

**Assessing the effect of complex ground types on ground-dwelling arthropod movements with video monitoring: dealing with concealed movements under a layer of plant residues**

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## Abstract

- 1 Understanding the effect of ground types on foraging movements of ground-dwelling  
arthropods is a key step to managing their spatial distribution as required for successful  
conservation biological control. Indeed, fine movements at the centimetre scale can strongly  
influence the foraging ability of pest predators. However, because RFID or harmonic tracking  
techniques are not yet suitable for small species and video tracking focuses on uniform and  
light backgrounds, foraging movements have rarely been studied in relation to ground types.
- 2 We present a method to track a ground-dwelling arthropod (the earwig *Euborellia caraibea*) at  
night, walking on two contrasted ground types : bare soil and soil partly covered with a  
stratum of banana plant residues allowing individuals to hide periodically.
- 3 The tracking of individuals within these ground types was achieved by infrared light, tagging  
individuals, video treatments and semi-automatic cleaning of trajectories. We tested different  
procedures to obtain segments with identical durations to quantify speeds and sinuosities.  
These procedures were characterised by the junction time gap between trajectory fragments,  
the rediscretisation time of trajectories, and whether or not to use interpolation to fill in  
missing points in the trajectories.
- 4 Earwigs exhibited significantly slower and more sinuous movements on soil with banana plant  
residues than on bare soil. Long time gaps for trajectory junction, extended rediscretisation  
times and interpolation were complementary means to integrate concealed movements in the  
trajectories. The highest slowdown in plant residues was detected when the procedure could  
account for longer periods under the residues.
- 5 These results suggest that earwigs spent a significant amount of time concealed by the  
residues. Additionally, the residues strongly decreased the earwigs' movement. Since the  
technical solutions presented in this study are inexpensive, easy to set up and replicate, they  
represent valuable contributions to the emerging field of video monitoring.

43 **Keywords**

44 Insect, Mesocosm, Monitoring, Movement ecology, Spatial heterogeneity, Video tracking

## 1 Introduction

Ground type quality and spatial configuration are key factors for managing the spatial distribution of organisms for conservation purposes or improving the efficacy of conservation biological control. At the landscape scale, the effect of ground type and spatial distribution on dispersal have been extensively studied (Baguette & Van Dyck, 2007; Haddad et al., 2015), resulting in the development of management practices like movement corridors (Peng et al., 2017; Russell et al., 2018).

In contrast, at the patch scale, foraging movements of ground-dwelling arthropods (Bell, 1991) have primarily been studied in relation with the distribution of trophic resources (Kareiva & Odell, 1987; Valeix et al., 2009) but not the ground type distribution. Yet, there is evidence that ground type could influence the foraging movement of ground-dwelling arthropods, by providing a wider and more complex range of resources, such as favourable microclimatic conditions or protection from predators, or by deterring movement by increasing its risks and costs. A typical example is the reluctance of biological control agents to move inside the agricultural plot despite the presence of trophic resources, a frequently proposed explanation for failures in conservation biological control (Al Hassan et al., 2013; Albrecht et al., 2020). Individual-based models and a meta-analysis suggest that the interaction between movement behaviour and ground type spatial distribution could solve this problem (Albrecht et al., 2020; Collard et al., 2018; Delattre et al., 2019). Therefore, new data on the effect of ground type on patch-scale foraging movement are necessary for improving conservation biological control at this scale.

Analysing movements inside an agricultural plot requires collecting high-resolution data on a small spatial scale, which raises technical obstacles. Mark-Recapture (M-R) studies may provide insights on inter-patch movements but generally lack the resolution needed to document intra-patch movements especially for small ground-dwelling species (e.g., arthropods) that represent a high proportion of species of agronomic interest. Even the most recent advances in M-R techniques using radio frequency identification (RFID) tags are limited to the relatively large species that can handle the chip weight. Moreover, these techniques provide coarse-grained data (Kissling et al., 2014; Noskov et al., 2021;

Vinatier et al., 2010). Harmonic radar seems to hold the best promises for the future, with small tags and high-resolution data over a 1 km range. However, this technique has yet to be proven functional in complex vegetation covers (Daout et al., 2017; O'Neal et al., 2004). Its complex development process strongly reduces its immediate availability.

An alternative to *in-situ* observation techniques resides in mesocosm studies, in which one or several ground types (e.g., earthy soil, sand, plants) can be replicated in an enclosed arena, and the behaviour of the target organism is monitored by video (Reynolds & Riley, 2002). Since mesocosm studies allow for high-resolution data collection, they are well suited for studying foraging behaviours. However, they generally focus on diurnal movements on a uniform and light background to preserve a high contrast with the targets and allow automatic movement tracking. Some more advanced computing methods have been employed to track individuals in more complex environments and simultaneously track several individuals (Bernardes et al., 2021; Imirzian et al., 2019; Romero-Ferrero et al., 2018). Nevertheless, to our knowledge, the slightly more heterogeneous and realistic backgrounds were studied in open areas with no vegetation layer, filmed in a rather tight shot allowing only short movements to be recorded (Kindvall et al., 2000) and rarely addressed nocturnal movements (but see Imirzian et al., 2019).

Observing the effect of diverse ground types on movements using heterogeneous mesocosms and video monitoring is challenging, because not all ground types provide good contrast, especially at night-time, with some concealing parts of the movement paths. Thus, the difficulties of these types of studies resides in (1) separating the target animal from the background by image analysis and (2) reconstructing and analysing the scattered paths caused by complex three-dimensional covers (e.g., shelters above ground). In this study, we developed a method to track ground-dwelling arthropods in mesocosms that mimic real agricultural ground types. This method can track nocturnal individuals in ground with two strata that hide them periodically.

We utilised this technique to track the earwig *Euborellia caraibea* (Hebard), an endemic polyphagous predator of *Cosmopolites sordidus* (Germar) in the Caribbean islands (Brindle, 1971; Carval et al.,

2016; Mollet et al., 2014). Individuals were tracked in mesocosms mimicking two banana field ground types, bare soil and banana plant residues. In banana fields, *E. caraibea* seem to prefer the banana plant residues (Collard, pers. data), likely due to the humidity and shelter they provide (Burr, 1939). Herein, we addressed the problem of night-time and partially concealed earwig movements, focusing on the differences among individuals and ground types in terms of speed and sinuosity.

