# Relative roles of resource stimulus and vegetation architecture on the paths of flies foraging for fruit

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Many animals use their perceptual abilities to orient and locate resources in architecturally complex environments. However, it is not well known how the strength of a stimulus source affects the geometry of animal movement in architecturally complex environments. We mapped the 3D vegetation architecture of four apple trees of varying morphology and age and recorded the paths of apple maggot flies *Rhagoletis pomonella* foraging for artificial fruit. We compared the observed movement with the one obtained from a random walk model on a graph to estimate both 1) the attraction radius and strength of a fruit and 2) the relative roles of the architecture of vegetation and of the strength of attraction of a fruit on the movement of flies. The attraction radius is the maximal distance at which a stimulus source biases the movement of individuals and the attraction strength measures how strong this bias is. Plant architectural complexity is defined according to both foliage density and its 3D distribution within the canopy. A single fruit induces a bias in the path orientation of an insect that is at a large distance, relative to a tree volume, but it has no effect on the step length of moves. The plant complexity makes a minor contribution to defining the radius of the sphere of attraction, but a large contribution to the attraction strength. Conditional on visiting the location, the plant architecture plays a minor role compared to that of the presence of the fruit. Our findings show that the complexity of the environment can alter the use of sensory information, which has important implications for animal movements in complex environments. The importance of our results in animal dispersal and foraging is considered.

All animals exploit environmental information to locate resources and shelter, or to avoid areas with predators (Olden et al. 2004, Reynolds et al. 2007, Humphries et al. 2010, Schmidt et al. 2010). However, the perceptual range of individuals limits the spatial extent from which environmental information is obtained. Thus, the perceptual range determines the distance from which an external stimulus can affect the orientation and movements of animals (Lima and Zollner 1996, Olden et al. 2004). Many animals use environmental information while moving in geometrically complex environments. Examples include parasitic wasps searching for their hosts among grass stems (Randlkofer et al. 2010), spider monkeys searching food within the forest (Boyer et al. 2006), and invertebrates searching for prey at the leaf litter surface (Morice et al. 2013). Although there has been some work on modelling animal movement in complex vegetation structures (Cuddington and Yodzis 2002, Gingras et al. 2002, Hanan et al. 2002, Hannunen 2002, Skirvin 2004), we are not aware of any study which tested the role of vegetation architecture on both the perceptual range and movement of animals that forage in vegetation.

The perceptual range is closely related to the fine-scale movement of animals, so it can also influence a wide range of processes, from the dispersal of individuals to their foraging behaviour (Wiens et al. 1993, Lima and Zollner 1996). Dispersal is a key process that determines the dynamics and persistence of spatially structured populations (Hanski 1999). Connectivity among patches largely determines the colonization–extinction dynamics and the perceptual range is an important determinant of the dispersal success (Zollner and Lima 2005). Most work estimating the perceptual range of animals aimed to study how this range affects the detection of patches and thus the connectivity of populations in heterogeneous landscapes (Schooley and Wiens 2003, Bridgman et al. 2012). This is of importance when predicting how habitat fragmentation may limit the dispersal and the viability of populations (Lima and Zollner 1996, Flaherty et al. 2008). Perceptual range also plays a central role in animal foraging. Predators utilize sensory cues to locate prey and vice versa. Thus, the perceptual abilities of both prey and predators could affect, in principle, encounter rates and the functional response of predators, which describe their feeding rates (Hein and McKinley 2013). Most work, however, focused on estimating the perceptual range of animals – the maximal distance at which a stimulus source biases the movement of individuals –, but has traditionally neglected

to study the attraction strength of stimuli, which measures how strong animal movements are biased by stimuli.

In the last decade, some researchers have also incorporated a dynamic component into the notion of the perception radius of animals: several studies have shown that environmental features can influence the perceptual range of animals. For example, the amount of vegetation or the wind direction may modify the visual and the olfactory perceptual range in two species of marsupials and a cactus bug, respectively (Schooley and Wiens 2003, Prevedello et al. 2011). There is thus differential perception depending on the environment experienced, and Olden et al. (2004) highlighted the importance of using context-dependent perceptual ranges to model animal movements more accurately. Nevertheless, when estimating the perceptual range of animals, ecologists have generally simplified the fine-scale architecture of the habitat and consequently the bias that an external stimulus can introduce when animals move (Mech and Zollner 2002, Schooley and Wiens 2003, Prevedello et al. 2011). In particular, the architecture of the vegetation in which the animals live is of special importance because it can largely determine the movements of the animals, and, in turn, the trophic interactions (Andow and Prokrym 1990, Casas and Djemai 2002, Cronin and Haynes 2004, Gols et al. 2005, Morice et al. 2013). The term plant architecture is used for the geometrical information that describes the orientations and the 3D distribution of foliage, but not the topological information describing which components are connected with others (Godin 2000). As a consequence, there is still no complete understanding of how an external stimulus biases the movement of animals in geometrically complex environments (Morice et al. 2013). Estimating the effects of vegetation architecture on the perceptual range and attraction strength can be a daunting task, but it is a necessary step to understand animal movement in complex vegetation architectures.

In this study, we 1) estimated the attraction radius and strength of a foraging stimulus – an artificial fruit – and 2) investigated the relative roles of the architectural complexity of vegetation and of the strength of a foraging stimulus on the movement geometry of apple maggot flies *Rhagoletis pomonella*. The attraction strength of the fruit was estimated as a function of the distance to it. We compared the observed probabilities of visiting the stimulus source location, with the null probabilities of visiting the same location in the absence of the fruit, for varying distances. If the observed probabilities are higher than the null visit probabilities, the fly is assumed to be attracted to the stimulus source. The null visit probabilities were estimated using random walks in graphs; this is a powerful method for modelling the movement of animals in structured environments.

