Tracking butterfly flight in the field from an unmanned aerial vehicle (UAV): a methodological proof of principle.

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13 Abstract 14 Tracking and understanding the movements of animals in the wild is a fast-growing area of 15 research, known as movement ecology. However, tracking small animals such as flying insects, 16 which cannot easily carry an electronic tag, remains challenging as existing field methods are 17 costly either in terms of equipment or tracking effort (e.g. VHF radio-tracking, scanning 18 harmonic radar). Here we attempted to record the movements of free-flying butterflies from an 19 unmanned aerial vehicle (UAV), maintaining a static position in the sky and recording video 20 vertically downwards. With an appropriate flight height and image filtering algorithm, we 21 recorded 166 flight tracks of Pieris butterflies (P. brassicae and P. rapae), with a median tracking 22 length of 40 m (median flight duration 13 s), and a high temporal resolution of 30 positions per 23 second. Average flight direction varied significantly over the course of the flying season, from a 24 northward azimuth in June and early July, to a southward azimuth in September, congruent 25 with a trans-generational migratory behaviour that has previously been documented by field 26 observations or experiments in flight cages. In addition, UAV imagery unlocks the possibility to 27 measure high-resolution flight movement patterns (e.g. path tortuosity and transverse 28 oscillations), which will possibly help understand perceptual and locomotor mechanisms 29 underlying spatial behaviour. We explore the technical details associated with UAV tracking 30 methodology, and discuss its limitations, in particular the biases associated with a 2D 31 projection of 3D flight movements, the limited spatial scale, and the difficulty to distinguish 32 between visually similar species, such as P. brassicae and P. rapae.

34 *Keywords:* UAV image-based tracking, insect flight, insect migration, movement ecology.

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Introduction

37 Tracking the movements of an animal in the wild provides insights on its ecology, such as 38 habitat use (e.g. Da Silveira et al 2016), dispersal and migration behaviours (Whitfield et al. 2024, 39 Rotics et al. 2016). When the movement data are detailed enough, both spatially and 40 temporally, it is also possible to extract biological information on the animal's locomotor 41 biomechanics (Sherub et al. 2016, Hedrick et al. 2018, Ruaux et al. 2023), its spatial search 42 strategies (Shepard et al. 2011, Hernandez-Pilego et al. 2017, de Margerie et al. 2018), and more 43 broadly the perceptual and cognitive processes involved in movement (Kashetsky et al. 2021). 44 All of these biological and ecological aspects of animal movement have been advantageously 45 integrated into a synthetic movement ecology framework (Nathan et al. 2008, Abrahms et al. 46 2017, Joo et al. 2022), that is progressively articulated with other major fields of biological 47 research (e.g. community ecology: Schlägel et al. 2020; animal physiology: Hetem et al. 2025).

48 However, not all animal species are easy to track. Large-enough animals (approx. > 100 g) 49 can carry GPS receivers (Cagnacci et al 2010, Wilmers et al 2015), which are now often enhanced 50 with additional sensors (accelerometers, barometers, cameras) to better infer the animal's 51 behaviour along its route (Kays et al 2015, Joo et al. 2022). To track the movements of smaller species such as flying insects, tracking tags need to be much lighter, and alternative 52 53 technologies to GPS are employed. Beacons emitting simple VHF radio beeps have been used 54 successfully for decades to track the movements of flying and non-flying insects (Kissling et al. 55 2014). Yet, VHF radio-tracking involves following the animal with one or multiple antennae (or 56 deploying a fixed antennae array; e.g. Knight et al. 2019), and the spatio-temporal resolution is 57 inferior to GPS tracking. Even lighter, passive tags (of a few mg, without any battery) can be 58 used to track the movements of flying insects (Ovaskainen et al. 2008, Lihoreau et al. 2012, 59 Maggiora et al. 2019). The downside of these passive tags is that a scanning harmonic radar 60 (SHR) - a heavy and expensive device - has to be deployed in the field. The tracking range of SHR 61 is near 1 km, and the temporal resolution of the data is one position every 3 s (Ovaskainen et al. 62 2008). Other shorter-range, passive-tag tracking systems also exist (portable harmonic radar, 63 RFID tags; see Kissling et al. 2014, Batsleer et al. 2020, Rhodes et al. 2022 for reviews).

For all animal-borne tracking systems, whether GPS receivers or other types of tags, the impact of the tag on the animal's movements is a matter of concern. The carried mass, but also the drag, the position, or the method of attachment of the tag must be carefully considered. Impact studies are often necessary, both from an ethics point of view and in terms of the reliability of the collected movement data (Wilson & McMahon 2006, Batsleer et al. 2020).

69 There are other routes to track flying insects, without having to place tags on animals. First, 70 the classic mark-recapture method allows to demonstrate the movement of an individual from 71 one point to another, and was thus used for studying insect dispersal and migration (e.g. 72 butterflies; Chowdhury et al. 2021, 2022). Trapping techniques along flight routes, sometimes 73 combined with isotope analyses to determine the geographical origin of individuals, can also 74 provide information on large scale movements (e.g. dragonflies; Knoblauch et al. 2021, Oelman 75 et al. 2023). At a finer, local scale, if the insect flies slowly enough, in an open environment where 76 it remains visible, it can be followed by foot and its passed positions can be drawn on a map 77 (Brussard & Ehrlich 1970) or recorded by a GPS receiver carried by the observer (Delattre et al. 78 2013, Fernandez et al. 2016). Tracking butterflies crossing a body of water from a small boat is

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another possible technique (Srygley & Oliveira 2001). Also, when flying insects move in swarms
of many individuals, radars (weather surveillance radars or smaller scale biological radars) can
be used to detect and measure the direction of these flights (e.g. Stefanescu et al. 2013). With
biological radars, individual movement variables such as flight direction, height and ground
speed can be extracted (Bauer et al. 2024).

To complement these "tagless" tracking approaches, sometimes called "passive sensing" (Rhodes et al. 2022), we wondered whether flying insects could be tracked in video images filmed from a UAV (Unmanned Air Vehicle, or drone) positioned above them in the sky.

87 Image-based tracking from ground-based cameras is a known technique to reconstruct the 88 2D and 3D trajectories of animals, and in particular flying insects, with a high sampling 89 frequency (>1 Hz). It can be used in laboratory settings (e.g. Lihoreau et al. 2016a), semi-natural 90 outdoor insectaries (Kitamura & Imafuku 2015, Le Roy et al. 2021, Kleckova et al. 2024) or even 91 natural environments (Stürzl et al. 2016, Jackson et al. 2016). Most often used to address 92 biological questions related to perception, cognition or locomotion, image-based tracking 93 techniques, which are less invasive, are also attracting growing interest in ecology (Dell et al. 94 2014). Hybrid techniques tracking tagged animals in videos are also being developed (Crall et 95 al. 2015, Walter et al. 2021).

96 On the other hand, in the last decade, commercial UAVs have greatly improved in terms of 97 compactness, stability and image resolution, while decreasing in cost, making them valuable 98 tools for wildlife inventory and conservation (Wang et al. 2019, Charbonneau & Lemaître 2021). 99 Tracking animal movements using videos recorded from a UAV is a next logical step, and it has 100 already been achieved for a variety of large species (e.g. reef shark: Rieucau et al. 2018, wild 101 dog: Haalck et al. 2020, zebras and geladas: Koger et al. 2023). For flying insects, UAV-image-102 based tracking has been proposed previously (Ivosevic et al. 2017), but remains to be tested 103 and validated. Most recently, Vo-Doan et al. (2024) successfully tracked a honey bee from a 104 special UAV-borne optical system (Fast Lock-On), but this technique requires that the insect 105 carries a reflective marker.

