Ground beetle dispersal: how to bridge the scales?

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Abstract: Beneficial arthropods that provide biological control of aphids or weed seeds use a variety of habitats in agricultural landscapes. Information on the movement behaviour of these arthropods between these habitats is needed to develop conservation strategies that sustain pest suppression in agricultural landscapes. Models for movement behaviour may help to understand and explore biocontrol functions. As measurements of behaviour at the landscape scale are technically difficult to make, measurements are often made at smaller scales. It is then necessary to upscale to larger scales, using movement models. Here we present a case study on such upscaling. The first results indicate that upscaling from small scales to large scales, using a correlated random movement model, may result in errors. An alternative approach, to be tested in further work, is to fit the movement model directly to the large scale data.

Keywords: Ground beetle movement, correlated random walk, dispersal, scaling-up

Introduction

Naturally occurring predators provide the ecosystem service of biological control in field crops. These predators require resources in the landscape for overwintering, shelter against adverse conditions in the field, and alternative food sources. A key issue for the design of pest suppressive landscapes is how predators move between these resources (Bianchi et al. 2006).

Movement can be studied at several scales. Studies of behaviour can be made in small arenas using automated equipment as well as at field and landscape scale by manually tracking the movement of individuals. An alternative approach is to study population redistribution in space, the population-level consequence of movement. Population redistribution in space can be monitored, for example, by mass mark-recapture experiments. Via reverse engineering we can then infer the movement behaviour that gave rise to the population redistribution pattern.

Random walk models are often used to predict the large scale population redistribution pattern of animals (Hengeveld 2007). For any modelling approach, a key question is at which scale the behaviour should be measured. And is it possible to predict events at a larger spatial scale on the basis of a behavioural model parameterized with data that are collected at a smaller spatial scale?

Here we address this question by fitting a correlated random walk model to data collected in small scale dispersal experiments. This model is then used to predict results of a large scale dispersal experiment, and predictions are tested against the data.
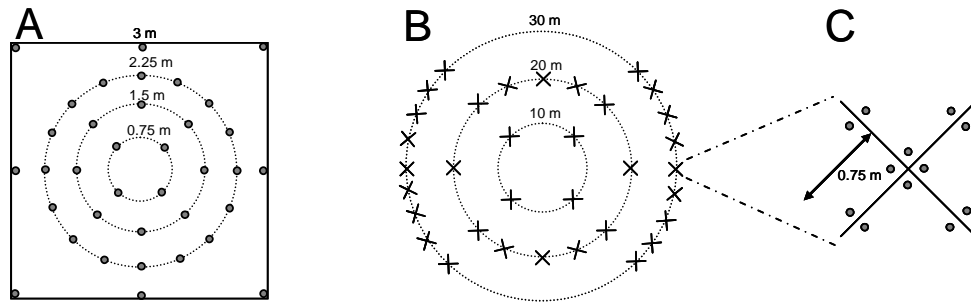
Figure 1. Map of the traps in the 6 x 6 m fenced plot (A) and at the larger 30 x 30 m scale (B). Trap sites in B consist of 12 pitfalls and a plastic cross, as shown in C.

Materials and Methods

Small scale population redistribution (6x6 m)

Four replicates of a small scale mass mark-recapture experiment were conducted in a triticale field, undersown with grass/white clover, at the Droevendaal Organic Farm of Wageningen University in June 2009. *Pterostichus melanarius* (Illiger) were collected on the farm by pitfall trapping in the weeks before the release. They were marked with a water-based paint (Posca paint marker) or red nail polish (HEMA, long lasting nr. 84).

On 3, 9, 15 and 20 June 2009, thirty beetles (15 male and 15 female) were released in the centre of a 6 x 6 m plot. The plot was fenced with 50 cm high plastic barriers that were dug 10 cm into the soil. Different colour marks were used to discriminate between beetles from the four releases. Recaptures were made using pitfall traps (Ø 8 ½ cm) arranged in three concentric circles around the centre of the plot and additional pitfalls at the borders (Figure 1A). Beetles were collected 2, 4, 6 and 8 days after release, but only the data from day 2 were used to calibrate the random walk model.

Large scale population redistribution (30x30 m)

This experiment was similar in setup to the small scale experiment, but the scale was larger and there was no border. The experiment was done in the same triticale/grass/clover field one week after the small scale dispersal experiment.

On a single occasion 1000 marked beetles (500 male, 500 female) were released in a square release area of 6x6 meter. Beetles were marked with red nail polish (HEMA, long lasting nr. 84) and recaptured in pitfalls in three concentric circles at 10, 20 and 30 meter from the centre of the release square (Fig. 1B). To enhance the recapture rate a cross was placed at each trap site (Fig. 1C). The number of recaptured beetles per trap site was counted daily for 14 days.

Model calibration

A random walk model was fitted to the mark-recapture data obtained at the 6x6 m scale. In this model beetles walk with a fixed move length (x). The turning angle from one move to the next is taken from a wrapped Cauchy distribution with a mean turning angle $\theta_0 = 0$, and a scale parameter γ (Batschelet, 1981). This distribution represents a bell shape wrapped around a circle. The scale parameter is calculated from ρ, the mean of the cosines of turning angles as:

$$\gamma = 2\tan^{-1}\left(\frac{1-\rho}{1+\rho}\right)$$

ρ is also referred to as the mean vector length (Batschelet, 1981; Bartumeus, 2005). It is a measure of concentration of the distribution of turning angles about the mean. If $\rho = 0$, the distribution is uniform on the circle. The corresponding walk is uncorrelated, i.e. the heading of the beetle is uniform on the circle, corresponding to a Brownian motion. If $\rho = 1$, the distribution is a spike at θ_0, and the walk has complete directional persistence, i.e. the movement path is straight, which is also referred to as 'ballistic'. As ρ increases from 0 to 1, there is a smooth transition from a uniform distribution of turning angles to this spike via ever narrower bell shapes, and the resulting movement pattern is a correlated random walk, whereby ρ expresses the degree of correlation. The parameters ρ, move length (x), number of moves (N) and trap efficiency (T) were fitted to the total number of beetles recaptured per distance per replicate, using maximum likelihood, assuming a Poisson error distribution. The prediction quality of the model at small scale was assessed by "leave one out cross validation" whereby – each time – three replicates were used to calibrate the model, and predict the fourth replicate. Reflecting boundary conditions were assumed.

