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Dphil Dissertation Submission

Exploration of human search behaviour: a multidisciplinary perspective

Marcos Francisco Rosetti Sciutto

Declaration

I hereby declare that this thesis has not been and will not be, submitted in whole or in part to another University for the award of any other degree.

Signature:

Marcos Francisco Rosetti Sciutto

Abstract

The following work presents an exploration of human search behaviour both from biological and computational perspectives. Search behaviour is defined as the movements made by an organism while attempting to find a resource. This work describes some of the principal procedures used to record movement, methods for analysing the data and possible ways of interpreting the data. In order to obtain a database of searching behaviour, an experimental setup was built and tested to generate the search paths of human participants. The test arena occupied part of a football field and the targets consisted of an array of 20 golf balls. In the first set of experiments, a random and regular distribution of targets were tested. For each distribution, three distinct conspicuity levels were constructed: a cryptic level, in which targets were painted the same colour as the grass, a semi-conspicuous level in which targets were left white and a conspicuous condition in which the position of each target was marked by a red flag, protruding one metre from the ground. The subjects tested were 9-11 year old children and their search paths were collected using a GPS device. Subjects did not recognise the spatial cues regarding the way targets were spatially distributed. A minimal decision model, the bouncing search model, was built based on the characteristics of the childrens search paths. The model produced an outstanding fit of the children's behavioural data. In the second set of experiments, a new group of children were tested for two new distributions obtained by arranging the targets in patches. Again, children appeared unable to recognise spatial information during the collection processes. The children's behaviour once again produced a good match with that of the bouncing search model. This work introduces several new methodological aspects to be explored to further understand the decision processes involved when humans search. Also, it illustrates that integrating biology and computational science can result in innovative research.

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Chapter 1

Introduction

The objective of this work is to provide an organised procedure exemplifying a possible method to record, analyse and model the searching behaviour of biological organisms. Searching, understood as the movements made while attempting to find a resource, is a ubiquitous behaviour in mobile organisms. One cannot underestimate the importance and complexity of search behaviour accross the life spectrum: It is produced by different systems of locomotion, occurs throughout all media and spatio-temporal scales and is guided by a coordinated set of external and internal processes. In this work, the focus is on the characteristics of the movement an individual makes when searching, the choices involved in the decision mechanism and finally, a comparison of this mechanism with the set of choices derived from a standard optimisation procedure.

For the purpose of obtaining a detailed record of search behaviour under controlled conditions, an experimental situation was designed. The experiment involved human participants searching in a bounded arena for targets whose spatial distribution and visual conspicuity was manipulated by the experimenters. Simultaneously, their path was tracked using a GPS (Global Positioning System). The analysis of the searching paths were used to construct a statistical model based on a simple set of rules. The model followed a simple design: an artificial searcher would follow a linear trajectory until it collided with the boundary of the arena or one of the targets. Conspicuity was simulated as the radius of the circle surrounding each target, in which the size of the radius was proportional to the degree of conspicuity. The collection of a target would occur when the

searchers path intersected with any of these circles. Thus, the searcher appears to bounce off any sensory encounter, hence the name *bouncing search*. Finally, this model was embedded into an optimisation procedure to observe whether the decision points (namely, the turning angles after a collision) would be able to accommodate a systematic sweep of the arena, producing a search strategy that guarantees the collection of all the targets in any spatial distribution.

The present work has the following goals:

- To produce and test an experimental setup where it is possible to obtain search paths under controlled conditions involving significant time constraints.
- To produce a simple model from the searching paths, which is easily implemented and whose complexity can be adapted to further findings.
- To test the viability of obtaining a systematic search as the result of an optimisation procedure.

1.1 Multidisciplinary approach to search behaviour

Historically, biology has demonstrated an ongoing interest in search behaviour. Search behaviour presents an excellent case study for several biological disciplines: Searching is fundamental to the life of mobile organisms, which combines the use of proximate decision-making with the development of search strategies that are of evolutionary relevance. Proximate mechanisms influence local decisions. For example, in the case of a foraging hummingbird or bee, an association is made between the size or colour of a flower and the amount of nectar that it may hold. Evolutionary strategies favour fixed systematic movements, as in the case of ants who undertake foraging trips from and back to their nest with a shorter travelled distance between sequential visits to resources. Searching relies heavily on the sensory and motor capacities of an organism, but some of the search choices reflect efficiency measures shaped by evolutionary pressures. For example, while searching in a patch, or an area where resource density is high, it's important to

move slowly and look carefully for resources. However, evolutionary pressures influence the amount of time a searcher spends in a particular patch. Searching efficiency is central to the economics of an organism: individuals must make the best use of their limited time and energy to search under conditions of reduced information and in many cases, the targets are not static. Search behaviour has been studied extensively in the biological sciences, which is further emphasised by the popularity of 'Optimal Foraging Theory' (Pyke, Pulliam and Charnov, 1977; Stephen and Krebs, 1987; Pyke, 1984), as well as the numerous examples that illustrate these cases in a huge variety of organisms (Bacteria (Stibora and Sommer, 2003), Parasites (Lozano, 1991), Insects (Charnov, 1976; Scheirs and De Bruyn, 2002), Fish (Werner and Hall, 1974), Birds (Goss-Custard, 1977), Mammals (Heth, Golenberg and Nevo 1989), Humans (Winterhalder, 1980; Winterhalder and Smith E.A. 2000).

Historically, searching problems have been relevant to computer science and biology alike: Questions concerning shortest paths between a defined set of coordinates are highlighted in the famous travelling salesman example. In this scenario, a salesman wonders how to travel the shortest distance between a set of houses and towns he must visit (Lawler et al., 1985). Another example includes the behaviour of robotic and simulated agents having to move and find specific items within intricate sets of artificial or real world data (Goss and Deneubourg, 1992; Yamaguchi, 1998). Also, problems regarding search paths have similar constraints in biology and computer science: energy, time, and other factors relating to search behaviour are among the crucial parameters around which efficient solutions revolve. This common ground marks an interesting area for multidisciplinary work. Aside from understanding biological phenomena, it is possible to analyse behaviour and to derive the algorithmic components that construct it (Webb, 2001). This is mutually beneficial, as algorithms provide models of behaviour that lead to a better understanding of the underlying mechanisms. Hence algorithms derived from evolutionary processes are useful resources to be tested in computational situations (Webb, 2000). These algorithms may not always be optimal, but are often parsimonious solutions, based on a simple set of rules, and are therefore computationally accessible.

There are other contexts in which searching is integrated in both a biological and a computational process. Some authors have compared the similarity between the fundamental aspects of foraging and some of the distinctive features of how humans browse the information on the World Wide Web (Pirolli, 2005; Mantovani, 2001). Others use the principles of foraging to explain the process in which the memory remembers words by invoking semantic networks, in which patches of similar words become associated (Hills, Todd and Jones, 2009). This extrapolation from the principles of searching show how extensive the range of applications can be. Similarity between these procedures is important because it might suggest cost-efficient ways to deal with searching through large amounts of information on the web or in our minds. The fact that similar aspects of searching can be detected at different levels of information processing (looking at an image or a webpage, remembering words or constructing them using letters drawn at random, looking for a book in a library or a can of soup in the supermarket, foraging for mushrooms in the forest, etc.,) suggests that central, and minimally cognitive mechanisms are involved in searching that are scalable to a range of dimensions and situations, as opposed to mental mapping and navigational planning or orientation, which are probably situation and scale dependent.

In this work a multidisciplinary approach to searching is adopted. An experimental paradigm was built to obtain the searching paths from human participants. Analysis, measurements and pre-processing procedures where integrated into a toolbox to systematically uncover relevant features of the paths. A simple model was used to study the properties of the hypothetical mechanisms underlying the search behaviour observed in the experimental setup. The same model was used to test an evolutionary procedure attempting to obtain systematic search paths under the constraints of the bouncing search model.

1.2 Outline of the thesis

• Chapter II presents a literature review of path analysis. It describes important aspects of path analysis and it's processes: From recording and pre-processing to

detailed examples, the main features of random walk models and suggestions on how to detect the existence of finer patterns within a searching path's structure. It is organised into three main sections:

- The first section offers guidelines on how to record the movement process. It
 also describes the main elements of a path and the principle techniques used
 when dealing with either missing data or excessive detail.
- The second section introduces the main statistical models that have been used to study biological behaviour. It describes several types of random walk variations, the characteristics that define them and the statistical processes used to identify them. Also, it contains a brief discussion on the use and misuse of pseudo-paths, a common bootstrapping method used when studying the statistical nature of trajectories.
- The third section addresses, in more detail, the detection and interpretation of
 repetitive patterns in a path structure in the context of environmental cues. It
 includes the case of foraging, highlighting the importance of specific mechanisms related to efficiency and decision-making.
- Chapter III presents the results obtained from the recording, analysis and modelling of search behaviour. The introduction stresses the importance of testing search behaviour under natural conditions and in a task that involves movement, rather than through computerised or highly constrained testing conditions. Also, it provides a justification for the type and age of the subjects tested. Details on the experimental setup used for testing search behaviour are followed by a description of the bouncing search model. Results describe the influence of environmental cues on the subject's performance. The main findings are summarised in the discussion, along with some recommendations for future studies.
 - The contents of this chapter form the basis for a paper that has been accepted for publication in:

Physica A: Statistical Mechanics and its Applicationsas a paper titled:

A experimental and theoretical model of childrens' searching behavior in relation to target conspicuity and spatial distribution with co-authors:

Rosetti, M, Pacheco-Cobos, L and Larralde, H and Hudson, R. See Appendix C.