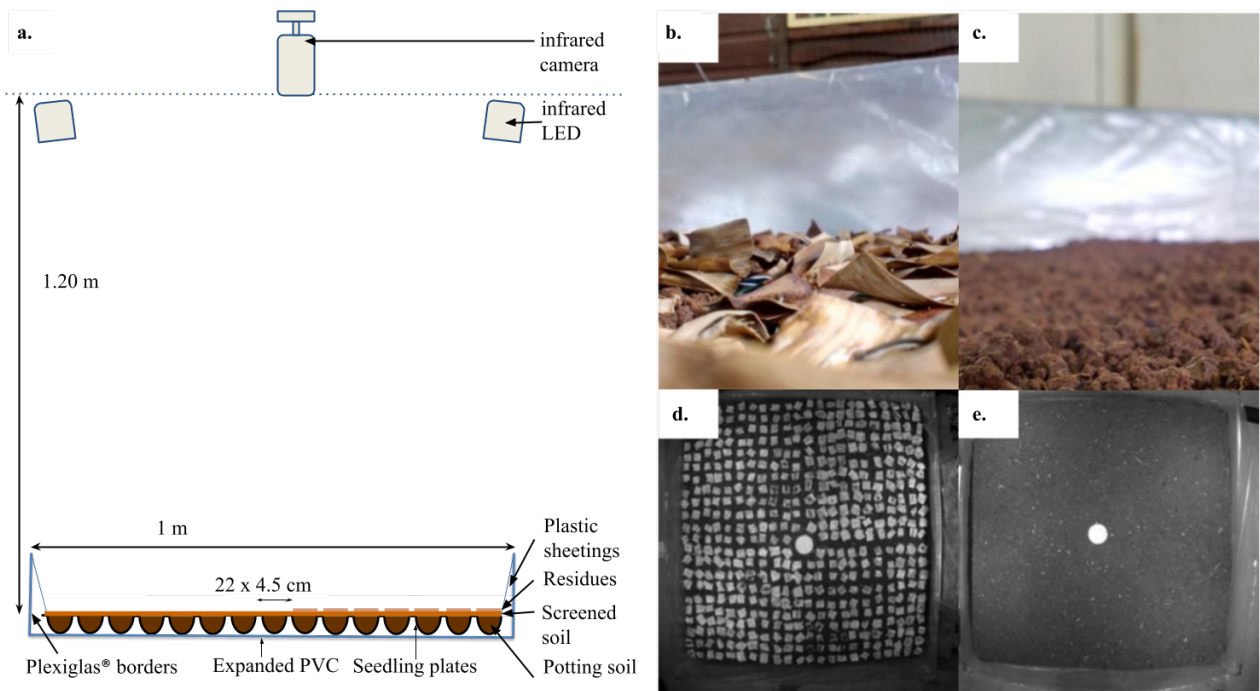
## 2 Materials and methods

### 2.1 Capture and laboratory maintenance of *Euborellia caraibea*

Thirty-five *E. caraibea* adults were caught in a field at the Petit Morne site in Martinique (14°37'N, 60°58'W). Species and sex determinations of individuals were performed according to Brindle (Brindle, 1971). In the laboratory, each individual was placed and kept in 6 cm diameter non-hermetic boxes at 25 °C (12:12, Light:Dark) until being placed in the arenas for 5 to 34 days. Each box contained a water source, food *ad libitum* and a shelter constructed of corrugated cardboard (see maintenance device in **Appendix A**).

### 2.2 Experimental mesocosms design and movement monitoring

Two 1 × 1 m mesocosm arenas were set up at the CIRAD facilities in Martinique (**Fig. 1a**; see details in **Appendix B**). One arena mimicked a ground with banana plant residues (hereafter referred to as "residues"; **Fig. 1b** and **1f**), and the second arena mimicked a ground of bare soil (hereafter referred to as "bare soil"; **Fig. 1c** and **1e**). For the "residues" arena, 3 × 3 cm units of overlaid dried banana leaves were placed evenly over the bare soil, with free space between them to allow the detection of the earwig's movement (**Fig. 1a** and **1f**). Circular white platforms of 6.5 cm diameter were positioned in the centre of each arena to accommodate the earwig in its shelter at the beginning of the experiment (5:00 pm). Individuals were chosen following their order of capture to homogenise the time spent in captivity. Each earwig was randomly assigned to one of the two arenas. We tested 17 and 18 *E. caraibea* (including five males per group) on "bare soil" and "residues", respectively.



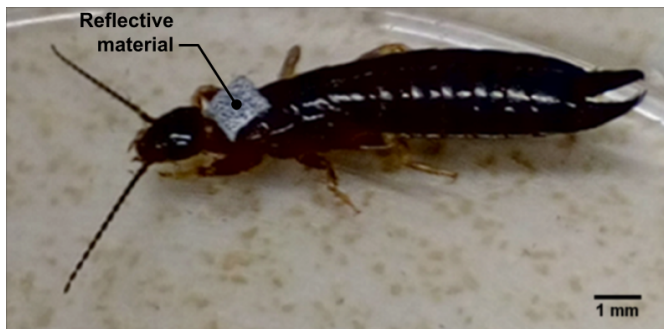
**Fig. 1: Experimental design for monitoring *E. caribbea* movements in heterogeneous environments : a. arena diagram, b. and d. photos of the "residues" arena, c. and e. photos of the "bare soil" arena. d. and e. images extracted from infrared night-time videos.**

The day after the experiment, the arenas were transferred outdoors, the residue grid was removed (for the "residues" treatment), and the bare soil was exposed to the sun to remove or, at a last resort, kill individuals from previous experiments and any organisms that might have entered the arena. A total of 28 earwigs were removed: 14 out of 17 on the bare soil and 14 out of 18 on the residue arenas.

Each arena was placed under one Trendnet TV-IP310PI infrared camera (3.2 megapixels, 2048 × 1536), and four projectors containing 48 infrared LED each, were placed on the corners of each arena to provide more uniform lighting (**Fig. 1a**, see details in **Appendix B**). The two arenas, video devices and infrared lights were placed in a climatic chamber maintained at 25 °C, with the LED produced artificial white light (Linear power led, 25W/4000 K, 2500 LM, Lamentin) providing a 12:12 (L:D) photoperiod (**Fig. 1a**). The two cameras filmed the arenas in parallel using a network switch, a Synology DS216 NAS and its Surveillance Station software, from 5:30 pm to 8:00 am (i.e., the entire night period, which starts at 6:00 pm). This period corresponds to the estimated activity period for *E. caribbea* under natural outdoor lighting conditions (see the preliminary experiment in **Appendix C**).