106 Here we explore the validity of a UAV as a platform for remote, passive observation of the 107 movements of untagged insects in flight. The motivation for this exploration is the many 108 potential benefits of such an approach, namely (1) non-invasiveness, i.e. tracking of animals 109 moving freely, without tags and associated capture procedures, (2) in an open natural 110 environment, over distances greater than in an insectary, (3) with a spatio-temporal resolution 111 superior to VHF, SHR or GPS tracking. If this type of fine movement data in natural conditions 112 can be collected easily, it could be very useful for bridging the gap between laboratory studies 113 on perceptual, cognitive and locomotor mechanisms, and movement patterns observed in the 114 natural environment at the local scale (daily routine movements) or beyond (insect dispersal or 115 migration).

116To begin this methodological exploration with a relatively simple case, we have focused on117Pieris butterfly species (large white Pieris brassicae and small white Pieris rapae) because of118their relatively slow flight, good visibility and abundance in the field. We limited the present119study to the simple situation of a single, static UAV in the sky, filming vertically downwards (Fig.1201A) to reconstruct flight trajectories in only 2 horizontal dimensions. We also chose to record121flights accross areas with low ecological resources, which are likely to promote simple directed

movements rather than highly tortuous, resource-searching movements (Schtickzelle et al.2007, Fernandez et al. 2016, Schlagel et al. 2020).

124 Material and Methods

This section describes the general methods we used to film butterflies in the field, reconstruct their flight trajectories and describe their movements. We later explored and validated these data using diverse specific methods and statistics, which are detailed at the start of each results sub-section, for ease of reading.



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Figure 1 – UAV field of view (FOV). (A) Video recording geometry, showing the influence of UAV flight height (*H*) and camera angular horizontal FOV (*hFOV*) on ground horizontal FOV (*ghFOV*) and ground pixel pitch (*gPP*). (B) Aerial view of the study site, showing FOV over western (WF) and eastern field (EF). Source for aerial photography: geoportail.gouv.fr
(C) Variation of *ghFOV* and *gPP*, as functions of *H*. These linear relationships depend on camera angular *hFOV* and recorded image width *IW* (see equations 1-2). (D-E) Examples of video frames recorded on July 8th 2021, over WF and EF, respectively. White arrows identify 2 reference crosses painted 20 m apart on the road, and used for image scaling.

138 Study site

We recorded butterfly flights from June to September 2021, in an agricultural area near the city of Rennes, France (coordinates 48.105444, -1.560029). The local landscape is covered with cultivated fields, few tree patches, small roads and farms, with the closest urbanized area situated 1.7 km away. We filmed butterflies flying above 2 fields situated on each side of a narrow road (Fig.1B). The western field (WF) contained an organic mixed crop (mainly wheat, fava and lucerne) which was harvested in August, whereas the eastern field (EF) contained forage grass, which was cut in June and August. We chose to record butterflies above two

146 different fields (filmed in alternance) to test our image filtering method above various 147 backgrounds, and also control whether the flight trajectories could be influenced by ground 148 vegetation: while EF crop was devoid of any identified ecological ressource, WF contained a few 149 nectar-bearing flowers that might attract butterflies, and hence influence their flight trajectory. 150 On the central road were the UAV takeoff/landing area, the UAV pilot (EDM), the technical 151 assistant (KM), and an ultrasonic anemometer (Gill Maximet 501) recording wind speed and the 152 direction from which the wind originates every second, at 2 m height. We painted two 153 permanent red crosses 20 m apart along the central road (Fig.1D, E), as a reference line segment 154 for positioning the UAV, and later for scaling the video frames. The ground slope in the recorded 155 area was less than 2°.

156 UAV video recording

157 We used a Mavic Air 2 UAV (DJI, Nanshan, Shenzhen, China), which is a small commercial 158 quadricopter (takeoff weight 570 g, retail price ~1000 € in 2021). This UAV has a CMOS sensor 159 $(6.4 \times 4.8 \text{ mm})$ which can record 3840×2160 pixel videos (i.e. "4K" images, with 16:9 aspect 160 ratio). According to the UAV manual, the camera lens has an f/2.8 aperture and an 84° field of 161 view. As most recent UAVs can record with various aspect ratios and resolution levels (which 162 may involve sensor cropping, i.e. digital zoom), we prefered to measure FOV in the lab, by 163 placing the UAV camera at a known distance from a wall, and measuring the horizontal distance 164 along the wall that is effectively included in the UAV camera image. The "horizontal" FOV (hFOV, 165 i.e. along image width), was measured at 68.3° in the default "4K wide" recording mode, that 166 we used throughout the present study. This angular hFOV value was used to choose a flight 167 height. We computed the horizontal field of view on the ground (ghFOV, in meters) when the 168 UAV camera aims vertically downwards:

169 (1)
$$ghFOV = 2H \tan\left(\frac{hFOV}{2}\right)$$

170 where *H* is the UAV height (m), and *hFOV* is the horizontal angular FOV (°).

Proportional to *ghFOV* is the corresponding pixel pitch on the ground, i.e. the distance on the ground covered by a single pixel side (*gPP*, m):

174 (2) gPP = ghFOV / IW

- 175 where *IW* is the video image width, in pixels.
- 177 The total recorded ground area (*gaFOV*, m²), can also be of interest:

178 (3)
$$gaFOV = \frac{IH}{IW}ghFOV^2$$

179 where *IH* is the video image height, in pixels.

Based on these relations, we chose a 45 m UAV flight height, which covers a *ghFOV* of 61 m $(gaFOV = 2096 \text{ m}^2)$, and corresponds to a *gPP* of 16 mm (Fig. 1C). This pixel pitch value was

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voluntarily chosen at a fraction of the body size of the *Pieris* species we wanted to track, whichhave a forewing length around 30 mm.

185 We performed preliminary tests in the field that confirmed that at *H* = 45 m, *Pieris* butterflies 186 flying near the ground were projected in recorded images as pixel "blobs" with an area around 10 pixels, which is large enough to be reliably tracked from frame to frame (see Fig. 2A, C). 188 Higher camera height would allow larger FOV area on the ground, and hence longer tracking 189 durations, but automatically tracking smaller blobs would become less reliable.

Note that at *H* = 45m, the butterflies are not visible to the UAV pilot through the live video feedback on the UAV controller screen. The video feedback has lower resolution (*IH* = 720 or 1080 pixels) than the recorded video, and the controler screen (Ipad Mini 5, Apple, Cupertino, USA) also has limited magnification and contrast in outdoor conditions. Butterflies in UAV footage were only detectable *a posteriori*, when playing recorded videos at full resolution on a computer screen in the lab.

All videos were recorded at "30 fps" (29.97 video frames per second), which in 4K resolution produced video data at a rate of 13 MB/s. The UAV firmware automatically cut videos lasting more than 5 min in multiple 4 GB files, which can be stitched in post-processing, but with the loss of one video frame between files (this may depend on the UAV model), For simplicity, we decided to keep each video duration below 5 min. Recording at 60 fps was another possible option, but with a 15 MB/s data rate, this implied less data collected per video frame. We sticked to 30 fps, aiming to obtain the best possible image quality per video frame.