Model testing at the larger scale

The average parameter values from the four model calibrations were used to simulate walking paths of beetles at the large scale. Simulated catches were compared to observed catches after fourteen days in the large scale dispersal experiment. No allowance was made for the crosses at each sample site. To represent the larger capture domain of sample sites, the diameter of traps was calibrated so that the simulation results at the 10 m traps matched the data.

Results and Discussion

Model calibration and validation

Calibration at the small scale resulted in an average move length $x = 14.8$ cm (ranging from 12-17 cm), a number of moves $N = 265$ in 2 days (ranging from 140-400), a mean cosine of turning angles $\rho = 0.525$ (ranging from 0.5-0.6), and an average trap efficiency $T = 0.45$ (ranging from 0.4-0.6). The predicted and observed pattern of recaptured beetles in the fenced plot showed satisfactory correspondence (Fig. 2A), with $R^2_{prediction} = 0.64$ (Turchin, 2003).

Pterostichus melanarius is active for approximately 4.8 hour per day (Firle et al. 1998), hence the *speed* of movement, calculated as the ratio between move length and move duration, is 3.9 to 8.3 cm/min, which is in good accordance with an observed speed of 4 cm/min in direct observations of movement of *P. melanarius* by Wallin and Ekbom (1988).

Model testing at the larger scale

Model predictions, using average parameter values from the calibrations at the small scale, underestimated population redistribution at 20 and 30 meters by an order of magnitude (Fig. 2B). A first attempt to bridge the scales entailed checking which parameters might be responsible for the discrepancy. Since calibrated movement speed was in agreement with field observations on *P. melanarius*, we conjecture that directional persistence of movement at the large scale may have been greater than estimated from the small scale data. Increasing the directional persistence, by increasing ρ, gave indeed a better fit. While it cannot be ruled out that a difference in directional persistence between experiments resulted from biological variability, the result also alerts to the possibility of an intrinsic problem with measuring directional persistence in small scale experiments and extrapolating this to larger scales.

The methodology of reverse engineering that we used to infer movement behaviour from a population redistribution pattern seems a promising way forward to improve insight in

movement behaviour. Calibrating the random walk model to the large scale population redistribution pattern, and a comparison with direct observations on movement behaviour in the field, will elucidate if reverse engineering indeed can help us understand how predators move at the landscape scale.
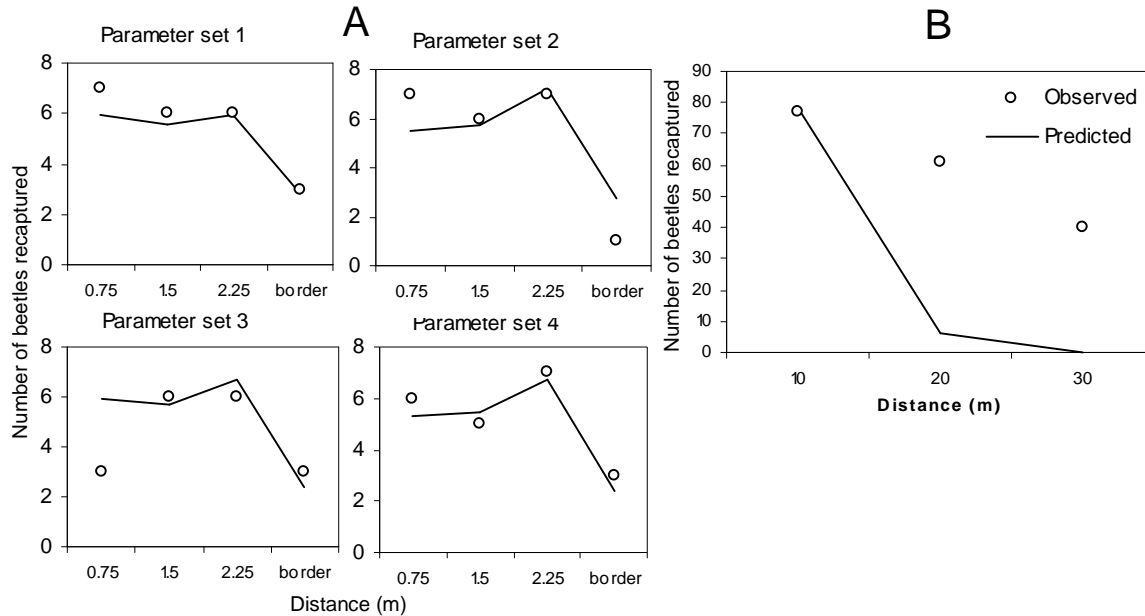

Figure 2. Number of beetles recaptured per distance in (A) the small scale experiment after two days and (B) the large scale experiment after fourteen days. Panel A shows data (circles) and predictions (lines) for one replicate based on parameters estimated from 3 other replicates. Panel B shows data (circles) and a prediction based on parameters averaged from 4 replicates in the small scale experiment.

Acknowledgement

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