The cameras created an image distortion depending on their distance from the arenas. It was estimated that 1 cm of the object corresponded to an average of 6.82 pixels over the entire arena with a standard error of  $\pm 0.01$  cm (see details in **Appendix B**). We obtained  $35 \times 14.5$  hours of videos (resolution  $1024 \times 768$  pixels;  $1 \text{ frame.s}^{-1}$ ) between April 26 and May 29, 2017.

Each tested individual was tagged with a  $1 \times 1$  mm square of reflective material (SKU Ref. HEBBR09001, Lecyclo, France) to allow the infrared light reflection enhancing the visibility of the individuals in the arena. The tag was fixed to the earwig's pronotum with a strong adhesive (cyanoacrylate, Super Glue®) at least 24 hours before testing (**Fig. 2**; see detailed tagging protocol in **Appendix D**).

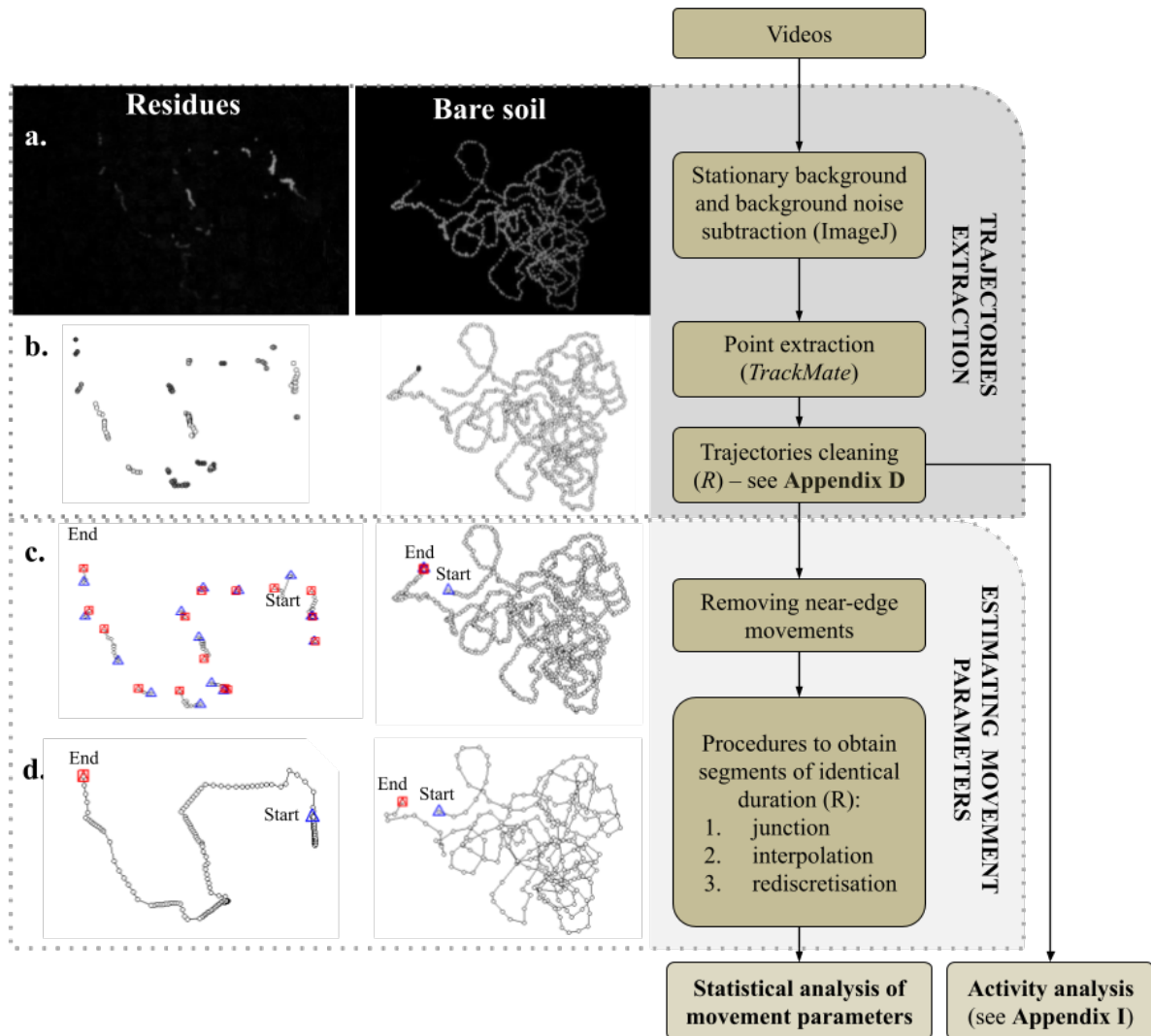


**Fig. 2: Picture of a tagged earwig *E. caraibea* (personal picture)**

### 2.3 Trajectories extraction from videos

We developed a method to extract trajectories from videos to characterise the movements (i.e., speed, sinuosity, and earwig activity) in both ground types (**Fig. 3**). The trajectories are defined as a time series of locations of one individual (= points), and each point is characterised by its coordinates and time. Points were grouped into a given trajectory if separated by less than a time gap  $tg$  and a distance gap  $dg$  (hereafter referred to as junction criteria) (Tinevez et al., 2017).



