Radiotelemetry unravels movements of a walking insect species in heterogeneous environments

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The study of movements of individual organisms in heterogeneous environments is of primary importance for understanding the effect of habitat composition on population patterns. We developed a new experimental methodology to measure individual movements of walking insects, based on radiotracking. Our aims were to understand the link between habitat heterogeneity and moving patterns, and to characterize the movements with dynamic models of diffusion. We tracked individual movements of adults of *Cosmopolites sordidus* (Coleoptera: Curculionidae) with passive radio frequency identification (RFID) tags under different field management practices. Diffusion models based on recapture data indicated a subdiffusive movement of this species. Substantial variation was found between individual paths, but this variation was not sex dependent. Movement of released *C. sordidus* was affected by banana planting pattern and the presence/absence of crop residues but not by the presence of a cover crop between rows of bananas or by banana variety. These results show that the RFID technology is useful for evaluating the dispersal parameters of cryptic insects in heterogeneous environments.
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The dispersal of individuals is a fundamental process affecting the metapopulation dynamics of organisms (Chapman et al. 2007). Dispersal affects foraging choices, habitat selection and home ranges (Clobert et al. 2004); it allows population spread and redistribution between patches of suitable habitat (Stacey & Taper 1992; Doak 2000); it varies according to size, geometry and suitability of patches (Tscharntke et al. 2002; Kreyer et al. 2004); and it explains some of the spatial patterns of populations, such as clumping (Lopes et al. 2007; Vandermeer et al. 2008). Good measurements of individual dispersal behaviour in the wild are therefore needed to address these ecological processes (Samietz & Berger 1997). Movement processes inform the foraging ecology of organisms (Ramos-Fernandez et al. 2004). Fitting movement processes based on quantitative data allows us to predict long-distance dispersal and therefore assess population persistence and cohort strength (Coombs & Rodriguez 2007).

Most studies of insect dispersal are based on mark–recapture techniques, where insects are trapped and checked for the presence of the marker (Cronin et al. 2000; St Pierre et al. 2005; Arellano et al. 2008). Simple methods such as paint (St Pierre & Hendrix 2003), ink, dust or mutilations (Delattre 1980) are used for visual marking of insects (Hagler & Jackson 2001). Regular tracking of the same individuals is impossible because insects need to be trapped for identification. Other methods allowing regular tracking exist, such as direct observation by eye (Banks & Yasenak 2003) or with video recording (Hardie & Powell 2002; Robinson et al. 2009; Sendova-Franks et al. 2010) for diurnal organisms as well as artificial illumination, fluorescent powders (Turchin & Thoeny 1993) or reflective material for nocturnal organisms (Kindvall 1999). Tracking methods should account for individual variability in movement, which is influenced by sex, age or gene pool. For example, dispersal can be sex biased (Gros et al. 2009) or highly variable between individuals of the same sex (Bengtsson et al. 2004).

Among the methods for studying individual movement patterns of organisms, radio frequency identification (RFID) tagging is the most promising technology. It is a wireless sensor technology, based on the detection of electromagnetic signals emitted by a tag. It can be used to detect tags through a variety of habitats, for example a layer of soil (Mociño-Deloya et al. 2009). This method allows researchers to track organisms regularly in time and with limited disturbance of their behaviour, keeping the individual information of movements. RFID tags may be active (i.e. with

a built-in battery) or passive (i.e. based on the electromagnetic field generated by the RFID reader; Domdouzis et al. 2007). Detection distance ranges from several centimetres for passive tags to several hundreds of metres for active tags. It is only during the last decade that radiotransmitters have become sufficiently small to be attached to invertebrates (Reynolds & Riley 2002). Active tags have been used on tarantulas, *Aphonopelma hentzi* (Janowski-Bell & Horner 1999) and large insects (Riecken & Raths 1996; Hedin & Ranius 2002; Lorch et al. 2005). Passive tags have been used on social insects such as bumblebees, *Bombus terrestris* (Molet et al. 2008) and honeybees, *Apis mellifera* (Streit et al. 2003), and also on walking insects such as ants (Robinson et al. 2009) to study activity patterns.

Until now, RFID tags have not been used to study dispersal parameters of walking insects in their natural environment, such as the banana weevil, *Cosmopolites sordidus* (Germar). This insect attacks only wild and cultivated clones of the genus *Musa* (banana, plantain, abaca) and is recognized as a major pest of banana crops (Gold et al. 2001). The adult has a long life span and low fecundity; it is nocturnally active and gregarious. Banana weevils are hygrotactic (Roth & Willis 1963) and prefer habitats with a high humidity such as banana plants and crop residues (Gold et al. 2001). Males emit an aggregation pheromone that attracts both males and females (Beauhaire et al. 1995). Although *C. sordidus* adults have functional wings, they have never been observed flying and are assumed to move only by crawling (Gold et al. 2001). The movement of *C. sordidus*, however, has not been studied in detail. The insect's cryptic, nocturnal behaviour does not allow the use of direct visual marking techniques. Furthermore, *C. sordidus* has limited dispersal abilities (Gold et al. 2001). Banana fields can be infested with *C. sordidus* through the planting of infested material, through spread from a heavily infested neighbouring field, or through adults that have survived the last planting, which result in random, linear or patchy distributions, respectively (Delattre 1980; Treverrow et al. 1992). The weevil is able to colonize new banana plants from heavily infested plants.

