

1 Tracking individual honeybees among wildflower  
2 clusters with computer vision-facilitated pollinator  
3 monitoring

4

5 Malika Nisal Ratnayake<sup>1</sup>, Adrian G Dyer<sup>2,3</sup>, Alan Dorin<sup>1\*</sup>

6 <sup>1</sup> Faculty of Information Technology, Monash University, Melbourne, Australia

7 <sup>2</sup> Department of Physiology, Monash University, Melbourne, Australia

8 <sup>3</sup> School of Media and Communication, RMIT University, Melbourne, Australia

9

10 \* Corresponding Author

11 Email: [alan.dorin@monash.edu](mailto:alan.dorin@monash.edu) (A.D.)

12 **Short Title**

13 Tracking honeybees in outdoor environments

## 14 **Abstract**

15 Monitoring animals in their natural habitat is essential for advancement of animal behavioural studies,  
16 especially in pollination studies. Non-invasive techniques are preferred for these purposes as they  
17 reduce opportunities for research apparatus to interfere with behaviour. One potentially valuable  
18 approach is image-based tracking. However, the complexity of tracking unmarked wild animals using  
19 video is challenging in uncontrolled outdoor environments. Out-of-the-box algorithms currently present  
20 several problems in this context that can compromise accuracy, especially in cases of occlusion in a 3D  
21 environment. To address the issue, we present a novel hybrid detection and tracking algorithm to  
22 monitor unmarked insects outdoors. Our software can detect an insect, identify when a tracked insect  
23 becomes occluded from view and when it re-emerges, determine when an insect exits the camera field  
24 of view, and our software assembles a series of insect locations into a coherent trajectory. The insect  
25 detecting component of the software uses background subtraction and deep learning-based detection  
26 together to accurately and efficiently locate the insect among a cluster of wildflowers.

27 We applied our method to track honeybees foraging outdoors using a new dataset that includes complex  
28 background detail, wind-blown foliage, and insects moving into and out of occlusion beneath leaves  
29 and among three-dimensional plant structures. We evaluated our software against human observations  
30 and previous techniques. It tracked honeybees at a rate of 86.6% on our dataset, 43% higher than the  
31 computationally more expensive, standalone deep learning model YOLOv2. We illustrate the value of  
32 our approach to quantify fine-scale foraging of honeybees. The ability to track unmarked insect  
33 pollinators in this way will help researchers better understand pollination ecology. The increased  
34 efficiency of our hybrid approach paves the way for the application of deep learning-based techniques  
35 to animal tracking in real-time using low-powered devices suitable for continuous monitoring.

36 **Keywords:** individual behaviour, flying insect, deep learning, animal movement, occlusion

37

## 38 **Introduction**

39 Studying animal behaviour helps address key questions in ecology and evolution, however, collecting  
40 behavioural data is difficult [1]. While direct observation by ethologists is useful, this approach has low  
41 sampling resolution [2] and create bias due to attentional limitations [3], which makes it difficult to  
42 monitor fast moving animals such as insects [4]. Additionally, the accuracy of data may later be  
43 questioned since visual records of incidents are not preserved [5]. Video recordings potentially help  
44 overcome some methodological limitations by preserving observations. Unfortunately, manually  
45 extracting animal behaviour from video remains time consuming, and error prone due to the attentional  
46 limitations of human processing [3]. Recent advances in automated image-based tracking tackle these  
47 problems by extracting and identifying animal behaviours and trajectories without human intervention  
48 [5,6]. Whilst these techniques promise improved sampling of data, performance is still limited, in this  
49 case by environmental and animal behavioural complexity, and computational resources.

50 One area in which accurate, fine-scale behavioural data is particularly valuable is the study of insect  
51 pollination. Pollination is an integral requirement for horticulture and ecosystem management – insect  
52 pollinators impact 35% of global agricultural land [7], supporting over 87 food crops [8]. However, due  
53 to their small size and high speed whilst operating in cluttered 3D environments [4], insect pollinator  
54 monitoring and tracking is challenging. Since pollination is an ongoing requirement of crops and  
55 wildflowers alike, it would be ideal to establish field stations that can provide ongoing data on pollinator  
56 behaviours. To be practical, such a solution would need to be cheap to assemble and install. They would  
57 need to provide low cost, reliable and continuous monitoring of pollinator behaviour. These  
58 requirements exclude many current approaches to insect tracking, but the challenge is suitable for  
59 innovations involving imaging and AI.

60 Previous research has developed both invasive and non-invasive insect tracking methods. Invasive  
61 methods for example mark insects with electronic tags such as Passive Integrated Transponders (PIT)  
62 [9–12] or tags facilitating image-based tracking [13]. PIT-based tracking requires an electronic tag (e.g.,  
63 harmonic radar, RFID) to be attached to an insect's body. Although, these methods can track insects

64 over expansive areas and thus provide important larger scale information [14], the spatiotemporal  
65 resolution of collected data is lower than that of image-based tracking [5]. The latter approach is  
66 therefore better for data collection on fine insect movements likely to provide insight into cognition and  
67 decision making. Attaching tags to insects adds to their mass and may increase stress and alter behaviour  
68 [5,15,16], and, tagging individual insects is laborious, especially outdoors. For continuous season-long  
69 insect monitoring, attaching tags to populations of wild insects and managed honeybee hives containing  
70 potentially thousands of colony members is infeasible. Therefore, non-invasive methods such as  
71 unmarked image-based tracking can potentially make important contributions to our knowledge. Any  
72 improvements made to supporting technology can increase the scope and value of the approach.

73 Following unmarked insects is a difficult image-based tracking problem [17]. Previous tracking  
74 programs have been developed to research insect and small animal behaviour [17–22]. But their  
75 application is often confined to laboratories offering constant backgrounds and illumination needed for  
76 accurate tracking [17–21] or require human intervention [22]. Behavioural research on animals shows  
77 that environmental factors such as wind, temperature, humidity, sky exposure, may affect behaviour  
78 and interactions [23,24], and these are exactly the kinds of factors that field monitoring must explore.  
79 It is therefore essential to track insects outdoors in a biologically relevant scenario, rather than in a lab.  
80 In this study, we present novel methods and algorithms to enable this. We illustrate the application of  
81 our methods by automatically tracking freely foraging honeybees.

82 Segmentation methods such as background subtraction and thresholding are widely used in image-based  
83 tracking to identify the position of animals in a video frame [17–19,25–28]. Background subtraction is  
84 efficient where background and illumination are constant, and significant background/object contrast  
85 exists [5]. This method has also been used to count and track honeybees [29–37] and bumblebees [1].  
86 Most of this research to date has been conducted in laboratories, or in front of and within beehives with  
87 relatively constant backgrounds. This makes the application of pure background subtraction  
88 challenging.

89 Recently, there has been increased use of deep learning and neural networks for animal tracking [38].  
90 Deep learning can detect and identify animals in a frame irrespective of the environment as it does not

91 rely on foreground-background segmentation. The application of deep learning however has a high  
92 computational cost, and detection rate and accuracy depend on the quality and quantity of training data  
93 [39]. For rare species, or for species not previously tracked, a requirement for large training datasets  
94 increases the difficulty in implementing a tracking algorithm. Together, these factors currently limit the  
95 use of deep learning for generalised animal tracking, and for its application in remote devices for  
96 ecological research extracting movement and behavioural data from high-resolution data. Previous  
97 tracking approaches have used convolutional neural networks (CNNs) to estimate honeybee posture  
98 [25], distinguish between pollen-bearing and non-bearing honeybees [40], monitor interactions of  
99 honeybees in a hive [13] and monitor hive entry/exits [41]. However, taking steps towards the efficient  
100 and autonomous video tracking of unmarked insects in complex outdoor environments remains key to  
101 improving pollination and insect behavioural studies.

102 Insects forage amongst trees, leaves and flowers subject to changing illumination and movements  
103 caused by wind and animals (Fig. 1). This increases tracking complexity [6] since the changes detected  
104 in a frame of the video may relate to instances where one, the other, or both insect and non-insect  
105 elements (such as wind-blown leaves or flowers manipulated by an insect) in the environment move  
106 with respect to the camera. Ideally, it is desirable to detect an insect and identify its position in all of  
107 these scenarios to enable accurate census of pollinators, and what flowers they visit. Further  
108 complications arise as insects don't always fly, sometimes they crawl among and behind vegetation  
109 [42–44]. This can cause the insect to be occluded from view, or the insect may leave the camera's field  
110 of view completely resulting in frames where no position is recorded. To maintain the identity of the  
111 insect and terminate tracking if necessary, it is important for accurate recognition of insects as they  
112 move through a complex environment. Although previous research has tracked insects through  
113 occlusions in an open arena [45–47], identifying occlusions and view exits in unbounded, complex  
114 outdoor environments has not been previously reported.

115

116 **Fig 1: Foreground masks of an image showing a honeybee on a carpet of flowers obtained using**  
117 **background subtraction.** The KNN background subtractor [48] was used to obtain foreground masks

118 when the background is (a) constant; (b) wind-blown. Moving objects are shown in white pixels, the  
119 honeybee is circled.

120

121 In this paper, we present a novel Hybrid Detection and Tracking (HyDaT) algorithm to monitor foraging  
122 insects outdoors. Our purpose is to accurately map a sequence of interactions between a particular insect  
123 and its foraging environment. Hence, our implementation tracks one insect at a time from its entry to  
124 its exit from view, or from the start of a video sequence to the conclusion. In order to extract multiple  
125 plant-pollinator interaction sequences (actually, sequences of interactions between a unique pollinator  
126 and a set of flowers) we re-run the software on each insect detected in a region / clip in turn. To  
127 demonstrate our software in action, we train the detection model and tune parameters to track  
128 honeybees. We compare the efficiency and effectiveness of our algorithm against human ground  
129 observations and previously described methods, and apply our approach to track foraging on flower  
130 carpets in a new dataset (78 minutes of outdoor video). Finally, we discuss our results and suggest future  
131 improvements.

## 132 **Materials and methods**

133 Our Hybrid Detection and Tracking (HyDaT) algorithm has four main components (Fig. 2). A hybrid  
134 detection algorithm begins at the start of the video and moves through the footage until it first detects  
135 and identifies an as yet untracked insect. If this insect is not detected within a subset of subsequent  
136 frames, the algorithm uses novel methods to predict if it is occluded or has exited the view. Positional  
137 data collected from the algorithm is then linked to synthesise coherent insect trajectories. Finally, this  
138 information is analysed to obtain movement and behavioural data (e.g. heat-maps, speed or turn-angle  
139 distributions).

140 **Fig 2: Hybrid Detection and Tracking (HyDaT) algorithm overview and components.**

## 141 **The hybrid detection algorithm**

142 We use a hybrid algorithm consisting of background subtraction and deep learning-based detection to  
143 locate an insect. As discussed in the introduction, background subtraction can detect movements in the  
144 foreground without prior training and works efficiently where the background is mainly stationary. In  
145 contrast, deep learning-based detection can detect and identify an insect irrespective of changes in the  
146 background, but it requires training with a dataset prior to use. We designed our hybrid detection  
147 algorithm to work with the strengths of each detection technique and intelligently switch between the  
148 two approaches depending on variations in the video's background. Prior to algorithm commencement,  
149 the deep-learning detection model must be trained on a dataset of the target insect species.

150 The algorithm begins using the trained deep learning model to initialise the detection process by locating  
151 the insect's first appearance in a video. This ensures identification of an insect with a low probability  
152 of false positives, even if the background is moving. After initial identification, the technique used for  
153 insect detection is determined by the number of regions of inter-frame change within a calculated radius  
154  $MDT_{DL}$  of the predicted position of the insect in the next frame (Data association and tracking, Equation  
155 4). If there is a single region of significant change identified between frames, the background subtraction  
156 technique is used to locate the insect. If a small number of regions of change are detected within the  
157 predicted radius of the insect, then the region closest to the predicted position is recorded as the insect's  
158 position. (With our setup, three regions of movement within the calculated radius around the predicted  
159 position of the insect offered an acceptable compromise between algorithm speed and tracking  
160 accuracy. This trade-off can be user-adjusted). However, sometimes the region within the radius around  
161 the insect's predicted position is too full of movement to be sure which is the insect. In this case,  
162 background subtraction is unusable, or perhaps insufficiently inaccurate, so the hybrid algorithm  
163 switches to deep learning. In addition, whenever the background subtraction technique fails to detect  
164 movement likely to indicate the insect's position, deep leaning is used.

165 The hybrid detection algorithm consists of a modular architecture allowing state-of-the-art deep  
166 learning and background subtraction algorithm plug-ins to be incorporated as these tools advance.  
167 Details of deep-learning and background subtraction algorithms we use appear below.

## 168 **Deep learning-based detection**

169 We use a convolutional neural network (CNN)-based YOLO (You Only Look Once) [49] object  
170 detection algorithm to detect insects in a video frame because it is well supported and convenient.

## 171 **Background subtraction-based detection**

172 We use K-nearest neighbour (KNN)-based background/foreground segmentation [48] (OpenCV 3.4.1  
173 [50]) to detect foreground changes in the video. The KNN background subtractor works by updating  
174 parameters of a Gaussian mixture model for better kernel density estimation [51]. The resulting binary  
175 image includes changes of the foreground assuming a constant background. A median filter and an  
176 erosion-based morphological filter are applied to the segmented image to remove noise. The resulting  
177 image contains changes in the foreground caused by insects and moving objects. Next, contours of the  
178 foreground detections (blobs) are extracted from the binary image and filtered based on their enclosing  
179 area to remove areas of movement less than a predetermined minimum pixel count covered by the focal  
180 insect. The position of the insect is designated by the centroid of this filtered blob (Fig. 3).

181

182 **Fig 3: Detecting an insect with background subtraction.** (a) Honeybee and flower shown at pixel  
183 resolution typical of that we employed for our study; (b) Binary image extracted using KNN background  
184 subtractor [48]; Resulting image with (c) median filter; (d) erosion-based morphological filter (centroid  
185 indicated) .

186



## 187 **Identifying occlusions**

188 In the event that the focal insect is undetected, our algorithm analyses the variation in insect body area  
189 before its disappearance to identify a possible occlusion. Background subtraction is used to measure  
190 this change from the video. Variation of visible body area is modelled linearly using a least squares  
191 approach (Equation 1) to determine whether the insect is likely to have been occluded by moving under  
192 foliage.