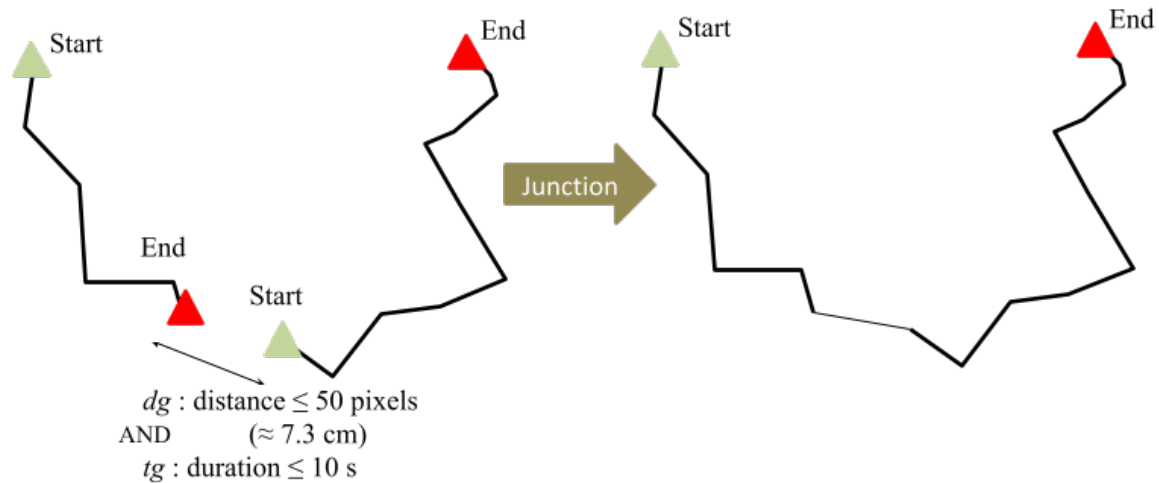


**Fig. 3: The successive steps to extract trajectories and estimate movement parameters. Each step is illustrated with a 30 minute-long data selection from both "residues" and "bare soil" treatments. a. Images representing the maximum intensity obtained for each pixel over a video of 30 min after stationary background and background noise subtraction. b. Locations extracted via the *TrackMate* plugin and after cleaning with *R* software. Examples of trajectories obtained with a specific procedure: c. a short junction (criteria 10 s, 50 pixels) with a rediscritisation at 1 s without interpolation, and d. a long junction between trajectories (criteria 5 min, 50 pixels) and a rediscritisation at 5 s with interpolation (for definitions, see section 2.4).**

The experimental design of this study posed some specific problems that made the extraction of trajectories from the videos difficult, including (i) significant background noise caused by heterogeneous backgrounds and the infrared light and (ii) the simultaneous presence of several individuals in an arena for some replicates where a previous individual had not been found and

removed. Moreover, not all earwigs could be systematically recovered at the end of the experiment, such that 40% of the replicates may have contained several earwigs simultaneously (three maximum), representing eight and six replicates for residues and bare soil, respectively.

To account for these issues, we used (i) a technique to subtract background and residual noise from the videos (more details in **Appendix E**) and (ii) semi-automated *cleaning* of the trajectories in R to eliminate conflicting and interacting trajectories (more details in **Appendix F**). After background and residual noise subtraction from the videos (i), the trajectories were extracted using ImageJ, an image processing software (Schindelin et al., 2012), its *TrackMate* plugin (Tinevez et al., 2017) and the R software (R Core Team, 2018). The moving points were identified and associated within trajectories according to the junction criteria  $dg$  (30 pixels, i.e.,  $\approx 4.3$  cm), and  $tg$  (5 s) without signal (more details in **Appendix E**). Once the conflicts were removed by cleaning (ii) and the confusion between individuals and noise was no longer observed, the trajectories were reconstructed with less restrictive junction criteria ( $dg = 50$  pixels and  $tg = 10$  s) (**Fig. 3b** and **Fig. 4**).



**Fig. 4: Diagram of the junction of two trajectories according to junction criteria  $dg$  (distance gap) and  $tg$  (time gap)**

## 2.4 Estimating movement variables

We developed a method to estimate movement variables that quantify the sinuous or slow nature of an individual's movements in both ground types (**Fig. 3**). The movement variables were the time-series of distances and relative angles calculated from segments with identical durations. Two successive points within a trajectory define a segment. A distance is the length of a segment. A relative angle is calculated between the direction of a segment and the direction of the previous segment. Therefore, it takes two successive segments to obtain a relative angle.

### Removing near-edge movements

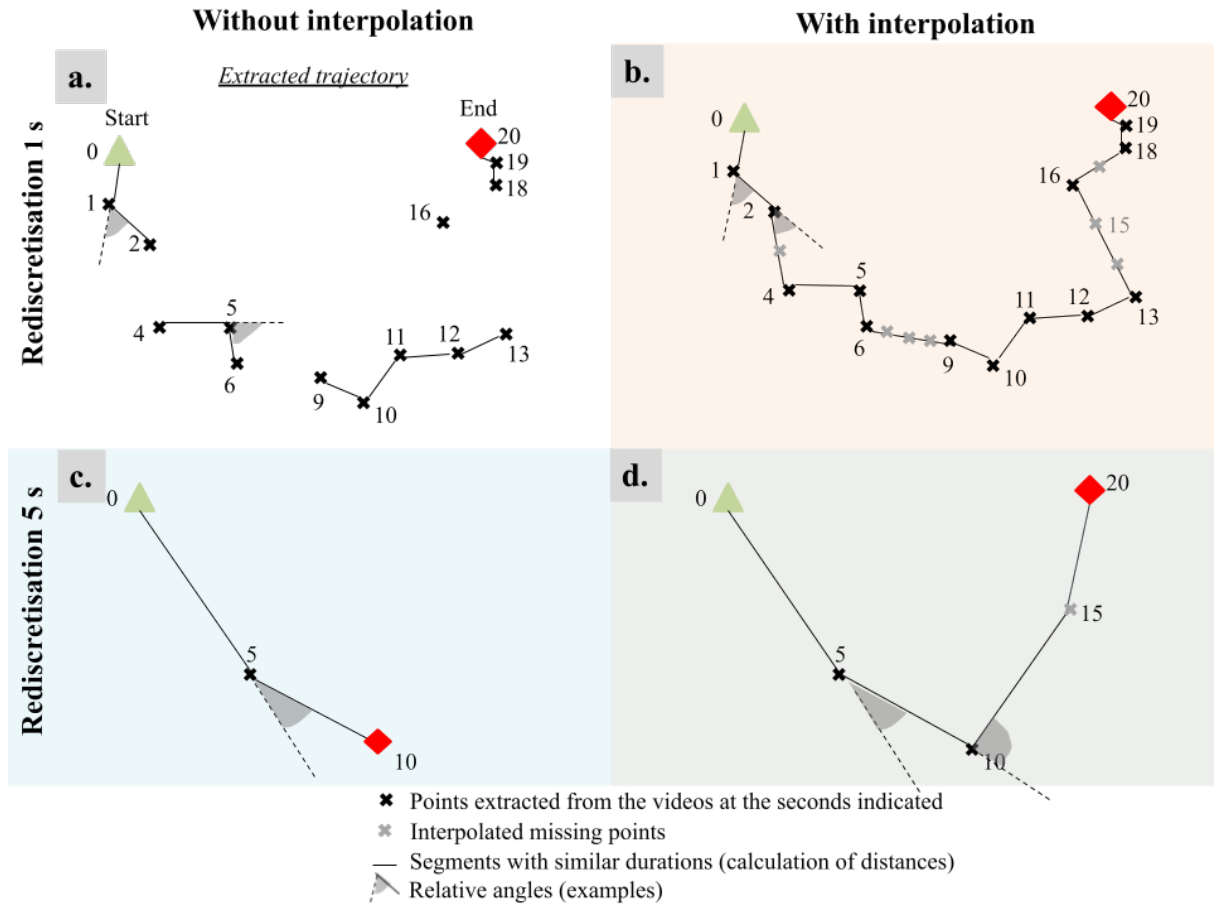
To estimate movement variables that were not biased by the arena's edges, we removed all trajectory points within 35 pixels ( $\approx 5.1$  cm) of the arena borders (**Fig. 3**). This treatment split some trajectories into several trajectories. This operation was always performed after conducting the junction operation for specific time and distance gaps (see next paragraph).

