats of various species faced increased collision risk in forested landscapes or areas with more trees, although they could not model this effect on short-range echolocators like *B. barbastellus*. Similarly, Russell et al.²² suggested that bats exhibit a heightened collision risk with increasing canopy cover; noting an absence of carcasses in locations lacking canopy cover within 15 m of the road, but a rise in mortalities when canopy cover was closer to the road. However, their study did not determine whether this observed increase in mortalities was a consequence of higher bat densities within these habitats or altered flight behaviour, as observed within this study.

A decrease in the canopy cover in the vicinity of roads resulted in a reduction in *B. barbastellus* flight speed (Fig. 5b). This finding contradicted our hypothesis, as we had anticipated that bats might increase their speed in open areas to minimise exposure time to perceived predation risk⁴⁶. Controlled experiments have also demonstrated that bats fly faster in open spaces compared to environments with artificial trees introduced⁶⁴. A reduction in speed is expected in these more cluttered habitats, as it would provide additional time to manoeuvre through woodland. However, considering that *B. barbastellus* was found to fly closer to the road surface when near canopy, there may be enough open space to navigate relatively unhindered by obstacles.

The probability that flight trajectories were following the road increased with decreasing distance to canopy cover (Fig. 5c). In other words, on wooded or tree-lined roads, bats were more likely to show behaviour consistent with foraging^{34,35}. Forest edges and linear landscape features such as roads may be used as commuting³³ and foraging sites for edge-adapted species such as *B. barbastellus*^{34,35}. Therefore, if roads provide significant advantages for commuting and foraging, as shown by Myczko et al.⁶⁵, *B. barbastellus* may spend more time along them. However, it's essential to recognise that these advantages might not fully compensate for the associated collision risk by vehicles, warranting further research into these cost-benefit dynamics. Interestingly, bats were more likely to directly cross the road when the mean canopy height was greater (Fig. 5c). This may suggest that tall canopy offers greater protection and a clearer flight corridor, leading bats to cross more directly, potentially avoiding the risk of flying along the road where there may be fewer escape options or greater exposure to vehicles.

We found no evidence that *B. barbastellus* adjusted its flight behaviour (i.e., speed, height, orientation) in response to traffic density. This challenges our hypothesis that bats would fly higher and more directly across roads to minimise risk under higher traffic conditions. Although increased traffic density raises the likelihood of bat-vehicle co-occurrence by reducing the time gaps between vehicles, short-range echolocators such as *B. barbastellus* have been shown to mitigate this risk by being less likely to fly within the collision risk zone when a vehicle is present⁶³. This suggests that *B. barbastellus* may rely on temporal avoidance to reduce collision risk, rather than altering its flight height or orientation. It is also possible that *B. barbastellus* exhibits some degree of road avoidance in response to traffic noise, as has been demonstrated in several other species⁶⁶. However, Kerth and Melber³⁶ observed commuting *B. barbastellus* flying directly over a motorway with heavy traffic, where other species used underpasses, indicating limited road avoidance despite the likely high level of traffic noise. Such behaviour may help explain the frequent road mortalities reported by Lesiński, Sikora, and Olszewski²³, particularly if bats are not adjusting their height in response to traffic.

Several recommendations for managing roadside vegetation and planning new road schemes can be drawn from the findings of this study. Firstly, it is advisable to avoid siting roads in areas with a high percentage of canopy cover, such as woodlands, where a high proportion of *B. barbastellus* bats fly at heights that pose a significant collision risk. Conversely, areas with fewer trees near roads should be prioritised, as bats in these areas are less likely to fly within the collision risk zone and tend to cross roads more directly. Whilst no evidence was found that vegetation height directly influenced flight height, bats were more likely to make direct crossings in areas with taller vegetation, potentially spending less time at risk. Therefore, maintaining tall vegetation and/or selecting of sites with a lower percentage of canopy cover could help mitigate collision risk.

For roads where *B. barbastellus* activity is known to be high, limiting night-time traffic and restricting large vehicles could be a cost-effective and easily implemented measure to reduce collision risk. Such traffic restrictions would help minimise bat exposure to vehicles, particularly during peak activity times. Although reducing canopy cover around roads, either through tree trimming or selective removal, might also decrease collision risk by encouraging bats to fly at greater heights, this approach should be pursued cautiously. It could have unintended consequences, such as the loss of habitat and connectivity for other species⁶⁷, and might hinder landscape permeability, potentially increasing the barrier effect for *B. barbastellus*, with implications for foraging and roosting site access¹³. Due to the complexities associated with data processing within our study, we were often unable to obtain a complete set of reconstructed trajectories for an entire night. Therefore, we could not accurately model the influence of roadside vegetation on the barrier effect of roads through an analysis of bat activity rates. Whilst our acoustic data could have alternatively provided a measure of bat activity, different setups (i.e., directional microphones) would be needed to discern whether recorded activity occurs over the roads, as discussed previously. Therefore, the management of trees and their canopies needs to be approached

with careful consideration of alternative routes for bats and a comprehensive understanding of the movement of individuals within a colony before implementing mitigation strategies. Further research is needed to understand these potential implications in more detail.

Understanding how the environment around roads influences bat behaviour is essential for effective conservation and mitigation strategies. We have shown that a high level of detail on the spatial movement of bats along roads is achievable using 3-D tracking approaches, offering novel insights into bat behaviour. This approach allowed us to identify the important influence of canopy structure on the flight behaviour of a woodland bat species and the subsequent implications for collision risk. Importantly, our findings challenge prior assumptions about how bats interact with roads, contradicting our initial hypotheses based on established research and conceptions, highlighting the need to reassess current mitigation strategies in light of species-specific behavioural responses. Although road avoidance behaviour could not be explored due to limitations in the cameras' field of views, future research could incorporate complementary tools, such as directional microphones, to detect bat activity and movement patterns beyond the cameras' range. Additionally, examining flight height centiles within trajectories could help quantify the frequency of high-risk drops in flight height, providing a more refined understanding of collision risk. The methods developed in this study, combined with these additional techniques, could be used to evaluate the impact of road developments (e.g., bridges) and mitigation structures (e.g., bat gantries, green bridges, hop-overs) on bat behaviour, provided sites are surveyed before and after implementation⁶⁸. The integration of tracking technology into these survey designs can, therefore, represent an important step-change in our understanding of bat-road interactions.

Data availability

The dataset, videos displaying reconstructed flight trajectories, and R code for this study are publicly accessible in the Figshare data repository (<https://doi.org/10.6084/m9.figshare.26124277.v3>)⁶⁹.

Received: 28 August 2024; Accepted: 30 July 2025

Published online: 23 October 2025

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Acknowledgements

We would like to thank the West Sussex County Council for giving us permission to undertake this study at the road sites; Frank Greenaway for providing both advice and radio-tracking data to help inform site selection; Daniel Whitby for loaning equipment for testing and calibrating; and Chris Damant and Iain Hysom for providing advice on lighting and survey design.

Author contributions

K.D.O. carried out the data collection, statistical analysis, conceived and coordinated the study, and drafted the manuscript. F.M. and H.S. conceived the study, advised on statistical analysis, and helped review and edit the manuscript. A.C. advised on survey design, assisted with data processing, and helped review and edit the manuscript. D.H. and P.G.R.W. helped review and edit the manuscript. All authors approved the final manuscript prior to publication.

Declarations

Competing interests

The authors declare no competing interests.

Additional information

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1038/s41598-025-14315-2>.

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