193

$$m = \frac{n \sum Af - \sum A \sum f}{n \sum f^2 - (\sum f)^2} \quad (1)$$

194

195 Where  $m$  is the gradient of the linear polynomial fit,  $n$  is the number of frames considered,  $f$  is frame  
196 number, and  $A$  is visible insect body area in frame  $f$ . When the insect crawls or flies under foliage, the  
197 variation of visible body area before disappearance shows a negative trend ( $m < 0$ ). Our algorithm  
198 utilises this fact to identify whether the insect is occluded from view due to movement under foliage  
199 (Fig. 4). If the insect disappears along a frame edge designating the camera's field of view, then the  
200 disappearance is assigned to a possible exit from the field of view, as discussed below. The algorithm  
201 for insect occlusion is not executed in this case.

202

203 **Fig 4: An example of an insect occluded under foliage.** Scatterplot shows the variation of insect  
204 visible body area before occlusion, and the corresponding least squares polynomial fit. Pixel intensity  
205 in the greyscale image represents the amount of change detected in the foreground.

206

207

## 208 **Identifying an insect exiting the field of view**

209 To identify an insect's exit from view, we use Algorithm 1 to calculate an exit probability value  $\beta$  when  
210 it has been undetected for a threshold of  $\bar{\tau}$  consecutive frames. If  $\beta$  is higher than a predefined threshold  
211 value  $\bar{\beta}$ , the algorithm pauses tracking the focal insect, and begins to search for new insects to track. If  
212 an insect is re-detected near the point of disappearance of the original focal insect before a new insect  
213 appears, the algorithm resumes tracking it, assuming this to be the original focal insect (see Discussion  
214 on Identity Swap management). Otherwise, the algorithm terminates and stores the previous track. Any  
215 new insect detections will be assigned to new tracks.

---

**Algorithm 1:** Calculating exit probability  $\beta$

---

**Input:** Insect speeds,  $d_e$

**Output:**  $\beta$

initialisation;

**if**  $\tau == \bar{\tau}$  **then**

$i = 1.00$ ;

**else**

$i = \text{last } i$ ;

**end**

$d_t = \tau \times \eta_i$ ;

**if**  $d_t > d_e$  **then**

**while**  $d_t < d_e$  **do**

$i -= 0.01$ ;

$d_t = \tau \times \eta_i$ ;

**end**

**else**

    return;

**end**

$\beta = (1 - i) \times 100\%$

---

$\beta$     Exit probability

$d_e$     Shortest distance to frame boundary from insect's last  
detected position

$d_t$     Predicted distance travelled by the insect during  $\tau$   
number of undetected frames

$\tau$     Consecutive number of frames insect is not detected

$\bar{\tau}$  Threshold number of consecutive frames insect is not  
detected  
 $i$  Quantile value  
 $\eta_i$   $i^{th}$  quantile value of speed of the insect

---

216

217

## 218 **Data association and tracking**

219 For applications discussed above, our algorithm tracks one insect at a time from its first appearance  
220 until its exit from view, before it is re-applied to track subsequent insects in footage. As a given frame  
221 may contain multiple insects simultaneously foraging in a region, a "predict and detect" approach is  
222 used to calculate the focal insect's track over successive frames. In a set of three successive frames, the  
223 predicted insect position in the third is calculated from the detected positions in the first two frames,  
224 assuming constant insect velocity over the three frames [35,52]. The predicted position  $P_k$  of the insect  
225 in frame  $k$  of the video is defined as:

226

$$P_k = [x_{pk}, y_{pk}]^T = A * [D_{k-1}, D_{k-2}]^T \quad (2)$$

227

228 Where,

$$A = \begin{bmatrix} 2 & 0 & -1 & 0 \\ 0 & 2 & 0 & -1 \end{bmatrix}$$

229

230 In equation (2)  $x_{pk}$  and  $y_{pk}$  refer to coordinates of the predicted position of the insect in the frame  $k$   
231 and  $[D_{k-1}, D_{k-2}]$  are the detected positions of the insect in the two previous frames.

232 When an insect is first detected, the predicted position for the next frame is assumed to be the same as  
233 its current position (as there are no preceding frames). In the case of occlusions or frames in which no  
234 insect is detected, the predicted position is carried forward until the insect is re-detected.

235 In cases where multiple insects are detected within a single video frame using the hybrid algorithm, it  
236 is necessary to assign the predicted position of the focal insect to an individual detection within the  
237 frame. This is done using a process derived from the Hungarian method [53] which minimises the  
238 distance between assigned detections and predictions. To avoid recording false-positive detections, a  
239 detection is not associated with a prediction if the distance between the two surpasses a maximum  
240 threshold calculated using equations (3 & 4), based on distances travelled by the focal insect between  
241 consecutive frames within previously analysed data. Different detection thresholds are used for  
242 background subtraction ( $MDT_{BS}$ ) and deep learning-based detection ( $MDT_{DL}$ ) techniques, with  $MDT_{BS}$   
243  $< MDT_{DL}$  since background subtraction-based detections are more prone to false positives.  
244 Thresholds are defined as follows.

245

$$MDT_{BS} = \max \{d_{int}, d_{max}\} \quad (3)$$

246

$$MDT_{DL} = 2 \times \left( MDT_{BS} + \eta_{\min\left\{\frac{\max\{0, (\tau - \bar{\tau})\}}{100}, 0.99\right\}} \right) \quad (4)$$

247

248 Where  $d_{int}$  is the initial value for  $MDT_{BS}$  set to the average body length (in pixels) of the target insect  
249 species,  $d_{max}$  is the maximum recorded distance travelled by the focal insect between consecutive  
250 frames,  $\eta_i$  is  $i^{th}$  quantile of recorded speeds of the insect,  $\tau$  is the number of consecutive frames during  
251 which the insect is not detected, and  $\bar{\tau}$  is the predefined threshold number of consecutive frames during  
252 which the insect has gone undetected.

253

## 254 Experiments and results

255 In this section, we evaluate the performance of our method (HyDaT) on honeybees (*Apis mellifera*).  
256 Honeybees are social insects that forage in wild, urban and agricultural environments. They are  
257 widespread, generalist pollinators of extremely high value to the global economy and food production  
258 [5], making honeybees particularly relevant organisms suited for testing our tracking.

259 We selected a patch of Scaevola (*Scaevola hookeri*) groundcover as the experimental site to evaluate  
260 our methods because of the species' tendency to grow in two dimensional carpets and to flower in high  
261 floral densities. Due to the undercover's structural density, honeybees both fly and crawl from flower  
262 to flower as they forage. Honeybees often crawl under the foliage to visit flowers that are obscured from  
263 above. These complexities in honeybee behaviour in Scaevola help us evaluate the robustness of our  
264 methods.

265

## 266 Data collection for experiments

267 Videos required for experiments were recorded on the grounds of Monash University's Clayton campus,  
268 Melbourne, Australia (lat. 37.9115151° S, long. 145.1340897° E) in January 2019. All the videos were  
269 recorded between 10:00 am – 1:00 pm, ambient temperature 23 °C – 26 °C, wind speeds 9 – 26  $kmh^{-1}$   
270 . The study area contained ~446 flowers making a density of ~2340  $flowers/m^{-2}$  . A Samsung  
271 Galaxy S8 phone camera (12 MP CMOS sensor, f/1.7, 1920 × 1080 pix, 60 fps) mounted on a tripod  
272 was set 600 mm above the groundcover to record videos (

273 **Fig 5: Experimental setup for recording videos.**) A ruler placed in the recorded video frame was  
274 later used to convert pixel values to spatial scale (millimetres). Recorded videos covered an area of  
275 600 mm × 332 mm with a density of 10.24  $pixels/mm^{-2}$ . Average area covered by a honeybee was  
276 1465 ± 531  $pixels$  (e.g. see Fig 3a).

277

278 **Fig 5: Experimental setup for recording videos.**

## 279 **Software development**

280 We developed the software using Jupyter Lab (Python 3.7.1), Computer Vision Library (OpenCV) 3.4.1  
281 and Tensorflow 1.13.1. A Dell Precision 5530 workstation with Intel(R) Core i7-7820HQ (2.90 GHz)  
282 CPU, 32 GB Memory, 512 GB (SSD) storage and Microsoft Windows 10 Enterprise OS was used for  
283 processing. Data analysis was conducted using NumPy 1.16.2, Pandas 0.24.2 and Matplotlib 3.0.3. The  
284 code is available at [github.com/malikaratnayake/HyDaT\\_Tracker](https://github.com/malikaratnayake/HyDaT_Tracker).

285 A YOLOv2 object detection model [54] was used as the deep learning-based detection model in HyDaT.  
286 A Darkflow [55] implementation of YOLOv2 was trained using Tensorflow [56]. Images required for  
287 training the deep learning-based detection model were extracted from videos recorded in Scaevola  
288 groundcover using FrameShots [57]. Extracted images were then manually filtered to remove those  
289 without honeybees. The 2799 selected images containing honeybees were manually annotated with  
290 bounding boxes using LabelImg [58]. The annotated images and trained YOLOv2 model can be found  
291 in *SI Data*.

## 292 **Experiment 1: Detection rate and tracking time**

293 We evaluated the detection rate and tracking time of HyDaT using a data set of seven video sequences  
294 of honeybees foraging in Scaveola. These videos were randomly selected from continuous footage of  
295 foraging honeybees. Each video was between 27 and 71 seconds long, totalling 6 minutes 11 seconds  
296 of footage in all. HyDaT was tuned to track the path of a honeybee from its first appearance in the video  
297 to its exit. All videos contained natural variation in background, lighting and bee movements. Fig. 6  
298 provides an explicit representation of each video sequence's changeability. One or more honeybee  
299 occlusions from the camera occurred in all of the videos.

300

301 **Fig 6: Number of image region changes per frame in test videos.** Box plot showing the distribution  
302 of number of image regions with greater than one pixel change per frame in test videos. The filled red  
303 diamond indicates the mean number of region changes per frame.

304 *Detection rate* is our measure to evaluate the number of frames where the position of the insect is  
305 accurately recorded with respect to human observations. For the purpose of the experiment, frames  
306 where the honeybee is fully or partially hidden from the view were considered to be *occlusions*. If the  
307 algorithm recorded the position of the honeybee in an area that was in fact covered by the body of the  
308 bee, this was considered as a *successful detection*. The time taken by the algorithm to process the video  
309 was recorded as the *tracking time*.

310 We also compared the detection rate and tracking time of HyDaT to the stand-alone deep learning-  
311 based YOLOv2 [49] model after using the same training dataset for each. The aim of this was to evaluate  
312 the improvement in detection rate our methods can achieve compared to a deep-learning model under  
313 the same training regime and limitations. Parameters of our algorithm and the stand-alone YOLOv2  
314 detection model were tuned separately to achieve maximum detection rates for each and allow it to  
315 operate at its best for comparison purposes (S2 Table). To benchmark our results further, we also  
316 processed the seven honeybee videos using Ctrax [18], current state-of-the-art insect tracking software.

317 Results are provided in Table 1. HyDaT detected the position of the honeybee and associated it to a  
318 trajectory in 86.6% of the frames in which it was visible to human observation. Compared to the stand-  
319 alone deep learning-based method YOLOv2 [49] model, HyDaT achieved higher detection rates for all  
320 seven test videos, a 43% relative increase in detection rate and a relative reduction in error of 66%.  
321 HyDaT processed the seven videos totalling 6 minutes 11 seconds (22260 frames at 60 fps) of footage  
322 in 3:39:16 hours, a reduction in tracking time of 52% over YOLOv2. This improvement in speed is  
323 possible because 91% of detections by HyDaT were made with background subtraction which requires  
324 much lower computational resources than purely deep learning based models. Ctrax, an existing animal  
325 tracking package we used for comparison, was completely unable to differentiate the movement of the  
326 honeybee from background movement. Its attempts to locate the honeybee were unusable and it would  
327 be meaningless to attempt to compare its results in these instances. In addition, when the honeybee was



328 occluded for an extended period, Ctrax assumed it had left the field of view and terminated its track.  
 329 Therefore, in these cases also it is meaningless to compare Ctrax’s outputs with HyDaT. Tracks of  
 330 honeybees extracted using HyDaT are shown in

331 **Fig 7: Trajectories for a single honeybee in test videos.** Tracks were extracted using HyDaT from  
 332 seven test video files..

333 **Table 1: A quantitative comparison of HyDaTs’ tracking performance against a stand-alone**  
 334 **deep learning-based model (YOLOv2) [49] of honeybees foraging in Scaevola.**

Video (Scaevola)	Number of frames		Detection rate (%)		Tracking time (hh:mm:ss)		HyDaT’s Detection method utilisation (%)	
	Video	Honeybee visible	HyDaT	YOLOv2	HyDaT	YOLOv2	Background Subtraction	Deep Learning (YOLOv2)
V1	3540	2670	<b>97.7</b>	76.4	<b>00:29:29</b>	01:18:26	94.9	5.1
V2	2940	2148	<b>51.5</b>	36.9	<b>00:45:45</b>	01:03:55	95.8	4.2
V3	3600	3016	<b>91.9</b>	63.1	<b>00:33:51</b>	01:19:20	85.2	14.8
V4	2820	1612	<b>72.6</b>	50.1	<b>00:38:16</b>	00:53:05	98.7	1.3
V5	3480	2802	<b>89.2</b>	26.9	<b>00:30:26</b>	01:05:40	94.5	5.5
V6	4260	3882	<b>97.1</b>	84.0	<b>00:28:58</b>	01:22:11	87.6	12.4
V7	1620	1414	<b>89.1</b>	77.3	<b>00:12:32</b>	00:33:17	88.2	11.8
Overall	22260	17544	<b>86.6</b>	60.7	<b>03:39:16</b>	07:35:54	91.0	9.0

335 Algorithm performance is assessed by detection rate (percentage of frames where the position of the  
 336 honeybee accurately corresponds to human observations) and tracking time (the time taken to process  
 337 a video). The “detection method utilisation” column shows the percentage of frames our algorithm used  
 338 background subtraction versus deep learning methods to detect honeybee position. The best performing  
 339 algorithm is indicated in bold.

340

341 **Fig 7: Trajectories for a single honeybee in test videos.** Tracks were extracted using HyDaT from  
 342 seven test video files.

## 343 **Experiment 2: Occlusion identification and exit frame estimation**

344 The performance of the occlusion identification algorithm and the insect frame exit estimation were  
345 evaluated against human observations using a continuous video of duration 8 min. 15 sec. (29,700  
346 frames) showing foraging honeybees in Scaevola. For this evaluation we only consider trajectories of  
347 bees visible for more than 120 frames (2 seconds at 60 fps). Threshold number of consecutive  
348 undetected frames,  $\bar{\tau}$ , was set to 15, and the threshold exit probability,  $\bar{\beta}$ , was 85%. The following  
349 guidelines were followed when conducting the experiment and determining the human ground  
350 observation values.