203 Constant, manual exposure was tested initially, but proved unpractical as the ground
204 luminance could vary by several exposure values (Ev) when cloud shadows crossed the FOV.
205 Hence, we used auto-exposure with an exposure compensation of -0.7 to -1.3 Ev, as it improved
206 the contrast between the white butterflies and the background.

207 Time distribution of UAV flights

208 In order to distribute observations accross the Pieris flight season (which in France can span 209 from April to October; Lafranchis et al. 2015), we chose to collect videos once a week, over the 210 months of June, July and September 2021. Each week, we chose a day that was favorable for 211 butterfly flight, i.e. with a weather forecast as warm, sunny and not very windy as possible. We 212 went on site in the afternoon (14:00-16:30). After takeoff, the UAV was positioned at H = 45 m 213 above the EF. The UAV camera was tilted to a vertically-downward position, and the pilot used 214 the video feedback to place the scale points on the road to the left margin of the FOV (see Fig. 215 1E). The pilot started the video recording, and the UAV then relied on its own sensors (GPS, 216 altimeter, etc.) to maintain its position without any pilot input, for about 4 min 30 s. Then the 217 video recording was stopped, the UAV was relocated to the WF, height and scale alignment (now 218 on the right margin of the FOV, see Fig. 1D) were checked, and another 4 min 30 s video was recorded. Repeating these steps, we could record a second EF video and a second WF video 219 220 before the UAV battery dropped to 20-30% of capacity, inciting landing the UAV and swapping 221 its battery. With this sequence, each UAV battery (rated at 11.6 V, 3500 mAh, 40.4 Wh) allowed 222 to record about 18 min of video. As we used 3 fully charged batteries per field session, we were 223 able to collect about 1 hour of video per field session. Weather allowing, 3 field sessions could 224 take place in June (1st, 9th, 15th), 4 field sessions in July (1st, 8th, 15th, 22nd) and 4 in September 225 (6th, 16th, 22nd, 29th), for a total video duration of 10.7 hours (48.8% over WF, 51.2% over EF).

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231 Video processing

232 In order to automate the tracking of butterflies in videos, pixels corresponding to the 233 butterfly should be easily distinguished from the background. In the present case, Pieris 234 butterflies appear in the raw video as blobs of bright pixels, but the background formed by the 235 vegetation also has multiple bright areas (Fig. 2A), which rules out a simple detection of the 236 butterfly by thresholding the raw video luminance levels. In addition, as the UAV is not perfectly 237 static, and the wind can cause vegetation on the ground to move slowly, the background is 238 moving, which does not favour background subtraction approaches (Piccardi 2004). We found 239 a solution to this issue by designing a custom filter that selects the pixels that blink in the video: 240 when a butterfly passes over an area, the pixels in that area become brighter for only 1 frame, 241 and then revert to the background luminance. To apply this filter, we first transformed the RGB 242 video frames into greyscale. Each pixel then has a single luminance value (v) in the range [0, 243 255]. Then the "blink" filter script performs the following calculations:

245 Pixel value variations from current frame (t) to next (t+1) and previous (t-1) video frames:

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If both variations have the same sign, there was a luminance peak (positive or negative), and a blink value (b) is computed. On the contrary, if variations have different signs, there was no blinking, only monotonous pixel value variation.

251	(6)	$if sgn(\Delta v_n) = sgn(\Delta v_p)$	\rightarrow	$b_t = -sgn(\Delta v_n) * \min\left(\Delta v_n , \Delta v_p \right)$
252	(7)	else	\rightarrow	$b_t = 0$

Note that *b* can be positive (bright blob passing over darker background) or negative (dark
blob passing over brighter background).

Interestingly, when going through a series of successive video frames, keeping memory of
 extreme *b* values for each pixel (notated *B*) can be used to reveal flight trajectories as a series
 of blobs, in a synthetic, diachronous image.

 $\begin{array}{cccc} 259 & (8) & \quad \text{if } |b_{t+1}| > |b_t| & \rightarrow & B = b_{t+1} \\ 260 & (9) & \quad \text{else} & \rightarrow & B = b_t \end{array}$

For easy display of *b* frames (and *B* synthetic images), pixel blink values are rescaled from [-255, 255] to [0, 255].

263 (10) b = (b + 255)/2

As a result, background appears as medium grey (*b* = 128), with blinking pixels as lighter or darker gray blobs. Fig. 2 shows example results of the blink filter.



Figure 2 – Video frame filtering. (A) Magnified view of an original video frame, containing a *Pieris brassicae* image (as identified after butterfly capture). (B) Same view after applying the blink filter (i.e. *b* frame). (C) A hypothetical 30 mm forewing length *Pieris*, with wings fully stretched, projected onto a pixel grid with a 16 mm *gPP*. If all partially covered pixels appear brighter, the pixel blob area would be around 12 pixels. (D) Merging successive *b* frames reveals *P. brassicae* flight trace in a synthetic, diachronous image (i.e. *B* image). (E) Example trace of *Pieris rapae*. (F) Example trace of *Melanargia galathea*. (H) Example trace where the shadow of a *Pieris* butterfly is also visible (contrast ×1.5).

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We used the blink filter in two processing steps. For the initial exploration of our videos, we cut each video into 20 s bouts, and generated a single *B* image summarising each bout. This enabled us to quickly detect which video bouts contained butterfly tracks. On this basis, the FOV entry and exit times of each butterfly were precisely noted by playing the original videos on a large screen. Based on these time limits, we then generated for each butterfly track a new greyscale, uncompressed video file, containing the series of *b* frames. This filtered greyscale video was then used to automatically track the blobs.

We used DLTdv8 (Hedrick 2008) to extract blob coordinates (in pixels) in successive video 284 285 frames. The blob was manually digitized (i.e. mouse clicked) in the first few frames, and then 286 DLTdv8 uses a Kalman filter and 2D cross-correlation to find the blob in following frames 287 (without thresholding). As blob size and contrast can vary, and filtered b frames still contain 288 some noise in the background, the automatic tracking process needed human supervision and 289 frequent manual corrections, but with a convenient user interface to navigate through video 290 frames, DLTdv8 offered vast time savings compared to a fully manual digitization. The average 291 time spent on screen to process the videos was approximately 15 min per track. There are 292 numerous alternative options to DLTdv8 for tracking blobs through video frames (e.g. Sridhar 293 et al. 2019, Lauer et al. 2022, Chiara & Kim 2023). Regardless of the tracking software used, 294 starting from the blink-filtered video will help solve the natural, moving background issue.

295 For scaling the butterfly track to real-world coordinates, we measured pixel coordinates of 296 the two painted reference crosses in one video frame (at mid-duration of the track), and fitted 297 a geometrical transformation (combining rotation, scaling and translation; fitgeotrans function 298 in Matlab) that resulted in (0, 0) and (0, -20) coordinates in real-world meters. This same 299 transformation was then applied to the whole butterfly coordinate series, transforming 300 coordinates in pixels to meters. We had measured with a compass in the field that the central 301 road had a 6°E azimuth. We checked and refined this value in a GIS software 302 (https://www.geoportail.gouv.fr), and thus applied a 5.83° CW rotation to all butterfly 303 coordinates, so that in all graphical representations, y axis has a 0°, northward azimuth.