### Procedures to obtain segments of identical duration

Due to the disappearance of the tag and missing points within the trajectories in the "residues" arena, in particular, segments with an identical duration, necessary for calculating the movement variables, were rare. We developed different procedures to obtain segments of identical duration from the trajectories to account for this issue. We transformed the extracted trajectories with three different operations for each procedure to obtain such segments: a junction, an interpolation and a rediscritisation of the trajectories (cf. **Fig. 4** and 5). All operations were performed with the R software (R Core Team, 2018) and the *adehabitatLT* package (Calenge, 2006).

The junction operation consisted of reconstructing trajectories with a less restrictive junction time gap (*tg*) (**Fig. 4**). The interpolation operation involved placing one point for each missing point within trajectories (**Fig. 5**), utilising linear interpolation between the previous and following extracted points (see interpolation function proposed by *adehabitatLT*). By filling in the missing trajectory points, interpolation allowed the disappearance periods to be included in the speed calculation. The

209 rediscritisation operation consisted of modifying the fixed duration of the segments required to  
 210 estimate the movement variables within each trajectory.



211

212 **Fig. 5: Trajectory procedure scheme for rediscritisation at 1 or 5 s, with or without interpolation. The segments for**  
 213 **calculating distances and examples of relative angles are shown for each procedure. Interpolation was performed**  
 214 **before rediscritisation. Consequently, point 15 (Fig. d) is taken from the interpolated point 15 (Fig. b) and not by**  
 215 **linear interpolation between points 10 and 20.**

216 In the absence of interpolation, the segments with identical duration were selected from successive  
 217 direct observations corresponding to the selected rediscritisation time (**Fig. 5a, c**). If there were no  
 218 observations exactly at the next re-discritisation time, the segment and consequently the distance and  
 219 the relative angle were not calculated. In the case of interpolation (**Fig. 5b, d**), rediscritisation  
 220 consisted of placing all missing points with interpolation and selecting the segments corresponding to  
 221 the chosen rediscritisation times. Therefore, each dataset of movement variables obtained by a  
 222 specific procedure was based on a specific way of obtaining segments with identical duration.

## **Sensitivity of movement variables to operation values**

Choices made for the three main operations used to obtain segments of identical duration (junction, interpolation, rediscritisation) may affect the values of movement variables describing the paths (i.e., distances and relative angles). Long junction values ( $tg$ ) allow the inclusion into the trajectories of longer times spent under the residues but may lead to a higher occurrence of missing values within the trajectories. Every rediscritisation value reveals the individual movement at a different scale and requires a different interpretation. Short rediscritisation values indicate the detailed individual trajectory and permit the calculation of mobility parameters like maximum velocity. Long rediscritisation values reveal individual net displacement over the corresponding period, allowing the inclusion into the trajectories of longer times spent under the residues in the limits permitted by the dimensions of the arena. Linear interpolation makes it possible to keep all the information in a trajectory but artificially translates time spent under the residues into a straight displacement of equivalent velocity. Thus, the calculation of relative angles was only performed on trajectories without interpolation.

To investigate those potential effects, we tested the impact of procedures on movement variables with all combinations of the following values: (i) junctions ( $tg$ ) of 10 s, 30 s, 1 min and 5 min; (ii) rediscritisations of 1, 5, 10, 20, 30, 40, 50 and 60 s, (iii) with and without interpolation.

## **2.5 Statistical analysis of movement variables**

We tested the effect of residues on travel speed and sinuosity by comparing the movement variables of trajectories (distances and relative angles) between the two ground types. We considered the autocorrelation of successive segments in our analyses by testing the effect of ground types for different rediscritisation values (i.e., at different time scales) and taking an individual resolution for our statistical analyses (Fieberg et al., 2010).

Distances were compared between ground types using datasets of all procedures with enough replicates (i.e., at least 10 individuals with at least 10 distance records per ground type). We did not get enough replicates to allow statistical comparison of distances for 23 (over 64) procedures, with

some displaying high rediscritisation values, short junctions or no interpolation (see **Appendix G**). Statistical analyses were performed using mixed linear models (package *lme4*) with individuals as a random effect and a square root transformation of distances expressed in pixels ( $\sqrt{distance}$ ). Model residuals were inspected for dispersion, uniformity and outliers with the “DHARMA” R package (Hartig, 2020). The effect of the individual's sex and its interaction with ground type were removed from the model since they had no significant effect on distance (see analysis in **Appendix H**).

Relative angles were compared between ground types for all procedures without interpolation and with a junction of 10 s comprising at least 10 individuals with at least 10 relative angles records per ground type. Only one junction time gap was tested because, in absence of interpolation, the junction time gap does not affect the relative angles used for analysis. We did not obtain enough replicates to allow statistical comparison of relative angles for 24 (over 32) procedures, only procedures with rediscritisation values of 1 and 5 s were tested (see **Appendix G**). Two individual-based statistics were used to test the effect of ground type on the distribution of relative angles: the mean direction (mean relative angle) and the concentration (1 - the variance of relative angles around the mean). Concentration is a measure of the sinuosity of a trajectory, ranging from 0 to 1, with low values corresponding to sinuous trajectories. Statistics developed on R by Pewsey et al. (2013) were used. These analyses rely on the large sample test statistics of Watson (1983) and the non-parametric test statistics of Wallraff (1979) and allow the comparison of two circular statistical distributions for the mean direction and the concentration, respectively. A randomization test was performed on these test statistics. The statistical distribution under  $H_0$  was constructed by calculating 1000 statistics obtained after random permutations of the individuals between the ground types to account for the differences in numbers of calculated angles among individuals. The p-values were calculated by comparing the observed statistics with the statistical distribution under the null hypothesis  $H_0$  of similar values in the two ground types.