- 351 1. An insect was considered to be occluded from the view if it was partially or fully covered by a  
352 flower or a leaf and if it was not detected for over  $\bar{\tau}$  frames.
- 353 2. An insect was considered to have exited the frame when it had completely left the camera view.

354

355 Results are given in Table 2. The video evaluated for the study consisted of 54 instances where the  
356 honeybee was undetected by the software for over threshold value  $\bar{\tau}$  (15) frames. The algorithm detected  
357 68.57% of occlusions and all honeybee field of view (FoV) exits when compared to human analysis of  
358 the video.

359 **Table 2: Occlusion detection algorithm performance and field of view (FoV) exit estimate for an**  
360 **8:15 minute video of honeybees recorded in Scaevola.**

Event	Actual no. of events	No. of events recorded (correct/incorrect)	No. of events missed	Detection rate (%)	Error in estimate (%)
Occluded	35	24 (24/0)	11	68.57	0.00
Exited FoV	16	19 (16/3)	0	100.00	15.79
Other	3	11 (3/8)	0	100.00	72.72

361 Detection rate = percentage of events correctly recorded compared to actual number of events; Error in  
362 estimate = percentage of incorrect recordings out of events recorded. “Other” in the Events column

363 refers to instances where the insect was visible and the detection algorithm failed to locate it for over  $\bar{\tau}$   
364 (15) continuous frames.

365

## 366 **Example data analysis**

367 To demonstrate the value of our approach for extracting meaningful data from bee tracks, we studied  
368 the behaviour of honeybees foraging in a Scaevola (*Scaevola hookeri*) as already discussed, and also in  
369 Lamb's-ear (*Stachys byzantine*) ground cover. We extracted spatiotemporal data of foraging insects and  
370 analysed their changes in position, speed and directionality. We tested our setup on both Scaevola and  
371 Lamb's-ear to assess the capability of our system to generalise, while simultaneously testing its ability  
372 to extend to tracking in three-dimensional ground cover, within the limits imposed by the use of a single  
373 camera.

374 We followed methods presented in Data collection for experiments section to collect study data. A  
375 dataset of 451 images was used to train the deep learning model of HyDaT on Lamb's-ear while the  
376 dataset used in experiments 1 and 2 was re-used for Scaevola (S3 Text). We extracted movement data  
377 from 38 minutes and 40 minutes of videos of honeybees foraging in Scaevola and Lamb's-ear  
378 respectively. Tracks longer than 2 seconds in duration were used for the analysis. Results of the study  
379 are shown in Fig 9.

380

381 **Fig 8: HyDaT algorithm tracking honeybee movement.** (a) Scaevola and (b) Lamb's-ear. Red  
382 indicates recorded positions.

383

384 **Fig 9: Data analysis of honeybees foraging in Scaevola (N = 47) and Lamb's-ear (N = 90).** (a)  
385 Honeybee trajectories, (b) Location heat-maps, and (c) Visibility duration for Scaevola and Lamb's-ear.  
386 Honeybee (d) Speed distribution, (e) turn-angle distribution in Scaevola. In (b) the heat-map scale  
387 shows the aggregate of durations honeybees spent in a region. Bin size of the heat-map is the average  
388 area covered by a honeybee in pixels. In (c) recorded time is divided into durations the honeybee spends  
389 on the flower carpet (visible), under the carpet (occluded), and un-estimated, based on the output of the  
390 occlusion identification algorithm. The red dashed line shows the mean foraging time of honeybees  
391 within the field of view of the camera.

392 Our algorithm was able to extract honeybee movement data in both two-dimensional (Scaevola) and  
393 three-dimensional (Lamb's-ear) ground covers. However, since our approach with a single camera is  
394 primarily suited to two-dimensional plant structures, the occlusion detection algorithm was unable to  
395 estimate the honeybee position in 36.5% of instances in the Lamb's-ear, compared to 8.8% of the  
396 instances in Scaevola (Fig. 9c). We did not plot speed or turn-angle distributions for Lamb's-ear since  
397 a single camera setup cannot accurately measure these attributes for three-dimensional motion, a  
398 limitation we discuss below.

## 399 **Discussion**

400 To address concerns about insect pollination in agriculture and ecosystem management, it is valuable  
401 to track individual insects as they forage outdoors. In many cases, such a capacity to work in real world  
402 scenarios necessarily requires handling data that includes movement of the background against which  
403 the insects are being observed, and movement of insects through long occlusions. We tackle this  
404 complexity using a novel approach that detects an insect in a complex dynamic scene, identifies when  
405 it is occluded from view, identifies when it exits the view, and associates its sequence of recorded  
406 positions with a trajectory. Our algorithm achieved higher detection rates in much less processing time  
407 than existing techniques.

408 Although we illustrated our method's generalisability in two differently structured ground covers, there  
409 remain several limitations associated with our method suited for further research. Our algorithm tracks  
410 one insect in sequence and must be restarted to track subsequent insects within a video. Future work  
411 could address this by considering models of multi-element attention [59], however this is unnecessary  
412 for the applications for which the software is currently being applied and was out of our scope.  
413 Regarding species other than honeybees; although we trained and tested our algorithm with honeybees  
414 as this is our research focus in the current study, tracking other species is feasible after retraining the  
415 YOLOv2 model and adjusting parameters for the area an insect occupies in the video frame and the  
416  $MDT_{BS}$ , maximum detection threshold. Another potential subject for future study relates to identity  
417 swaps during occlusions, in which a single track is generated by two insects. This is likely to be a

418 problem only in instances where insect densities are high and two insects cross paths, perhaps whilst  
419 occluded. Fingerprinting individual unmarked animals to avoid this is a complex image-based tracking  
420 problem [17,20,47] that, if solved, would enable such errors to be avoided. Previous research in the area  
421 has been conducted in controlled environments. Its application to the dynamic backgrounds necessary  
422 for our purpose of tracking insects in the wild will be challenging. Lastly, the accuracy of our single-  
423 camera method is diminished in three-dimensional plant structures such as the Lamb's Ear. Extending  
424 our method for multi-cameras would be worthwhile future work if insect behaviour within such plants  
425 was required for a particular study, although such solutions would increase cost base and complexity  
426 for surveying.

427 Our research's hybrid detection method combines existing background subtraction and deep learning-  
428 based detection techniques, to track honeybee foraging in complex environments, even with a limited  
429 training dataset. As applications of deep learning-based tracking is still relatively new to ecology, there  
430 is a scarcity of annotated datasets of insects. We also observe that the applicability of the datasets that  
431 are available currently to specific ecological problems will be dependent on the importance of the  
432 species documented and the environmental context in which the recordings were made. Therefore, in  
433 most instances ecologists will have to build and annotate new datasets from scratch to use deep learning-  
434 based tracking programs. Our methods will ease this burden on ecologists by enabling them to track  
435 insects with a relatively small training dataset.

436 Our algorithm is designed with a modular architecture, which enables any improvement to individual  
437 detection algorithms to be reflected in overall tracking performance. The current version of HyDaT was  
438 implemented with a KNN background subtractor and a YOLOv2 detection model. However, use of  
439 different combinations of detection models for background subtraction and for deep learning models  
440 may further improve detection rates and tracking speeds. This allows ecologists to quickly adopt  
441 advancements in deep learning or computer vision research for improved tracking.

442 Mapping interactions between insect pollinators and their foraging environments improves our  
443 understanding of their behaviour. Previous research has studied the movement patterns of insect  
444 pollinators such as honeybees [44,60–63] and bumblebees [42–44,62,64,65] to document their flight

445 directionality, flight distance, time on a flower, nature of movement etc. Most of this research relied on  
446 manual observations conducted inside laboratories or on artificial rigs. However, environmental factors  
447 such as wind, temperature and other conditions may play a role in driving insect behaviour outdoors  
448 [23,24]. Our tracking method facilitates researchers to study insect pollinators in their natural habitat  
449 and enables collection of accurate, reliable data. This capacity may be expanded across a network of  
450 monitoring sites to assist in the automatic measurement of behavioural traits such as flower constancy  
451 of bees in complex environments [66]. In addition, our algorithm can record when insects crawl under  
452 flowers, a frequent occurrence that previous algorithms have not considered.

453 Commercial crops such as strawberry, carrot and cauliflower flower in a somewhat flat carpet of  
454 inflorescences when compared against other insect-pollinated crops such as raspberry and tomato. Our  
455 algorithm is particularly suited to record and analyse the trajectories of insect pollinators on such two-  
456 dimensional structures and can therefore be used to monitor agricultural insect pollination in these  
457 circumstances. This enables growers and beekeepers to estimate pollination levels and take proactive  
458 steps that maximise pollination for better crop yield [67]. We hope that ultimately these findings will  
459 be helpful in pollinator conservation and designing pollinator-friendly agricultural setups[67] for  
460 increased food production.

461 While our main contribution is tracking insect pollinators in complex environments, our results are an  
462 important step towards real-time tracking and implementing deep learning-based object detection  
463 models in low powered devices such as the Raspberry Pi ([www.raspberrypi.org](http://www.raspberrypi.org)) which are suited to  
464 ongoing field monitoring of insect populations and behaviours. Through experiments, we have shown  
465 that combining computationally inexpensive detection methods like background subtraction with deep  
466 learning can increase the rate of detection and reduce computational costs. Hence, our hybrid approach  
467 may be suited to applications where low-powered devices should be used.

## 468 **Acknowledgements**

469 Authors would like to thank Prof. Dinh Phung for the valuable suggestions and helpful comments given  
470 in designing the methods and experiments and Dr. Mani Shrestha for assisting in species identification.

## 471 **Author Contributions**

472 M.N.R., A.G.D. and A.D. designed the study and planned the experiments. M.N.R. and A.D. designed  
473 the software. M.N.R. developed and further refined the software, collected and analysed the data and  
474 drafted the manuscript. All authors contributed critically to the drafts and gave final approval for  
475 publication.



## 476 **References**

- 477 1. Crall JD, Gravish N, Mountcastle AM, Combes SA. BEEtag: A low-cost, image-based  
478 tracking system for the study of animal behavior and locomotion. Gilestro GF, editor. PLoS  
479 One. 2015;10: e0136487. doi:10.1371/journal.pone.0136487
- 480 2. Dankert H, Wang L, Hoopfer ED, Anderson DJ, Perona P. Automated monitoring and analysis  
481 of social behavior in *Drosophila*. Nat Methods. 2009;6: 297–303. doi:10.1038/nmeth.1310
- 482 3. Simons DJ, Chabris CF. Gorillas in our midst: Sustained inattention blindness for dynamic  
483 events. Perception. 1999;28: 1059–1074. doi:10.1068/p281059
- 484 4. Rader R, Bartomeus I, Garibaldi LA, Garratt MPD, Howlett BG, Winfree R, et al. Non-bee  
485 insects are important contributors to global crop pollination. Proc Natl Acad Sci U S A.  
486 2016;113: 146–151. doi:10.1073/pnas.1517092112
- 487 5. Dell AI, Bender JA, Branson K, Couzin ID, de Polavieja GG, Noldus LPJJ, et al. Automated  
488 image-based tracking and its application in ecology. Trends in Ecology and Evolution. 2014.  
489 pp. 417–428. doi:10.1016/j.tree.2014.05.004
- 490 6. Weinstein BG. A computer vision for animal ecology. Journal of Animal Ecology. Blackwell  
491 Publishing Ltd; 2018. pp. 533–545. doi:10.1111/1365-2656.12780
- 492 7. FAO. Why bees matter; the importance of bees and other pollinators for food and agriculture.  
493 2018.
- 494 8. Aizen MA, Garibaldi LA, Cunningham SA, Klein AM. How much does agriculture depend on  
495 pollinators? Lessons from long-term trends in crop production. Ann Bot. 2009;103: 1579–  
496 1588. doi:10.1093/aob/mcp076
- 497 9. Osborne JL, Williams IH, Carreck NL, Poppy GM, Riley JR, Smith AD, et al. Harmonic radar:  
498 A new technique for investigating bumblebee and honey bee foraging flight. Acta  
499 Horticulturae. 1997. pp. 159–163. doi:10.17660/actahortic.1997.437.15

- 500 10. Riley JR, Smith AD, Reynolds DR, Edwards AS, Osborne JL, Williams IH, et al. Tracking  
501 bees with harmonic radar. *Nature*. 1996;379: 29.
- 502 11. Nunes-Silva P, Hrnčir M, Guimarães JTF, Arruda H, Costa L, Pessin G, et al. Applications of  
503 RFID technology on the study of bees. *Insectes Soc*. 2018; 1–10. doi:10.1007/s00040-018-  
504 0660-5
- 505 12. Roberts CM. Radio frequency identification (RFID). *Comput Secur*. 2006;25: 18–26.  
506 doi:10.1016/j.cose.2005.12.003
- 507 13. Boenisch F, Rosemann B, Wild B, Dormagen D, Wario F, Landgraf T. Tracking all members  
508 of a honey bee colony over their lifetime using learned models of correspondence. *Front Robot*  
509 *AI*. 2018;5: 35. doi:10.3389/frobt.2018.00035
- 510 14. Makinson JC, Woodgate JL, Reynolds A, Capaldi EA, Perry CJ, Chittka L. Harmonic radar  
511 tracking reveals random dispersal pattern of bumblebee (*Bombus terrestris*) queens after  
512 hibernation. *Sci Rep*. 2019;9: 4651. doi:10.1038/s41598-019-40355-6
- 513 15. Dennis RL, Newberry RC, Cheng HW, Estevez I. Appearance matters: Artificial marking  
514 alters aggression and stress. *Poult Sci*. 2008;87: 1939–1946. doi:10.3382/ps.2007-00311
- 515 16. Batsleer F, Bonte D, Dekeukeleire D, Goossens S, Poelmans W, Van der Cruyssen E, et al.  
516 The neglected impact of tracking devices on terrestrial arthropods. *Methods Ecol Evol*.  
517 2020;11: 350–361. doi:10.1111/2041-210x.13356
- 518 17. Pérez-Escudero A, Vicente-Page J, Hinz RC, Arganda S, de Polavieja GG. idTracker: tracking  
519 individuals in a group by automatic identification of unmarked animals. *Nat Methods*.  
520 2014;11: 743–748. doi:10.1038/nmeth.2994
- 521 18. Branson K, Robie AA, Bender J, Perona P, Dickinson MH. High-throughput ethomics in large  
522 groups of *Drosophila*. *Nat Methods*. 2009;6: 451–457. doi:10.1038/nmeth.1328
- 523 19. Mönck HJ, Jörg A, von Falkenhausen T, Tanke J, Wild B, Dormagen D, et al. BioTracker: An  
524 Open-Source Computer Vision Framework for Visual Animal Tracking. *arXiv Prepr*