304 Track selection

When we explored the *B* images synthesizing our videos, we mainly found flight traces of *Pieris* butterflies (large white *P. brassicae*, small white *P. rapae*), appearing as clearly visible white dotted traces (fig. 2D, E). These two species were also the most easily observed from the ground during the field sessions. We also found a few flight traces of other species, that we had observed in the field, such as the marbled white (*Melanargia galathea*), the red admiral (*Vanessa atalanta*) or the peacock (*Aglais io*). However, as these traces were less frequent, and usually barely visible and discontinuous (Fig. 2F, G), we did not analyse them further.

For some *Pieris* traces, the shadow of the butterfly formed a second, dark trace (Fig. 2H), which may potentially be used to determine the height of the butterfly relative to the ground (knowing the associated sun elevation angle). These shadows were only visible on almost bare ground (September videos, after crop harvest), and thus concerned a small number of *Pieris* traces. We have therefore not used this additional source of 3D data in the present study.

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318 Among the *Pieris* tracks, we applied the following exclusion criteria:

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- A 10 m wide strip, containing the road and the adjacent flowered ditches, was excluded
 from the analysis, so that each field (WF and EF) included a homogeneous area in terms
 of ground vegetation.
 - Many very brief tracks (< 5 s), often crossing just one corner of the FOV, were considered less informative and excluded from analysis.
- We chose to focus on butterflies in continuous movement: Tracks marking one or more stops while crossing the FOV were excluded (a stop being defined as remaining for at least 1 s within a radius of 0.1 m). These tracks with stops were in the minority (~ 1 out of 6 tracks).
 - Tracks in which the butterfly interacted with another individual (e.g. flight inflection towards another butterfly, chases) were also excluded (~ 1 out of 13 tracks).
- In the end, our sample comprised N = 166 *Pieris* flight tracks. Despite our constant sampling
 efforts, these were not evenly distributed through the season: we recorded 12 tracks in June,
 125 in July and 29 in September. Taking all these tracks together, 70524 butterfly positions were
 recorded, representing a total of 39 min of flight time, and a flight distance of 7.4 km.

When the tracks contained missing positions (caused by the absence of blob in some *b* frames), the (x, y) coordinates were linearly interpolated. These interpolated positions represented 2.2 % of the dataset (1544 positions). The interpolated positions were rarely contiguous, and the longest interpolated segment represented 7 successive positions (i.e. 0.23 s).

340 Track descriptive variables

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341 For this pilot study, we computed a small set of basic descriptive variables for each 2D track.

- Track duration is the time the butterfly remained within the FOV (road zone excluded).
- The change in 2D position from a frame to the next frame is named a step vector. Track
 length is computed as the sum of step vector norms.
 - Step speed is equal to step vector norm divided by the elapsed time (i.e. 1/29.97 s). **Average speed** is the arithmetic mean of the series of step speed values. It indicates how fast, on average, the butterfly flew along its 2D track. Average speed is also equal to track length divided by track duration. Note that average speed is a ground speed, not an air speed.
- A "beeline" vector is defined as the vector from the first to the last recorded position
 of the butterfly. The beeline vector is equal to the vectorial sum of step vectors, and
 hence represents the butterfly's resultant, directed movement across the FOV. Beeline
 azimuth was the direction of the beeline vector, a circular variable in the interval [0°,
 360°[, 0° corresponding to a northward azimuth.
- Track straightness is computed as the ratio of the beeline vector norm to the track
 length. Straightness value is in the interval [0, 1]: 0 indicates that the butterfly
 performed a loop (i.e. had the same entry and exit positions), while 1 indicates a
 perfectly straight flight path. Straightness is inversely related to path tortuosity. Track
 straightness is also known as "Net to Gross Displacement Ratio" (NGDR, Buskey 1984).

- Beeline speed is the norm of the beeline vector divided by track duration. It reflects
 how fast the butterfly, on average, progressed in its directed movement. Beeline speed
 is also equal to average speed multiplied by straightness. Note that beeline speed is
 also a ground speed, not an air speed.
- Wind speed and direction for each track were computed from the vectorial sum of the
 n wind vectors recorded during track duration, divided by n.

367 Processing and statistics software

Pixel blob tracking in videos was performed using DLTdv8 (Hedrick 2008;
<u>https://biomech.web.unc.edu/dltdv/</u>). Other analyses, from video processing to statistics, were
performed using Matlab R2018b (The MathWorks, Natick, MA, USA). We used the CircStat2012a
toolbox for circular statistics (Berens 2009). For a small number of captured butterflies,
forewing length measurement from field photographs were performed with ImageJ V1.54g
(<u>http://imagej.org</u>).



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Figure 3 – *Pieris* flight tracks description. (A) Reconstructed 2D tracks over WF and EF.
Black dots indicate last position of each track. (B-F) Distributions of descriptive variables:
(B) track duration, (C) track length, (D) average speed, (E) track straightness and (F) beeline speed.

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Results

380 Track general description

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Fig. 3 shows the reconstructed 2D tracks, and associated variable distributions. We collected 66 *Pieris* flight tracks over WF, and 100 tracks over EF. Tracks had a median duration of 12.8 s (range 5.1 to 56.5 s, Fig. 3B), for a median track length of 40.0 m (13.4 to 134.9 m, Fig. 3C). The median value for average speed was 3.3 m.s⁻¹ (1.9 to 9.2 m.s⁻¹, Fig. 3D), and 2.9 m.s⁻¹ for beeline speed (0.2 to 9.1 m.s⁻¹, Fig. 3F). Straightness distribution was strongly skewed towards straight tracks, with a median value of 0.93 (range 0.10 to 0.99, Fig. 3E). High straightness values imply similar values for average speed and beeline speed in most tracks.

We used two-sample Kolmogorov-Smirnov (KS) tests to assess distribution differences between WF and EF tracks, and found no significant difference for track duration ($D_{(66,100)} = 0.10$, p = 0.78), track length ($D_{(66,100)} = 0.09$, p = 0.86), average speed ($D_{(66,100)} = 0.09$, p = 0.86), or beeline speed ($D_{(66,100)} = 0.18$, p = 0.15). However, there was a significant difference between straightness distribution over WF and EF ($D_{(66,100)} = 0.26$, p = 0.009), with straightness for EF tracks being even more skewed towards 1 (median 0.94) than WF tracks (median 0.90; see Fig. 3E).

Beyond average speed and straightness, the 30 fps butterfly flight tracks extracted from UAV
 videos also contained fine-scale instantaneous information about flight speed and azimuth
 variation along the tracks. For example, Fig. 4 shows a track segment that depicts interesting
 movement patterns, in the form of meter-scale, sub-second transverse oscillations along the
 flight path.



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Figure 4 – Benefit of 30 Hz positional data. <u>A</u>12 s flight track segment, reconstructed with the present method, showing all recorded 2D positions (+, 361 in total). <u>The insert shows a magnified view.</u> The 5 circles represent the positions that could have been recorded with a SHR tracking system, that has a 90-fold lower sampling frequency (1 position every 3s.). Note that on the other hand, SHR benefits from a larger FOV, and hence longer tracking durations (see discussion).