We present here a new experimental methodology, based on radiotracking and quantitative analyses of individual movement paths. We applied this method to a cryptic insect to address the following questions. (1) Which movement process best suits the movement patterns of a walking insect? (2) How does habitat heterogeneity influence the spatial orientation of this organism? The study was conducted on *C. sordidus*, which shows cryptic and walking behaviours, in a heterogeneous natural environment composed of banana plants, bare soil, crop residues (leaves, pieces of old pseudostems and shoots) and cover crops.

METHODS

Insect Trapping, Sexing and Marking

Because *C. sordidus* was difficult to rear in the laboratory, adults were obtained from the field. Accordingly, instead of using cohorts of known age, we used large sets of individuals directly collected with pseudostem traps from one banana field (Rivière-Lézarde, Martinique, West Indies). To make pseudostem traps we cut banana plants into slices and lay them on the ground to attract weevils. This sampling method has been largely used in biological studies on *C. sordidus* (Delattre 1980; Kiggundu et al. 2007). We assumed that the distribution of ages of sampled individuals was similar to that of the field population. Insects were sexed according to Longoria (1968), based on punctuations of the rostrum that differ for male and female. Before they were released in experiments, insects were kept in the laboratory for up to 1 week in large plastic boxes (80 × 40 cm and 40 cm high) with soil and pieces of pseudostem at

room temperature. To prevent crowding effects we kept 25 adults per piece of pseudostem, which was much less than the density of weevils found on infested plants (Delattre 1980; Gold & Bagabe 1997). They were marked 2 h before release with passive RFID tags (TXP148511B, Biomark Inc., Boise, ID, U.S.A.) that were attached to the insect by braided fishing line (14 kg, 0.260 mm; Daiwa Sports Ltd, Wishaw, U.K.). Cyanoacrilate glue (superglue) was used to fix the tag to the line and the line to the insect's back (Fig. 1), and epoxy glue (Araldite) was used to smooth the surface of the tag. We attached the tag to the insect's back to avoid disturbing its burrowing behaviour. The ratio of tag mass to individual insect mass was 1:1 and the width of the tag was narrower than the insect. Each tag, and therefore each insect, was individually labelled with a unique identification label.

Laboratory Experiment

Insects with and without tags were followed for short distances (0.5 m) in controlled conditions at 25 °C to evaluate the possible bias from the tag weight on their dispersal capacities. Forty adults (20 tagged + 20 nontagged) were released in the morning (1000 hours local time, Martinique: GMT − 4 h) at the centre of a 1 m² wooden board that was covered or not covered with crop residues. The experiment was conducted separately for males and females and for boards with and without crop residues. For each individual, the time from release to arrival at the end of the wooden board was measured. Then recorded individuals were immediately removed. The release was repeated three times both for the covered and noncovered treatments, yielding a total of 120 individuals tested.

Field Experiments

Characteristics of experimental plots

Three experiments (named experiment 1, experiment 2 and experiment 3) were conducted in banana fields in Martinique, French West Indies (Table 1). Banana plants are considered to be semiperennial, and plants are successively replaced (as many as 50 times) by suckers emerging at irregular intervals from a lateral shoot of the mother plant (Turner 1994). Lateral shoots are selected by farmers so that there is only one shoot per mat. Mats of banana plants consist of one plant in young plantations and several plants in older plantations; mats include shoots, the so-called mother plant and the base of old plants resulting from former cycles. Banana plants were planted in double rows in experiment 1 (Fig. 2a, b; width of row: 1 m; width of inter-row: 5 m) and in staggered rows (width of inter-row: 2 m) in experiments 2 and 3 (Fig. 2c–g). Experiment 1 was carried out between January and February 2009 on a 4-year-old banana field. The objective of experiment 1

Figure 1. An individual *C. sordidus* with its tag.