- 525 arXiv180307985. 2018 [cited 22 May 2019]. Available: <http://arxiv.org/abs/1803.07985>
- 526 20. Sridhar VH, Roche DG, Gingins S. Tracktor: image-based automated tracking of animal  
527 movement and behaviour. Börger L, editor. *Methods Ecol Evol.* 2018; 1–16.  
528 doi:10.1101/412262
- 529 21. Rodriguez A, Zhang H, Klaminder J, Brodin T, Andersson PL, Andersson M. ToxTrac : A fast  
530 and robust software for tracking organisms. Freckleton R, editor. *Methods Ecol Evol.* 2018;9:  
531 460–464. doi:10.1111/2041-210X.12874
- 532 22. Haalck L, Mangan M, Webb B, Risse B. Towards image-based animal tracking in natural  
533 environments using a freely moving camera. *Journal of Neuroscience Methods.* Elsevier B.V.;  
534 2020. p. 108455. doi:10.1016/j.jneumeth.2019.108455
- 535 23. Berdahl A, Torney CJ, Ioannou CC, Faria JJ, Couzin ID. Emergent sensing of complex  
536 environments by mobile animal groups. *Science (80- ).* 2013;339: 574–576.  
537 doi:10.1126/science.1225883
- 538 24. Pawar S, Dell AI, Savage VM. Dimensionality of consumer search space drives trophic  
539 interaction strengths. *Nature.* 2012;486: 485–489. doi:10.1038/nature11131
- 540 25. Rodríguez IF, Branson K, Acuña E, Agosto-Rivera JL, Giray T, Mégret R. Honeybee  
541 Detection and Pose Estimation using Convolutional Neural Networks. *Congrès Reconnaiss des*  
542 *Formes, Image, Apprentiss Percept.* 2018; 1–3.
- 543 26. Yamanaka O, Takeuchi R. UMATracker: an intuitive image-based tracking platform. *J Exp*  
544 *Biol.* 2018;221: jeb182469. doi:10.1242/jeb.182469
- 545 27. Pennekamp F, Schtickzelle N, Petchey OL. BEMOVI, software for extracting behavior and  
546 morphology from videos, illustrated with analyses of microbes. *Ecol Evol.* 2015;5: 2584–  
547 2595. doi:10.1002/ece3.1529
- 548 28. Risse B, Berh D, Otto N, Klämbt C, Jiang X. FIMTrack: An open source tracking and  
549 locomotion analysis software for small animals. Poisot T, editor. *PLOS Comput Biol.* 2017;13:

- 550 e1005530. doi:10.1371/journal.pcbi.1005530
- 551 29. Ngo TN, Wu KC, Yang EC, Lin T Te. A real-time imaging system for multiple honey bee  
552 tracking and activity monitoring. *Comput Electron Agric.* 2019;163: 104841.  
553 doi:10.1016/j.compag.2019.05.050
- 554 30. Babic Z, Pilipovic R, Risojevic V, Mirjanic G. Pollen Bearing Honey Bee Detection in Hive  
555 Entrance Video Recorded by Remote Embedded System for Pollination Monitoring. *ISPRS  
556 Ann Photogramm Remote Sens Spat Inf Sci.* 2016;3: 51–57. doi:10.5194/isprs-annals-III-7-51-  
557 2016
- 558 31. Kimura T, Ohashi M, Crailsheim K, Schmickl T, Odaka R, Ikeno H. Tracking of multiple  
559 honey bees on a flat surface. *International Conference on Emerging Trends in Engineering and  
560 Technology, ICETET. IEEE; 2012. pp. 36–39. doi:10.1109/ICETET.2012.25*
- 561 32. Kimura T, Ohashi M, Crailsheim K, Schmickl T, Okada R, Radspieler G, et al. Development  
562 of a New Method to Track Multiple Honey Bees with Complex Behaviors on a Flat  
563 Laboratory Arena. Wicker-Thomas C, editor. *PLoS One.* 2014;9: e84656.  
564 doi:10.1371/journal.pone.0084656
- 565 33. Kimura T, Ohashi M, Okada R, Crailsheim K, Schmickl T, Radspieler G, et al. Automatic  
566 tracking method for multiple honeybees using backward-play movies. 2017 6th International  
567 Conference on Informatics, Electronics and Vision and 2017 7th International Symposium in  
568 Computational Medical and Health Technology, ICIEV-ISCMHT 2017. IEEE; 2018. pp. 1–4.  
569 doi:10.1109/ICIEV.2017.8338596
- 570 34. Jun Tu G, Kragh Hansen M, Kryger P, Ahrendt P. Automatic behaviour analysis system for  
571 honeybees using computer vision. *Comput Electron Agric.* 2016;122: 10–18.  
572 doi:10.1016/j.compag.2016.01.011
- 573 35. Magnier B, Ekszterowicz G, Laurent J, Rival M, Pfister F. Bee hive traffic monitoring by  
574 tracking bee flight paths. 2018. doi:10.5220/0006628205630571

- 575 36. Luo S, Li X, Wang D, Li J, Sun C. A Vision-Based Bee Counting Algorithm for Electronic  
576 Monitoring of Langstroth Beehives. *J Food Eng.* 2015;69: 1–17.  
577 doi:10.1016/j.compag.2016.07.023
- 578 37. Campbell J, Mummert L, Sukthankar R. Video monitoring of honey bee colonies at the hive  
579 entrance. *Vis Obs Anal Anim insect Behav ICPR.* 2008;8: 1–4.
- 580 38. Manoukis NC, Collier TC. Computer Vision to Enhance Behavioral Research on Insects. *Ann*  
581 *Entomol Soc Am.* 2019;112: 227–235. doi:10.1093/aesa/say062
- 582 39. Bowley C, Andes A, Ellis-Felege S, Desell T. Detecting wildlife in uncontrolled outdoor video  
583 using convolutional neural networks. *Proceedings of the 2016 IEEE 12th International*  
584 *Conference on e-Science, e-Science 2016.* 2017. pp. 251–259.  
585 doi:10.1109/eScience.2016.7870906
- 586 40. Sledevic T. The application of convolutional neural network for pollen bearing bee  
587 classification. *2018 IEEE 6th Workshop on Advances in Information, Electronic and Electrical*  
588 *Engineering, AIEEE 2018 - Proceedings.* IEEE; 2018. pp. 1–4.  
589 doi:10.1109/AIEEE.2018.8592464
- 590 41. Kelcey M. Counting bees on a Raspberry Pi with Convolutional Network. brain of mat kelcey.  
591 2018. Available: [http://matpalm.com/blog/counting\\_bees/](http://matpalm.com/blog/counting_bees/)
- 592 42. Cresswell JE. A comparison of bumblebees' movements in uniform and aggregated  
593 distributions of their forage plant. *Ecol Entomol.* 2000;25: 19–25. doi:10.1046/j.1365-  
594 2311.2000.00230.x
- 595 43. Geslin B, Baude M, Mallard F, Dajoz I. Effect of local spatial plant distribution and  
596 conspecific density on bumble bee foraging behaviour. *Ecol Entomol.* 2014;39: 334–342.  
597 doi:10.1111/een.12106
- 598 44. Kipp LR, Knight W, Kipp ER. Influence of resource topography on pollinator flight  
599 directionality of two species of bees. *J Insect Behav.* 1989;2: 453–472.

- 600           doi:10.1007/BF01053348
- 601   45.   Fasciano T, Dornhausy A, Shin MC. Multiple insect tracking with occlusion sub-tunnels.  
602           Proceedings - 2015 IEEE Winter Conference on Applications of Computer Vision, WACV  
603           2015. IEEE; 2015. pp. 634–641. doi:10.1109/WACV.2015.90
- 604   46.   Fasciano T, Dornhaus A, Shin MC. Ant tracking with occlusion tunnels. 2014 IEEE Winter  
605           Conference on Applications of Computer Vision, WACV 2014. 2014. pp. 947–952.  
606           doi:10.1109/WACV.2014.6836002
- 607   47.   Rodriguez A, Zhang H, Klaminder J, Brodin T, Andersson M. ToxId: An efficient algorithm to  
608           solve occlusions when tracking multiple animals. *Sci Rep.* 2017;7: 14774.  
609           doi:10.1038/s41598-017-15104-2
- 610   48.   Zivkovic Z, Van Der Heijden F. Efficient adaptive density estimation per image pixel for the  
611           task of background subtraction. *Pattern Recognit Lett.* 2006;27: 773–780.  
612           doi:10.1016/j.patrec.2005.11.005
- 613   49.   Redmon J, Farhadi A. YOLO9000: Better, faster, stronger. *Proc - 30th IEEE Conf Comput Vis*  
614           *Pattern Recognition, CVPR 2017.* 2017;2017-Janua: 6517–6525. doi:10.1109/CVPR.2017.690
- 615   50.   Bradski G. The OpenCV Library. *Dr Dobbs J Softw Tools.* 2000;25: 120–125.  
616           doi:10.1111/0023-8333.50.s1.10
- 617   51.   Trnovszký T, Sýkora P, Hudec R. Comparison of Background Subtraction Methods on Near  
618           Infra-Red Spectrum Video Sequences. *Procedia Eng.* 2017;192: 887–892.  
619           doi:10.1016/j.proeng.2017.06.153
- 620   52.   Yang C, Collins J. A model for honey bee tracking on 2D video. *International Conference*  
621           *Image and Vision Computing New Zealand.* IEEE; 2016. pp. 1–6.  
622           doi:10.1109/IVCNZ.2015.7761542
- 623   53.   Kuhn HW. The Hungarian method for the assignment problem. *50 Years Integer Program*  
624           *1958-2008 From Early Years to State-of-the-Art.* 2010;2: 29–47. doi:10.1007/978-3-540-

- 625           68279-0\_2
- 626   54.   Park C. Soccer-Ball-Detection-YOLOv2. 2018. Available: [https://github.com/deep-](https://github.com/deep-diver/Soccer-Ball-Detection-YOLOv2)
- 627           diver/Soccer-Ball-Detection-YOLOv2
- 628   55.   Trieu. Darkflow. 2016. Available: <https://github.com/thtrieu/darkflow>
- 629   56.   Abadi M, Barham P, Chen J, Chen Z, Davis A, Dean J, et al. TensorFlow: A system for large-
- 630           scale machine learning. Proceedings of the 12th USENIX Symposium on Operating Systems
- 631           Design and Implementation, OSDI 2016. 2016. pp. 265–283.
- 632   57.   EOF Productions. FrameShots. 2019. Available: <https://www.frame-shots.com/>
- 633   58.   Tzutalin. LabelImg. 2019. Available: <https://github.com/tzutalin/labelImg>
- 634   59.   Viswanathan L, Mingolla E. Dynamics of Attention in Depth: Evidence from Multi-Element
- 635           Tracking. *Perception*. 2002;31: 1415–1437. doi:10.1068/p3432
- 636   60.   Ginsberg H. Honey bee orientation behaviour and the influence of flower distribution on
- 637           foraging movements. *Ecol Entomol*. 1986;11: 173–179. doi:10.1111/j.1365-
- 638           2311.1986.tb00292.x
- 639   61.   Waddington KD. Flight patterns of foraging bees relative to density of artificial flowers and
- 640           distribution of nectar. *Oecologia*. 1980;44: 199–204. doi:10.1007/BF00572680
- 641   62.   Willmer PG, Bataw AAM, Hughes JP. The superiority of bumblebees to honeybees as
- 642           pollinators: insect visits to raspberry flowers. *Ecol Entomol*. 1994;19: 271–284.
- 643           doi:10.1111/j.1365-2311.1994.tb00419.x
- 644   63.   Garcia JE, Shrestha M, Dyer AG. Flower signal variability overwhelms receptor-noise and
- 645           requires plastic color learning in bees. *Behav Ecol*. 2018;29: 1286–1297.
- 646           doi:10.1093/beheco/ary127
- 647   64.   Nakamura S, Kudo G. Foraging responses of bumble bees to rewardless floral patches:
- 648           Importance of within-plant variance in nectar presentation. *AoB Plants*. 2016;8: plw037.