407 Controlling UAV stability

408During video recording, the UAV was not perfectly static, and whether this could have an409effect on the reconstructed flight tracks was an important issue. For a small random subset of410tracking videos (N = 10), we digitized the two reference points painted on the road, describing411a 20 m reference segment (RS), not only at mid-duration, but on every video frame (using

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415 <u>automatic tracking in DLTdv8</u>, which allowed to monitor how the RS was transformed 416 throughout the duration of tracking, due to UAV movements. We assumed that a combination 417 of rotation, scaling and translation could affect the RS projection. Using the *fitgeotrans* function 418 in Matlab, we obtained the geometric transformation matrix from the first frame's RS to each 419 following frame, which allowed to monitor rotation, scaling and translation movement 420 components separately.

421 Fig. 5 shows that the RS projected image was indeed affected by a combination of geometric 422 transformations through time. Over the investigated tracking durations (13 to 40 s), rotation of 423 the RS could attain 0.26° (Fig. 5A), and was on average 0.07° (root mean square, RMS). Scaling 424 variation could attain ± 1.13 % (0.36 % RMS; Fig. 5C). Horizontal (x) or vertical (y) translation of 425 the RS image (Fig. 5B) could reach ± 11.2 pixels (3.6 pixels RMS), which represents less than 0.3 426 % of image width, or 0.18 m when projected on the ground. The amounts of transformation 427 usually did not grow monotonically through time, reflecting that in the absence of pilot input, 428 the UAV does not simply drift away from its initial position, but uses inputs from its onboard 429 sensors to try and maintain position and azimuth. Digitizing the RS only once at track mid-430 duration - i.e. assuming that the UAV is fully static during each track - resulted in a maximal 0.28 431 m error (0.08 m RMS) on the butterfly reconstructed 2D position (Fig. 5D). For the present work, 432 we considered these levels of error to be acceptable, which is why we used the single RS 433 digitizing method for all the remaining tracks. 434



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Figure 5 - UAV movements. Reference segment transformation through time for 10 tracking videos, decomposed into (A) rotation, (B) translation and (C) scaling components. (D) Resulting 2D error on the butterfly 2D position, when only a single digitization of the RS is performed at mid-duration.

441 Controlling butterfly flight height

With the present recording geometry, the flight tracks of all butterflies passing through the pyramidal FOV (Fig. 1A), regardless of their flight height, are projected on a single sensor plane.

We reconstructed these tracks in 2D by assuming that the butterflies moved in the same plane as our reference 20 m segment, i.e. flew at ground level. How this simplification departed from the 3D reality needed investigation. We were especially interested in the possibility that some butterflies might have crossed the FOV at a significant height (10-40 m), which would result in vastly overestimated flight speeds in our ground-projected reconstructions.

449 During field work, we visually monitored the fields under the UAV, and noted each time we 450 saw a Pieris butterfly passing at a low height (defined as below the observer visual horizon, i.e. 451 less than ~2 m above the ground). By comparing our field notes with the timestamps of the 452 reconstructed tracks, N = 45 out of 166 tracks (i.e. 27 %) corresponded to visually-detected 453 butterflies flying at low height (LH group). The remaining tracks were qualified as "unknown 454 height" (UH group, N = 121), and may correspond either to high-flying butterflies (visually 455 undetected because of low contrast against the sky), or to low-flying butterflies that remained 456 undetected (because the observer's attention was regularly directed at the UAV rather than at 457 the ground).

458We compared the beeline speeds of the low-height (LH) and unknown-height (UH) groups.459Both groups had very similar speed distributions (Fig. 6A), as confirmed by statistical tests : LH460 $(2.9 \pm 1.0 \text{ m.s}^{-1}, \text{ mean } \pm \text{ SD})$ and UH tracks $(3.1 \pm 1.3 \text{ m.s}^{-1})$ did not significantly differ for mean461speed in a *t*-test ($t_{(164)} = 0.84, p = 0.40$), and were not drawn from different distributions according

462 to a KS test ($D_{(45,121)} = 0.11, p = 0.79$).





464Figure 6 - Speed distribution and flight height. (A) Ground beeline speed distribution465observed for low height (LH) and unknown height (UH) butterfly tracks. (B) Kernel466probability density estimation for LH and UH tracks, and for simulated tracks with467uniform height distribution (see text).

468In order to visualize what speed distribution would be obtained for butterflies flying far from469the ground, we simulated 10^5 straight horizontal tracks, with flight speeds sampled from a470normal distribution copied form the LH group ($2.9 \pm 1.0 \text{ m.s}^{-1}$), but crossing the FOV at heights471uniformly distributed between 0 and 45 m. Simulated tracks crossing the FOV, and with a track

472 duration of at least 5 s (to simulate comparable track selection), had a ground-projected speed 473 distribution that was flatter and shifted towards high (i.e. overestimated) speeds when 474 compared to both LH and UH tracks (see Fig. 6B). This further suggests that the UH group in our 475 track sample mainly comprises low-flying butterflies that went visually undetected in the field. 476 Still, we cannot exclude that a small number of tracks in the UH group (on the right tail of speed 477 distribution, e.g. with reconstructed speed > 6 m/s) might correspond to high-flying butterflies. 478 Using the pixel blob area as a proxy to measure flight height was not considered a valid option, 479 as the blob area can vary considerably even for a single individual flying at low height (see next 480 section).

481 Exploring blob area as a specific signature

482 We explored the possibility to discriminate P. brassicae from P. rapae tracks, based on pixel 483 blob area in the videos. During field work we captured a small number (N = 8) of Pieris 484 individuals that had just passed through the UAV's FOV. Each individual, captured with a 485 butterfly net, was briefly placed in a thin transparent box with a grid-patterned back, 486 photographed with its wings stretched for later identification and size measurement, and then 487 immediately released. Back in the lab, we measured each individual's forewing length (from 488 wing base to wing tip, Van Hook et al. 2012) using ImageJ. The UAV video recordings 489 corresponding to these individuals were filtered and digitized with the same methods as 490 previously described, but were later re-analysed to measure the blob size in each filtered video 491 frame. As a simple approach, the blob was defined as connected pixels with grey level b > 138, 492 i.e. departing by more than 10 grey level from the mean background grey of 128. Sometimes the 493 simple thresholding approach detected no blob, but this method still allowed to obtain many 494 (269 to 654) blob area values per individual, that could be compared to the animal's real size. 495 Note that 4 out of the 8 tracks used for the present blob area analysis were not part of the final 496 flight track sample (N = 166), because these captured individuals had flown near the road, or 497 performed stops along their flight (see Track selection section).

Five captured individuals were identified as *P. rapae* (2 females + 3 males), with forewing length ranging from 22.8 to 28.0 mm. The 3 other captured individuals were *P. brassicae* (2 females + 1 male), with longer forewing, ranging from 31.2 to 36.7 mm. These values were in line with the literature, with the largest *P. rapae* individuals being close in size to the smallest *P. brassicae* specimens (Cook et al. 2022).

503 Fig. 7 shows the blob area distributions observed for all 8 captured individuals. When 504 considering only the median blob area for each individual, it was positively correlated to the 505 forewing length of the animal (Spearman rank correlation, $r_{(6)} = 0.73$, p = 0.047). However, the 506 relationship was not monotonically increasing (r < 1), and there was extensive overlap between 507 blob area distributions. In other words, a smaller butterfly could often project as a larger pixel 508 blob than a larger butterfly, depending on the compared video frames. As a result, we 509 considered unreliable to use recorded pixel blob areas as a direct mean to discriminate P. rapae 510 and P. brassicae flight tracks in the present work.