Table 1
Characteristics of field experiments

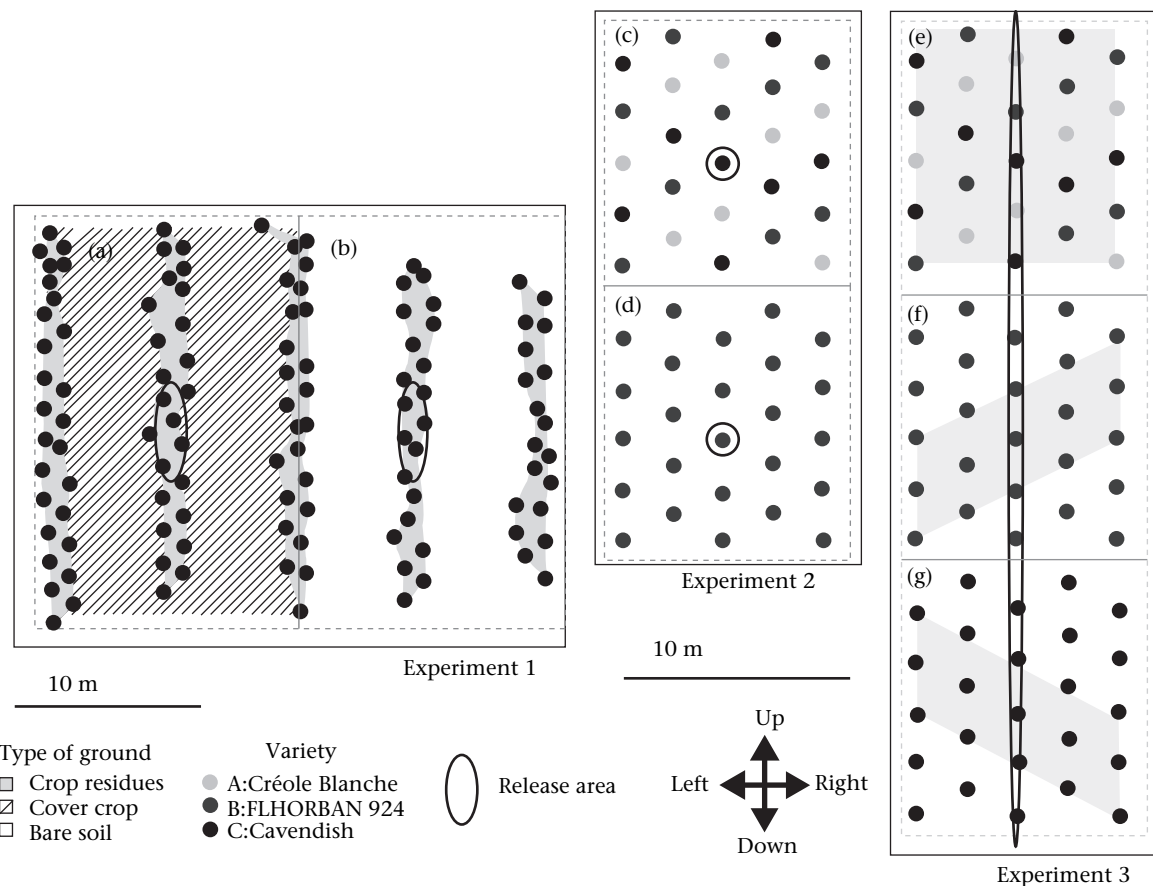|	Experiment 1	Experiment 2	Experiment 3
Site name	Rivière-lézarde	Petit Morne	Petit Morne
Site location	14°39′N, 60°58′W	14°37′N, 60°58′W	14°37′N, 60°58′W
Field area (m²)	2400	1300	1300
Area per plot (m²)	400	100	100
Plantation	Double row	Staggered rows	Staggered rows
Number of banana planting cycles	4	1	1
Banana stage	Flowering	Flowering	Flowering
Design	Randomized complete block	Randomized complete block	Randomized complete block
Treatments	2	4	4
Number of replicated plots/treatment	3	3	3

was to evaluate the effect of a cover crop on insect dispersal. Experiment 1 included two treatments: with and without a cover crop in the inter-row; each treatment was represented by three replicate plots.

Experiments 2 and 3 were carried out on banana fields recently planted with three varieties: A (*Musa* spp., AAB group, cv. Créole Blanche); B (*Musa* spp., AAA group, cv. FLHORBAN 924); and C (*Musa* spp., AAA group, cv. Cavendish Grande Naine). A is susceptible and C is tolerant to immature stages of *C. sordidus*; B is intermediate (Kiggundu et al. 2003).

The objective of experiment 2, which was carried out between May and June 2009, was to test the effects of banana plant variety on dispersal capacities and habitat preference of *C. sordidus*. The varieties A, B and C were planted in pure stands (one plot per variety) and in a plot containing a random mixture of the three varieties; all plots in experiment 2 had bare soil (Fig. 2). These four types of plot were replicated three times, giving a total of 12 plots.

The objective of experiment 3 was to test the effect of different spatial arrangements of crop residues (homogeneously distributed or in strips) on weevil movements. We compared the absolute angles of movement paths of weevils released on bare soil (outside residues) for plots planted with varieties A, B or C in pure stands with residues in strips (Fig. 2f, g; five and four replications, respectively) to those of weevils released in the same relative places in plots planted with a random mixture of varieties, where residues were homogeneously distributed (Fig. 2e; three replications). The distribution of absolute angles was expected to be nondirectional when crop residues were homogeneously distributed over the plot, and oriented towards crop residues when residues were in strips. Experiment 3 was carried out between July and August 2009.

We tested the effect of climate variables on movement patterns. Mean $\pm$ SD temperature, rainfall, wind strength and relative humidity of air were 26.2 ± 1.6 °C, 6.7 ± 10.5 mm/day, 1.62 ± 0.34 m/s and $75.3 \pm 5.2\%$, respectively. We found no significant effect of climate variables on the percentage of recaptured tags, the mean

Figure 2. Diagrams of the three field experiments used to measure the effects of various factors on movement of *C. sordidus* individuals with RFID tags. An example of each treatment is presented (a–g). Treatments a–e, f and g were replicated three, five and four times, respectively. Dashed lines indicate plot edges. Experiment 1 compared the effects of (a) a cover crop or (b) bare soil between the banana rows. Experiment 2 compared the effects of banana varieties planted in (c) a random mixture or (d) pure stands (where variety B is shown as an example). Experiment 3 compared the effects of crop residues (e) covering the whole treatment area (with mixed varieties) or (f–g) arranged as a strip (with varieties planted in pure stands). Black ellipses represent the release area of each experiment; *C. sordidus* individuals were released in a patch, a plant, and on a line in experiment 1, experiment 2 and experiment 3, respectively.

distance moved per day and the number of movements during the experiments (Pearson test: $P > 0.05$). The only exception was an effect of the relative humidity of the air on the distance moved per day ($R^2 = 0.20$, $N = 40$).