## Material and methods

### Maintenance of flies

Flies were obtained from infested apples collected from unsprayed orchards. Apples were kept in baskets filled with moist vermiculite. After one month, the developed puparia were collected and stored at 5°C for 6 months. When flies

were needed, puparia were placed in a glass container at 24°C with 90% RH, 16L:8D until adults emerged. Adults were held in 25 cm³ plexiglas cages and fed with sucrose, enzymatic yeast hydrolysate and water. To ensure that all the flies were in a similar physiological state as relevant to fruit foraging, we allowed each to lay an egg on a host fruit both before release and after the experiment. Only the individuals (n = 250) that laid an egg before and after the experiment – i.e. sexually mature, gravid female – were included in the statistical analysis (further details in Aluja and Prokopy 1993).

### Tree architecture

The experimental setup is detailed in Aluja et al. (1989) and Aluja and Prokopy (1993). We only provide relevant additional details here. The three-dimensional structure of two apple trees planted in the field was mapped first in 1984 and again in 1985, i.e. the same two trees were mapped during two consecutive years. To capture the essence of the main architecture, the trees were first divided into $14^3$ imaginary $20 \times 20 \times 20$ cm cubes. A tree map data sheet was prepared containing the cube identification number, the x-y-z coordinates of the cube centre, and whether it contained any vegetation (e.g. leafs, twigs, branches etc.) or not. Vegetation present in each of the cubes was then marked with masking tape strips ($1.5 \times 0.8$ cm) containing the cube number, to quickly identify the location of the insect within the tree. The cubes represent a 3D lattice in which flies moved, hereafter called 'landing points' (Fig. 1). This 3D representation is equivalent to that used in the RATP model (Sinoquet et al. 2001). Because the trees in 1984 were six years old, they were still growing and hence added vegetation during that year: in 1984 the trees had, on average, 46.95% fewer landing points (tree A: 393 and B: 409 landing points) than the same trees in 1985 (tree A: 849 and B: 684 landing points). We refer thereafter to vegetation density, which is the number of cubes occupied by vegetation divided by the total of $14^3$ imaginary cubes. Plant architectural complexity is defined according to both foliage density and its 3D distribution within the canopy. The trees were not grown according to any particular standard to maximize fruit number or quality.

Prior to the experimental set-up, we first removed all fruit from the trees. The tree architecture was manipulated to keep it constant over the experimental period of eight weeks and to ensure a clear view of all the cubes in the tree: some branches and twigs were pulled and fastened with string or nylon; and 40% of all leaves were removed, without altering the total number of cubes. Branches were pulled so as to modify their original orientations only slightly, and the leaves removed were mostly those clustered around big leaves. We believe that this manipulation did not alter the general tree architecture for two reasons. First, the number of vegetated cubes was kept constant. Second, the cubes still contained a large total landing surface area despite the removal of leaves to facilitate observation. Each tree was enclosed in a 3.5 m diameter × 3.5 tall cylindrical clear-screen cage. The cages were 60 m apart.

### Fly movements

Fly movements were recorded in the trees with and without a wooden red sphere of 7.5 cm diameter visually mimicking
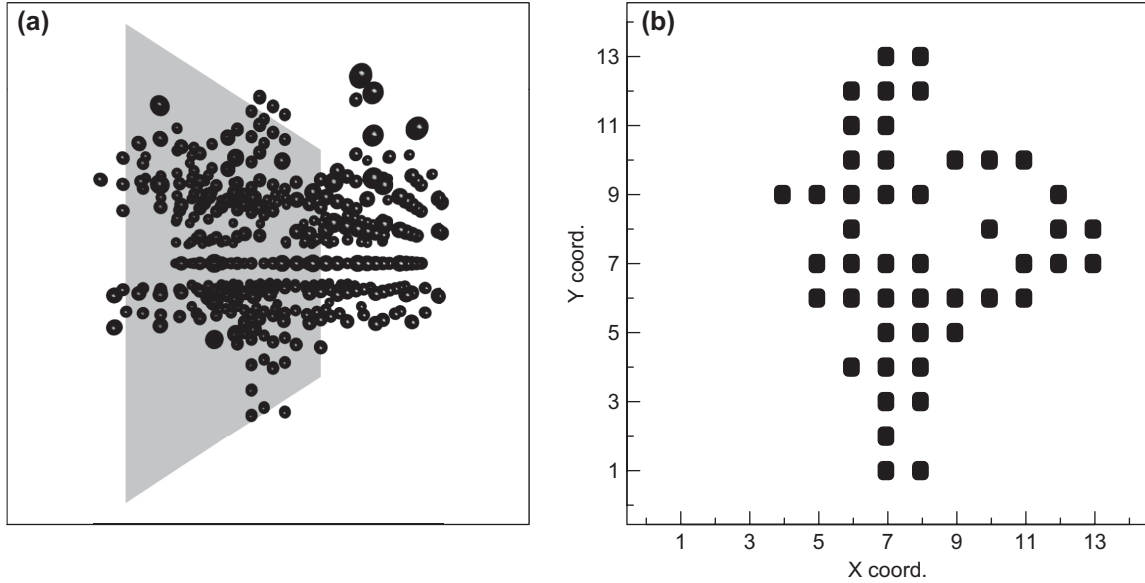
Figure 1. Lattice points from mapping the 3D structure of a tree canopy (a) and 2D representation of the plane illustrated in (a) of the same tree (b).