649 doi:10.1093/aobpla/plw037

650 65. Pyke GH. Optimal foraging: Movement patterns of bumblebees between inflorescences. *Theor*  
651 *Popul Biol.* 1978;13: 72–98. doi:10.1016/0040-5809(78)90036-9

652 66. Chittka L, Gumbert A, Kunze J. Foraging dynamics of bumble bees: Correlates of movements  
653 within and between plant species. *Behav Ecol.* 1997;8: 239–249. doi:10.1093/beheco/8.3.239

654 67. Dorin A, Dyer A, Taylor T, Bukovac Z. Simulation-governed design and tuning of  
655 greenhouses for successful bee pollination. *The 2018 Conference on Artificial Life.*  
656 Cambridge, MA: MIT Press; 2018. pp. 171–178. doi:10.1162/isal\_a\_00038

657

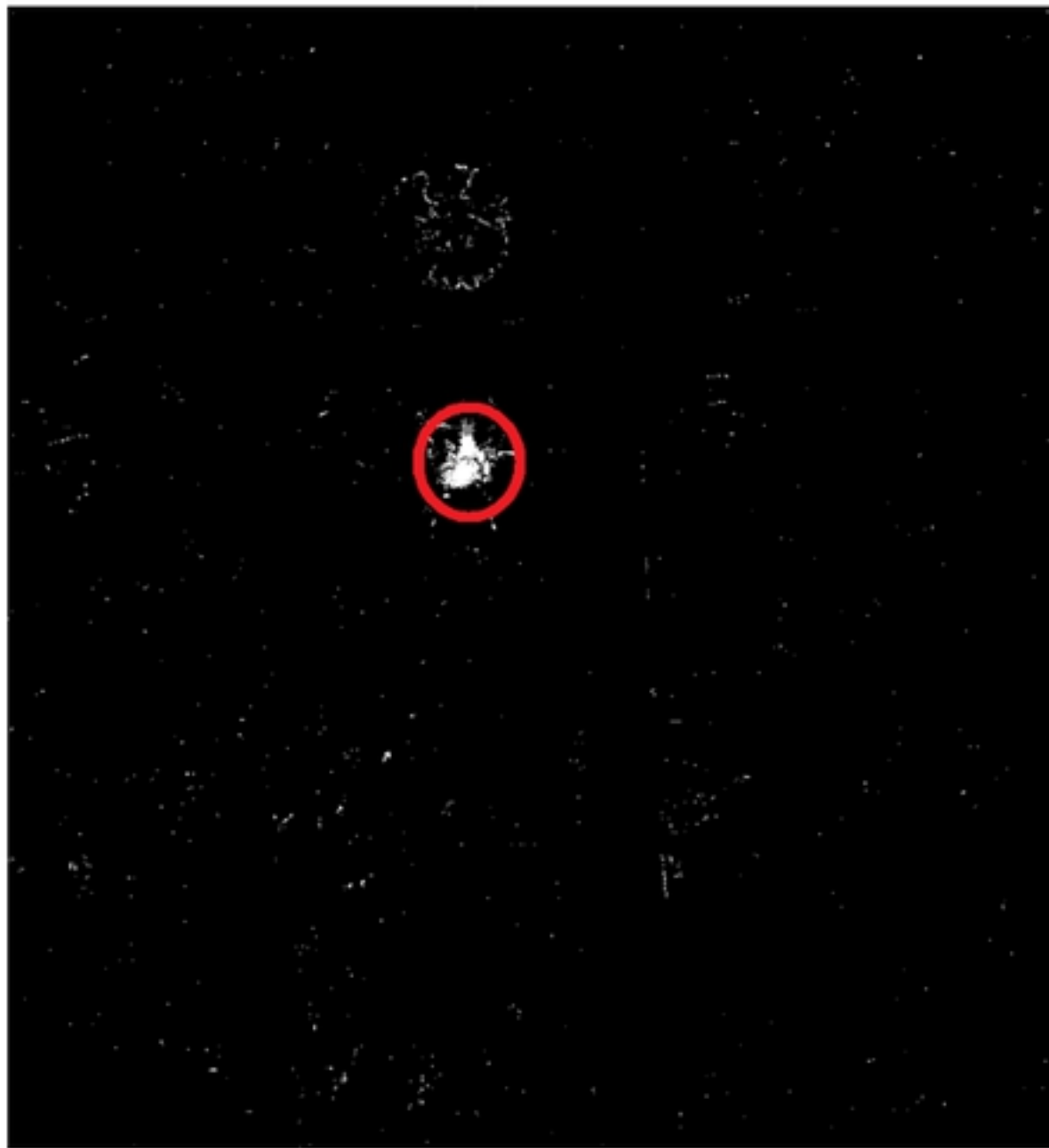
## 658 **Supporting Information**

659 **S1 Data. Honeybee video tracking data.** Annotated images for training YOLOv2, video files,  
660 experiment results, and tracks of insects recorded in example data analysis can be accessed through  
661 <https://doi.org/10.26180/5f4c8d5815940>

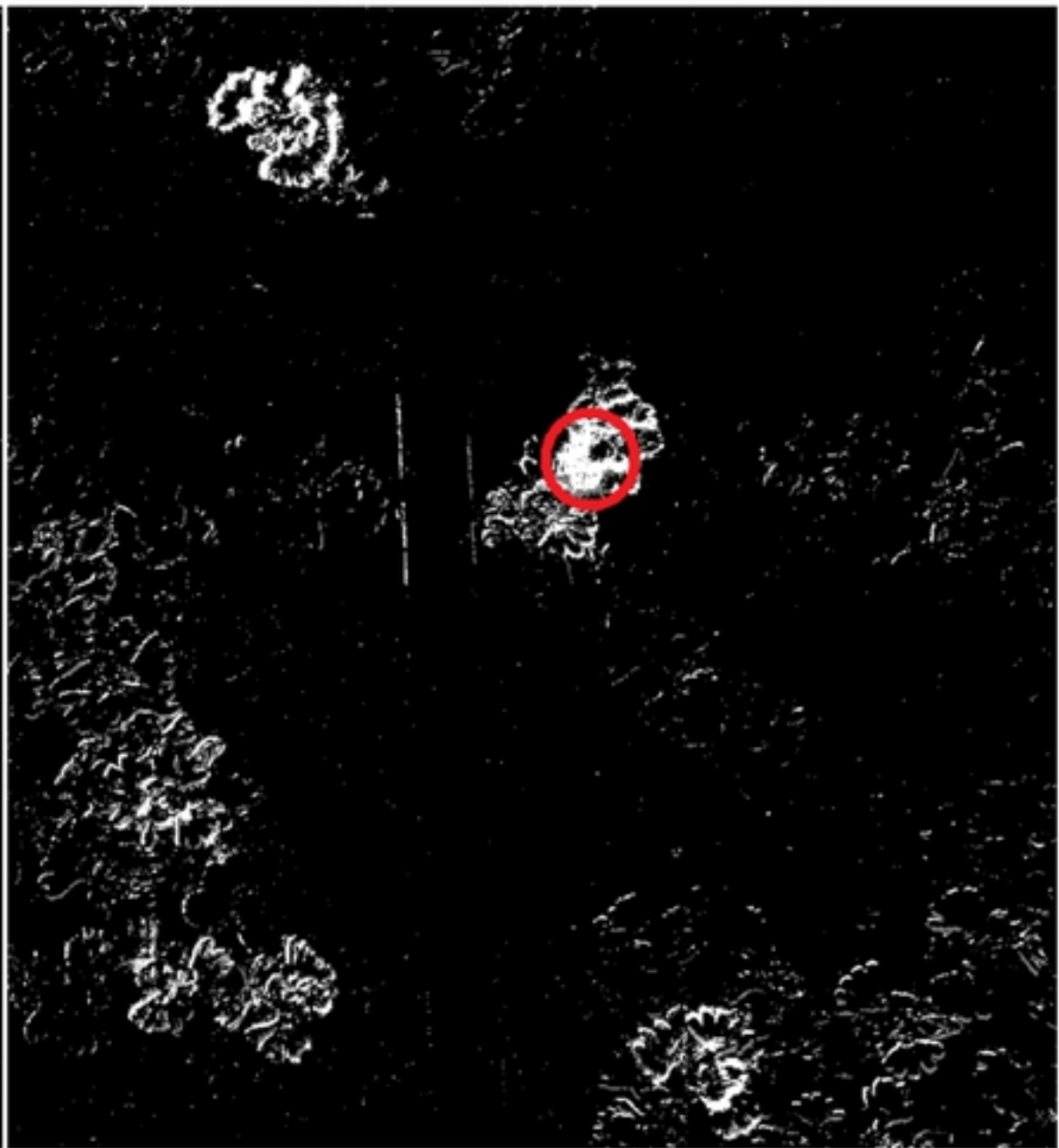
662 **S2 Table: Parameter settings used in experiments.**

663 **S3 Text: Data Collection details for experimental data analysis.**





(a)



(b)

Fig1

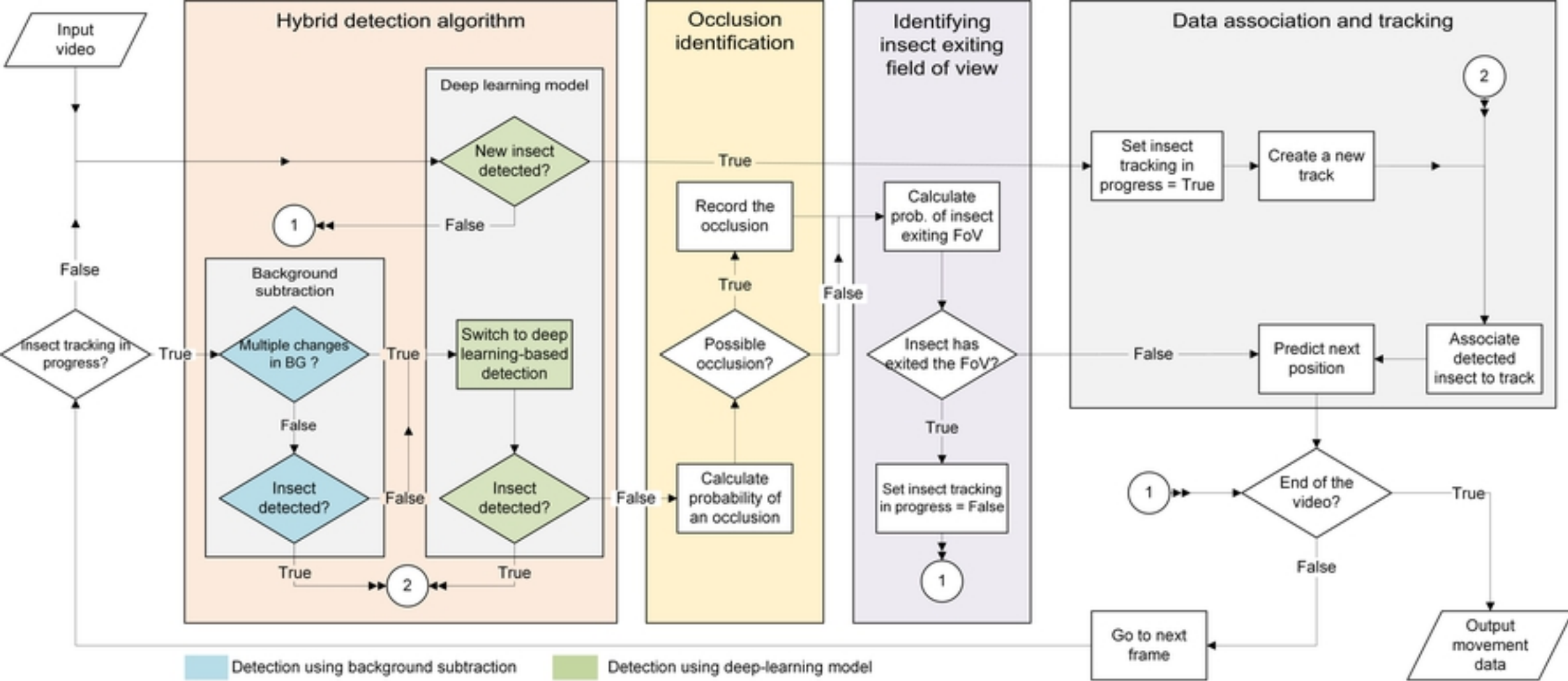
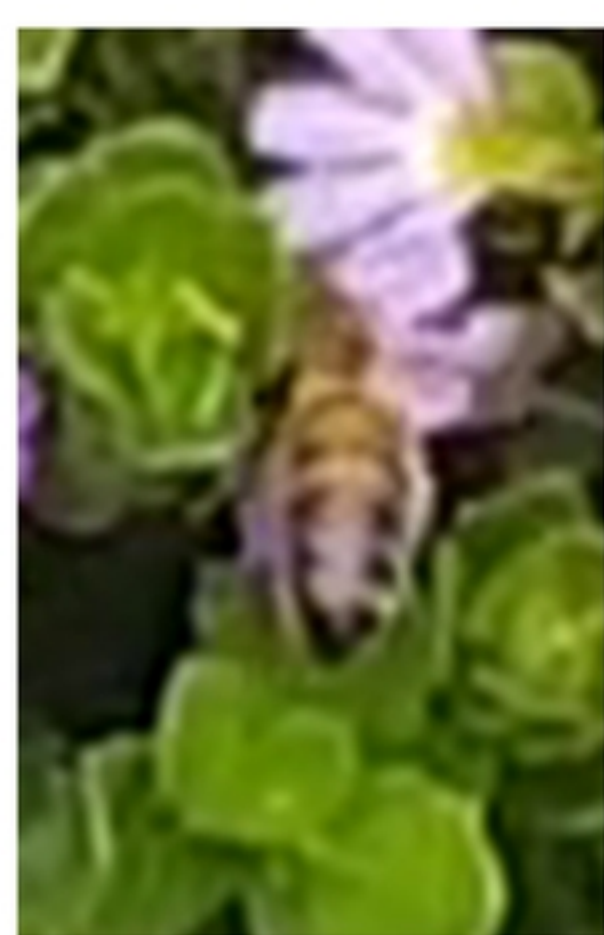


Fig2



(a)



(b)



(c)



(d)