Releasing and monitoring of the tagged insects

For experiment 1, 204 tagged individuals (34 per plot) were released on 12 January 2009. Insects were released in the centre of each plot on a patch 2 m long and 0.3 m wide in the double row (Fig. 2a, b). For experiment 2, 360 tagged individuals (30 per plot) were released on 11 May 2009. Insects were released near the central banana plant of each plot, on a circle of 1 m diameter (Fig. 2c, d). For experiment 3, 360 tagged individuals (30 per plot) were released on 16 July 2009. Insects were in a line with alternate male and female individuals 20 cm apart (Fig. 2e, f). Orientation of the weevil's body on the ground and sex of released weevils were random for the three experiments.

Insect location was monitored during 38, 22 and 30 days for experiments 1, 2 and 3, respectively. Individuals were monitored daily during the first week, three times per week during the second week, two or three times per week the following weeks, and once the last week of the experiment leading to 18, 13 and 16 measures for experiments 1, 2 and 3, respectively. A RFID antenna with a Destron Pit tag reader (model FS2001 FR/ISOCB) was used to locate insects at the base of banana plants, on the surface of bare soil, and on the surface of soil covered with crop residues. The detection distance, which was measured in the field with tags alone, was between 0 and 20 cm. When a tag was detected, the power of the signal increased with the proximity to the tag; the precision of the signal's position was 10 cm. A stake with its code was sunk near the tag position, and this position was indicated on a 1/100 map of the observation area, with an overall precision of 30 cm. Each tag was spatially localized, and its local environment was recorded. For experiment 1, the recorded environments were 'near a banana', 'on a mother plant', 'on a shoot' or 'on an old plant'. For experiment 2, they were 'on bare soil' or 'on a mother plant' and for experiment 3, 'on bare soil', 'under the crop residues' or 'on a mother plant'.

At the end of each experiment, all the tags were systematically searched for and removed from the field. The state of each tag was recorded (attached to a living weevil, attached to a dead weevil or separated from the weevil).

Analysis of insects' paths

Basic geometric and quantitative properties of the path of each insect were defined according to Patterson et al. (2008) as follows. A path consists of several segments, named steps, linking time-indexed positions of an individual over the study period. Paths were located on an orthogonal plane with plot axes (left–right and up–down) as indicated in Fig. 2. We calculated the length of each step, the length of the path, the absolute angle between the segment linking the beginning and end of the path and plot axes, and the relative angle (called the turning angle) between two successive steps, as well as the mean squared displacement between each step (R_n^2). Lengths of steps were divided by time (in days) between two successive observations to take into account unequal times between observations. For individuals found alive at the end of the experiment, the monitoring period then stopped. For individuals found dead or not found at the end of the experiment, the monitoring period stopped at the last recorded movement. Movement metrics and all parameters were calculated taking into account individual monitoring periods, the monitoring period of each individual being defined as the time between release and the last recorded movement. Movements of length less than 10 cm were not recorded.

For testing the movement process that best suits the movement patterns of *C. sordidus*, we plotted the mean squared displacement (R_n^2) of each individual versus time (t) and we tested whether the diffusion model was subdiffusive or superdiffusive by fitting a power model on the resulting curve:

$$R_n^2(t) = at^b \tag{1}$$

where a and b are parameters. The coefficient b of the power model indicates whether the curve is concave or convex, suggesting a subdiffusive or a superdiffusive movement, respectively (Uchaikin 1999; Yadav & Horsthemke 2006).

A model of equation 1 was fitted to the data using nonlinear least squares (Bates & Watts 1988). The coefficient R^2 of the fitting was estimated using a log transformation of the data for linearization (Turchin & Thoeny 1993).

Statistical Analysis

All statistical analyses were performed with R software (R Development Core Team 2009) using basic packages, and specialized packages such as 'spatstat' (for spatial analyses and mapping) and 'circular' (for circular analyses).

The effect of the tagging method (tagged or nontagged) on the dispersal capacity (laboratory experiment) was assessed using a t test, after testing the normality of the data with the Shapiro test (Royston 1982). Repeatability of recapture rates over time was calculated from a one-way analysis of variance using among-plots and within-plots variances (Lessells & Boag 1987).