a fruit. The wooden sphere, covered with Tarter Red Dark enamel paint, mimicked the spectral reflectance curve of the red apples from the trees (Aluja and Prokopy 1993). The nature and the order of the treatments within each tree were assigned at random every day. Usually, individuals land and start foraging from the lower to the upper parts of the vegetation (Aluja et al. 1989, Aluja and Prokopy 1993, Casas and Aluja 1997). Thus, female flies were released individually at a point situated in the central-lower vegetated part of the tree. The coordinates of all the cubes visited by the fly over a period of 20 min were recorded. Flies move intermittently, by hopping between different parts of the vegetation. A step length was defined as the distance of a hop between two different cubes, roughly estimated as the distance between these cubes. Therefore, within cube movement was not recorded. The observation period was stopped once the predetermined time had elapsed (20 min) or if the fly left the tree and flew to the cage wall. If the fly was lost for more than 1 minute, the observations were discarded. Overall, we observed 4199 moves by 157 flies in trees without a wooden red sphere and 1966 moves by 93 flies in trees containing the wooden red sphere. Note that part of the dataset – fly movements in trees without an artificial fruit – is the same as in Casas and Aluja (1997), but that we greatly expanded the use of this dataset to include the moves of flies in trees with an artificial fruit.

**The null model: a random walk on graphs**

We constructed a random walk model in trees without stimulus (Casas and Aluja 1997), which we call the null model. In view of the findings reported by Casas and Aluja (1997) from the fly movements in trees without an artificial fruit, we assumed the absence of correlation between successive steps and between length and direction. We also assumed that individuals do not have any preference for direction, and that they move with the same step length distribution as observed for individuals moving in trees devoid of fruit.

The purpose of this model was to extract the null probabilities of visiting the stimulus source location so as to allow comparison with the observed visit probabilities in trees with an attractive stimulus source (Goodwin et al. 1999, Fletcher et al. 2013). Also, we used the model to estimate the attraction radius of the fruit, and the attraction strength of the fruit within the attraction radius. Below, we explain how the random walk model works and then place it in the context of the theory of random walks on graphs.

To calculate the next fly position from a given point we proceed in two sequential steps. First, a step length that defines the radius of a search sphere centred on the fly is selected randomly from the observed step length distribution (values range from 1 to 14). Secondly, one point on the sphere surface (i.e. at a distance equal to the chosen step length) is randomly chosen and the fly is assumed to move to it. The process continues until the total number of steps ($n = 21$, the mean number of steps per individual moving in an empty tree) is reached. Hence, a time step is always defined as a change in position. If there are more landing points available upwards than downwards on the sphere surface, the fly will most likely move upwards, and reverse. Consequently, the architecture of the tree itself governs the paths of the individuals and the likelihood of any particular landing point being chosen. Thus, due to the heterogeneity of the vertical distribution of vegetation, this size-based sampling often leads to an upwards bias, to the areas with more vegetation. This is exacerbated by the fact that flies are released in the lower part of the canopy. The concept of edges is not easily applied for networks and was not incorporated into the model.

Movement is thereby modelled as a random walk on a graph. Trees can indeed be represented as graph structures with landing points connected by edges. Cubes without any vegetation in them are absent from this type of representation. Let $M = \pi_{ij}$ be the matrix of transition probabilities between all the landing points, where the value $\pi_{ij}$ describes

the probability of going from point $i$ to point $j$. From one point there are as many connections (i.e. edges) as other points, and all the transition probabilities of one point must add up to 1.

The transition probabilities are calculated from the distribution of observed step lengths of insects moving in trees without stimulus and from the distance matrix between the landing points. Hence, the probability that a fly will visit point $j$ from point $i$ is first given by the probability that the fly will move that distance. Then, because other points might be also accessible from that distance, each one will have a probability of being visited of 1 / 'connectivity'. Connectivity denotes the number of points accessible using that step length. The transition probabilities $\pi_{ij}$ are thus computed as follows:

$$\pi_{i \to j} = k_i \left[ P(d_{ij}) \times c_d^{-1} \right]$$

$$k_i = 1 \Big/ \sum_{j=1}^{n} P(d_{ij}) \times c_d^{-1}$$

where, $P(d_{ij})$ is the probability of moving a step length equal to the distance between the point $i$ and $j$, $c_d$ the connectivity of the vertex $i$ when the step length equals $d$ and $k$ is a normalization constant to make all the probabilities add up to 1.

With this formalism, we calculated the null probabilities, averaged from all the directions, of visiting the stimulus source coordinates, called $S$, from a given distance. For this, we proceed in four sequential steps:

1. First, we obtained the probabilities of visiting any point $j$ (including $S$) from any other point $i$ in the $n$th step. These probabilities are given by the $ij$-entry of the matrix $M^n$ (Lovasz 1996).
2. Secondly, we obtained the probabilities of visiting any point $j$ from any other point $i$ but without having visited the specific point $S$. These probabilities are given by the $ij$-entries of $M^{n*}$, which is the same as the $M^n$ matrix but with $\pi_{i \to s} = 0$.

3. Third, we calculated the matrix of probabilities of visiting the point $S$ at least once during n steps of movement. This new matrix is called $_sM^n$ and is calculated by subtracting the previous two matrices: $_sM^n = M^* - M^{n*}$.
4. Finally, we calculated the probability of going from $i$ to $S$ at least once during n steps – $P(i \to S)_n$ – by adding all the probabilities of moving from point $i$ to all the other points $j$:

$$P(i \to S)_n = \sum_{j=1}^{k} \left( _sM^n \right)_{i,j}$$

Averaging $P(i \to S)_n$ of the $i$ coordinates that are at the same distance from the coordinate $S$ gives the probability of visiting $S$ in n steps from a given distance.