Fig3

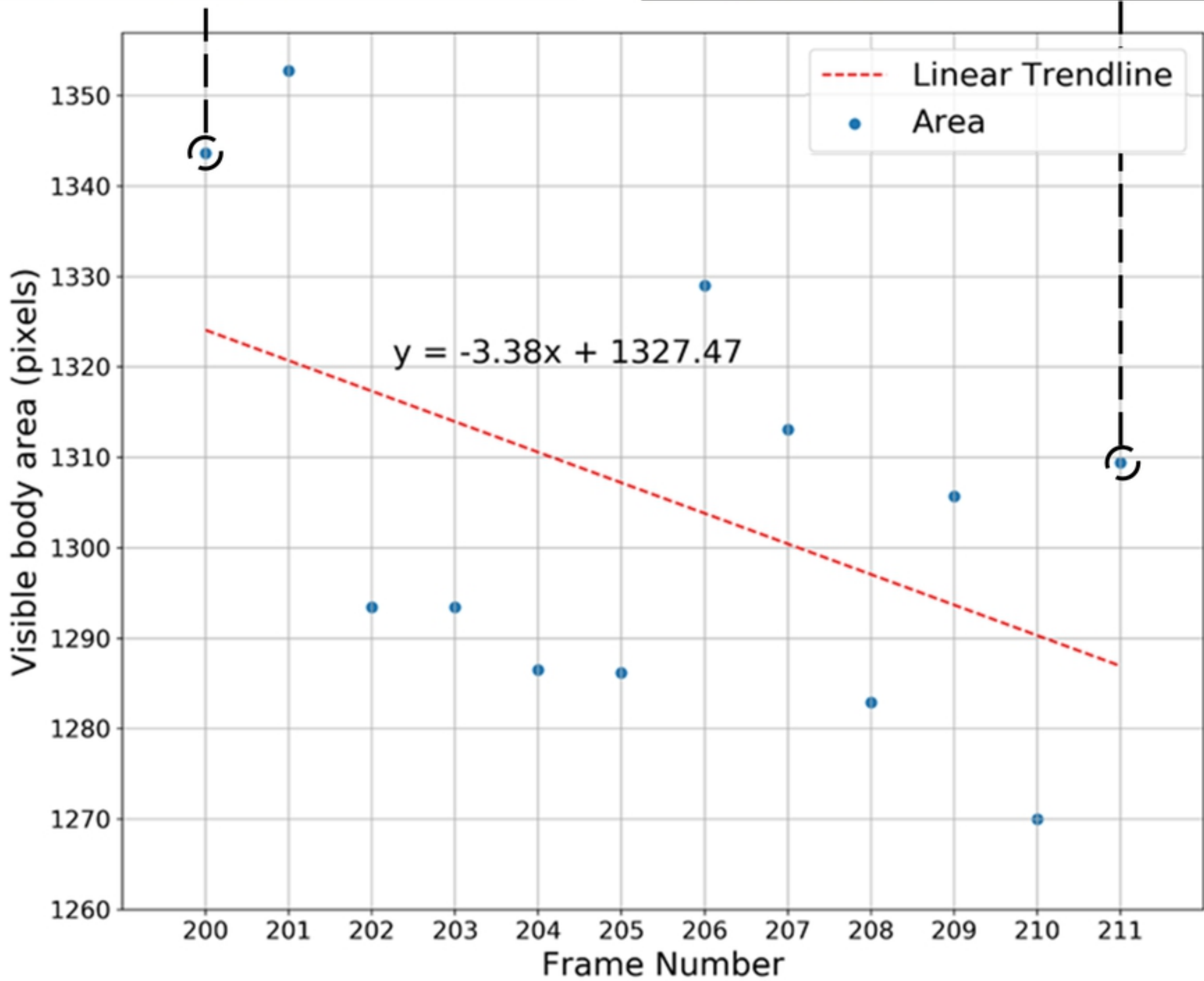
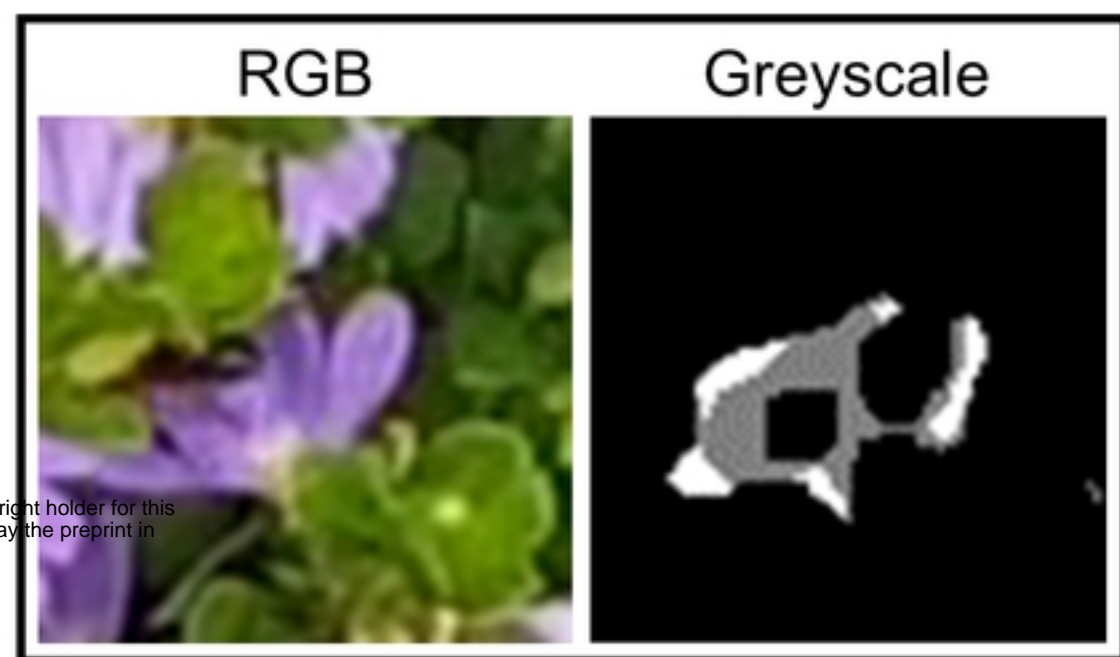


Fig4

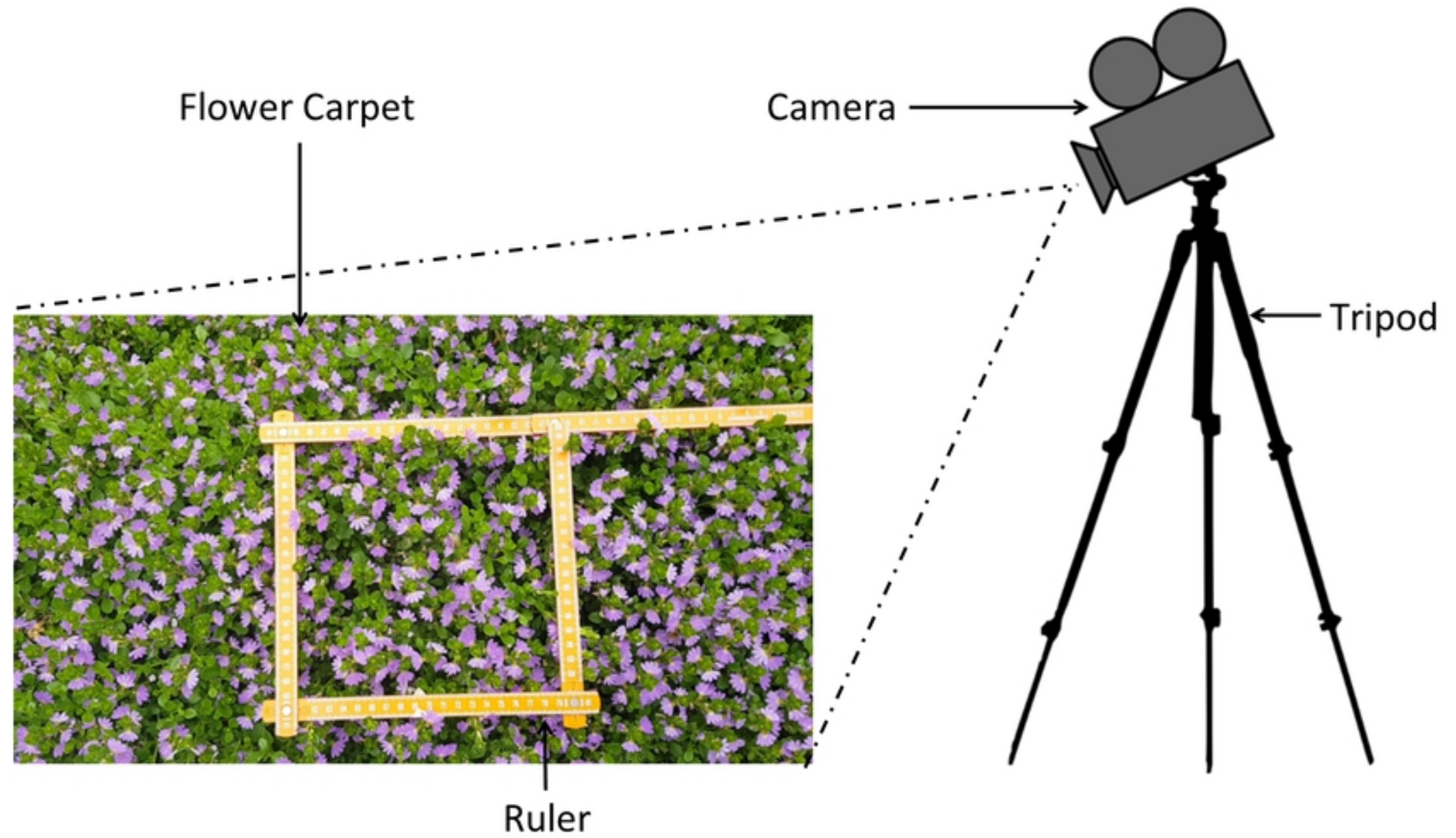


Fig5

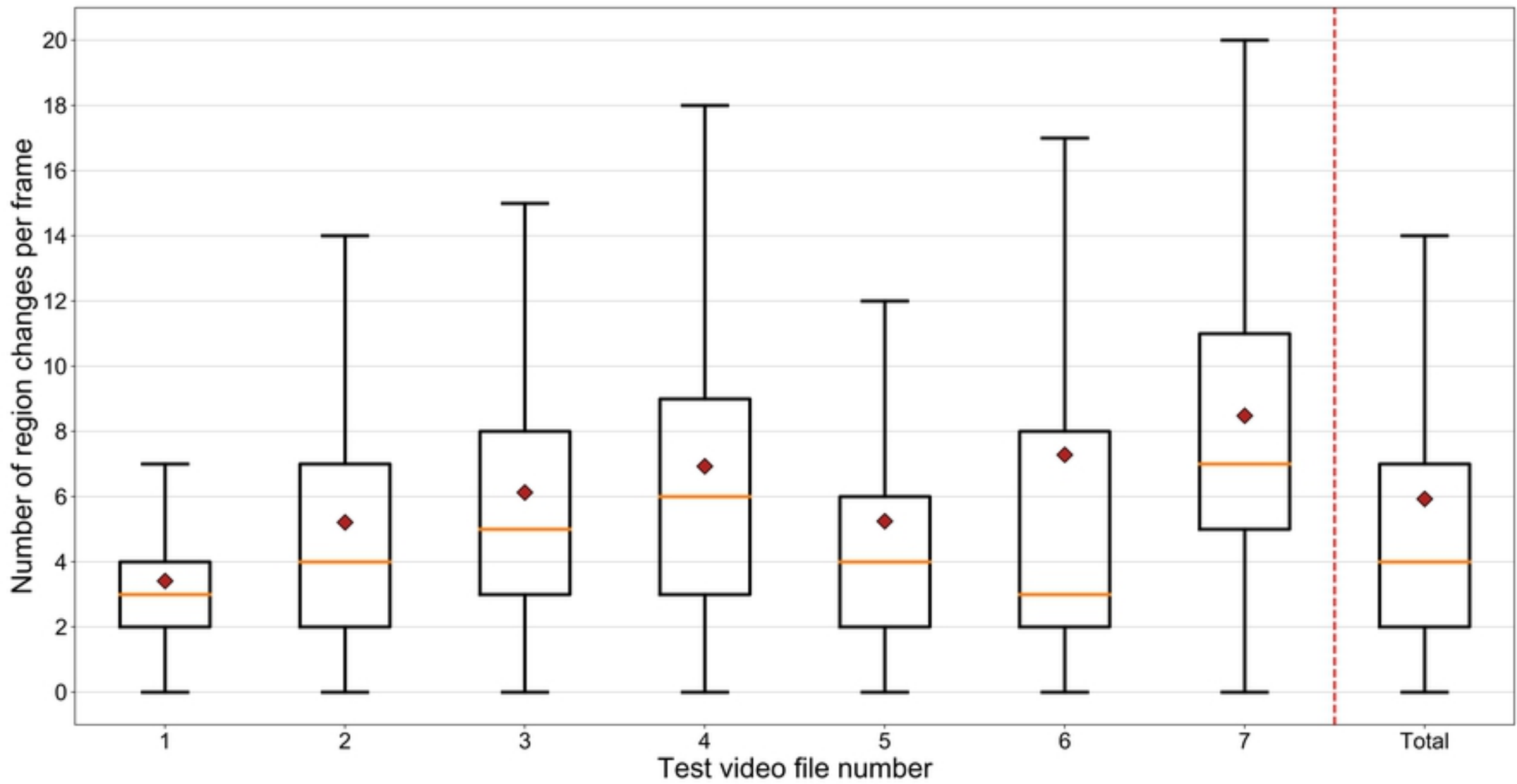


Fig6

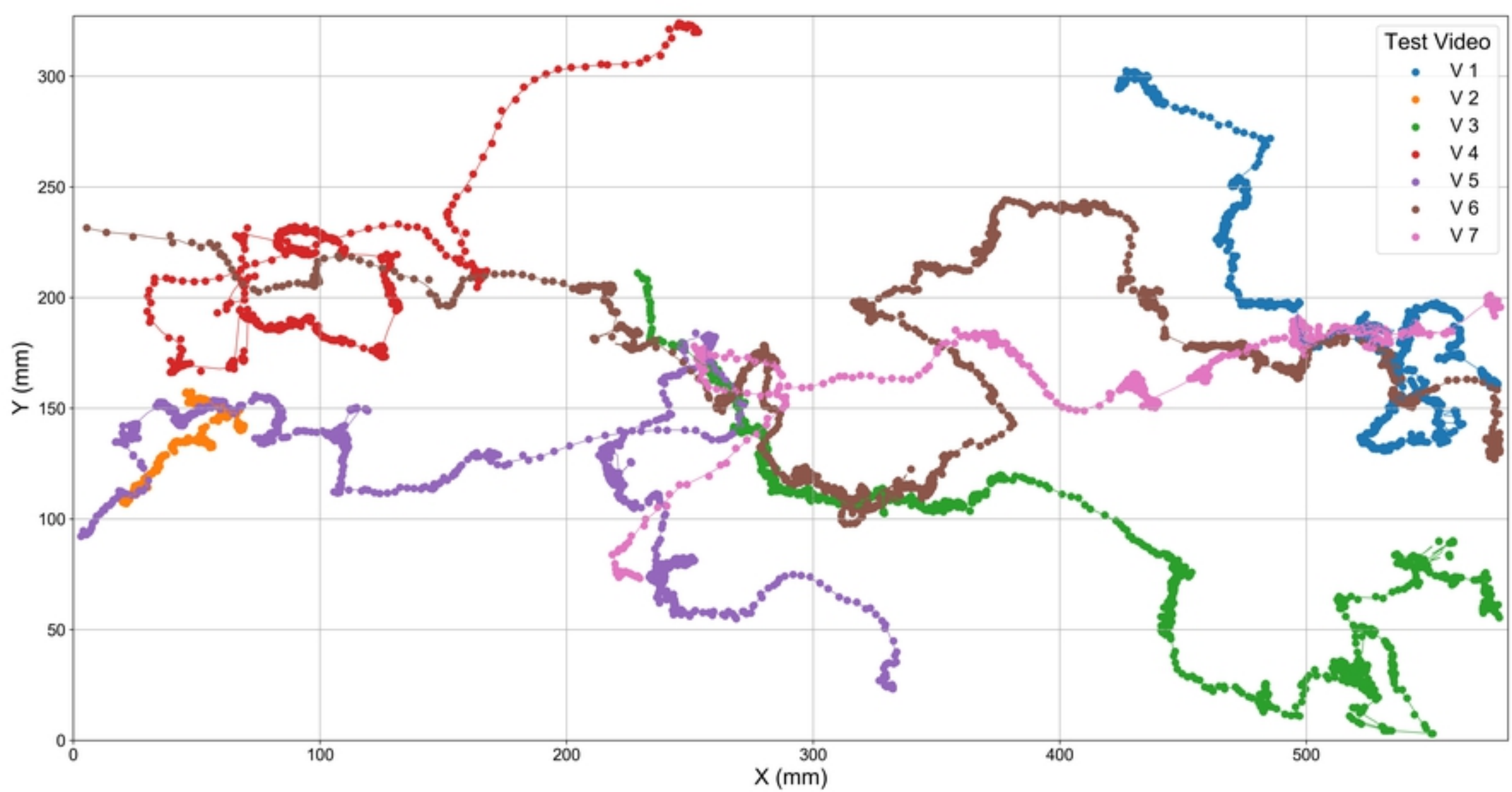


Fig7



(a)