- Chapter IV presents the recording and analysis of search behaviour in a new set of experiments constructed to challenge the findings of Chapter III. The numerical quantification of conspicuity provided the measures necessary for the construction of patchy distributions of targets. Conspicuity was manipulated in the same way as in Chapter III, but a new condition was added, in which the subjects are given some hints regarding the distribution of targets. The children's search paths were indistinguishable from the model's predictions. This chapter also presents a set of performance measures, related to the structure of patches, that were obtained from the search behaviours of children and artificial agents.
- In Chapter V, the performance of the paths produced by an optimisation procedure is evaluated. General conclusions are drawn regarding the nature of the search strategies that might prove successful in the constrained setup of the bouncing search.
- Chapter VI presents the main conclusions of this work. It further emphasises the
 importance of adopting a multidisciplinary approach to search behaviour by combining computer science and biology. This chapter summarises the main findings of
 this work. Finally, the section on future work provides some useful recommendations for improving the search task and model, for which optimisation procedures
 can prove useful.

1.3 Thesis contributions

Among the main contributions of this work are:

• The successful development of a versatile experimental task: The manner in which the experimental setup was designed allows the exploration of several questions related to the search performance of humans by testing modified versions of the experimental setup. Experimental conditions guarantee that results are consistent amongst trials, but the dimensions of the experimental field and the playful nature of the task suggests that subjects enjoy the task and that energetic decisions may play a role in their performance.

- The experimental series described here constitutes one of the first examples for the evaluation of searching performance through the study of search paths. The use of GPS recordings for human behaviour has a recent history, but has never been used in an experimental task up until now.
- The development of a simple algorithm to explain the performance of humans whilst searching in a bounded environment. A simple model with a large predictive power suggests the use of simple heuristics in search behaviour.
- Finally, the simulation and posterior attempts to optimise the bouncing search experiment represents an example of the possibility of how the tools of computer science can provide insights into biological processes.

Chapter 2

A review of path recording, analysis, modeling and interpretation

In this chapter, relevant concepts and methods related to path analysis are introduced. The purpose here is to summarise the large amount of information that exists on path analysis, while placing it within a framework that provides a set of instructions to be used in the following chapters. Many of the concepts and methods explained here are illustrated with plots and examples generated solely for this purpose.

2.1 Introduction

From bacteria to humans, it is through changes of location that individuals contribute to the dispersion of a population, explore their home-range, avoid predators, find food, mates and shelter or improve their current circumstances by migrating to more favourable conditions. Movements of organisms can be described in enormous detail and in a huge variety of contexts, yet it can also be summarised as a path encoded as a discrete time series of spatial co-ordinates. The analysis of paths can be used to measure and quantify features of movement relevant to several types of behavioural questions, such as animal distribution, habitat use and selection, habitat connectivity, recruitment, migrations, and foraging strategies (Tremblay, 2009).

Analyses commonly aimed at records of individual movement stem from relatively

different fields of research. Some questions address theoretical aspects, such as the statistical properties of movement in bacteria, while others are concerned with practical applications, for instance, helping fisheries predict the location of fish schools. The time and distance scales over which movement occurs ranges from excessively large to extremely small and detailed. Thus, this work presents an integrative effort to deal with these differences using referenced approaches, methods, models and other efforts, which serve as a list of background studies that have dealt with such issues.

In this chapter an effort has been made to classify and describe the essential characteristics of the methods used for pre-processing path data, the models with which to interpret the resulting path features, and the frameworks for the identification and interpretation of possible mechanisms that give rise to particular features. The goal is to provide a type of flow chart to aid with the sequential choices needed to be made when studying the paths produced by moving organisms.

In the first section the consequences of the sampling criteria are discussed, followed by a description of the principal pre-processing methods which typically follow any sampling. The consequences of under and oversampling are also addressed, along with how pre-processing follows either case, as well as the effects these methods will have on the statistical structure of the components of a path. The next section focuses on the relevance of random walk models for the description and understanding of biological movement. Variations of random walk are introduced, it's principal characteristics, as well as the biological models for which they have proven useful. Next, an overview of the situations found to be optimal search strategies is presented together with quantifiable ways to recognise them. Finally, guidelines for more detailed path interpretations with an aim to distinguish strategies and mechanisms are presented. These include a closer look at the dynamic processes by which a path is formed and the relationship between the environmental parameters and the properties of the path. The special case of searching is discussed in order to exemplify the case where energy demands place constraints on the characteristics of displacement.

2.2 Methods of sampling and pre-processing

2.2.1 Sampling

Movement data is recorded through systematic procedures typically sampled at either fixed time or distance intervals, or at behavioural events chosen by the observer. For example, movement in E. coli is marked by a tumbling behaviour, which these prokaryotes use to change direction; path segments can then be taken to be linear interpolations between tumbling events (Reviewed in Berg, 1975; Adler, 1975). Automated observation of microscopic paths rely on motion-recording software set to sample individual trajectories with fixed time intervals, as observed with the paths of sea urchin spermatozoids (Corkidi et al., 2008) or the movement of leukocytes as they migrate and interact with tissues and other cells. (Mempel et al., 2004). Movement occurring at a visible scale can be video recorded and sampled using physical references of space. Analysis of videos to sample movement in a fixed time frame is a common method used for small mammals (Pacheco-Cobos et al., 2003; Sokoloff et al., 2002) and invertebrates (Baatrup and Bayley, 1993). The quantitative recording of movement from a video can be achieved by mapping the motion against physical references that are either artificially constructed (e.g. placing pickets arranged in a spatial distribution with defined distance intervals, Bovet, 1968; or with a lattice reference, see Pacheco-Cobos et al., 2003), or naturally occurring, such as landscapes (e.g. distance between trees or a group of flowers).

Longer displacements can be tracked with satellite positioning (Jouventin and Weimerskirch, 1990; Weimerskirch *et al.*, 2002) or telemetry (Keating *et al.*, 1991), involving an automated sampling process which depends on fixed intervals set by the observers and is limited by the resolution and storage capacity of the recording apparatus (Ryan *et al.*, 2004; Hays *et al.*, 2001). On other occasions, movement is detected by indirect evidence of animal activity, such as hair, droppings, or track marks (Whittington *et al.*, 2004); paths detected this way can be recorded, for example, by recording their position with any of the methods mentioned above at the desired resolution. Given the previous examples, it is clear that different sampling methods may produce path representations with different

details and features (Behamou and Bovet, 1992). The path of a bee inside a patch of flowers can be represented as the linear sequence between landings, while sampling at fixed time intervals can capture features of the path between the flowers, which might be useful in a more detailed analysis. Also, while fixed time intervals are convenient for accurately representing speed, recording motion at fixed distance intervals might be used to produce a gapless representation of the distance travelled, which is especially relevant if the particular organism has lengthy resting times (Getz and Saltz, 2008).

An important characteristic of the recording method chosen to study a path is it's resolution, i.e. the distance or time in which the movement will be sampled, relative to the distance or time in which movement normally occurs (Codling, 2005). Ideally, the resolution should reflect the characteristics of the motion in terms of the length scale that the study wishes to analyse. Realistically, however, the resolution is more than often limited by the methodological and technical capabilities of the study, which generates underor over-sampled paths whose direct interpretation can lead to errors (Turchin, 1998). If under-sampled, the points making up the path do not provide sufficient resolution to accurately represent the movement of the subject/s under study. For instance, if an organism moves in a spiralling fashion, and is sampled using large intervals, the lines between successive points will depict a rugged forward movement rather than it's true spiralling movement. Conversely, over-sampling may capture more detail than is necessary, resulting in the creation of artefacts that make it difficult to interpret the path. For example, recording movement with a too high resolution produces records that may be interpreted as movement features that are, in fact, mere body shifts naturally associated with gait. This is more extensively discussed by Turchin, who refers to the wobbling motion of cockroaches (1998, p. 131).

Thus, as a general rule it is risky to attempt to interpret paths directly from sampling, since their resolution is frequently not optimal and limited by the available recording methods. Pre-processing methods can provide criteria that help decide which data to use, which to discard and can even improve under-sampled paths. Overall, it is advisable to favour over-sampling rather than under-sampling, since pre-processing strategies are

better able to deal with over-sampled data, and make less assumptions. Thus, by setting intervals of high resolution as a general guideline, flexibility can then be gained during pre-processing (Turchin 1998, Benhamou and Bovet, 1992).