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Figure 7 - Forewing length vs. pixel blob area distribution for 8 tracked and captured *Pieris* butterflies. Blue: *P. brassicae* (N = 3); Green: *P. rapae* (N = 5). Distributions are displayed as Kernel probability density estimates. Circles indicate the median blob area value for each butterfly.

516 517

518 Effect of advancing season on flight azimuth.

519 By observing the tracks at different times in the flight period, it appeared visually that the 520 flight azimuths have varied over the season (Fig. 8).

521 To further quantify seasonal variations in azimuth distributions, we computed the beeline 522 azimuth of tracks crossing a 30 m diameter disc located at the centre of the camera's FOV (Fig. 523 8). Indeed, the rectangular shape of the camera FOV is less likely to record trajectories parallel 524 to the longer side of the FOV (see Fig. S1), and this bias can be corrected by considering only an 525 area enclosed by a circle inside the FOV. When a track did not cross this central disc, it was 526 therefore removed from the sample for circular statistics. When a tortuous track crossed this 527 disc more than once, only the longest segment inside the disc was considered. This restriction 528 of the FOV to a central disc had the effect of reducing our sample from N = 166 to N = 119 (for 529 this section only).





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Figure 8 – *Pieris* flight tracks broken down by flight period (vertically) and field (horizontally). Black dots indicate last position of each track (N = 166). 30 m diameter circles represent the area considered for azimuth statistical comparisons (N = 119).

We tested the effects of period (June to September) and field (WF vs. EF) on beeline azimuth, using a two-factor ANOVA for circular data (Harrison & Kanji 1988, in Berens 2009). As we observed many more trajectories in July, we subdivided the month of July: *early July* (field sessions on July 1st and 8th) and *late July* (July 15th and 21st). We then tested the uniformity of the azimuth distributions for each period, using Rayleigh tests (Fisher 1995, in Berens 2009).

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Figure 9 – Circular distributions of *Pieris* **beeline azimuth**, broken down by period (vertically), and field (horizontally). Arrows represent <u>mean</u> resultant vectors. The right column shows azimuth distributions for both fields pooled (WF + EF), with red arrows representing significant <u>directional preference</u> according to a Rayleigh test. <u>The Rayleigh</u> test asks how large the mean resultant vector length *R* must be to indicate a non-uniform distribution (Fisher 1995, in Berens 2009).

547 The ANOVA for circular data detected a significant effect of period on azimuth ($\chi^2_{(6)}$ = 43, p = 548 1.2×10^{-7}), but no effect of field side ($X^2_{(2)} = 0.51$, p = 0.77), and no interaction between the two 549 factors ($X^{2}_{(3)}$ = 5.5, p = 0.14). The distribution of azimuths during the 4 periods is shown in Fig. 9. 550 In June, the butterflies flew most often to the north-east (Rayleigh test, N = 7, R = 0.65, p = 0.04; 551 mean azimuth 24°). In early July, they flew most often to the north-west (N = 51, R = 0.56, p = 4552 \times 10^{\circ}; mean azimuth 317°). In late July, tracks in all directions were observed, without any 553 dominant azimuth, so that the azimuth distribution was not significantly different from a 554 homogeneous distribution (N = 42, R = 0.15, p = 0.41). Finally, in September, tracks were most 555 often oriented to the south (N = 19, R = 0.59, p = 0.001; mean azimuth 173°).

Although our data was collected in low wind conditions (median wind speed 1.9 m.s⁻¹), wind could still influence the butterflies' trajectory. To verify if the above results were influenced by wind, we first tested whether butterfly beeline azimuth was correlated with wind direction, using a circular-circular correlation test (Jammalamadaka & Sengupta 2001, in Berens 2009). a supprimé: resultant vectors

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561 The test returned no significant correlation (c = -0.01, p = 0.95; Fig. 10A). We also assessed 562 whether butterfly preferentially flew downwind, crosswind or upwind, by computing the 563 angular difference between beeline azimuth and wind direction, and testing whether this 564 "angle to wind" variable departed from a uniform distribution. Results suggested that 565 butterflies did not preferentially fly at a specific angle to wind (Rayleigh test, N = 119, R = 0.15, p 566 = 0.06; Fig. 10B), but the test was close to statistical significance, despite a small resultant vector 567 (i.e. small effect size). Therefore, as a supplementary verification, we focused on tracks 568 recorded during stronger winds (> 2 m.s^{-1} , N = 64), as these butterflies were expected to be the 569 most affected by a possible wind influence. Both circular-circular correlation (c = -0.04, p = 0.75) 570 and Rayleigh test on angle to wind (N = 64, R = 0.08, p = 0.67) returned non-significant results 571 (Fig. 10C, D). This comforted the conclusion that wind direction did not significantly bias 572 butterfly flight azimuth in our data.



574	Figure 10 – Wind and Pieris flight azimuth. (A) Beeline azimuth vs. wind direction for N
575	= 119 tracks. (B) Angle to wind for N = 119 tracks. 0° corresponds to upwind flight, 180° to
576	downwind flight. (C-D) Same graphics for the N = 64 tracks where wind speed exceeded
577	2 m.s ⁻¹ .

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Discussion



We show that UAV-image-based tracking can be used to reconstruct free-flying butterfly paths. With light, affordable and easily-deployed gear in the field, we were able to track numerous wild, untagged *Pieris* butterflies, over an area of 2100 m², with track lengths averaging 40 m. Given an average flight speed of about 3 m.s⁻¹, this translates to tracking durations most often near 10-20 s (Fig. 3B-D), depending on each butterfly's flight speed and straightness. This scale of recorded movement is larger than what can be achieved in most insectaries (e.g. Kleckova et al. 2024: 15 m²; Le Roy et al. 2021: 36 m²; Kitamura & Imafuku 2015:

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182 m²; Lihoreau et al 2016b: 880 m²), but remains modest compared to other open field
methods such as SHR (Ovaskainen et al. 2008: 2.5 km²; Lihoreau et al. 2012: 1.5 km²; Maggiora
et al. 2019: 0.7 km²) or human-held GPS tracking (e.g. Fernandez et al. 2016: 100 m average track
length).

591 The spatial scale of the present method is directly constrained by the UAV camera FOV, 592 which was voluntarily limited to 61×34 m (from a 45 m UAV height). This was needed to 593 maintain a butterfly blob area around 10 pixels, for reliable blob tracking throughout video 594 frame series (see Methods section). A first possible way to enlarge FOV would be to use an UAV 595 with higher camera resolution (e.g. 6K or 8K sensor, with matching optics quality), which could 596 potentially fly higher and record a wider ground area, while maintaining a centimetric pixel 597 pitch on the ground. Moreover, a higher signal-to-noise ratio in video frames (e.g. from larger 598 sensors and/or less compressed video file formats) might allow to reliably detect smaller blobs 599 throughout frame series, which in turn would allow larger pixel pitch values, and even higher 600 UAV flight height. A FOV exceeding 100 m in side length (i.e. ~5000 m²) is probably already 601 possible with current high-end commercial UAVs, which might be a large enough area to record 602 routine flight movements in some species with limited home ranges (e.g. Fernandez et al 2016). 603 An alternative way to greatly increase recorded movement length would be to try and follow 604 butterflies with the UAV. This would necessitate (1) that the video feedback to the UAV pilot is 605 of sufficient magnification for a live view of individual butterfly blobs and (2) a different 606 approach to video frame filtering (accounting for quickly moving image background), but these 607 are interesting perspectives for future methodological developments, that might allow 608 recording butterfly movements at a much larger spatial scale, closer to the real scale of 609 dispersal or migration movements.