### 3 Results

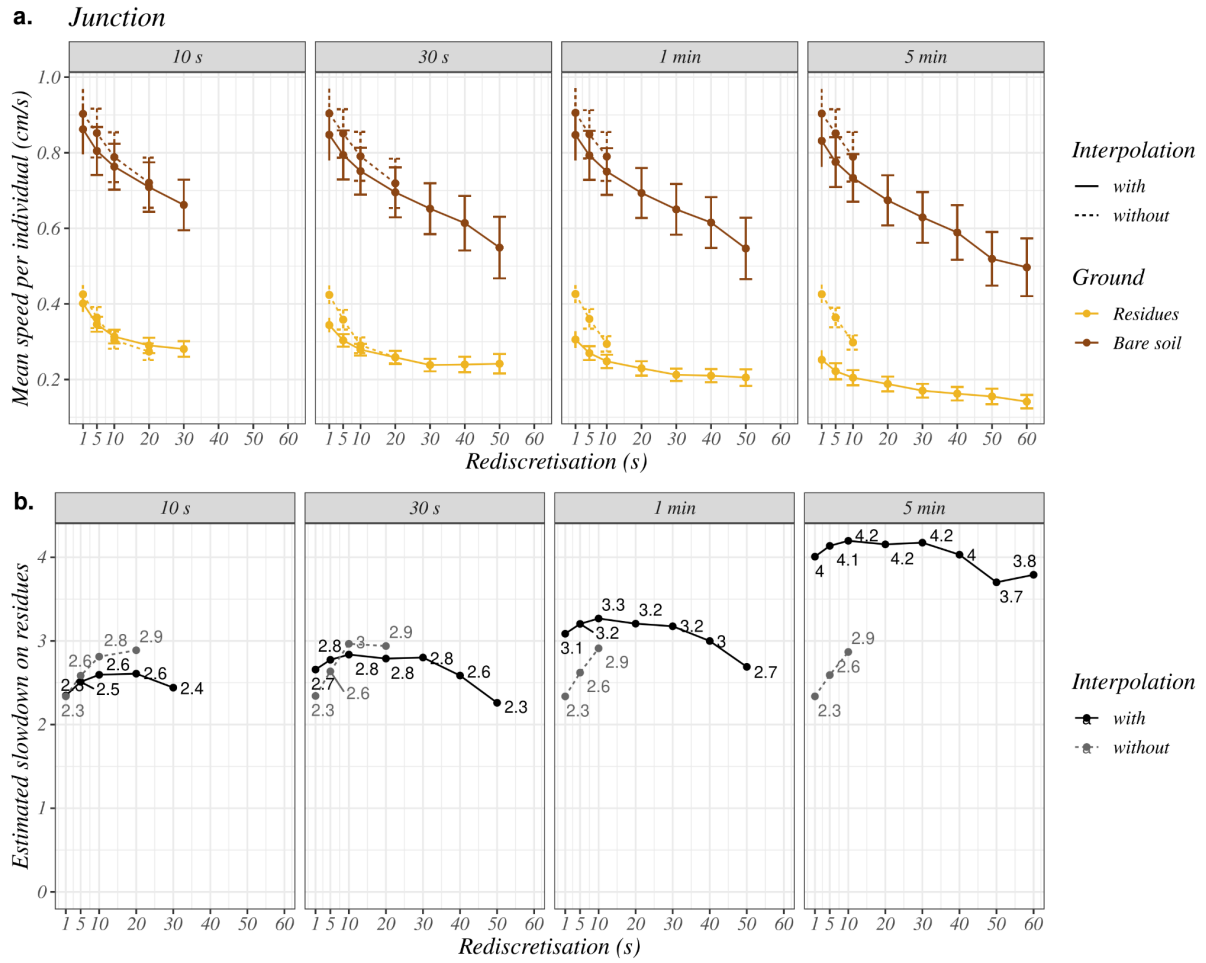
The earwigs under investigation revealed a highly variable activity pattern (intensity and distribution over time). The result depended on each individual's identity and was not linked to ground type (see

**Appendix I).** The trajectories selected for the movement analysis (excluding near-edge movements) represented  $31.9 \pm 18.6$  % of the total seconds of movement (inter-individual mean  $\pm$  standard deviation).

### 3.1 Speed

Speeds were calculated from distances as the ratio between distances and the rediscratisation value and are presented to simplify the comparison between the different rediscratisation values. During their movements, earwigs reached maximum speeds of  $2.19 \pm 0.84$  cm.s<sup>-1</sup> (inter-individual mean  $\pm$  standard deviation calculated from trajectories with rediscratisation at 1 s without interpolation), with a maximal speed of 4.93 cm.s<sup>-1</sup> registered for an individual on residues.

For all tested procedures (**Fig. 6**), the earwigs' mean speeds were estimated 2.3 to 4.2 times slower on residues than on bare soil (all p-value  $< 10^{-3}$ ). For example, the inter-individual mean speed was  $0.36 \pm 0.11$  cm.s<sup>-1</sup> ( $\pm$  standard deviation) on residues vs  $0.85 \pm 0.27$  cm.s<sup>-1</sup> on bare soil, for a procedure with few assumptions, i.e., junction of 10 s, without interpolation, rediscratisation of 5 s. Estimated slowdowns on residues varied depending on the procedure (**Fig. 6b**). Stronger slowdowns were estimated with long time gaps for junction (starting from 1 min), intermediate rediscratisations (10 to 30 s) and interpolation. Junction only affected slowdown for procedures with interpolation. In particular, allowing a junction of 5 min with interpolation strongly increased the estimated slowdown. Rediscratisation had different effects with and without interpolation. Without interpolation, rediscratisations of 5 s and more increased the estimated slowdown. With interpolation, increasing rediscratisation values (starting from 30 s) tended to decrease slowdown. The standard error associated with model estimates also increased for high rediscratisation values (see **Appendix J**).