In general, movement can occur in one, two or three dimensions. Although the following text will deal mainly with two dimensions, most of the analysis can be applied to a different number of dimensions. Obviously, dimensionality is strongly related to the physical medium in which the motion is taking place, however, when possible, dimensionality should be simplified, since situations can become increasingly complex due to the higher number of options yielded by the use of more dimensions.

2.2.2 Path characteristics

Once the methodological details have been decided with the help of the criteria and examples discussed above, and the paths are sampled, one can begin to resolve the characteristics of the path. Sampled movement, by whichever method, becomes a discrete path represented by a time series of sequential co-ordinate points (x_i, y_i) in a reference system. At this stage, the path can also be represented using a time series of another set of important elements:

• The step lengths, quantifiable as the series of the lengths (l_i) of the line segments between successive sampling points, can be calculated as:

$$l_i = \sqrt{(x_{i+1} - x_i)^2 + (y_{i+1} - y_i)^2}$$
 (2.1)

Where (x_i, y_i) and (x_{i+1}, y_{i+1}) are values of the consecutive coordinates that make up the path.

• The turning angle θ , which is the change of bearing between two consecutive steps, can be calculated as the difference between the angles of successive path segments, measured with respect to an arbitrary system of reference. For each segment, its angle θ_i can be computed as:

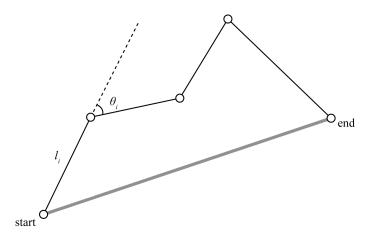


Figure 2.1: Path Characteristics: A simplified path segment is used to illustrate a) the length of a step, which is the segment between two consecutive fixed points, b) the turning angle, or the change of bearings between steps and c) the beeline between the start and ending point of the path segment (in grey).

$$\theta_{i} = \begin{cases} if \quad y_{i} < [sgn(\Delta x_{i})y_{i}\pi + arctan\left(\frac{\Delta x_{i}}{\Delta y_{i}}\right)] \\ else \quad arctan\left(\frac{\Delta x_{i}}{\Delta y_{i}}\right) \end{cases}$$
 (2.2)

Where the sgn function is defined as:

$$sgn(x) = \begin{cases} for & x < 0 & -1 \\ otherwise & 1 \end{cases}$$
 (2.3)

The turning angle $\Delta\theta_i$ is calculated as the difference between successive values of θ or:

$$\Delta \theta_i = \theta_{i+1} - \theta_i \tag{2.4}$$

A third characteristic is the change of bearing (ψ) of every step which is calculated as the angle between the orientation of a step as referenced from the horizontal axis (Figure 2.2).

These features of the path are simple to calculate (See figure 2.1), and provide a ground for comparing the performance between organisms with regards to energy expen-

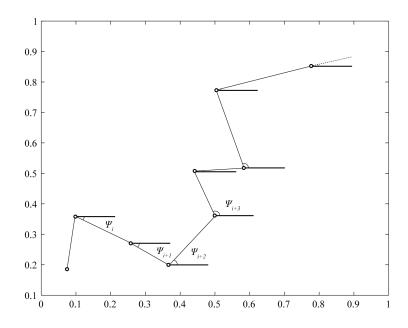


Figure 2.2: Measuring ψ (a)

diture, coverage, efficiency and directionality. Moreover, they form the basis for comparison with other statistical models of movement. For instance, the total path length L which is given by the sum of the lengths l_i of the segments, and the *beeline*, which is the straight line between the first and last point of the path. It's orientation with respect to an arbitrary axis represents the path's main bearing. Also, the ratio between the length of the beeline and the total path length can be used to estimate the tortuosity of a path. Yet, these values are likely to vary depending on the sampling procedure, and the criteria used by the researcher, when the path is sampled as behavioural events. To reduce this variability and to transform the data into a form more convenient for the intended analysis, the data should undergo pre-processing procedures that correct for over- and, when possible, under-sampling.

2.2.3 Pre-processing

In path analysis, pre-processing consists of a series of optional steps designed to manipulate data in order to select or, when necessary, create data from the sampled process that most accurately represent the characteristics of the movement. Typically, any sampled path will undergo a great deal of pre-processing. This includes interpolation for paths

which are suspected to be under-sampled or have missing records, and re-discretisation and coarsening, for paths that are over-sampled.

Interpolation

Interpolation involves the insertion of new co-ordinate locations between sampled points to enhance the representation resulting from an under-sampled path. The most direct interpolation algorithm is linear interpolation where an interval is subdivided into smaller ones by adding new co-ordinates over the line drawn between (x_a, y_a) and (x_b, y_b) . For example, choosing the value of x_{new} as the x-coordinate for an interpolated point, the corresponding value of y_{new} can be calculated with:

$$y_{new} = y_i + x_{new} - x_i \left(\frac{y_{i+1} - y_i}{x_{i+1} - x_i} \right), \quad for \quad (x_i, x_{i+1})$$
 (2.5)

Linear interpolation is often used to fill in the gaps left by missing points when sampling is made in a *conservative* manner (Tremblay, 2006). While nothing is gained by interpolating a correctly sampled path, linear interpolation relies on the assumption of linear displacement to complete a defective sampling process by placing steps inside the gaps, which are arbitrarily determined by, for instance, by the sampling frequency.

Of course, linear interpolation is not the only choice: there are an infinite number of curves which can be chosen to interpolate between any two sample points (for the result of a few arbitrary choices, see figure 2.3). However, some interest has been directed towards the use of splines to represent movements (Turchin, 1998). Splines are curves obtained by evaluating a set of low-degree polynomials, each one defined over a different subinterval of the path coordinates. Splines can be chosen to produce a smooth curve with seamless unions at each of the path sample points, interpolations can then be chosen as points along the spline. There are several types of splines with different properties, though the choice of which to use that best represents movement remains arbitrary. Spline interpolation has been attempted with limited success in aquatic environments, since they best model the movement of particles in the atmosphere or oceans, in which movement operates in a curvilinear manner due to the forces that influence fluid properties, like density gradients

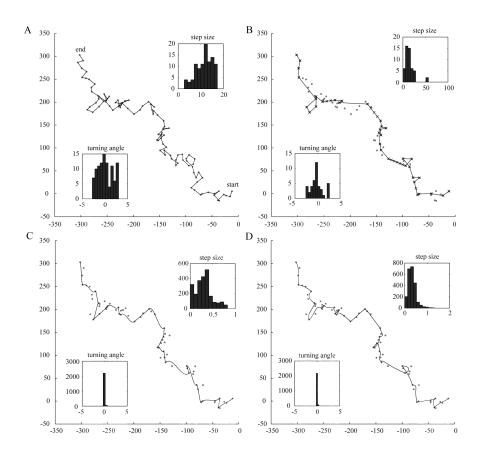


Figure 2.3: Example of interpolation. A regularly sampled path (a). The subsequent interpolation efforts when the original path has randomly lost 10% of the original sampling points by (b) linear interpolation, (c) cubic splines, and (d) a set of bezier curves.

and Coriolis forces (Vogel, 1994). Also, the movements of animals tracked in fluids or the atmosphere, such as birds in flight or aquatic organisms, are heavily affected by wind or current. Curvilinear tracks are consistent with marine animals moving in fluid, curvilinear structures (Tremblay *et al.*, 2006). Given this observation, Tremblay *et al.*, (2006) evaluated interpolation using curvilinear algorithms for tracks of different species, observing not only a more accurate description of the actual movement of certain marine species but also a higher accuracy when estimating the length of paths from fewer data points.

Rediscretisation

Rediscretisation is the calculation of a new path over an old one using a constant step length (Turchin, 1998). This is generally useful for finding a length scale in which steps are not self correlated (the statistical simplicity of independent steps is discussed below), even if at some scale they accurately represent the nature of the movement. Rediscretisation is commonly used when self correlation is considered a spurious consequence of over-sampling.

Self-correlation can be dependent on the sampling interval, hence, by increasing step length until the correlation disappears, it may be possible to reconstruct the path as a series of steps with independent turning angles (Figure 2.4). Even though rediscretising path information results in information loss and decreased resolution of the path, the gain of representing the path as a sequence of independent steps can prove valuable for statistical models and bootstrapping techniques (Turchin, 1998; Dray, Royer-Carenzi and Calenge, 2010). One of the possible ways in which rediscretisation can be implemented is found in *box 1.0*. When using a rediscretisation procedure to remove correlations and oversampling, the choice of length for the new step should, ideally, involve knowledge of the organisms activity (Turchin, 1998). The link ¹ contains my own Matlab implementation of the process described in box 1.0.