611 On the other hand, a strength of the movement data we collected is the 30 Hz temporal 612 resolution, which is orders of magnitude higher than non-image-based field tracking methods 613 applicable to flying insects: 1 Hz for human-held GPS tracking (Fernandez et al. 2016), 0.33 Hz 614 for SHR (Ovaskainen et al. 2008), and lower (usually < 0.01 Hz) for automated radio-tracking 615 (Kays et al. 2011). Here, with one location every ~10 cm along the flight path, the reconstructed 616 tracks reveal fine-scale movement patterns (see Fig. 2, 4, 8), and offer access to flight speed and 617 tortuosity in the wild, with improved accuracy. Such refined movement data may provide 618 interesting insights on biomechanical and/or orientation processes at work during butterfly 619 flight. More detailed analyses focused on the effect of wind on flight speeds, and the oscillation 620 patterns along Pieris flight paths are envisaged, but as they imply many additional analyses (e.g. 621 Srygley & Oliveira 2001), they were beyond the scope of the present UAV methodology 622 presentation. Note that in environments richer in ecological resources (e.g. patches of host 623 plant or nectariferous flowers) and conspecifics, having fine access to flight speed and 624 tortuosity will be useful to study less directed, routine flight behaviours, such as foraging or 625 mate searching (Schtickzelle et al. 2007, Fernandez et al. 2016).

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627Another limitation of the present method is the projection of the FOV, a pyramidal 3D air628volume that butterflies can cross at various height, onto a virtual 2D surface at ground level. For629a UAV at height H and a butterfly flying at height h, this 2D projection at ground level causes an630overestimation of flight speed by a factor of H / (H-h). For example, the speed of a butterfly flying

631 at h = 15 m under our UAV at H = 45 m would be overestimated by a factor of 1.5. In our dataset, 632 we were able to verify by direct observation that at least 27 % of tracked butterflies flew at less 633 than 2 m above ground level. For these tracks, the 2D ground projection implies only a small 634 error on flight speed (overestimation factor \leq 1.05). For other butterflies, for which we were 635 unable to confirm flight height, we showed that their projected flight speeds are no higher than 636 confirmed "low flyers", and thus conclude that they probably also crossed the FOV at low height 637 (Fig. 6). This remains indirect evidence, and we cannot exclude that for a small minority of 638 tracks, we might have significantly overestimated flight speed because the butterfly crossed 639 the FOV at a higher height.

Note that, in the hypothetical situation where butterflies move mainly in horizontal planes,
but at various heights, the reconstruction of flight speeds will be heterogeneously
overestimated, but the angular and temporal variables (e.g. variation of azimuth through time)
remain unaffected by flight height.

644 Beyond the average flight height, all the vertical (z) movements of the butterflies are lost 645 when projected onto a (x, y) horizontal plane. For following studies, it is therefore important to 646 observe the 3D flight behaviour of butterflies beforehand, depending on the species, the type 647 of investigated movement (e.g. foraging, patroling, dispersal or migration), the relief of the 648 terrain and vegetation, and to assess from these necessary preliminary behavioural 649 observations whether a 2D projection might overlook relevant information about the animals' 650 movements. If the investigated movement is mainly in the horizontal plane and at low height, 651 then the present method can be appropriate. In the case where the 3D flight trajectory or 652 elevation relative to the ground are necessary data for a study, one should either find a zone 653 where the butterfly's shadow is also visible in the image (Fig. 2H) and derive 3D track data, or 654 opt for other natively 3D optical methods, based on multiple views of the flight volume 655 (Theriault et al. 2014, de Margerie et al. 2015). 656

657 When the UAV receives no command from the pilot, its flight control algorithm seeks to 658 maintain its horizontal position, height and azimuth, using sensory-motor regulation loops 659 based on many on-board sensors (GPS, barometric altimeter, magnetic compass, 660 accelerometers, gyroscopes, downward vision system). Commercial UAVs have made 661 spectacular progress on stability in the last decade, and we were able to verify that, at least over 662 the tracking durations used here (< 1 min), the movements of our UAV were indeed very limited 663 (Fig. 5). This allowed us to assume that the drone was static in the sky, at the cost of a drift under 664 30 cm in the reconstructed position of the butterfly, which we found acceptable for the question 665 posed here (i.e. the measurement of the beeline azimuth over several tens of meters). Still, note that most UAVs use barometric sensors for regulating flight height, and that atmospheric 666 667 pressure might vary significantly across flight times longer than a few minutes.

For studies requiring lower error caused by the drone's position, it is possible to <u>perform a</u> continuous measurement of the reference segment on every video frame (by <u>auto-tracking the</u> <u>2 reference points</u>), or <u>even</u> to perform a more refined calibration of the projected image by continuously tracking multiple points on <u>a grid to fully monitor any complex image</u> <u>transformation or distortion</u>. If the drone's movements really need to be more closely controlled, more advanced commercial drones are available, using positioning technologies

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such as Differential GPS (DGPS) or Real Time Kinematic (RTK), which can monitor the UAVposition with centimeter accuracy.

681 Our video tests suggest that other butterfly species are potentially detectable using the 682 present method, whether they appear light against a dark background (resulting in white blobs 683 in filtered video frames) or dark against a light background (black blobs, Fig. 2F). The blink filter 684 proved efficient for erasing background textures, while also tolerating a fair amount of 685 background movement, caused either by the slow drift of the UAV, or vegetation being blown 686 over by the wind. Hence, we hope to see following studies tracking other butterfly species in 687 various open landscapes. In more cluttered landscapes, where the butterflies can fly through 688 or below vegetation, the present optical method will not be appropriate.

689 Unfortunately, depending on the location and the flight season, it is possible to run into the 690 issue that two (or more) species with similar sizes and colors get filmed simultaneously, and 691 this is the problem we encountered here with two Pieris species. This problem of distinguishing 692 species and individuals is often encountered with tagless, image-based or radar-based tracking 693 (Schlagel et al. 2020). We were not able to discriminate P. brassicae from P. rapae based on pixel 694 blob area (Fig. 7). The wide, overlapping distributions of blob areas for each individual butterfly 695 is not surprising: Flying butterflies can have any posture, from fully stretched to fully closed 696 wings on different video frames, as a result of (1) flapping wing movement and (2) variable roll 697 and pitch angles of the body along the flight path. Moreover, pixel blob area can also be affected 698 by other factors such as (3) contrast with the local background, (4) "blob-clipping" (i.e. when 699 the distance covered between two consecutive frames is less than the body length, which 700 interferes with the filtering method), and (5) flight height. Note also that the relationship 701 between butterfly size and blob area is expected to follow discrete steps (pixels), especially 702 when the pixel pitch is close to animal body size (Fig. 2C).

Provided that some of these sources of blob area variation can be better controlled, we do
 not rule out that pixel blob area could help discriminate butterfly species in future studies
 (and/or monitor flight height), but this would need more refined blob classification processes
 than what we implemented here.