## Data analyses

In this article we analyse a) the step length distributions, b) the probabilities of visiting the location of the fruit, c) the attraction radius of the fruit and d) the attraction strength of the fruit. Figure 2 briefly summarizes how these four variables were estimated from the data, and Table 1 shows the independent variables used in each analysis.

We performed Kolmogorov–Smirnov (K-S) tests to compare the step length distributions of individuals that moved in the absence and presence of a fruit, and to compare the step length distribution obtained from the random walk model with that of individuals that moved in the absence of a fruit.

The attraction of the fruit was analysed by comparing the observed probability of visiting the fruit in the next step with the expected null probability of visiting its location, which we calculated using the random walk model. If the observed visit probability is higher than the expected visit probability, a fly is assumed to be attracted to the stimulus source. We used a generalised linear model (GLM) with a logit link function. Using the observed paths, we coded each step with a 1 or 0 according to whether the animal visited or did not visit the fruit. Using simulated data, we multiplied and
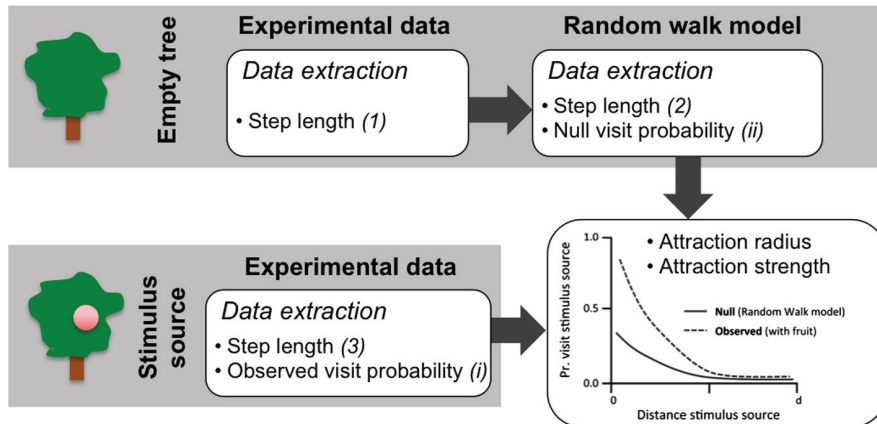


Figure 2. Movement paths were extracted from individual flies moving in trees with and without a fruit. A random walk model was constructed using the step length distribution of individuals moving in an empty tree; this model was used to estimate the null probabilities of visiting the location of the fruit. The null visit probabilities were compared to the observed probabilities of visiting the fruit, to estimate both the attraction radius and strength of the stimulus source.

Table 1. Dependent and independent variables used in the analyses.

| Dependent variable | Presence/absence stimulus source | Distance to stimulus source | No. of steps | Young/old tree |
|---|---|---|---|---|
| Step length | X | – | – | – |
| Visit probability | X | X | X | X |
| Attraction radius | – | – | X | X |
| Attraction strength | – | – | X | X |

rounded the exact null probabilities to obtain an equivalent number of 1's and 0's for each distance. The probability of visiting the stimulus source location was analysed as a function of 1) the 'stimulus' (present versus null random walk), 2) the 'distance' between the fly and the stimulus source location, 3) the number of 'steps' (n) and 4) the 'age of tree' (young versus old vegetation). The data available from middle to long distances was low when the numbers of steps (n) was of 6 or more, leading to large amplitude errors of the estimated probabilities to visit the fruit location. Due to the loss of statistical power when n > 6, only values of n from 1 to 5 were used. We performed a stepwise model selection based in the Akaike information criterion (AIC) to select the most parsimonious model (Venables and Ripley 2002). We calculated p-values of the selected model using the likelihood ratio test (Venables and Ripley 2002).

***Estimation of the attraction radius and strength***
The radius of attraction $R$ is defined as the maximal distance between the fly and the fruit at which the observed probability of the fly visiting the fruit's location is higher than the null probability. The attraction strength $\Delta$ is a measure of the difference between the observed and the null probabilities of visiting the fruit 'within' the attraction radius, and represents how strongly a stimulus source biases the movement of individuals. The attraction radius and strength were averaged across all directions, assuming that the effects of the stimulus source on the movement of individuals do not depend on any particular direction. Although we adopted the fruit as the world centre, a reversal of point of view with the fly at the centre is equally valid.

To estimate the attraction radius and strength we used the previously observed and expected fitted probabilities of visiting the fruit as a function of the distance to it. The distance at which the two curves became undistinguishable was set as the perception radius. We considered that a threshold of 0.05 in probability difference indicates the distance at which the two curves are undistinguishable. This value corresponds to the smaller distance at which the difference in probabilities (i.e. observed null) is small. Differences smaller than 0.05 imply perception radius that are negligibly larger. During the experiment, we removed some leaves, without altering the tree architecture, to facilitate the observation of flies. Although this manipulation could have increased the probability that flies detected and moved to the fruit, it does not invalidate the comparison between years, as the removal of foliage was of a similar magnitude.