 $^{^{1}}http://docs.google.com/Doc?docid=0AXBqPCRUKfQHZGRnYnI0Z21fMjByY3YzODZjNA\&hl=en2deltahter.$

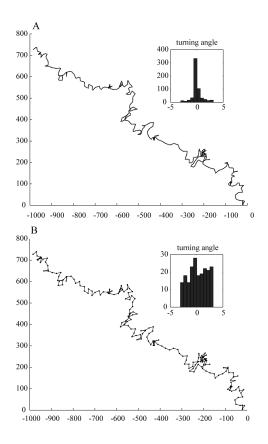


Figure 2.4: Effect of rediscretization:(a) A path consisting of frequent sampling points and normally distributed turning angles (a, inset), and after (b) rediscretization procedure. The number of steps is reduced but changes the turning angle distribution to a uniform distribution (b, inset), thus removing the directional persistence of the previous turning angle distribution.

Box 1.0 The following box contains an easily computable algorithm to rediscretize a path. First, a new step length d' is chosen by the researcher. For a correlated path, the rediscretization step at which the correlations are lost is λ , which can be found by attempting rediscretization with sequential increments.

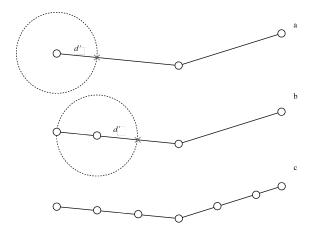


Figure 2.5: Illustrated rediscretization procedure.

Over the original path, a circle is drawn using the first point on the path as the center and d' as the radius. Figure 2.5 (a). The first step of the rediscretized path goes from the center or the circle to the closest point where the circumference intersects the path. The intersection coordinates can be calculated with the following formulae:

$$x = \frac{D\Delta y \pm sgn(\Delta y)\Delta x \sqrt{r^2 d_r^2 - D^2}}{d_r^2}$$

$$y = \frac{-D\Delta x \pm |\Delta y| \sqrt{r^2 d_r^2 - D^2}}{d_r^2}$$

where, d_r , D

$$d_r = \sqrt{\Delta x^2 + \Delta y^2}$$

$$D = x_1 y_2 - x_2 y_1$$

Then, the center of the circle is moved to the next point (the first point of the rediscretized path, figure 2.5 (b)) and the process is repeated until the end of the path is reached. The resulting path has a fixed step length equal to d' (Figure 2.5 (c)).

Coarsening

Coarsening is another popular preprocessing technique, which potentially reduces an oversampled path into a smaller sequence of distinct *effective* steps of appropriately vary-

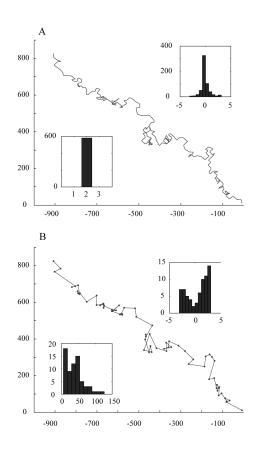


Figure 2.6: Effect of coarsening: (a) An oversampled path, with a turning angle distribution centred around zero (a, inset), can be resampled (b) in steps of varied size through coarsening, which usually reduces the number of steps and changes the shape of the turning angle distribution (b, inset).

ing length (Turchin, 1998). In essence, by coarsening, the path variations which fall within a given threshold are removed and the steps involved are joined into a single *effective step*. One of the possible ways in which to implement this procedure is illustrated in *box 1.1*.

The threshold of variation for a step to be joined is decided by an arbitrary parameter w. The choice of w is based on observation of path structure and does not necessarily reflect any biological information, this justifies incrementing systematically the parameter w to find the most suitable *effective steps*. The link 2 contains the Matlab implementation of the process described in box 1.1.

Similar to rediscretisation, coarsening can also remove sequential turning angle correlations, but there is no need to choose a step size, rather, the procedure gives rise to a path with variable step sizes (Figure 2.6). However, a problem with this procedure is a

²http://docs.google.com/Doc?docid=0AXBqPCRUKfQHZGRnYnI0Z21fMjJnY25kMzdnZw&hl=en

potential larger loss of information compared with rediscretisation. The reduction in the number of steps may be far greater when coarsening, thus, first attempting a rediscretisation procedure may help in cases where step number is an issue.

The potential gain may outweigh the loss of resolution, since having paths of variable step lengths, and independent turning angles, greatly increases the chances of successfully using several bootstrapping methods as well as allowing for the comparison of data with statistical models (these are described in the next section).

Box 1.1 First, a threshold value w is defined (a). This value roughly represents the amount of variation to be removed from the path. A rectangle crossed in the middle through its longest length by the line between P_o and P_{i+2} , and whose shorter side is 2w is drawn (a). Then, the coordinates between P_o and P_{i+2} are examined to see whether between they fall within the rectangle borders (b). If the coordinates fall within the rectangle, the rectangle is drawn again for the interval P_o to P_{i+3} (c). This procedure is repeated until the coordinates in between the interval fail to fall inside the rectangle (c) or the path ends. When the coordinates fall outside the rectangle boundaries, the interval, up to when the coordinates still fall inside the rectangle is joined into a single step $(P_o - P_{i+4})$ and the end point if the new single step is used to repeat the process (d) until the path ends (e).

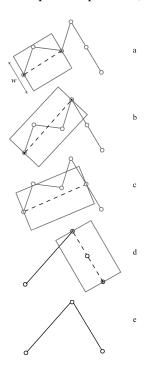


Figure 2.7: An example coarsening procedure, illustrating my own implementation

Note: For both preprocessing procedures, there are values which are chosen by the experimenter (d' in rediscretization, w in coarsening). In order to find the value for these parameters which returns the desired effective step and angle distribution, the pre-processing should try out systematically increasing values, testing the effect of different values on the resulting distributions. In both cases the effective paths can be reached once the sequential turning angle disappears or the shape of the turning angle distribution remains relatively stable.

Correlation is usually caused by the natural tendency of an organism to move in a

straight line, a reflection of the biased distribution of the sensorial systems attributed to cephalization and bilateral symmetry, or even willfully maintained as an effective searching strategy. It is common to study autocorrelated data in order to evaluate and distinguish between kinesis and taxis in an organisms movement. Choosing to analyze autocorrelated features of a path over those arising as the product of rediscretization or coarsening, implies the choice of a length scale and does not discard the phenomena occurring at a different (usually larger) one. In fact, the long steps commonly produced by coarsening represent the instances where the organism travelled in a correlated manner, although the focus is rather placed on the reasons and places where the direction changes are occurring . For the cases where correlation occurs with larger angles, such as in systematic movements, coarsening may in fact enhance the correlation of the turning angles. Identification of the most salient features of systematic movement are discussed further in this chapter.

Pre-processing may change the attributes of the original path, such as the shape of the step length and turning angle distributions. It may also remove the presence of self-correlated turns and step lengths. If steps and turns are uncorrelated, and therefore independent processes, it may be possible to represent the path as a random walk, a topic described with more detail in the next section.

On the detection and removal of self-correlations

A correlated movement process implies that the probability of the choice of turning angle or step length at every step is influenced by previous turning choices or step lengths. There are several ways in which correlation can be detected. A simple way to detect correlations between successive step directions is to calculate the mean $\cos(\theta)$ of the turning angles, where a value approaching 1 denotes absolute correlation for a path that travels in straight line, while uncorrelated steps yield a value 0 and a value of -1 denotes a negative correlation, or a path where the walker makes a complete directional change on every step.

Another way to detect self-correlated turning angles or step lengths is the computation of the autocorrelation function for these values. Autocorrelation can be detected in a time

series by comparing a signal with lag-shifted versions of itself. An issue that arises when working with an autocorrelation function to detect self-correlations in a path, is the need for fixed units, which in the case of pre-processed paths is *n* or the tag attached to each step (Dray, Royer-Carenzi and Calenge, 2010).

Another technique that could to detect autocorrelation in a path is normally applied to the detection of correlations in the underlying signals in time series and involves the use of the Fourier transform. The Fourier transform gives the amplitudes of corresponding to each frequency when we represent the signal as a superposition of periodic functions (sines and cosines). Structure in the frequency domain relates to an underlying structure (correlations) in the functions that give rise to the time series. Conversely, a constant power spectrum in the frequency domain indicate an uncorrelated, *white*, signal. (Brillinger, *et al.*, 2004). Something similar can be achieved by using wavelets, which are a special case of Fourier transforms that involve the simultaneous representation of time and frequency of a signal (Polansky, *et al.*, 2010). As with any time series, it is also possible to divide a path in smaller segments and test for local self-correlation.

Sometimes it is possible to remove correlation so that the individual steps can be treated as independent events, which is useful if the case requires the use of bootstrapping techniques. Self-correlation can be dependent on the sampling interval and therefore by increasing step length until the correlation disappears, it may be possible to represent the path as a series of steps with independent turning angles (Dray, Royer-Carenzi and Calenge, 2010). Pre-processing involves changing the scale with which steps are represented; thus, ideally, a scale can be found a scale can be found where the step properties are no longer self-correlated. Correlation might still exist, but on smaller scales. Hence, during pre-processing, one goal is to find the smallest scale at which correlations disappear.