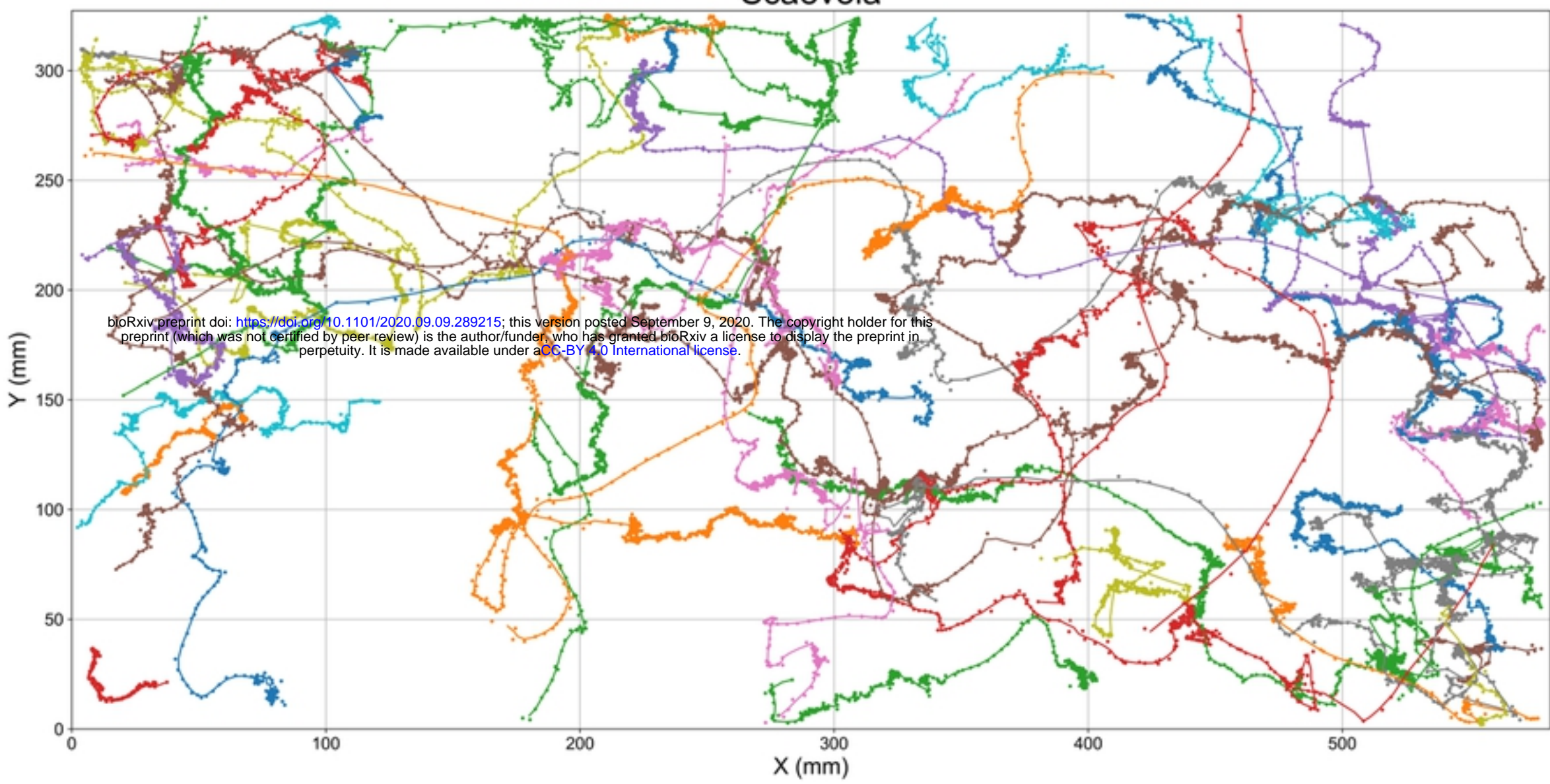


(b)

Fig8



# Scaevola



# Lamb's-ear

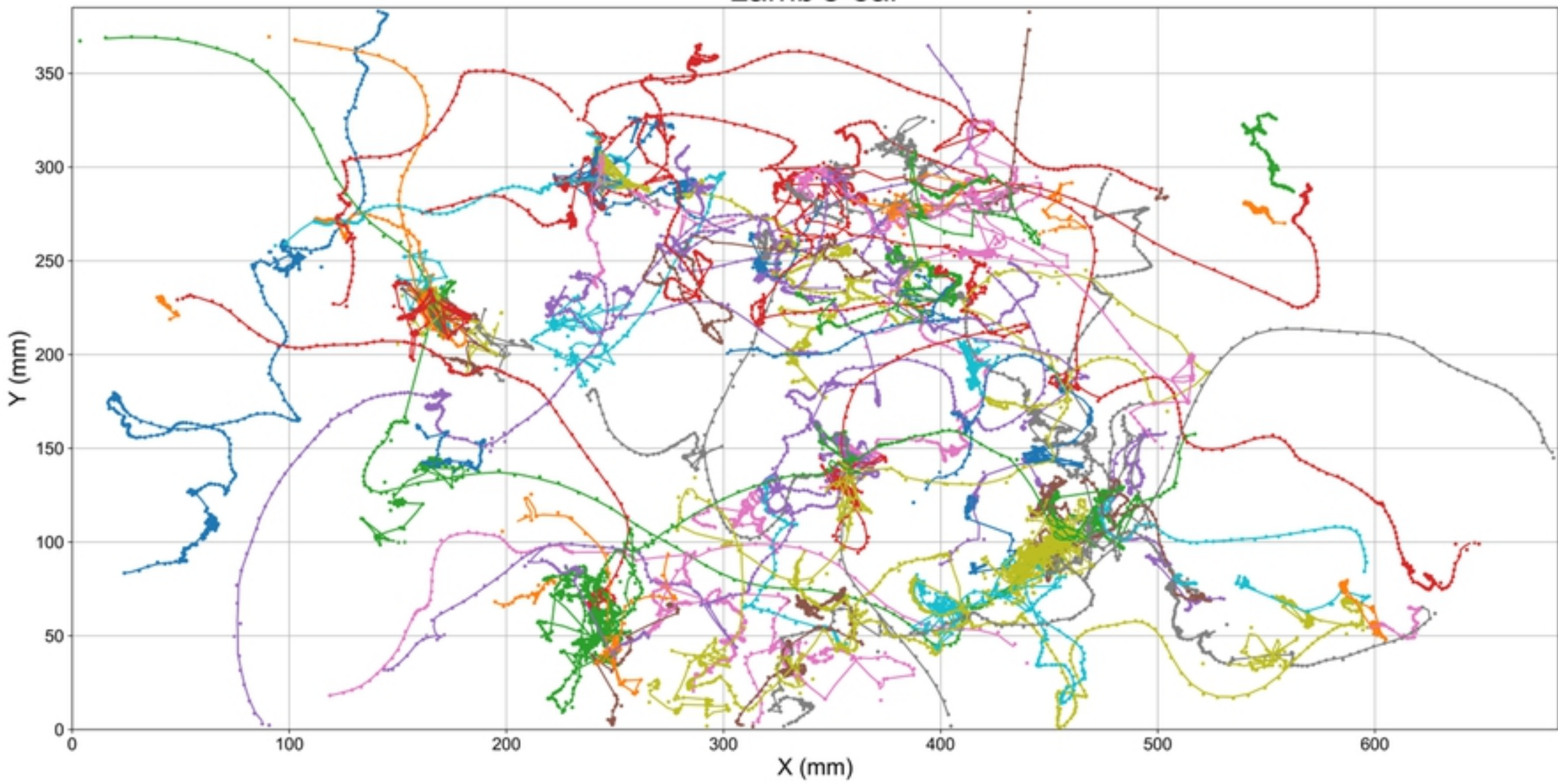
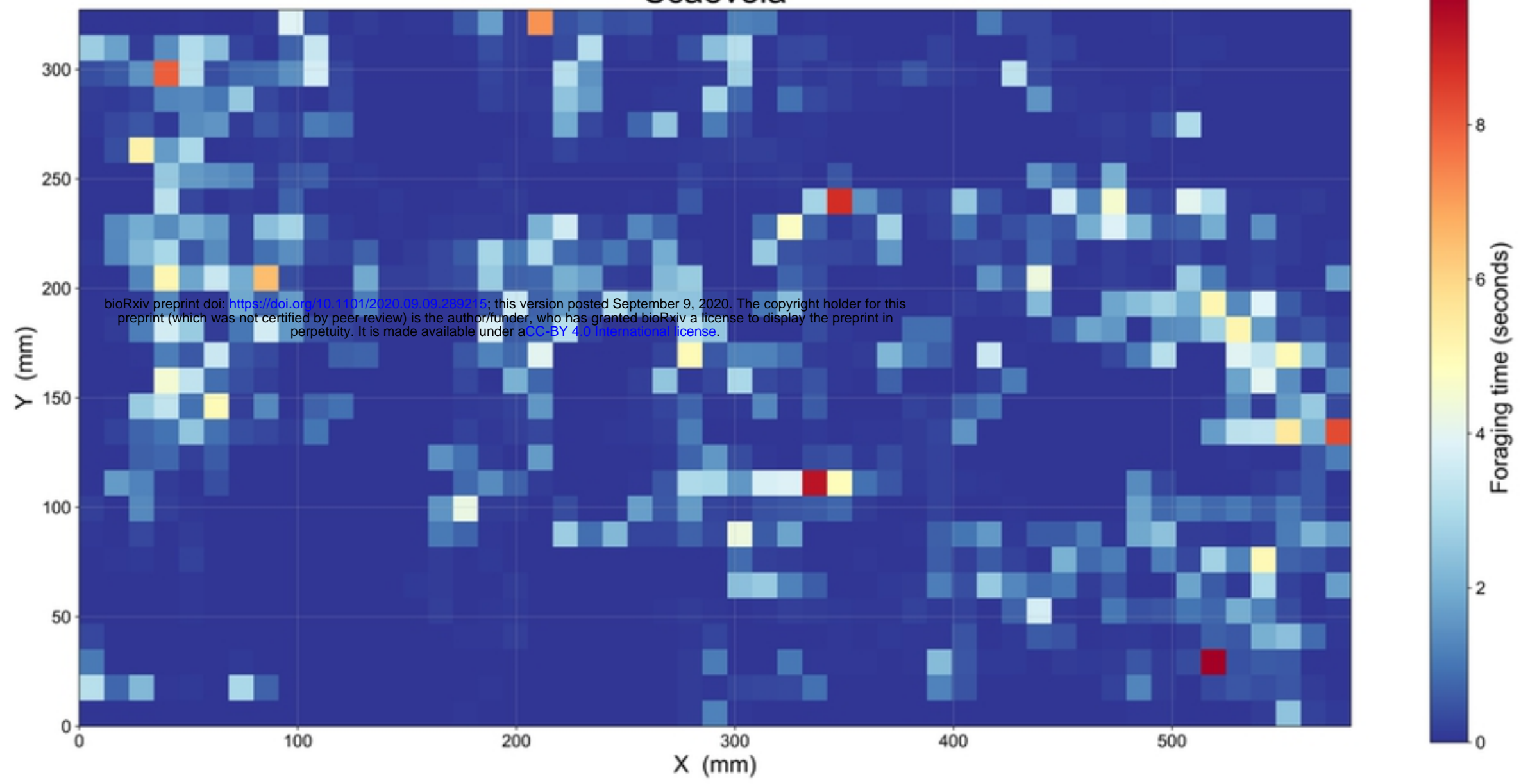