The attraction strength was estimated as the difference between the areas under the two curves that describe the observed and the predicted probabilities of visiting the stimulus source:

$$\Delta = \int_{R_0}^{R} f_{observed}(r)\,dr - \int_{R_0}^{R} f_{null\,model}(r)\,dr$$

where $R$ is the attraction radius, and $R_0$ the minimum distance before visiting the fruit (i.e. one cube). The areas of the functions $f_{observed}(r)$ and $f_{null}(r)$ were calculated from the indefinite integral of the logistic function:

$$\int_{R_0}^{R} f(r)\,dr = F(R) - F(R_0)$$

$$F = \int f(r)\,dr$$

where the indefinite integral $F$ is obtained from:

$$f(r) = \frac{1}{1 + e^{-(a+br)}}$$

$$\int f(r)\,dr = \frac{\log\left(1 + e^{-(a+br)}\right)}{b}$$

A fly might approach the fruit by a succession of several steps. We therefore estimated the attraction radius and strength by calculating the probability of visiting the fruit in as many as $n$ steps (n being between 1 and 5 inclusive), and compared the attraction radius and strength across different movement steps. Thus, the definition of a radius of attraction does not change, but the number of steps required to reach the fruit needs to be quantified. Also, we compared attraction radius and strength values in different foliage densities (i.e. dense versus sparse) to estimate how foliage density influences the perception of the fruit.

***Relative roles of architectural complexity and fruit attraction on insect movement***
We calculated the relative contributions of vegetation architecture and fruit attraction to influencing the visit of the fruit location in n steps at a given distance from its location. To calculate the relative contributions we assumed that no other factors than fruit attraction (e.g. internal state or environment) motivated the movement of individuals. The relative contributions were calculated as follows:

Stimulus contribution = $P(Fly \rightarrow S)/[P(Fly \rightarrow S) + P(RW \rightarrow S)]$

Vegetation contribution = 1-Stimulus contribution

where $P(Fly \rightarrow S)$ is the probability that the fly visits the fruit location due to the presence of the fruit effect, and $P(RW \rightarrow S)$ is the null probability of visiting the fruit location obtained from the random walk model.

All the analyses and the developed code for the random walk model were performed with R ver. 2.15.

## Results

### Stimulus source and movement patterns

The presence of a fruit in the trees had no detectable effect on the step length distribution (K-S test: D = 0.21,
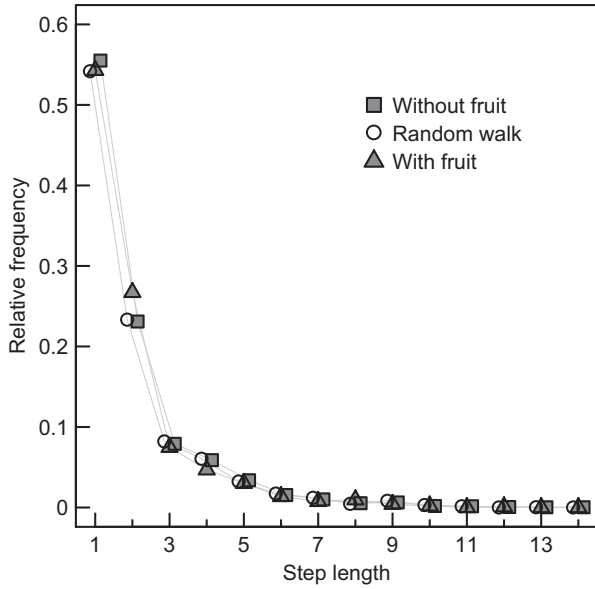
Figure 3. Relative frequencies of observed step length distribution (in cubes, 1 cube = 20 cm). Triangles and squares correspond to step lengths for flies moving in trees with or without the fruit, respectively. Circles indicate the step lengths extracted from the random walk model.

Table 2. Results of likelihood ratio tests predicting the probability to visit the fruit for the best model selected by stepwise AIC. Dist: distance to fruit, Fruit: presence versus absence of a stimulus source, Year: young versus old tree, Steps: number of steps allowed to move. Values in bold indicate the significant higher-order interactions.

|  | Estimate | SE | $\chi^2$ | DF | p-value |
|---|---|---|---|---|---|
| Dist | −1.65 | 0.15 | 1506.80 | 1 | <0.01 |
| Fruit | 1.78 | 0.47 | 1193.80 | 1 | <0.01 |
| Year | 0.29 | 0.32 | 73.28 | 1 | <0.01 |
| Steps | −0.02 | 0.10 | 249.08 | 1 | <0.01 |
| **Dist × Steps** | **0.16** | **0.03** | **44.61** | **1** | **<0.01** |
| Fruit × Steps | 0.14 | 0.12 | 0.84 | 1 | 0.36 |
| Dist × Fruit | 0.60 | 0.17 | 2.14 | 1 | 0.14 |
| Dist × Year | 0.44 | 0.12 | 2.82 | 1 | 0.09 |
| Fruit × Year | 0.85 | 0.39 | 40.57 | 1 | <0.01 |
| Dist × Fruit × Steps | −0.07 | 0.04 | 3.14 | 1 | 0.08 |
| **Dist × Fruit × Year** | **−0.68** | **0.13** | **31.21** | **1** | **<0.01** |

p = 0.90; Fig. 3). Also, the step length distribution obtained from the random walk model was not different from the distribution of steps of individuals that moved without a fruit (K-S test: D = 0.14, p = 0.99; Fig. 3). However, we found an interaction between the distance from the fruit, the presence of a fruit, and the age of tree, on the probability that a fly visited the fruit location (Table 2). The shorter the distance from the fruit,

the greater the tendency of the fly to move towards it, and the presence of a fruit significantly increased the probability that the fly moves towards it from shorter distances. Moreover, the age of tree (i.e. tree complexity) affected the probability that the fruit biased the movement of flies towards it (Fig. 4). Also, we found an interaction between the distance from the fruit and the number of steps (Table 2). Flies were more likely to reach the fruit location if, for a given distance, they made several steps to the fruit, and this effect was stronger when the distance to the fruit location was shorter (Fig. 4).