Removal of self-correlations may be desirable in order to address the process generating the path as a series of independent events. Having independent steps allows for a great simplification of the statistics describing movement and allows the comparison of the recorded paths with some of the simplest random walk models. Also, correlations are

undesired because they frequently are a consequence of the recording method, however, it is possible that sequential correlations might be a feature of interest in the path. Within this work, emphasis is placed in processing the data as to arrive at the simplest set of choices, and independent steps guarantee the simplest statistical explanation.

2.3 Probabilistic models of movement paths

The use of statistical movement models allows for the description of path features within a greater framework of probability that has a long research history and hence, many testable predictions. One of the most basic descriptions obtained is from the visual inspection of the shape of the step length and turning angle distributions. For instance, if paths can have steps of variable length, the shape of the distribution of step length values may be measured. The shape of the distribution suggests many features of movement, whether steps are normally distributed or perhaps the path is better described as a series of small steps interrupted by the rare appearance of extremely long steps. Similarly, the distribution of turning angles yields information on the statistical arrangement of successive bearings of the path. A distribution of turning angles centred around a mean of zero signifies the most frequent direction taken, and that the walker moves more frequently to those places.

2.3.1 The mean squared displacement

Amongst the first statistical descriptions that can arise from a path's characteristics is the squared displacement. The step length and change of bearing are combined to compute the squared displacement, which is an account of the length that an individual searcher has travelled from it's point of origin in a given number of steps, or $|\bar{R}|^2$. It is mainly useful to calculate *mean square displacement* for theoretical paths or groups of organisms by averaging several paths at each step and the rate at which the variance grows can help determine the rate of diffusion of that particular set of paths, or the probability to find any of the walkers at a certain distance after a given time period.

The mean (thus μ) of the square displacement ($\langle |\bar{R}_{\mu}|^2 \rangle$) is computed as:

$$\langle |\bar{R}_{\mu}|^2 \rangle = \frac{1}{N} \sum_{\mu=1}^{N} \left[\left(\sum_{i=1}^{n} l_i \cos(\psi_i) \right)^2 + \left(\sum_{i=1}^{n} l_i \sin(\psi_i) \right)^2 \right]$$
 (2.6)

Where ψ_i is the angle resulting from the change of bearing at step i, l_i is the length of step i, n is the number of steps in a path and N is the total number of paths in the sample. While the square of the mean $(|\langle \bar{R}_{\mu} \rangle|^2)$ is:

$$|\langle \bar{R}_{\mu} \rangle|^{2} = \left[\frac{1}{N} \sum_{\mu=1}^{N} \sum_{i=1}^{n} l_{i} \cos(\psi_{i}) \right]^{2} + \left[\sum_{\mu=1}^{N} \sum_{i=1}^{n} l_{i} \sin(\psi_{i}) \right]^{2}$$
(2.7)

So then the variance (σ) is the difference between the mean of the square and the square of the mean:

$$\sigma = \langle |\bar{R}_{\mu}|^2 \rangle - ||\langle \bar{R}_{\mu} \rangle||^2 \tag{2.8}$$

The comparison between the variance of the mean squared distance calculated and that expected from a random process can be used to suggest the presence of orientation mechanisms and the diagnosis of non-random elements. Similarities (or differences) in the statistics of sampled paths over a limited time or space interval should not be considered as definite arguments to accept nor reject the model: the characteristics of paths are frequently affected by the scale of description and amount of data. Therefore, in order to attempt a comparison and to determine the similarities and differences that a particular set of paths hold to a random process, other characteristics should be tested.

In biology, we often find that the turning angles of the movement of many organisms draw normal distributions, with a mean centred around zero. Some authors have suggested another way of calculating the mean squared distance to take this fact into consideration. For instance, Kareiva and Shigesada (1983) suggested that calculation of \bar{R}_n^2 the following formula could be used. In this formula, only the mean cosine is taken into consideration, since the sine of small angles is close to zero. Also, note that n is used instead of mu, since it is for individual paths:

$$\bar{R}_n^2 = nm_2 + 2nm_1^2 \left(\frac{c}{1-c}\right) \left(n - \frac{1 - c^{\frac{n-1}{2}}}{1-c}\right)$$
 (2.9)

Where:

$$m_1 = \frac{1}{n} \sum_{i=1}^n l_i, \quad m_2 = \frac{1}{n} \sum_{i=1}^n l_i^2, \quad c = \frac{1}{n} \sum_{i=1}^n \cos(\theta)$$
 (2.10)

The expression within parenthesis gives importance to the mean cosine of turning angles in the first steps, so that for paths with a large number of steps (n >> 1):

$$\bar{R}_n^2 \approx n \left(m_2 + 2m_1^2 \frac{\psi}{1 - \psi} \right) \tag{2.11}$$

The variance around the mean squared displacement can be calculated by the difference between the squared displacement and the square of the displacement (McCulloch and Cain, 1989).

2.3.2 Random walks

The theoretical description of paths generated by a sequence of distributed steps, i.e. lengths and turning angles, falls within the framework of random walk models. In general, the basic assumption of a random walk is that paths are constructed by the successive concatenation of steps drawn from appropriate probability distributions. When a given random walk model is found to statistically fit a biologically observed set of paths, then the model can be used to make inferences about the efficiency with which the path covers space, the probability it has to encounter sparsely distributed random targets, the frequency it will revisit previously visited areas, etc. On the other hand, when a path is judged to be non-random, random walk models can be used as a null hypothesis to evaluate the internal or external reasons as to why the path differs from randomness. Of course, for cases consisting of few sampled paths, it may be hard or even impossible to distinguish among the many types of random walks, and thus to determine which model best represents the biological process. In what follows, all paths are represented as occurring on a two-dimensional surface, though it is also possible to represent them and measure their characteristics in one and three dimensions.

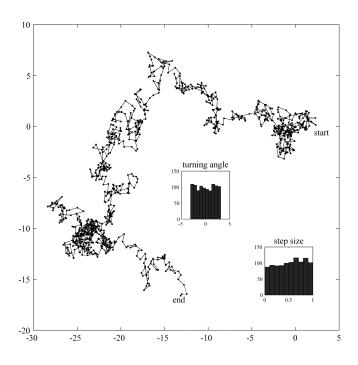


Figure 2.8: An example of a simple random walk, with the main statistical features (inset) a uniform turning angle and step length distribution.

Simple random walks

A simple random walk is the most basic form of a random walk involving step sizes and turning angles drawn from uniform distributions. It exhibits normal diffusion (linear growth of the variance of the mean squared displacement) and is characterised by the independence and isotropy (i.e. lack of a preferred direction) of the steps comprising the path (see example in figure 2.8). Basic random walks are still popularly used as models for movement in bacteria (Keller and Segel, 1971, Schnitzer *et al.*, 1990) and have proven useful when describing the movement of populations as a diffusion process (Okubo, 1980). Among the properties that have been studied, it is possible to calculate the chances that a random walk has to visit a certain number of sites, whether some sites have more probability of being visited, the number of times it will visit the same site, the time it may take to cover all the area, and several more properties.

Given the vast body of knowledge on the basic random walks, it is clear why it provides such a good testing ground for biological hypotheses. For instance, one could ask how different is the natural movement of an organism to a random walk. If the movement of an organism is like a random walk, what are the chances it might get back home? How

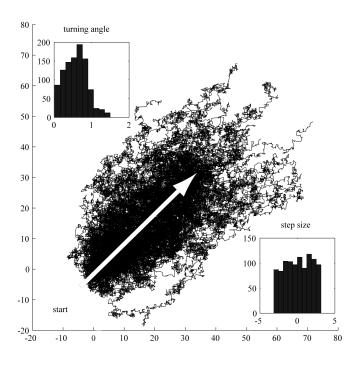


Figure 2.9: The directional bias of a set of 100 biased random walks is shown by a white arrow. The bias is created in this case by a preferential choice of a random turning angle (inset).

likely is it that it will encounter all the resources? Will it find the closest resources to home or will it look for the farthest ones? What happens if resources regenerate or move around? Amongst the advantages of a random walk as a null hypothesis is it's simplicity. If no other elements are taken into account and movement is said to be random in origin, how much would it differ from the movement we observe? On the other hand, this can prove to be a disadvantage - no organism can be said to move in a truly random fashion, nor in a boundless environment. Thus, in many cases, it's potential as a null hypothesis is limited. Many questions, however, might benefit from the use of random walk models by increasing the complexity to include other elements, such as energy expenditure or risk of death. What follows are some of the variants of the basic random walk found to be popular in the biological literature, which can be obtained by modifications of properties of the distributions on which the turning angle and step sizes are drawn.

Biased random walks

A biased random walk produces paths with an orientational bias. Although the individual components (step size and turning angle) are random, they might contain a slight bias. For instance, steps taken in a certain general direction (e.g., north) can be longer than those moving in any other direction (Figure 2.9). This type of random walk can also exhibit a linear growth in the diffusion rate, although sub diffusion (that is, a diffusion rate lower than expected for a simple random walk) can happen if the bias pulls the walker to the point of origin.