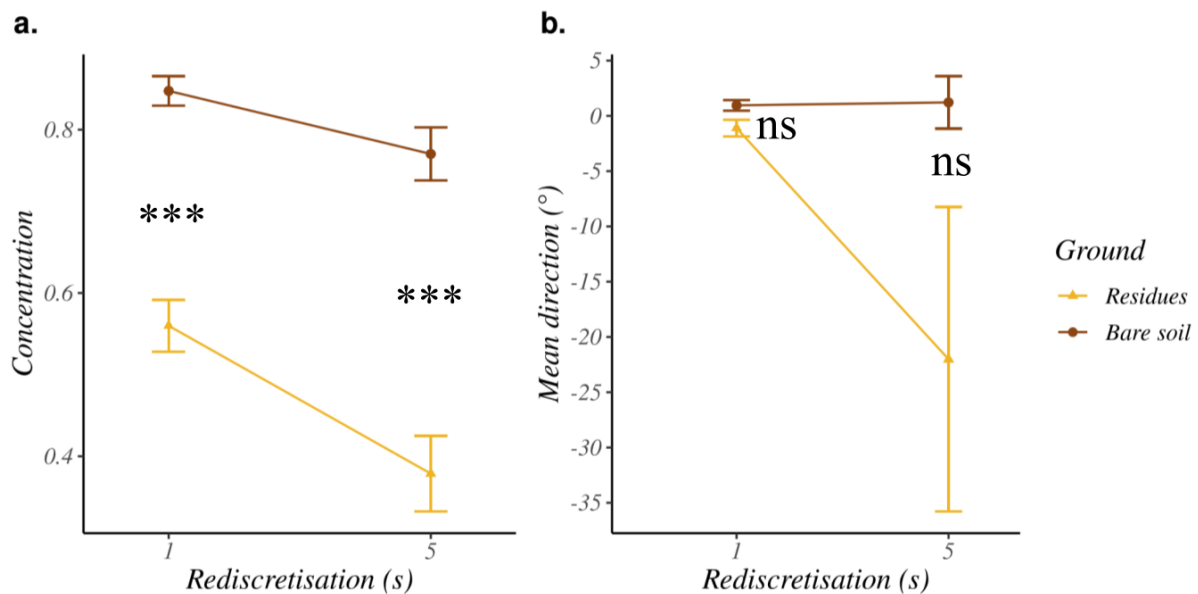
**Fig. 6: Effect of ground type on the speed of earwigs according to procedures. a.** Average mean speeds per earwig ( $\pm$  standard errors) according to ground type (yellow or brown lines), junction (horizontal division), rediscritisation (horizontal axis) and interpolation (solid or dotted lines). **b.** Estimated ratio of speeds on bare soil vs residues. These ratios were calculated with the predicted distances extracted with the “effects” R package (Fox & Weisberg, 2018). All procedures represented here show a significant effect of ground type on speed (all p-values  $<10^{-3}$ ).

### 3.2 Relative angles

The sinuosity of a trajectory increases as the concentration of relative angles decreases or as the mean direction moves away from 0. Trajectories obtained for short rediscritisation (1 and 5 s) showed significantly stronger sinuosities on the residues than the bare soil, caused by smaller concentrations and not changes in mean direction (**Fig. 7**). For the 5 s rediscritisation, concentrations were almost twice as large on bare soil (inter-individual mean  $\pm$  standard deviation:  $0.40 \pm 0.16$  on residues and  $0.77 \pm 0.14$  on bare soil, p-value  $< 10^{-3}$ , statistic = 219.81). Mean direction did not differ between ground types for both rediscritisations (1 s: p-value = 0.347, statistic = 108.65; 5 s: p-value = 0.461,



311 statistic = 35.47). For the rediscretisation of 1 s, the mean direction over the two ground types was  
 312 close to 0 (inter-individual mean  $\pm$  standard deviation:  $-0.55 \pm 4.35^\circ$ ; **Fig. 7b**).



313 **Fig. 7: Effect of ground type on concentration (a.) and mean direction (b.) of the earwig's relative angles. The**  
 314 **averages per earwig ( $\pm$  standard errors) of concentration and mean direction are represented according to ground**  
 315 **type (colour) and the rediscretisation value (without interpolation and junction at 10 s). The significance of the ground**  
 316 **type effect on the mean direction or concentration is represented by: "\*\*\*\*"  $p < 0.001$ , "ns"  $p \geq 0.05$ .**

## 317 4 Discussion

318 Analysing foraging movement of small organisms at a fine scale, over long periods and on realistic  
 319 ground is crucial for understanding their spatial and temporal dynamics and help managing them in  
 320 real agricultural environments. Based on generic video and trajectory processing, we developed a  
 321 method that made it possible to detect more sinuous and slower movements of the nocturnal earwig *E.*  
 322 *caraibea* walking on soil covered by banana leaf residues rather than on bare soil.

### 323 4.1 Tracking earwigs' movements with an experimental mesocosm and video recording.

324 Our experimental device made it possible to monitor several hours of movement on both ground types.  
 325 A crucial step of the method was to distinguish earwigs from the background. The use of reflective  
 326 materials on earwigs' pronotum was decisive in increasing the earwigs' contrast. In addition to video

treatments (**Appendix E**), semi-automatic cleaning of trajectories was necessary to suppress the remaining noise and to make robust choices between some simultaneous trajectories. The reflective materials and video treatments have made the manual editing more manageable given the number of hours, and the movement resolution registered [mean of  $3.5 \pm 8.6$  (standard deviation) trajectories to clean manually per individual; maximum of 34].

The experimental device developed in this study appeared to be more efficient for calculating speeds and highlighting differences in earwig movements for the fine temporal grains (rediscretisation  $\leq 30$  s). Indeed, we observed a decreasing trend in the estimated slowdown in the residues arena when the values of rediscretisation increased (starting at 30 s) with interpolation (**Fig. 6b**). Above 30 s, the dimensions of the arena ( $< 1 \text{ m}^2$ ) were probably too small, biasing the sampling of distances towards shorter distances than they might be in open ground. This limitation should be considered when extrapolating the study results to larger spatial and temporal scales, as the distances travelled do not change linearly with sampling time (Morales & Ellner, 2002).

This experimental device opens up the possibility for future analyses on the effects of a wide variety of ground types on the movement of ground-dwelling arthropods. Additional video treatments or improved tracker algorithms (e.g., Assali et al., 2020) may be required in more complex environments, such as plant cover, where background noise management for trajectory extraction and individual recovery is challenging. In all cases, the spatial distribution of the cover units that could hide individuals should be set to allow the brief but regular appearance of the target species. Previous knowledge of the species, their maximum and approximately mean speed can help optimise the cover design. Similarly to our case, studying cryptic species would probably require improving the contrast between the target and the cover. Thus, choosing an appropriate tag is critical and depends on the species targeted, the ground type tested, and the camera device chosen. In the case of diurnal species, there are more possibilities for distinguishing individuals from the background. Indeed, recording in visible light results in less noise than infra-red light (Semenishchev et al., 2018) and standard cameras under visible light return three values per pixel, providing more possibilities to find colours (not just

intensities) that distinguish individuals from the background (Sebastian et al., 2010; Wu et al., 2020 preprint). The standard infra-red camera used in this experiment returns only one value per pixel (intensity), suggesting that reflective material is probably the best option for nocturnal species.