## Tree complexity and fruit attraction

The age of tree affected the probability that a fly visited the fruit location both directly and indirectly through changes in perception of the fruit. First, both the observed and the
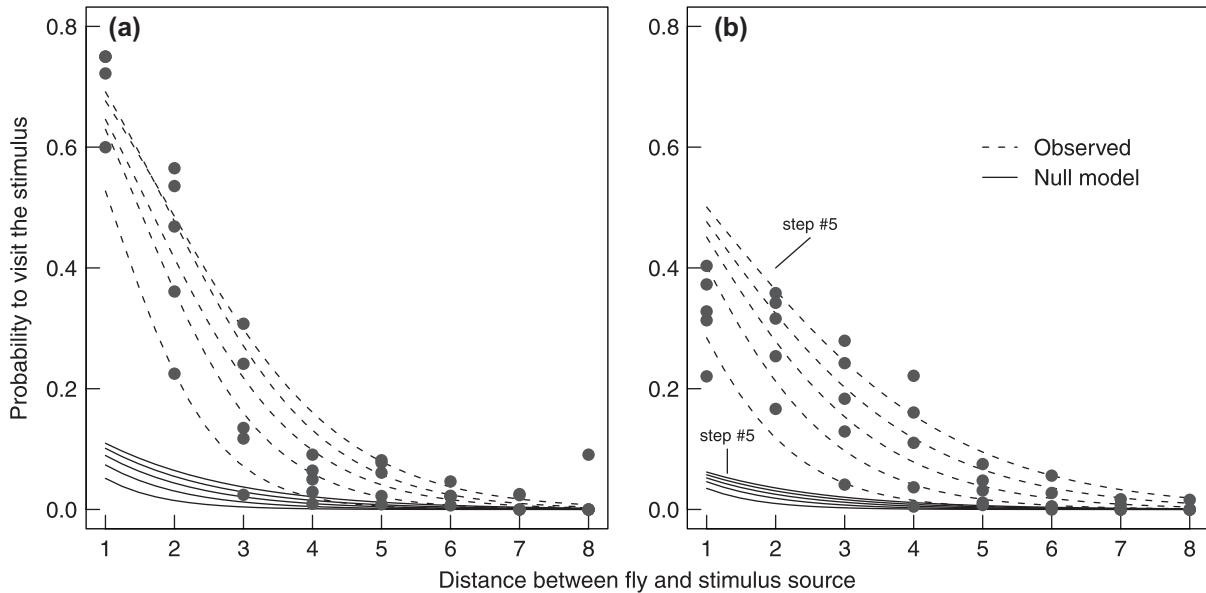


Figure 4. Probabilities of visiting the stimulus source as function of the distance (in cubes, 1 cube = 20 cm) between fly and fruit in (a) young (sparse) and (b) old (dense) vegetation. Points indicate the observed probabilities of visiting the fruit when it was present. The lines are observed (dashed) and null (solid) logistic fits for the visiting probabilities obtained from observed paths of flies moving in the presence of a fruit, and from the random walk model, respectively. The different curves represent the probabilities of visiting the fruit in the next n steps, from 1 (the lower curve) to 5 (the upper curve).

null probabilities of visiting the fruit location were lower when the trees were older (Fig. 4). Second, the attraction radius and strength were significantly different according to the age of tree (radius: $\chi^2 = 0.14$, DF = 1, p < 0.001; strength: $\chi^2 = 0.22$, DF = 1, p < 0.001; Fig. 4). Fruit in older trees had a shorter attraction radius and weaker attraction strength (mean ± SE: radius = 75.8 cm ± 6.51; strength = 0.61 ± 0.12) than fruit in younger trees (radius = 80.6 cm ± 4.93; strength = 0.98 ± 0.12). However, the age of tree affected the attraction strength more strongly than the attraction radius: the attraction strength was 37.76% lower for the older than for the younger trees, and the attraction radius only 5.95% lower. Both the attraction radius and strength tended to increase with increasing number of steps allowed for searching (radius: $\chi^2 = 3.24$, DF = 1, p < 0.001; strength: $\chi^2 = 0.58$, DF = 1, p < 0.001; Fig. 4). A complete 3D reconstruction of the sphere of attraction in both years was constructed: in both cases, the sphere occupies a significant portion of the total volume of the tree (Fig. 5). Finally, we show that the relative contribution of fruit attraction was much greater than that of vegetation architecture to influencing the visit to the fruit location, and that the contribution was similar for both younger and older trees (younger tree: fruit = 0.89, vegetation = 0.11, older tree: fruit = 0.91, vegetation = 0.09).
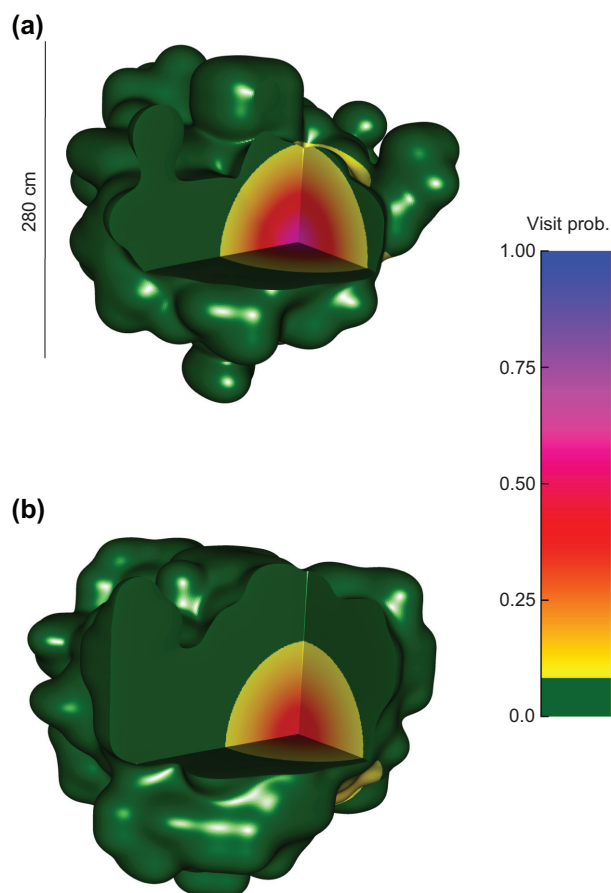
**(a)**



**(b)**



Figure 5. Probabilities of visiting the location of fruit in the next 5 steps in (a) a young (sparse) and (b) an old (dense) tree. The visiting probabilities are given by the colour bar on the right. The yellow perimeter of the sphere represents the limit of the sphere of attraction.