Biased random walks have been proposed as models for organisms which orient towards stimuli, for example, swimming bacteria with simple motor and navigational mechanisms, perform biased random walks to get closer to their objectives (Segall, 1986). Also, it can be an efficient searching strategy in heterogeneous landscapes, where distribution density exists as a gradient (Hill and Häder, 1997; Kamil *et al.*, 2009).

Knowledge of the biological system generating the path may be essential for the classification of these paths as biased random walks. Usually, by knowing the position of a potential attractor, it is possible to calculate the general direction towards which the bias is directed. In these cases, the variance of the turning angle might become relevant, as it can prove to be significantly different from that of a basic random walk.

Correlated random walks

Random walks where the turning angles are considered to be independently drawn from a distribution with a mean that peaks around zero (or any other mean, though in biology this value is usually close to zero) earn the name of correlated random walks (Figure 2.10). Once a direction is taken, it is more probable to find the walker somewhere along the initial angle. However, given that the first angle is also a random choice, dispersion also increases at a linear rate.

Correlated random walks are popular in references of biological movement, which can be explained by the fact that many animals have normal distribution of turning angles, i.e., they prefer to move forwards. The anatomical configuration of most animals is on

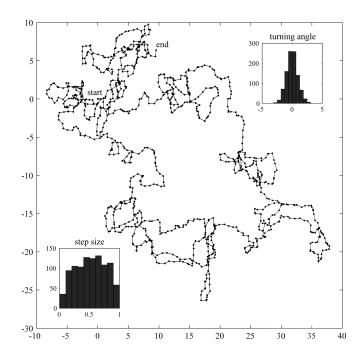


Figure 2.10: An example of a correlated random walk, in which the main feature is that turning angles appear to be drawn from a normal distribution (inset)

a longitudinal body axis, with the head on one of the endpoints (Bovet and Benhamou, 1988). The head usually concentrates the senses so navigation persists in this direction. This type of model has been described for the movement of *Eleodes* beetles (Crist *et al.*, 1992), caribou (Bergman *et al.*, 2000), swans (Nolet and Mooij, 2002) and many others species. Foraging habits resembling correlated random walks can be efficient under certain conditions, such as when searching for locations that can only be visited once, the higher frequency of small turning angles reduces the chances for the path to repeatedly visit the same place.

Lévy walks

Lévy Walks are random walks in which the length of constituent steps is best described by a Lévy distribution, in which the frequency of ever larger steps decreases as a negative power function of their length. An interesting property of Lévy walks is that they exhibit scale invariance on the step distribution, meaning that at several scales, it is possible to observe small steps punctuated by the rare appearance of extremely large ones (Figure 2.11). The length of each successive step (l) varies according to a truncated power-law of

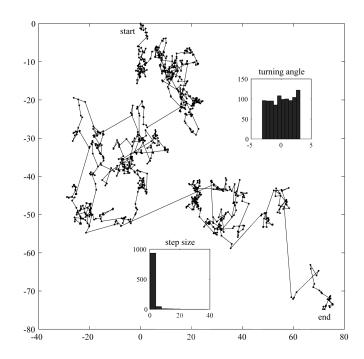


Figure 2.11: An example of a Lévy walk, where the steps are drawn from a Lévy distribution, which is a visually evident feature given the presence of rare but conspicuous long steps, punctuated by patches of smaller step lengths.

the form:

$$P(l) \sim l^{-\mu}$$

$$where$$

$$1 < \mu < 2$$
(2.12)

Lévy walks are frequently reported in the biological literature, particularly for foraging paths of animals. They have been reported for microplankton (Bartumeus *et al.*, 2003), albatross flights (Viswanathan *et al.*, 2006), foraging paths of deer (Mårell *et al.*, 2002), the movements in-between inflorescence made by bumblebees (Reynolds, 2005), spider monkeys in the Yucatan peninsula (Ramos-Fernández *et al.*, 2004), Peruvian purseseiners fishing trips (Bertrand *et al.*, 2005), humans, as estimated by travelling distances of marked currency (Brockmann *et al.*, 2006) and many others. This is relevant because some environmental features are also scale invariant, like the distribution of resource patches (Ramos-Fernández *et al.*, 2004). Large steps provide a way of moving between patches while small movements can be used to exploit the resources within a patch.

Léve walks are an efficient search strategy for sparsely distributed resources. The in-

frequent and extremely long steps move the searcher away from a certain area that may be closer to another patch. A visual inspection of the paths and the step size distribution can suggest a Lévy walk, particularly when looking for characteristics, such as the presence of single steps with a length similar to that of the whole path. A linear fit of the frequencies of the step size in a logarithmic plot (across as many scales as possible) can be a good estimator of scale invariance. A slope of the linear fit between 1 and 3 (optimally 2) can suggest a Lévy distribution of step sizes. Since histograms are sensitive to the choice of bin size, the number of bins has to be chosen geometrically, increasing the bin size logarithmically until a good match is found. A goodness-of-fit statistic should be used, as many distributions can resemble a Lévy distribution, leading to mistakes in identification of Lévy walks in several organisms (Edwards *et al.*, 2007). Other transformations greatly increase the accuracy of the identification, such as plotting the frequencies divided by the bin width against the geometrical bin width (Benhamou, 2007). A detailed account on minimising the error when identifying Lévy walks can be found in the work of Sims, Righton and Pitchford (2007).

2.3.3 Saltatory search

Saltatory search is a set of probabilistic models, which have received little attention (Anderson, 1997). These models contemplate searching as a series of runs and pauses, while placing emphasis on the characteristics of the distribution of waiting times, namely the intervals in which the organism does not move. Anderson (1981) identified that saltatory search was likely to occur when the functions relating body speed to benefits are concave-up, as opposed to cruise search occurring when those functions are linear or concave-down. That is, when an organism needs to move fast to catch it's prey, the more likely strategy adopted would be to wait and ambush. However, if prey moves slowly, organisms can cruise by and collect prey without adopting a saltatory search strategy. The characteristics of movement (step size or direction) can be replicated by any of the models described above. However, waiting times between steps is an easy way to implement fluctuations in the velocity that are not central to the description of random walk. Waiting

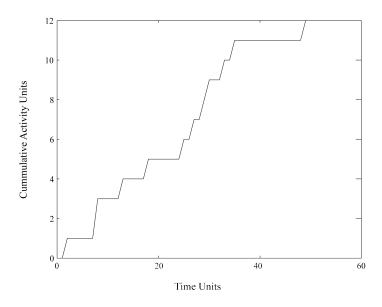


Figure 2.12: Step plot better represents the saltatory searches: the length of flat periods are the static searching periods, while the sudden increases in the cumulative activity show the brief periods where movement occurs.

times might be a qualitative feature worth studying in certain contexts. For example, when movement is particularly costly for a predator, or a prey is hard to detect it can pay off to make only few displacements to attempt to catch a target (Souto *et al.*, 2007). Where prey predictability is low, non-translational periods to scan the area can be beneficial. If prey are mobile, it could pay off to wait and ambush, especially in areas of high prey density or a scenario of great speed disadvantage. The velocity and duration of movement bouts can be adjusted to the size of prey to optimise the energy gain, as shown by the freshwater fish, white crappie (O'Brien, 1989).

When plotting the cumulative distance travelled versus the time spent, it is possible to identify the characteristic waiting times by analysing the frequency and length of the flat lines in the plot (Figure 2.12).

2.3.4 Pseudopaths and bootstrapping

When producing movement records, is not uncommon to obtain statistically challenged databases (i.e. recording only a small sample of searchers or search paths with a small number of steps) because of situations involving difficult recording terrain, an extensive effort needed from the observer to obtain a detailed record or rare sampling opportunities.

A usual statistical challenge faced by movement databases is that even after considerable experimental efforts, the number of sampled trajectories are still fewer than what is needed to make statistically-sound claims. However, some statistical methods allow one to make full use of even a small data set. For instance, it is possible to make full use of a reduced sample of paths by using bootstrapping procedures. Bootstrapping is an computational method that assigns measures of accuracy to statistical estimates (Efron, 1993). It can be used to approximate distributions, standard errors and confidence intervals and other statical characteristics by methodical resampling from an original data set. Resampling bootstrapping can be used on processed individual paths to learn more about their statistical characteristics.

Pseudopaths can be computationally-generated by determining the similarity of the path's characteristics to a certain probability distribution and then, using such distributions to generate populations of paths with similar characteristics (Tremblay, Robinson and Costa, 2009). In such a process, at least two distributions come into play: the shape of the step size and the turning angle distribution. At every step, a new coordinate is generated drawing the corresponding step size, or l_1 and a and a turning angle, θ_1 . This process can be repeated for n number of steps and for N number of paths. On the other hand, if a path's characteristics are clearly independent, that is are no self-correlations in the path or the path is not correlated with any spatial reference (which denotes orientation or taxis), constructing paths using reshuffled step sizes and angles is an alternative bootstrapping procedure. This can be done by randomly interlocking pieces of the path in any way. For instance, paths can be reversed, or any part of the path attached to any other part. Indeed, an alternative test of event independence, can be done by checking if statistical properties are maintained when paths are randomly reshuffled.