Distributions of movement metrics for male and female over the three field experiments were compared using the Kolmogorov–Smirnov test (Conover 1971). The Watson two-sample test was used to compare the circular distribution of angles (Jammalamadaka & SenGupta 2001). Mean and standard deviation of absolute and relative angles were calculated assuming von Mises distributions. This assumption was confirmed by the Watson test (Stephens 1970). The significance of mean direction of circular distributions was tested using the Rayleigh test (Jammalamadaka & SenGupta 2001). For applying circular statistics, bimodal distributions of absolute angles in experiments 1 and 3 were separated into two ranges, from $-180°$ to $0°$ and from $0°$ to $180°$.

Reaching a given row with or without a cover crop and being attracted towards a given variety were considered as Bernoulli experiments for statistical analyses. The effect of adding a cover crop on the proportion of individuals that reached the next row on the other side of the release point was analysed with a generalized linear model (GLM), assuming a binomial distribution of values. The global effect of varieties on movement metrics of insects was analysed with a GLM, assuming a Poisson distribution of number of movements during the experiment (Kolmogorov–Smirnov test: $D = 0.1231$, $P = 0.71$) and a gamma distribution of distance moved per day (Kolmogorov–Smirnov test: $D = 0.0739$, $P = 0.41$). The deviation from a theoretical distribution of the observed distribution of weevils on varieties in plots planted with a mixture of varieties was chi-square tested to analyse the attractiveness of varieties to weevils.

RESULTS

Efficiency of the Tagging Method

Table 2 presents the results of the laboratory experiment (tagged versus nontagged insects). For both the noncovered and the covered wooden boards, there was no significant difference for time to reach the edge of the wooden board between tagged and nontagged for both females and males. We also observed that

Table 2
Time (min) for individual weevils to reach the edge of the wooden board in the laboratory experiment

	Tagged individuals		Nontagged individuals		df	t test	P	95% Confidence interval
	Mean	Range	Mean	Range				
Noncovered experiment								
Female	13.1	(2.4–25.0)	13.2	(3.2–23.4)	118	0.113	0.91	(−1.6–1.8)
Male	12.0	(2.5–23.0)	11.0	(1.6–24.3)	118	−1.043	0.30	(−11.0–12.0)
Covered experiment								
Female	357.7	(40–574)	344.5	(58–585)	118	−0.496	0.62	(−65.7–39)
Male	357.7	(40–574)	326.7	(40–595)	118	−0.346	0.73	(−44.5–63.4)

Mean times were normally distributed (Shapiro test: $W = 0.9833$ and 0.9691, $P = 0.006$ and $P < 0.0001$ for noncovered and covered experiments, respectively).

tagged weevils maintained in boxes with pseudostem pieces were able to enter and leave the pseudostem freely.

The mean percentage $\pm$ SE of recaptured tags was $77.2 \pm 6.4\%$, $56.4 \pm 13.2\%$ and $61.3 \pm 6.7\%$ for experiments 1, 2 and 3, respectively. Repeatability of percentage of recaptured tags over time was 0.35, 0.57 and 0.14 for experiments 1, 2 and 3, respectively. The lowest level of repeatability for experiment 3 was due to a weak decrease of the recapture rate over the first few days (data not shown).

Dispersal Parameters

The individual monitoring period was 21.3 ± 11.5 days. A large proportion (0.74) of individuals remained in the 2 m area around the release site after 3 days. This proportion decreased to 0.43 after 29 days. Individuals moved on average 0.37 m/day for the three experiments, considering the ratio between path length and monitoring periods over all individuals. When periods of inactivity were removed, this rate of movement increased to 0.50 m/day. The maximal distance covered was 9 m in 1 day. The distribution of distances moved per day was not significantly different between males and females for the three experiments (Kolmogorov–Smirnov test: $D = 0.0455$, $P = 0.78$).

The power model of equation 1 explained 85% of the variation of the mean squared displacement (nonlinear least squares, R^2 on log-transformed data). As $0 < b < 1$ (95% confidence interval estimated from 1000 bootstraps: 0.44–0.67), the movement is subdiffusive. Subdiffusive movement is illustrated by the concavity of the curve on Fig. 3.
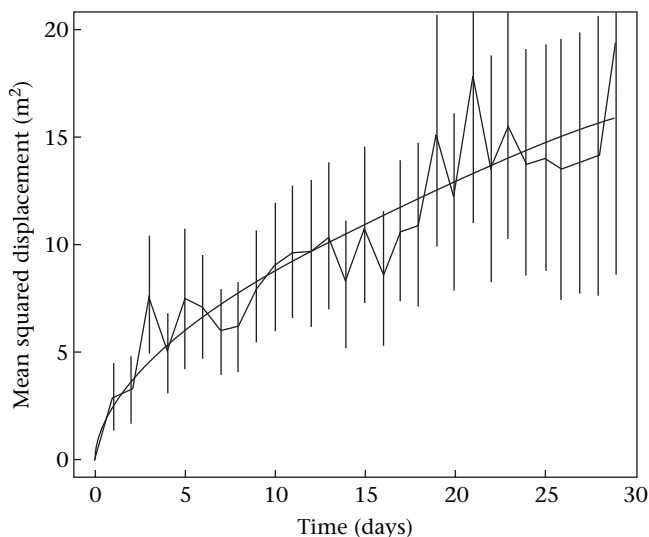
Figure 3. Fit of a power model (equation 1) on the mean squared displacement of individuals versus time since release. Error bars (SE) are indicated.