## 4.2 Characterising movements with trajectories containing missing points

Most trajectories included times where the location of the earwig was not known (missing points). Even on bare soil, missing points were rare but existed (**Appendix K**). Missing values within trajectories could have several explanations : (i) the individual hid under the soil, (ii) the individual movements were not captured by our device or (iii) the individuals were concealed by the residues. Since individuals hiding under the soil (situation i) were rarely observed, and situation (ii) corresponded to a short and random loss of the earwig's tag tracking (e.g., bad inclinations of the tag toward infrared LED), those missing points should not have significantly influenced the quantification of movement on bare soil.

We were interested in the period during which movements were concealed by residues (situation iii) because they could be the source of significant differences in movement variables between the two ground types. Because situation (ii) could also happen on residues, the time with missing points on residues did not exactly match the time individuals spent under residues (situation iii). However, in our experiment, the missing points between residues are unlikely to have affected the estimation of movement variables, particularly slowdown. Indeed, if we had lost track of individuals moving between two or more residues, resulting in an artificially long concealed period, these individuals probably travelled distances larger than the distance gap of 7.3 cm, such that the next data point would be the beginning point of a new trajectory. Herein, we used long time gaps for trajectory junction, long rediscritisations of trajectories and interpolation to include concealed movements in the trajectories used to quantify movement variables.

The duration of junction time gaps determined the maximum duration of concealed movements included in the trajectories. Long junction time gaps were necessary to account for long concealed movements (up to 5 min). These long junction time gaps affected the quantification of speed and

sinuosity only when (i) it was combined with interpolation (because numerous successive interpolated points were added), and (ii) rediscritisation was longer than the junction time gaps (because concealed periods shorter than this time gap could be included within a segment).

Varying the rediscritisation value without interpolation allowed to include concealed movements while making few assumptions, because only observed movements are taken into account. Short rediscritisations were adapted to analyse speeds and sinuosity on a fine time scale (1 to 5 s, **Fig. 6** and **Fig. 7**) because they provided enough replicates to perform statistical analyses without interpolation (**Appendix G**). Some slightly longer rediscritisations (10 and 20 s) generated enough replicates to compare speeds between ground types including longer concealed movements in trajectories (up to 19 s). However, because the inclusion of these longer concealed movements was only possible for long rediscritisation, it was not possible to disentangle the effects of concealed movement from those of time scale on speed and sinuosity. Notably, it has been proposed that each time scale can reflect different behaviours (Nathan et al., 2008). For example, individuals showing (i) a high sinuosity at a time scale but (ii) straight movement at a slightly longer time scale could have indicated a local avoidance of residues (i) while quickly crossing the arena (ii).

Interpolation was another means to include long concealed movements when calculating speeds (and not relative angles). This approach relies on the ability of the device to successfully track individual movements between residues and proved relevant for the analysis of speeds on larger time scales (5 to 30 s). In contrast to long rediscritisation, interpolation allowed for the analysis of the concealed movement effects regardless of time scale because it could be combined with both short or long rediscritisation values.

#### 4.3 Slower and more sinuous movements on the residues

Our study shows that the ground type strongly affected the movement of the earwig *E. caraibea*. Earwigs moved significantly slower on the residues, with speeds estimated to be two to four times slower than on bare soil (**Fig. 6b**). These results are particularly robust because they have been found

for all the procedures carrying enough replicates, whether with interpolated or observed trajectories, long or short junction and long or short rediscritisation values.

An increase in the sinuosity of visible movements on residues was also observed for short rediscritisations times of 1 to 5 s (**Fig. 7a**) (i.e., the fine movements of the earwig were more sinuous between (or on) the residues than on bare soil). Differences in sinuosity between the residues and the bare soil could not be analysed for longer rediscritisations because they could not generate enough replicates per individual. The residues, therefore, seem to have affected the fine movements of the earwigs, speeds, and sinuosity, even when they were visible and not hidden under them.

Furthermore, we estimated a larger slowdown on residues when concealed movements were included in the speed's calculation based on the observed trajectories using large rediscritisation values (10 or 20 s; **Fig. 6b**) or interpolated trajectories with long junctions (**Fig. 6b**). With those procedures, a larger part of concealed periods could be included in the analyses (mean concealed duration of 3.1 s and 12.1 s for bare soil and residues, respectively) (**Appendix K**). These results confirm that accounting for concealed movements matters. Earwigs seem to move slower or more sinuously (or both) under the residues than between them. Although procedures with long junction and interpolation must be interpreted with more care, the highest estimated slowdown of the earwigs (up to four times; **Fig. 6b**) obtained for the procedure with interpolation and with the longest junction value (5 min) indicates that earwigs likely stayed hidden for more than 1 min and that this stay strongly slowed down their exploration of the arena. Since the residues hid the earwig's movement from the camera, we expected longer concealed periods on residues. However, the signal loss caused by residues could not account for the strong slowdown by itself (see detailed analysis in **Appendix K**). Those long periods under residues suggest that residues have not simply slowed down the movements of earwigs as mere obstacles to movement (i.e., a barrier effect) but have caused a behaviour change, possibly related to the provision of trophic resources or the perception of safety (shelter).

The slowdown and sinuosity of earwigs on residues we observed in the present study are consistent with foraging theory (Andersson, 1978; Bell, 1991), the effect of artificial heterogeneity on movement

(Anselme, 2015), and the movement of larger animals on a larger scale (Fryxell et al., 2008; Morales et al., 2004; Owen-Smith et al., 2010). They confirm the importance of considering the effect of more realistic ground types on the movements of ground-dwelling arthropods if we want to optimise their spatial distributions for management practises such as conservation biological control.

#### **4.4 Conclusion**

To our knowledge, the method described in this study is the first to track the movement of nocturnal ground-dwelling arthropods in a realistic environment, with a high temporal resolution, an intermediate spatial extent (1 m<sup>2</sup>), and over an entire activity cycle. The technical solutions we set-up aimed to investigate how a terrestrial arthropod was affected by different ground types. Because they are based on generic principles, we think they are of great interest for the recent growing field of video monitoring and movement ecology. The relatively low cost of the cameras and the free software made it an inexpensive solution, easy to set up and replicate.

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#### **Conflicts of interest statement**

The authors declare no conflicts of interest.

## Authors contribution statements

BC, TD, PT, DC and CL conceived the ideas and designed methodology; BC collected the data; BC and TD analysed the data; BC and TD led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

## Data Availability Statement

We intend to publish in the nearest future the data of cleaned trajectories on CIRAD dataverse.

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