By generating large ($>10^6$) amounts of resampled paths through computer simulations, it is possible to observe of dispersion effects as well as bring out any statistical peculiarities that would not be noticeable in a small sample of paths (Dalziel, Morales and Fryxell, 2008). If events in the paths are not independent they can also be bootstrapped but the complexity of the path-generation process increases. For instance, if steps are cor-

related, it is important to create a path in which the correlation is kept. Pseudopaths can be generated to match any number of characteristics, and again, it is important to make the point that independent steps are only the simplest case. Bootstrapping by resampling cannot account for the possibility that the processes may not be stationary, limiting the power of the interpretation. Thus, bootstrapping provides method with which is possible to resample a small set of paths with the intent of researching their statistical characteristics, although it also has limited statistical assertiveness.

2.4 Mechanistic interpretation of movement paths

2.4.1 Mechanisms vs. models

As mentioned before, probabilistic models describe paths using global features - i.e the shape of the distribution of the turning angles or step lengths. Global probabilistic features can help predict movement features such as dispersion rate, collection efficiency, frequency of revisits to the same place, etc. However, movement characteristics of a path are rarely homogeneously distributed over time. When a particular variation occurs repeatedly under similar conditions we can suggest the presence of a mechanism.

For instance, if an organism moving mainly in straight lines with few turns enters a patch of densely packed resources, the movement of this organism might shift to small steps and an increased turning frequency. If there was a record showing the movement of such an organism, it will be evident that at some point it's behaviour changed, and if information about the environment were available, it could be possible to deduce, from this local change in path properties, a density-aware mechanism to increase collection rate. From a global perspective, the causes of the change in movement properties would only be important for their contribution to the statistical properties of the path, but no effort would be placed on understanding the factors that contributed to the local change in movement properties. So, in this thesis, a mechanism is defined as local changes in path features that can be traced to a particular environmental feature.

To study the changes in their inner structure, paths need to be systematically frag-

mented in sub-paths by criteria such as the occurrences of particular events, the collection of a resource, the detection of a stimulus or the collision against a boundary. To detect the presence of mechanisms in movement records is not always a feasible option. Usually, an extensive knowledge and description of the sensorial capacities of the organism and the spatial distribution of relevant stimuli is a requisite. In normal situations movement is caused by multi-sensory integration and feedback processes, and any attempt to establish a cause and effect relationship will be probabilistic at best. A great aid to pin down the relation between sensorial cues and a movement sequence are experimental testing situations where defined configurations of cues can be tested. The nature of the information input and processing falls outside the scope of this chapter, as interest is in defining how a set of movements comprises a mechanism, as well as the accompanying advantages and consequences.

In this section, discussion will be centred around the identification of common mechanisms based on the characteristics of the movement they produce. Particularly, by showing ways in which movement patterns and mappings of the environment can be overlapped. An arbitrary classification of the sensorial features involved in mechanisms is used, with increasing complexity as more cognitive mechanisms come into play. The last section focuses on foraging, which integrates several of the mechanisms, including memory, and holds an interest in the light of efficiency issues.

2.4.2 Systematic movements

While the environment may include potential cues to guide movement, under certain conditions, systematic movements provide the most viable solutions. In a set of computer simulations Zollner and Lima (1999) show that an exhaustive systematic search performed better than the best correlated random walk when mortality risks are low and energy reserves are high: increasing the range of detection of patches also favoured systematic searches. Systematic searches are easily recognisable, as they often have salient geometric features. Systematic movements are presumably achieved by ignoring cues that might be present to favour a set of systematic rules. Among the advantages of this type

of mechanisms is the simplicity of the underlying geometry, the systematic covering of surrounding space, the reduced cost on sensorial capacity, the reduced dependence on environmental information and finally, keeping track of the directional reference to the point of origin.

In the case *Hemilepistus reaumuri*, a desert isopod that lives in extreme temperatures and is often found in need of a burrow, success time is a crucial factor and a systematic combing of the area can be more rewarding and less costly to execute than searching in a random walk fashion, avoiding repeated visits to the same places without the use of positional references. Hoffmann (1983) described the searching movements of *H. reaumuri* as efficient homing behaviour independent of external orientation cues, that exploits an intrinsic structure that begins as an imperfect spiral with increasingly bigger loops, whose centre remains the starting point. By keeping track of the the simple geometric parameters of which a systematic search is composed, it is possible to locate the starting point by means of a path-integrator, or an integration of the information gathered during the journey, such as the number of steps, the distance from the nest, the total time travelled, etc. In a similar case, when foraging desert ants fail to return to the nest via path-integrators, they engage in systematic searches, consisting of loops of ever increasing size. The density of the systematic search pattern is correlated with the ants confidence in their path integrator, this confidence decreases with increasing foraging distances (Merkle *et al.*, 2006).

An almost unlimited number of systematic strategies may exist. However, for some which produce repeated geometric patterning, identification of the rules underlying a systematic search begins by determining a suitable geometric candidate from observing a plot and recognising structures in the path reminiscent of, for example, spirals (See examples in figure 2.13). A match can be corroborated by calculating a given parameter in the path and comparing it to the values generated by a simulation of the path drawn by the geometric pattern. Given the mechanistic nature of the origin of systematic movement, periodicity or steady changes should be found in some of the parameters, for example, distance to the origin over time, length travelled between steep turns, distance from the origin, etc.

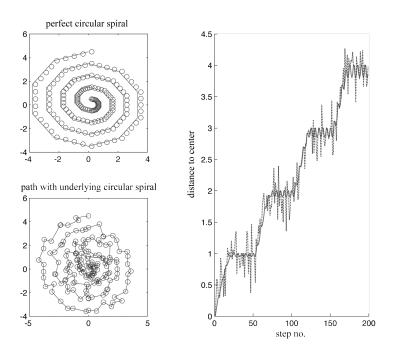


Figure 2.13: (a) An example of systematic movement, (b) systematic movement plus noise and (c) regularity in the path that can give it away as systematic movement.

2.4.3 Cues and working memory

Cue-based mechanisms attempt to relate the way in which an organism moves to its sensory capacity as well as the particular spatial arrangement of relevant information in order to determine the mechanisms employed to sample information and the accuracy of the decisions involved. For this, a map of the stimuli is needed with a resolution relevant to the organism's discerning capacity, as well as a movement record that is fine enough to relate directional changes of the organism in response to changes in environmental variables. For instance, the migration rate of the pseudo-plasmodia that drives the thermotaxis of the slug *Dictyostelium discoideum*. The migration patterns of these slugs display strong dependence of the range of temperature, moving only when located within a given range of temperature values and stopping their movement in higher temperatures (Poff and Skokut, 1977).

Due to their disperse nature, many stimuli occur in gradients, where intensity decreases as a function of the distance from the source. The movements an organism makes while responding to a gradient can either be classified as a kinesis or a taxis; they are considered positive when moving towards the source or negative if moving away from the

source. Taxis and kinesis are among the first orientation mechanisms derived from studying movement. They are particularly well described, classified and extensively illustrated with examples in the classic works of Fraenkel and Gunn (1961). The main difference between these orientation mechanisms is that in a taxis, orientation is achieved by movement with a directional aim while during a kinesis an organism manages to approximate a target by means of an increased turning frequency. As the organisms approach the desired value, movements might become increasingly accurate (reviewed in Benhamou and Bovet, 1992).

Gradients should disperse in concentric circles, yet physical obstacles in the surroundings, i.e. water or wind currents frequently shape them into linear plumes. When inside a gradient, the edges can be detected by a steeper drop in the range of the stimulus values, thus producing a corresponding change in behaviour. Movements towards the gradient source are oriented in a direction perpendicular to the gradient's edge. Zigzagging or *counter-turning* is the succession of alternating left and right turns, and is a common feature of the movements flying insects use to track an odour source (Kennedy, 1983). An illustrative example of the orientation mechanisms used within a gradient is provided by Baker and Kuenen (1982), where they describe the zigzag fashion movement used by male oriental fruit moths whilst flying along a stationary pheromone plume.

One of the most fundamental mechanisms for orientating in a gradient is to compare the difference between subsequent timed samples. This is where working memory becomes important - by sampling information, any current sensorial value must be compared to those sensed in the past in order to orient. Therefore, a positive difference can be followed to reach (or turn around to avoid) the source while a negative one can be used to turn and correct (or continue along to escape) the source. By increasing the sampling points (the information stored in working memory) it is possible to achieve a more accurate navigation through the gradient.