## Discussion

### Vegetation architecture determines step length and overall movement

We found that flies move according to a pattern that has been shown to be an effective movement strategy for locating randomly distributed resources (Bartumeus et al. 2005). Some animals can also adjust their moves according to the density of resources (Humphries et al. 2010). Here, we observed that the flies did not change their step length distribution in the presence of a fruit: either they do not change their movement patterns when exposed to fruit, or the presence of a single fruit is not sufficient to alter their searching behaviour. Moreover, the vegetation architecture was a major determinant of insect movements and their probabilities of finding the fruit. Our null model showed that vegetation density diminished the probability of finding it. This is in agreement with empirical work that found that, in general, the encounter rate between individuals or between individuals and different parts of the environment decreases as the architectural complexity of the environment increases (i.e. higher vegetation connectivity) (Price et al. 1980, Andow and Prokrym 1990, Grevstad and Klepetka 1992, Casas and Djemai 2002, Randlkofer et al. 2010).

### Towards a quantitative definition of a sphere of attraction

We defined the sphere of attraction of a stimulus and quantified its strength as the bias on the movements of individuals in complex vegetation architectures. A change in behaviour only occurs if the individual moves into the sphere of attraction, defined by a distance threshold (75.8 cm and 80.6 cm in old and young canopies, respectively). Moreover, as the distance from the fruit decreased, its attraction increased (Green et al. 1994, Zollner and Lima 1997, Rosenthal 2007). Also the probability of a fly visiting the fruit increased as the number of steps increased, and this increase was higher when the distance to the fruit was shorter. It is no surprise that the probability of visiting a given point increases with time and number of steps (Lovasz 1996). However, as the number of steps increased, the probability of the fly visiting the fruit increased over-proportionally with reference to the situation without fruit (i.e. null probability). This probably indicates that individuals employ intermittent locomotion: they detect the fruit from a distance and need to take several steps to reach it. This intermittent locomotion could be beneficial to flies because it may allow them to recover from fatigue, to stabilize their sensory field such that they can locate the resources more efficiently, or to avoid spider's webs (Kramer and McLaughlin 2001).

In our definition of the sphere of attraction both 1) the number of steps and 2) the value that indicates whether the null and observed curves are undistinguishable influence the radius of attraction. When the number of steps is large enough the probability to visit the fruit is close to 1 and the effects of distance disappear because the likelihood to find the stimuli by chance increases even from large distances. Since the observed probability to visit the stimulus location is not related with distance, the attraction range would be

overestimated. This is a rather unlikely scenario, as flies – and animals in general – tend to maximize the amount of energy obtained per unit time and give up a patch if no resources are found within a timeframe (MacArthur and Pianka 1966). To avoid an overestimated attraction range we should only use those number of steps from which there is a relationship between the probability to visit the stimulus source and the distance. Similarly, the value that indicates whether the null and observed curves are undistinguishable also influences the attraction range. While it is possible that animals could detect the stimulus source from far away than this threshold, the probability that the fruit significantly biased the movements of individuals at larger distances was negligible. Most of the influence that fruit exerts on the movement of animals is within the attraction radius defined by this threshold.

Some results confirm previous findings (e.g. distance dependent attraction: Green et al. 1994, Zollner and Lima 1997) and other approaches have been used to quantify the perceptual range of animals (Goodwin et al. 1999, Zollner and Lima 1999). Ours is the first to quantify the distance-dependent perceptual range as well as the strength of attraction of a stimulus source including the effects of a complex architecture (i.e. vegetation). We are thus in a unique position to disentangle the contributions of the architecture of canopies from the intrinsic strength of attraction of a given stimulus source on the probability of visiting the fruit. Conditional on visiting the landing site, the importance of the attraction by the fruit was much greater than that of the vegetation architecture (90% versus 10% respectively), and the pattern was similar between years (i.e. young versus old canopies). The effect of year was nevertheless small, despite a difference of 47% in vegetation density between them. We assumed that no other factors than fruit attraction affect the movement of individuals and their probability to visit the stimulus source. By using individuals reared in the laboratory and that previously laid an egg we minimized the effects of some variables – experience, memory or physiological state – that affect the movement of animals.