Another option could be to discriminate species based on flight speed or flight behaviour (e.g. tortuosity). A first issue with this approach is that in studies aiming at describing the flight behaviour, it could lead to circular inference. Moreover, Kleckova et al. (2024) reported that different species (*P. rapae* and *P. napi*) can have smaller differences in their flight parameters (measured in an insectary) than spring and summer generations of the same species.

712 Another route for reducing possible confusion between species could be a greater effort to 713 identify each individual's species (and sex) in the field, either by remote visual/photographic 714 identification, or by systematically capturing butterflies after they crossed the UAV's FOV. This 715 would be limited to low-flying butterflies, and also implies greater human presence and 716 movements in the field, which might affect the butterflies' movement patterns. As well, 717 capturing the butterflies before they cross the FOV, and tracking their movements once 718 released was not retained as a valid option, as released butterflies do not immediately display 719 their normal flight behaviour (Nikoleav 1974, Dudley & Srygley 1994).

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720 Observed flight speed and straightness distributions

721 Ground-based multi-camera settings can be used to measure butterfly flight speed in 3D, 722 most often inside insectaries (e.g. Kitamura & Imafuku 2015, Le Roy et al. 2021, Kleckova et al. 723 2024). Unfortunately, many butterflies species tend to fly slower in insectaries than in the wild 724 (Dudley & Srygley 1994), and captivity can also affect other flight parameters (e.g. glide 725 duration: Le Roy et al. 2021). The present data offers a nice opportunity to measure Pieris flight 726 speed in undisturbed, natural conditions, although in 2D only. The median average ground 727 speed we report, at 3.3 m.s⁻¹, comes out lower than some earlier measurements on smaller 728 samples of Pieris performing directed flight in the field (e.g. 3.6 m.s⁻¹ in P. brassicae, Nikolaev 729 1974; 4.4 m.s⁻¹ in *P. rapae*, Dunn 2024). More interestingly, across our relatively large sample 730 from multiple field sessions, we observed a wide speed range (from 1.9 to 9.2 m.s⁻¹ for track 731 average ground speed, Fig. 3D), not even accounting for flight speed variations within each 732 track. This again calls for a detailled (upcoming) analysis of instantaneaous ground and air 733 speeds, taking wind into account, that might provide novel insights on the flight behaviour of 734 Pieris (e.g. wind drift compensation; Gilbert & Singer 1975, Srygley & Oliveira 2001).

735 Flight speeds over WF (mixed crop) and EF (grass) did not differ, and most tracks had a very 736 high straightness value, compatible with a "directional, undistracted" flight behaviour that is 737 often understood as migratory in butterflies (Chowdhury et al. 2021). Still, we measured that 738 tracks over WF were not quite as straight as over EF (Fig. 3E), suggesting that the richer 739 vegetation in WF might have attracted butterflies to some extent, favouring slightly less 740 directed movement. Also, we note that some butterflies in our sample exhibited clearly 741 tortuous rather than directional flight (see Fig. S2 for 14 tracks with straightness < 0.6, which 742 were observed in equal numbers above WF and EF). Moreover, note that the speed and 743 straightness distributions we report would be different if we had included butterflies marking 744 stops along their flights. Thus, although most Pieris butterflies we observed in the field 745 exhibited a directed, possibly migratory behaviour, a minority appeared to be rather engaged 746 in undirected flight movements.

The higher number of butterflies passing over EF (*N* = 100 vs. *N* = 66 for WF) was intriguing.
After a close examination of sample sizes for each field session (see table S1), it appears that EF
and WF butterfly numbers only differed significantly for 1 out of 11 field sessions, thus we do
not conclude that EF consistently attracted more butterflies than WF.

751 P. brassicae and P. rapae migratory behaviours

In butterflies, migration often occurs over several generations, with successive generations 752 753 following different flight azimuths to achieve a round-trip annual travel (Chowdhury et al. 2021). 754 Within Pieridae, P. brassicae and P. rapae migratory behaviours have long been documented 755 from the observation of mass migrations (Williams et al. 1942, Vepsalainen 1968). These mass 756 migrations are now rarer due to the use of pesticides (Spieth & Cordes 2012), but see John et al. 757 (2008) and Dunn (2024) for recent reports of group migrations in P. rapae (and see Bauer et al. 758 2024 for radar-based studies on mass migrations in other insect species). Early attempts at 759 quantifying Pieris migratory flights used methods such as visually estimating the flight azimuth 760 in the field (e.g. Baker 1968), or difficult mark-recapture experiments (Roer 1959, 1961). More 761 recently, Jones et al (1980) used an egg marking method to study the movements of individual 762 australian P. rapae females, reporting directed flight with some northward bias. Gilbert &

763 Raworth (2005) observed in the Pyrenees mountains that a portion of the P. rapae population 764 migrated northward in spring and southward in autumn, in line with earlier observations in 765 England (Baker, 1968). For P. brassicae, Spieth & Cordes (2012) collected eggs from several 766 Western Europe regions, and later measured the spontaneous flight azimuth of adult female 767 individuals, in a 2 m octogonal flight cage. They showed that the preferred flight azimuth 768 depended on the season and the geographic origin: The first generation usually followed a 769 northward azimuth (modulated by the precise geographic origin), whereas the last generation 770 (2nd or 3rd depending on the region) flew southward. Using a similar flight cage, Larranaga et al. 771 (2013) confirmed a mean northward azimuth in both females and males P. brassicae of the first 772 generation.

773 Here, for a mixed sample of *P. brassicae* and *P. rapae* individuals, we observed flights that 774 were mainly directed northwards in the early season (June, early July), and a southward 775 azimuth in the late season (September). This appears congruent with the existing literature on 776 migration in P. brassicae (Spieth & Cordes 2012) and P. rapae (Gilbert & Raworth 2005). Hence, 777 despite the limited spatial scale of our movement data, it is probable that the highly directed 778 movements we recorded were segments of migratory flights. Note that the absence of a 779 dominant azimuth for late July might be the result of P. brassicae already shifting to southward 780 flight, with P. rapae still flying predominantly northward at this period (R. Baker, personal 781 communication).

782 Tracks recorded from a UAV allow an accurate measurement of flight azimuth, without the 783 need to capture or mark the butterflies (which can affect spontaneous flight behaviour: 784 Nikoleav 1974, Dudley & Srygley 1994), at an intermediate scale between a flight cage (or 785 insectary) and mark-recapture experiments. As a plus, high sampling frequency trajectories 786 contain previously unavailable fine-scale information on flight speeds, tortuosity of the flight 787 path, and patterns of rapid azimuth variation (transverse oscillations). This refined data may be 788 studied in greater detail and has the potential to reveal information on locomotor behaviour 789 and the perceptual mechanisms underlying spatial behaviour. Two major limitations of our 790 approach at this stage are (1) the limited spatial scale and (2) the confusion between P. rapae 791 and P. brassicae, because of their similar sizes and colors, and their concurrent flight in our 792 geographical area.

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Conclusion

794 Our results reveal that video tracking of butterflies from a UAV is possible, and capable of 795 providing movement data in fully natural conditions, at an unprecedented spatio-temporal 796 resolution, and at a modest cost. This fine-scale data could prove precious for understanding 797 the spatial behaviour of many butterfly species in open landscapes, and study their movement 798 ecology in various contexts, from routine ressource-searching flights in the local habitat, to 799 dispersal or even migratory flights. We hope that the present methodology exploration can 800 serve as a starting point and motivate other works using UAVs to study spatial behaviour and 801 movement ecology in flying insects.

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