In experiment 1, the proportion of individuals in crop residues decreased over time (Pearson product–moment correlation: $r_{16} = -0.65$, $P = 0.003$). The proportion of individuals in mother plants and in old plants was equal ($\chi^2_1 = 0.14$, $P = 0.71$) and considerably larger than the proportion in shoots ($\chi^2_1 = 42$, $P < 0.0001$; Fig. 4a). In experiment 2, all the individuals were found in planted bananas. In experiment 3, nearly 60% of the individuals were found in crop residues, about 40% were found in planted bananas consisting only of mother plants, and none were found on bare soil (Fig. 4b, c). Furthermore, the proportion of males in crop residues increased over time at the expense of the proportion in planted bananas (Pearson product–moment correlation: $r_{13} = 0.87$, $P < 0.0001$; Fig. 4c). The proportions of females in crop residues and on banana plants did not change over time in experiment 3 (Pearson product–moment correlation: $r_{14} = 0.039$ $P = 0.88$; Fig. 4b).

The distribution of turning angles between successive positions differed significantly from a uniform distribution for every experiment (Watson two-sample test: $U^2 = 0.217$, 0.648 and 2.203, $P < 0.001$ for experiments 1, 2 and 3, respectively). Turning angles were back oriented in the three experiments at $179.1 \pm 45.2°$ (mean direction of resultant vector $\pm$ circular variance; Rayleigh test: $P < 0.001$), indicating a tendency of weevils to do U-turns (Schtickzelle & Baguette 2003). Their distribution was not significantly different between males and females (Watson two-sample test: $U^2 = 0.0001$, $P > 0.10$).

Effect of Management Practices

In experiments 2 and 3, in which varieties A, B, and C were planted homogeneously, the variety of banana had no effect on the movement metrics of the insect, such as the number of movements during the experiment (GLM: $F_{2,62} = 0.79$, $P = 0.59$) and the mean distance moved per day (GLM: $F_{2,281} = 0.62$, $P = 0.43$). In the treatment where a random mixture of these varieties was planted, the proportion of individuals moving from the release point to a different variety was cumulated over repetitions, yielding $P_A = 11/31$, $P_B = 8/31$ and $P_C = 12/31$. These proportions were not significantly different from the proportions of the variety in the plot (1/3; $\chi^2_3 = 1.82$, $P = 0.61$).

At the end of experiment 1, weevils were significantly more abundant in their release row than in other rows ($\chi^2_1 = 19.3$, $P < 0.001$). There was no effect of the type of inter-row (bare soil or cover crop; $\chi^2_5 = 1.67$, $P = 0.89$; Fig. 2a, b) on the weevils that moved to another row. The absolute angles between paths of each individual and plot axes differed according to the experiment (Fig. 5). In experiment 1, paths of released individuals were oriented up and down (mean direction $= -85.2°$ and $82.3°$ for negative and positive angles, respectively; Rayleigh test: $P < 0.0001$; Fig. 5a), following the organization of planting rows. In experiment 2, the distribution of absolute angles between individual paths was not significantly different from a uniform distribution (Watson two-sample test: $U^2 = 0.105$, $P > 0.1$; Fig. 5b). In experiment 3, the distribution of absolute angles for individuals released on bare soil was significantly different from a uniform distribution (Watson two-sample test: $U^2 = 0.179$, $P < 0.01$; Fig. 5c). The mean directions of individuals released on bare soil were $-90.5°$ and $86.3°$ for negative and positive angles, respectively (Rayleigh test, $P < 0.0001$; Fig. 5c). In contrast, the distribution of absolute angles for individuals released under crop residues was not different from a uniform distribution (Watson two-sample test: $U^2 = 0.042$, $P > 0.1$; Fig. 5d).