Fig9a

# Scaevola



# Lamb's-ear

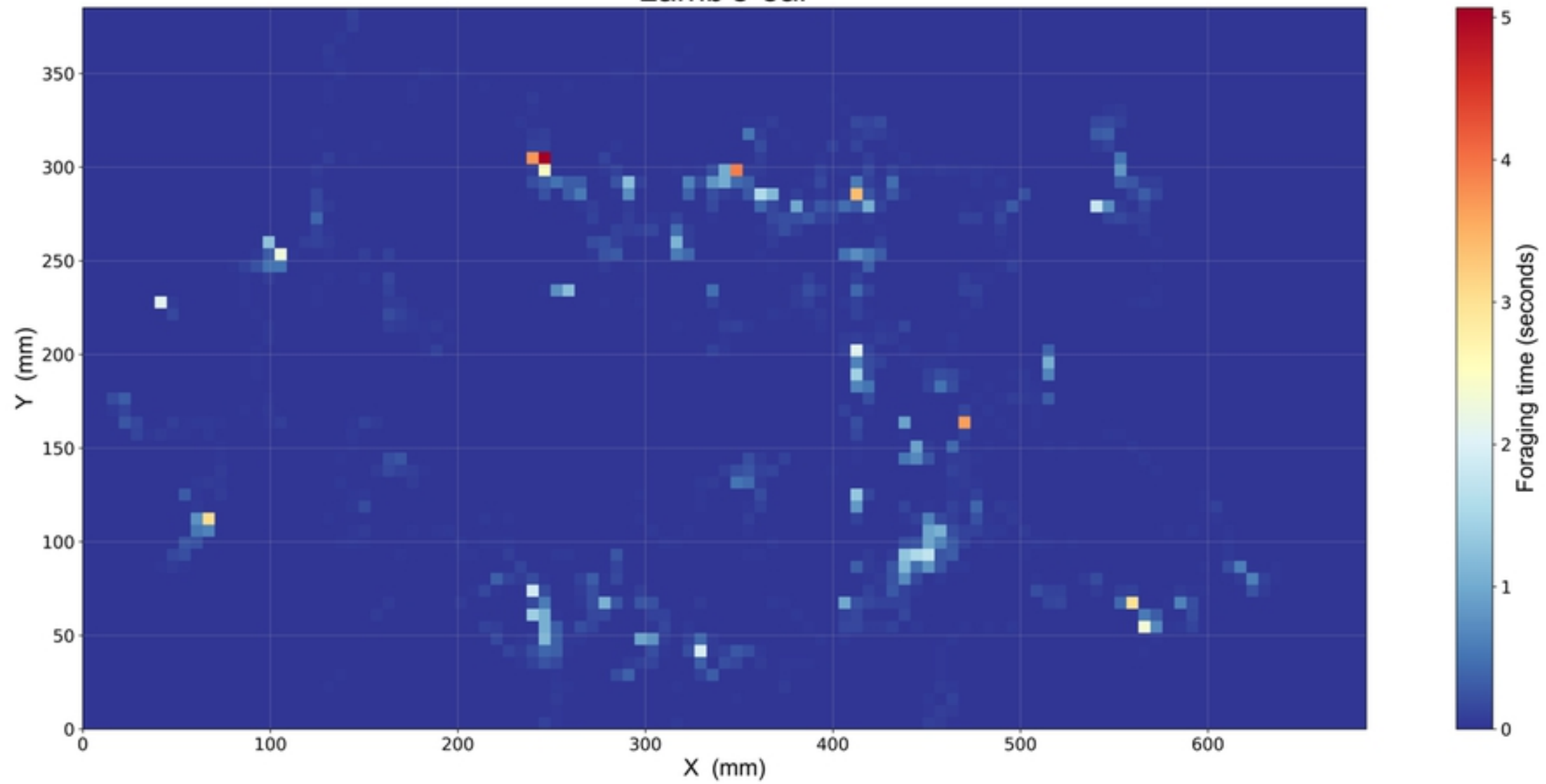


Fig9b

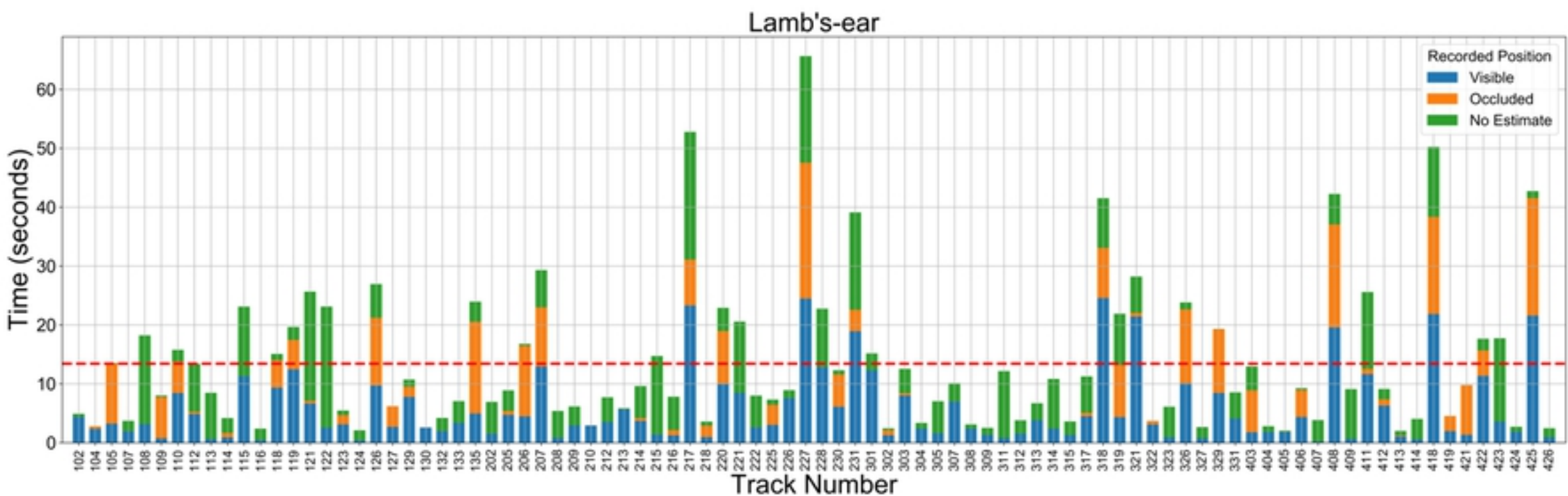
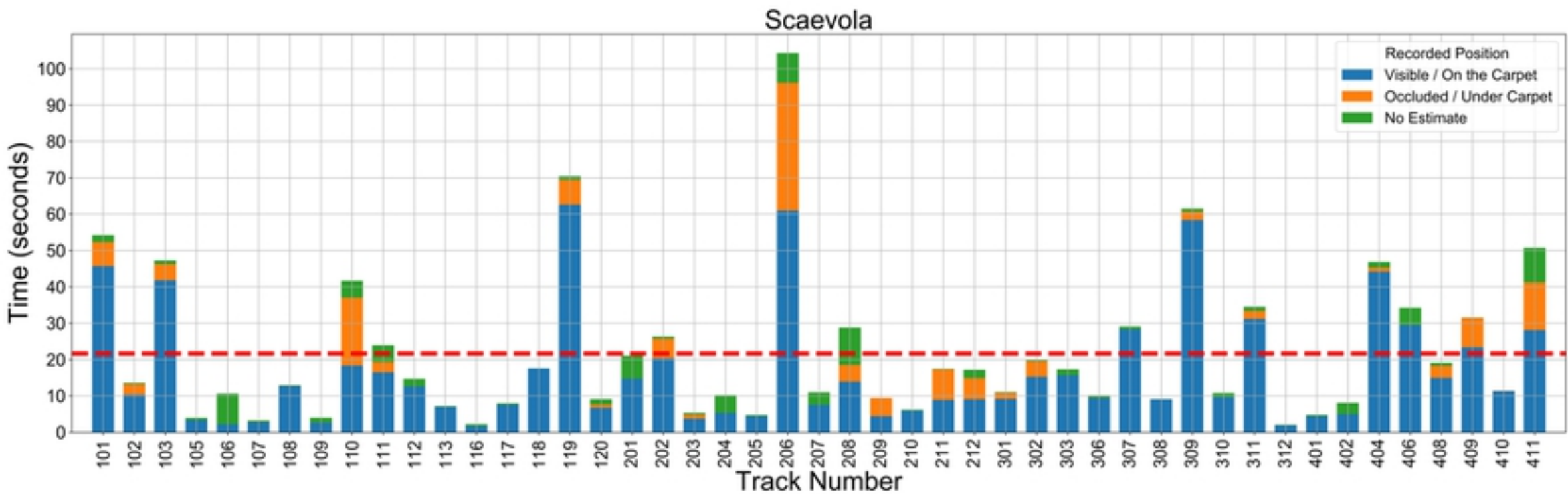


Fig9c

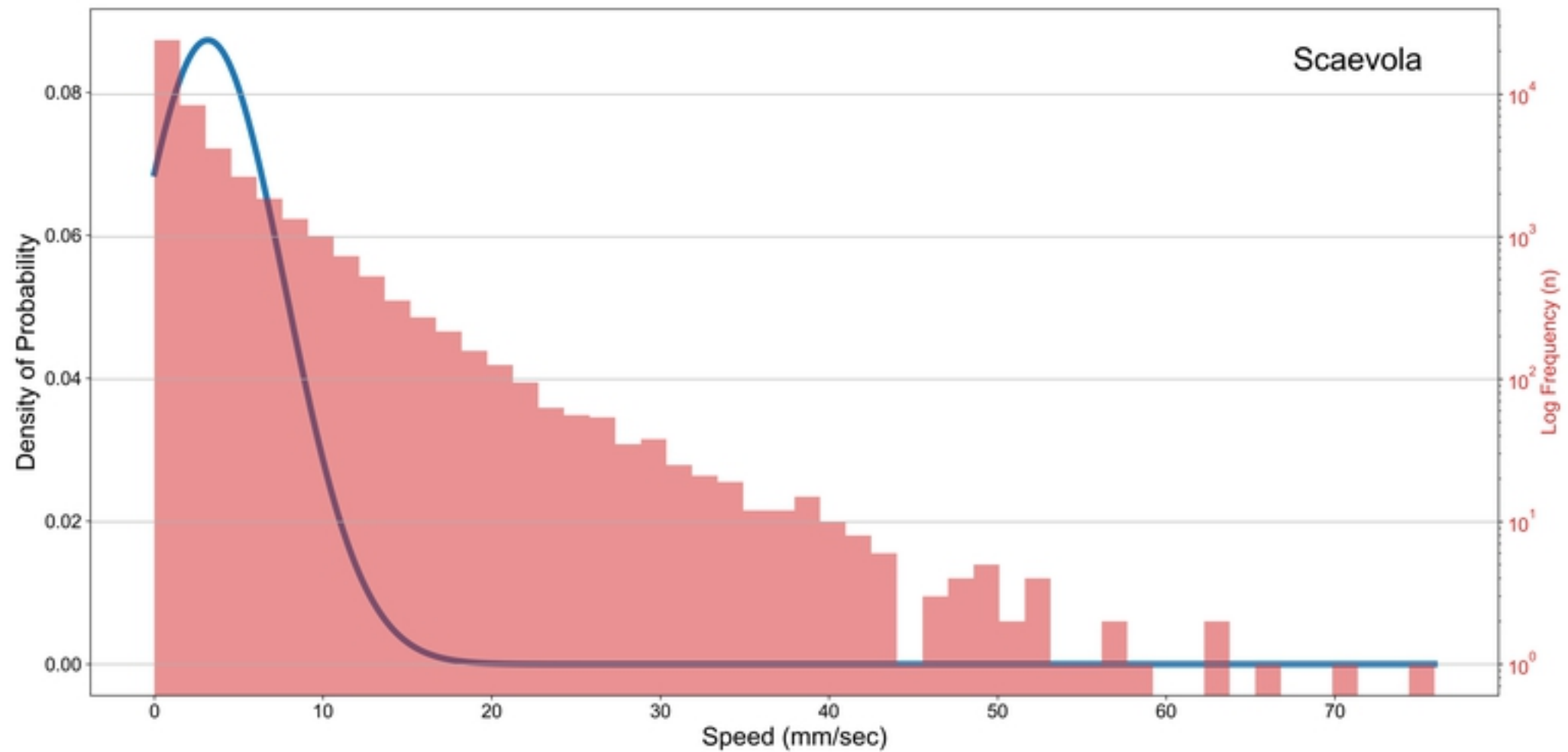


Fig9d

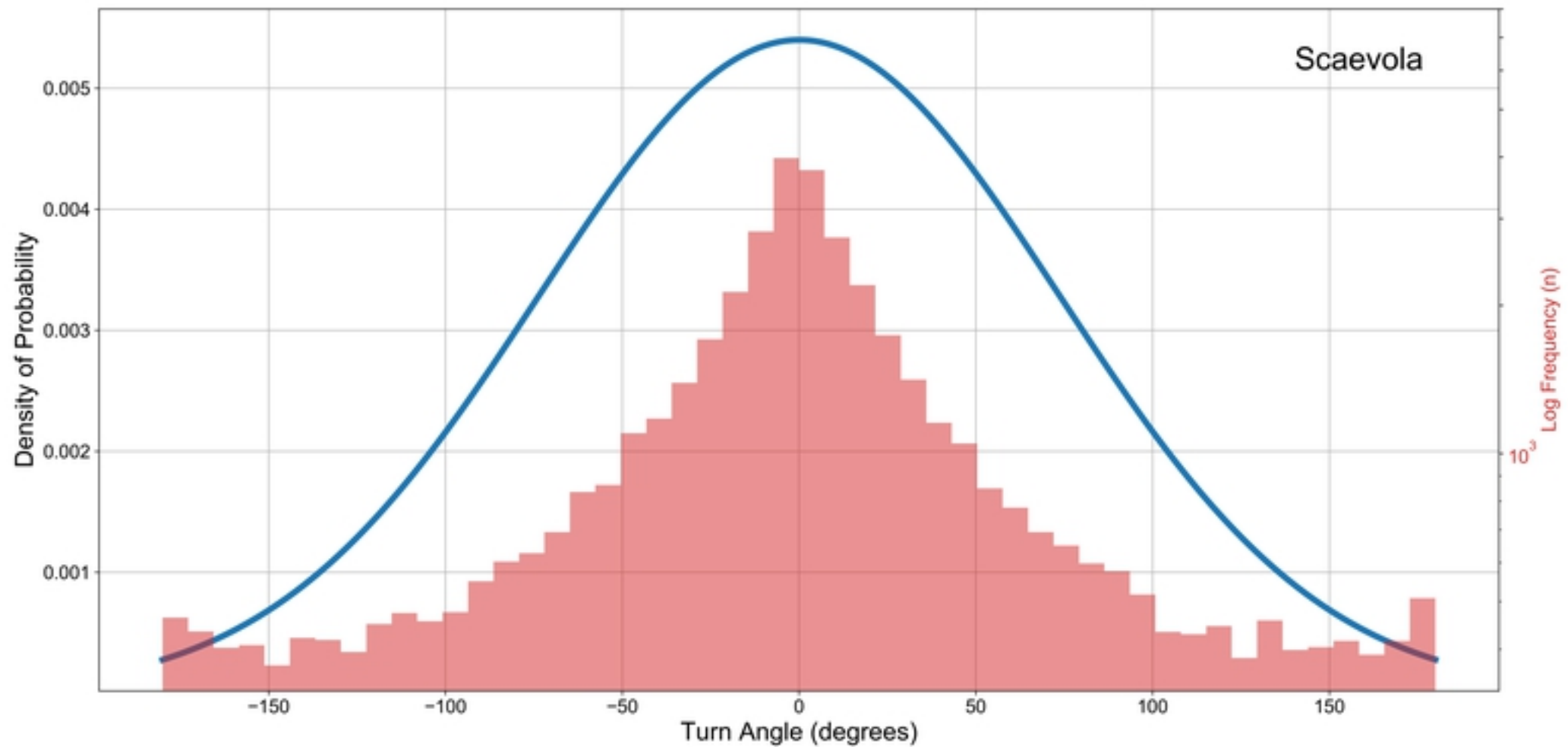


Fig9e