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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.

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

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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 m^2 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.