DISCUSSION

The new RFID-based methodology was successfully used to understand true fine-scale movements of an insect species in
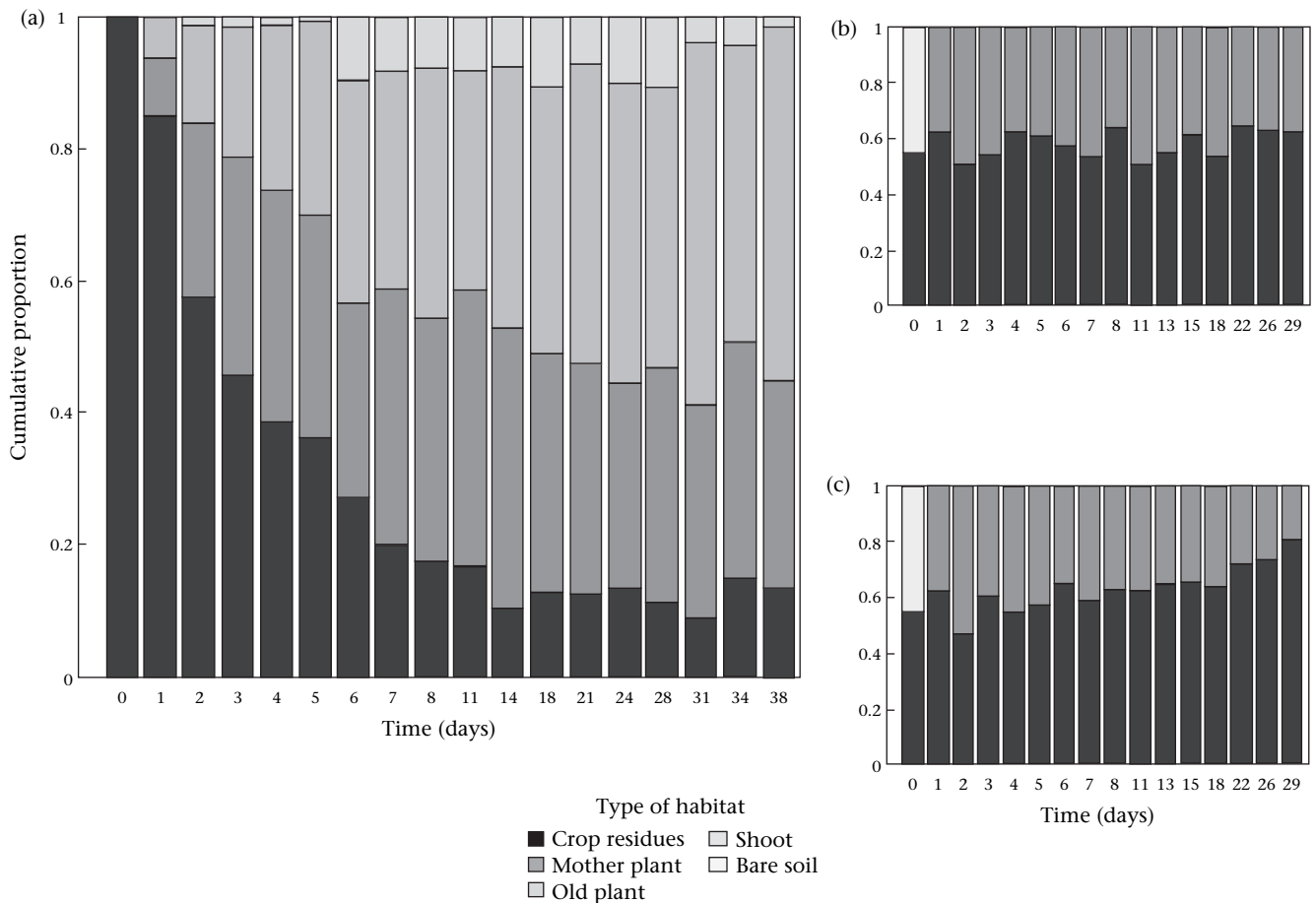
Figure 4. Relative cumulated histograms of distributions of released individuals of *C. sordidus* in different habitats in (a) experiment 1 and (b–c) experiment 3; (b) females and (c) males.

heterogeneous environment. First, the laboratory experiment showed that the tagging method did not affect movements of *C. sordidus*, although the weight ratio of tag to insect was almost 1:1. This ratio is generally lower for flying insects in mark-recapture studies, ranging from 0.025 to 0.05 (Ranius 2006). However, *C. sordidus* is a burrowing insect and is able to carry more than its weight, as is also the case for ants, which carry from 3.5 to 6.5 times their body weight (Burd 2000). Furthermore, the estimated frequency and range of dispersal movements were of the same magnitude as those estimated in the other mark-recapture studies on this insect. In our experiments, 74% of the weevils remained near their release site after 3 days, in accordance with Delattre (1980). The dispersal of *C. sordidus* appeared to be limited and slow. Adults moved on average 0.37 m/day, with a maximal distance moved in 1 day of 9 m, which agrees with a maximal weevil movement of 6 m and 15 m recorded by Wallace (1938) and Cendana (1922), respectively. After 29 days, weevils had remained within 10 m of the release site. Whalley (1957) and Cardenas & Arango (1987) reported that most banana weevils move less than 10 m over a period of several months. Second, recapture rates were higher than found with capture–recapture studies (Koppenhofer et al. 1994; Tinzaara et al. 2005). The error in location of individuals (0.3 m) was negligible in comparison to the range of displacements (1–10 m). However, RFID-tagged weevils may suffer from long-term effects such as exhaustion or a higher level of predation, which were out of the scope of this study which focused on short-term movements. For example, tagged weevils could be more visible to predators (toads, lizards or birds) when they disperse on

bare soil or egg-laying behaviour of females could also be influenced by the tagging. Further experiments will be needed to study this potential bias.

The relationship between the mean squared displacement and time since release was not linear as predicted by a simple diffusion model (Banks & Yasenak 2003). The analysis of this relationship revealed that the movement process of *C. sordidus* is subdiffusive rather than diffusive. This means that weevils are most active just after release. During this period, weevils may search for a suitable microhabitat.

The analysis of the circular distribution of turning angles characterizes the foraging strategies of *C. sordidus*. It suggested that individuals make frequent U-turns. As plots were surrounded by deep and large ditches and no weevils were found inside, U-turns could be attributed to weevils that hit the plot borders. Nevertheless, the high level of circular variance ($\sigma^2 = 45.2°$) of turning angles means that subsequent steps of the trajectory were poorly correlated, indicating a random walk movement of individuals. The high frequency of turns suggests an 'area-restricted' searching behaviour (Westerberg et al. 2008). This type of behaviour is usual when individuals are entering a resource patch (Dajoz 2002; Shuranova 2008; Garnier et al. 2009).