On the other hand, if we focus on the unconditional probability of visiting the fruit location, we found evidence that the tree complexity affected the strength of attraction of the stimulus: it was 37.76% lower in older than in younger trees. In older trees the density of foliage was 47% higher than in the same, younger trees. This difference in foliage density may have affected the physical properties of the environment and, in turn, the rates of attenuation and degradation of signals and the fruit detection (Endler 1993, Rosenthal 2007). Note that the strength of illumination can strongly influence the perceptual range of animals that use vision to obtain external information (Zollner and Lima 1999). The correlation between foliage density and age of tree, however, makes the statistical distinction between factors impossible. Foliage density may explain the differences in attraction strength, but also any other variable correlated with year that could have affected flight performance. Temperature and humidity, for instance, can affect searching behaviour by altering their movement rates (Taylor 1963, Bell 1990). Nevertheless, because the experimental period was of eight weeks and during the same season in both years, we expect the climatic variables to have similar ranges. Hence, we believe that vegetation density could likely explain the

differential attraction strength between years. Besides, our model (independent of any climatic conditions) showed that a higher density of vegetation lowers the probability of visiting the fruit location. Further studies in different tree architectures under otherwise constant conditions are required to confirm that vegetation density is the factor that explains attraction strength. Independent of which is the underlying causal factor, the differential attraction between years is real. This is of specially importance, because many ecologists have traditionally assumed that animals use a static perceptual range with equal attraction in all the distances from a stimulus source (Olden et al. 2004). Our results suggest that these assumptions may be erroneous.

## The power of renormalization

In a previous model (Casas and Aluja 1997), the authors imposed an explicit upwards bias on the movement of flies, i.e. a fly at a given height level had a probability fixed a priori to move upwards. The resulting model provided a very good fit for three of four trees, but it failed for a tree which was architecturally too different: not only was the tree markedly smaller than the others, but it also had a different distribution of foliage. Here, we implemented an upwards movement rule which is analogous to a renormalization procedure, in the spirit of scale invariance (Lesne 1998): flies are allowed to choose the next location at random within a set of landing points determined by the outer surface of a search sphere, the radius of which is set by the step length. The tree geometry and the fact that flies start foraging from the bottom, both imply that the number of landing points is, in most cases, greater above than below a fly. This proportional sampling produces a bias upwards. This approach requires no estimates of the exact height level at which flies find themselves in a tree, nor of the height of the tree in which they forage. It enables all trees of all shapes, irrespective of their foliage distribution or height, to be considered within the same model.

## Perspectives

### Towards a unified framework of perceptual range

In this study we developed a novel method to accurately estimate perceptual range and attraction strength from the movement trajectories of individuals. Perceptual range is an important trait that determines the availability of environmental information to make informed decisions, and has implications to understand animal movement. To date, most estimations of the perceptual range are based on translocations (i.e. captures and releases) of individuals at varying distance from a stimulus. The distance at which the orientation of individuals follows a non-uniform pattern indicates their perceptual range (Zollner and Lima 1997, Prevedello et al. 2011, Öckinger and Van Dyck 2012, Sozio et al. 2013). Since the translocation points are usually limited, the reported perceptual ranges are rough measures, usually given as an interval. Recently, other methods based on translocation experiments have been developed to better describe perceptual ranges. Fletcher et al. (2013) adapted the signal detection theory (SDT) to estimate the perceptual range of animals, and the theory is able to differentiate the

detectability of a stimulus from the response of the individuals to the stimulus, which are two independent measures of the decision-making process. All estimations of perceptual range that are based on translocations of individuals lack a control treatment – animal movement without a stimulus –. The control treatment is needed to differentiate the detectability of a stimulus from the response of the individuals (SDT) and to estimate the perceptual range and attraction strength. With our null model and recorded individual movement trajectories, we could reconstruct the null movements of individuals, a proxy of the control treatment, and analyse the data obtained from the translocation of individuals either with the SDT or our methodology. There is a great potential therefore in the integration of SDT and our methodology. Joining efforts to develop a combined framework could provide a better understanding of ecological processes such as dispersal and foraging, and how animals use external information to move.

### Landscape connectivity

Animals' perceptual range is key to determine patch finding and landscape connectivity. Understanding landscape connectivity is a fundamental step for conservation biology, as the degree with which different landscape elements are connected will determine the dynamics and persistence of spatially structured populations (Hanski 1999). Our methodology could also be used to determine the perceptual range of animals and theoretically estimate the probability of moving between one resource patch to another, which is a measure of landscape connectivity (Tischendorf and Fahring 2000). Furthermore, we distinguished between perceptual range and attraction strength, and we have shown that individuals may present the same perceptual range with different attraction strength. This is an important but neglected distinction, as we expect that landscape connectivity will be higher in animals showing higher attraction strengths for equal perceptual ranges. Recently, dispersal models have been developed that incorporate the perceptual range of individuals (Palmer et al. 2011, 2014, Pe'er et al. 2011), but the distinction between perceptual range and attraction strength is still lacking. With our methodology, the parameters obtained from empirical data could be easily included into dispersal models to better estimate landscape connectivity. Moreover, perceptual range and attraction strength can be parameterized as a function of vegetation complexity (i.e. matrix type). Dispersal models could, therefore, include the effects of certain characteristics of a landscape on connectivity.

### Foraging ecology

Individuals from many taxa use their sensory systems to make informed decisions while foraging. Different frameworks have been proposed to build mechanistic models of animal movement and include decision-based movements (Getz and Saltz 2008, Mueller and Fagan 2008, Nathan et al. 2008, Hein and McKinley 2012). Mechanistic models that include informed individuals have higher foraging success than models of animal movement resulting from a random walk process or area restricted search models (Okuyama 2009, Hein and McKinley 2012, Fronhofer et al. 2013). It is unusual, however, that mechanistic models of animal movement are combined with empirical data,

probably because of their complexity or the lack of adequate data. In this study we developed a novel method to estimate perceptual abilities from empirical data that will hopefully help to build a mechanistic model of animal movement and close the gap between theory and empirical data. Oriented movements such as the ones explored in our study are critical to understand animal movement, encounter rates, and search strategies. Given that animals use their sensory systems to make informed decisions and that they move and interact in heterogeneous environments, our approach might be of relevance to the myriad of other animals walking and searching in complex environmental structures.

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