Radiotracking revealed variation among individuals for movements and habitat selection. As shown by the error bars of mean squared displacements over time, some individuals moved faster than others. Individuals did not necessarily choose the same habitat whereas they were released at the same position (data not shown). However, individual variation in movement and in habitat selection
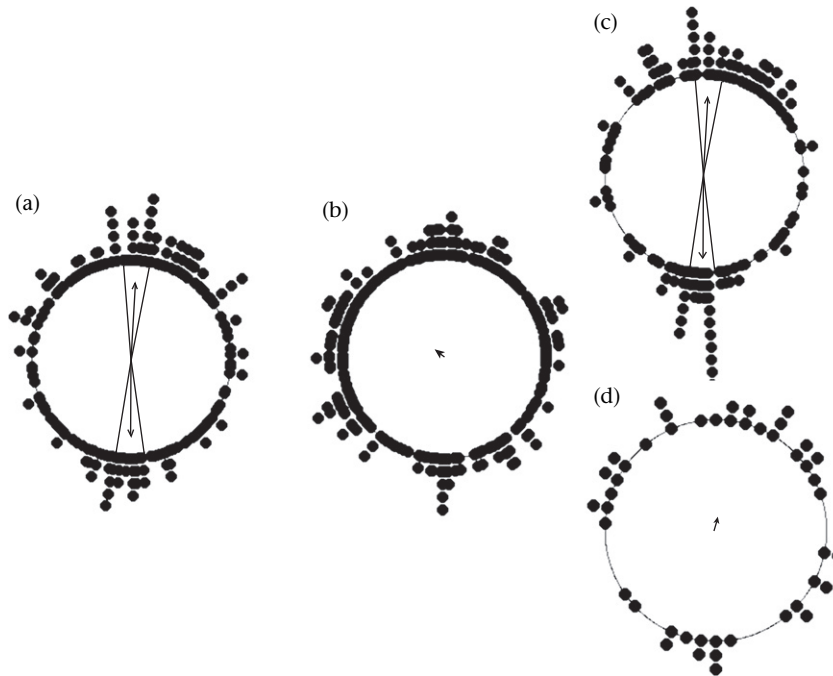
Figure 5. Frequency distribution of absolute angles between individual paths of *C. sordidus* and plot axes for (a *N*= 198) experiment 1 (see Fig. 2a, b), (b *N* = 284) experiment 2 (see Fig. 2c, d) and (c *N* = 155) experiment 3 for individuals released on bare soil (see Fig. 2f, g) or (d *N* = 46) in the same relative places under crop residues (see Fig. 2f, g). *N* refers to the number of individual paths used for the construction of the frequency distribution of angles. Arrows represent the mean direction of circular distributions. For (a) and (c), distributions are separated into two ranges (see Methods). Confidence intervals (0.95) are shown by black lines, except for (b) and (d) where the distribution of angles does not differ from a uniform distribution.

was not explained by gender. Movement parameters seemed generally similar for males and females, in accordance with Gold et al. (1999). Hedin et al. (2008) found the same result with *Osmoderma eremita*. The sex ratio is balanced for both *O. eremita* (Ranius 2001) and *C. sordidus* (Gold et al. 2001). Differences in movement patterns are generally observed for organisms with a biased sex ratio. Higher movement rates are found for males when the population is female biased (Young 2001; Gruber & Henle 2008; Kwiatkowski et al. 2008). In our experiments, however, we found fewer tagged males than females in banana plants. It is thus possible that females were less exposed to predators than males, perhaps because females must lay eggs in the less-exposed parts of the banana corm to increase the survival of immatures. We suppose that some of the individual variability of insect paths is determined by factors other than gender, such as age or fitness.

Our study suggests that habitat matrix heterogeneity affects the movement patterns of insects. Attractiveness of habitats may increase with the stage of the resource; for example, shoots of young banana plants were less attractive than older plants. It may also vary temporally: for example, crop residues would make old banana plantations more attractive. The analysis of absolute angles between subsequent steps of individuals clearly indicates that the spatial heterogeneity of the plantation and the spatial organization of residues affect the direction of individual paths. As movements of individuals are oriented towards crops and residues, the spatial arrangement of these elements may alter dispersal. However, some habitat elements, such as cover crop or varieties of banana in our case, do not affect the weevil's dispersal, which is consistent with McIntyre et al. (2004) who showed no effect of adding mulch on infestation patterns of *C. sordidus* in Uganda and with Pavis & Lemaire (1996) who suggested that the resistance of varieties was not related to attractiveness but rather to antixenosis.

In conclusion, we developed an experimental methodology that makes it possible to study the fine-scale movements of walking insects at the individual level, to derive movement patterns and to analyse the effects of habitat heterogeneity on movements. This offers the opportunity to implement individual-based models for pattern-oriented modelling (Grimm et al. 2005) such as that of Vinatier et al. (2009) on *C. sordidus*, thus helping to bridge the gap between individual and population studies.

Acknowledgments

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