For instance, the neural model of Mori and Ohshima (2002) for *Caenorhabditis elegans* thermotaxis involves mechanisms regulated by two interneurons in opposite directions: a difference in one direction positively stimulates the other direction to move

towards the source. The number of sampling points needed to track a source is small. This can be observed in paths resulting from the implementation of the algorithms of model cricket phonotaxis (Webb and Scutt, 2000) and lobster inspired, odour-tracking underwater autonomous robots (Atema, 1996). A crossed stimulation of sensors and motors allows the source of a gradient to be tracked down by measuring intensity at every time step. When the difference is not informative enough, random movement may ensue to produce a significant difference on which to act. Termites move randomly until detecting the odour of food sources: when these insects forage, a successful exploratory path leaves a pheromone recruitment trail, which becomes increasingly conspicuous as more individuals join in (Reinhard *et al.*, 1997).

As opposed to the type of changes provided by graded stimuli, some stimuli are simply detected in one sudden moment. Such is the case of visual (the sight of) or tactile cues (contact with) that may present an effect on the movement choices. In terms of movement records, the appearance of a visual cue or landmark can be monitored by a sudden change in the movement features, for instance, the sudden switch of a zigzag movement to a linear trajectory. In order to establish the association with the visual cue, it is possible to measure whether the distance between the path where the switch appears and the position of the landmark is coherent with the visual range of the organism. A linear path towards the visual cue indicates that it serves as a landmark while a path parallel to the cue shows that by following the cue it is possible to reach a particular point, such as an opening on the side of a large wall. Movement can follow more complex rules if memory comes into play. A visual cue might be associated by memory with the presence or absence of other stimuli and so forth, blurring the relation between the stimulus and movement. Nevertheless, it is extremely important for some organisms, as Ettiene et al. (1996) argues in a review explaining how mammals update their position using an array of cues derived from their locomotion to return home, but rely on visual landmarks to keep an accurate reference as distance from the point of origin increases.

Movement in bounded spaces

Contact cues define the area where movement may occur. This is frequently encountered in experimental situations, where arena walls influence the shape of movement by providing limits around the area of movement. Experiments in bounded spaces often leave unexplored the question of how exactly animals are using these boundaries, and whether it is contributing to the overall behaviour in the experiment (Andreassen, 1996). However, it is clear that arena boundaries may shape a path into a peculiar geometry, force organisms into corners and provide more information than was meant to be included in the study. For instance, in combination with a thermal gradient, a wall can help to establish a linear cue upon which to compare values of the gradient, like the newborn pups moving along the boundaries of an arena when placed on a surface with a thermal gradient, where they use the walls as a spatial referential thermometer (Pacheco-Cobos *et al.*, 2003). In other cases, boundaries can work as bouncing surfaces, marking the obligatory turning points to be made in order to be kept inside safe or resourceful areas (Rosetti *et al.*, 2010).

While random walk models dictate that it is not likely that a walker should follow a boundary, some organisms are often heavily dependent on boundaries for spatial references (Jeanson, 2003). Such is the effect of boundaries on newborn animals, whom have not developed many of the senses and thus, rely heavily on tactile stimuli to orient themselves. Also, some animals live in tight spaces and avoid open spaces. Such is the case with rats placed in bounded environments in order to perform anxiety tests that quantify the time spent near the wall or in the arena centre (Treit and Fundytus, 1988). Also, their use is not only circumstantial, they can provide useful information for simple orientation mechanisms, such as protection from the cold or predators and generally contribute to proprioception. Insects of the members *Trichogramma* genus, use the thigmotaxis along the edges of a leaf belonging to their host plants, while placing eggs all along the perimeter (Gingras *et al.*, 2008). This may be a simple mechanism to maximise the area where the eggs are placed. The simplicity of the reaction to borders observed in biological systems has inspired work in artificial agents, due to the ease of implementation and efficient navigation in situations where physical obstacles abound (May *et al.*, 2006).

Amongst the main mechanisms that can be identified in bounded environments are the proper thigmotaxis or wall following behaviour, which is movement that occurs consistently along the borders or sharp turns while approaching a boundary. If movement is permanent and linear along the border it can be considered a straight line as the boundary reduces the directional alternatives of movement (Neumeister *et al.*, 2004). Whereas when movement occurs on and off the bounds it is possible to compare the characteristics between the two places in order to understand the effect and the decisions involved in following and/or in detaching from the wall.

2.4.4 The case of foraging

Movement between patches

For very long searching bouts, it is possible to distinguish differences in the searching patterns when organisms are inside and outside a resource path. Changes in local resource density has been suggested as a mechanism to decide when to leave a particular patch (Charnov, 1976; Stephens and Krebs, 1986). Changes in time interval between collections produce consequent modifications of the turning and movement rates, leading to changes in foraging intensity.

Generally, it is assumed that foraging intensity can be quantified by the convolution of a path, an index that increases as turning rates increase or larger turning degrees appear more frequently. It is possible to calculate the tortuosity for different intervals of a path to try to identify the patch crossing segments and compare their characteristics with those segments involved in exploration or where the collection is marked by significantly fewer collection points. Tortuosity is the ratio of the distance travelled between two points to the beeline between these points. It is a measure of how much a path differs from linear movement. For instance, if an organism leaves it's home to forage, it can be calculated as the ratio of the foraging path to the linear distance between all the sequence of collection points:

$$T = \frac{\sqrt{(x_{i+1} - x_i)^2 + (y_{i+1} - y_i)^2)}}{\sqrt{(x_{c_{i+1}} - x_{c_i})^2 + (y_{c_{i+1}} - y_{c_i})^2}}$$
(2.13)

Where x_i, y_i are the coordinate points defining the path and x_{c_i}, y_{c_i} are the coordinate points defining a sequence of linear distances using fewer coordinate points than the path (for instance, those points that mark collections.) Sinuosity can be increased when foraging inside a patch to maximise area coverage, but not as much as to make the forager go over its own path and visit the same place repeatedly (Benhamou, 2004a). The sinuosity of the search path corresponds to the amount of turning associated with a given path length and is then given by:

$$S = \frac{\sigma}{\sqrt{p}} \tag{2.14}$$

Where σ is the variance of the turning angle distribution and p is the constant step size (remember, a path can be rediscretized). This calculation of sinuosity involves a constant step length and a turning angle with a null mean. A general definition of sinuosity, that is able to include any level of turning angle dispersion and a randomly variable step length follows:

$$S = \left[p(\frac{1+c}{1-c} + b^2) \right] \tag{2.15}$$

Where $c=exp(-\sigma^2/2)$ and $b=\sum_{i=1}^n(l_i-\bar{l})^2$ or the variance of the step length.

For instance, clown fish larvae display a clear shift in the complexity of their swimming paths after the onset of feeding: from a linear ranging mode when looking for a patch, they turn into a highly convoluted searching mode once a patch is located, also increasing their speed when a patch is found (Coughlin, Strickler and Sanderson, 1992). Similarly, ruddy ducks usually slow down and increase tortuosity and thus search intensity in areas with high concentration of a resource (Tome, 1988).

Movement inside patches (area restricted search)

By mapping movement paths over environmental variables, such as the availability of resources, it is possible to detect when the animal enters a resource-rich area and perhaps with enough detail, even the individual events of resource collection. Therefore, it is possible to relate the changes in movement characteristics to the changes of the resource spatial configuration.

Changes in the movement characteristics may be identified as mechanisms to increase the possibility of encountering a resource, such as slower movement, more scanning activity, smaller steps and larger turning angles. These mechanisms help an area concentrated search to maximise efficiency by matching the resource distribution or density within a patch. Regularities can be deduced by working out the changes that collection imposes on movement characteristics. In a given sequence of collections, the properties of the distribution for a particular characteristic of movement may be shifted dynamically after a few encounters to adjust performance during the foraging bout.

These mechanisms can be defined using the concepts of fast and frugal heuristics developed by Hutchinson and Gigerenzer (2005) and the framework given by the statistical decision theory proposed by Dall *et al.* (2005). Managing the amount of information to which an organism is exposed while foraging to produce an optimal decision seems a near-to-impossible task; and might be a futile one if the costs of the effort outweigh the benefits. Rather, it can be less costly to make decisions with a simple set of rules-of-thumb, influenced by few variables and little or no memory processing, while achieving an efficient solution. This behaviour can be observed by tracking modifications in the parameters of the turning angle and step size distribution along changes in resource density.

For example, a rule of thumb to follow during area concentrated search is to exploit heterogeneity of distribution by slowing down when a resource is found (more resources might be near), but increasing speed could result in a better search if the resources are uniformly distributed (Krakauer and Rodríguez-Gironés, 1995). Fortin (2002) showed how short term sampling of the quality of resources allows bisons to modify the characteristics of the searching paths to invest more effort in searching in areas with high quality

resources. Haskell (1997) studied how ferrets finely tune the characteristics of the search paths during area-concentrated search by lowering the sinuosity as resources become less clumped. In a classic example, Smith (1974) observed that scrubs performed small zigzag movements after encountering a resource.

2.4.5 Memory and movement

The role of memory in shaping foraging behaviour has been extensively studied. Until now, the discussed strategies have mainly dealt with the attempt to make the most out of reduced amounts of information, where resource distributions are depleted on a single visit, and thus have little use for more than working (or short-term) memory. However, several organisms commonly forage in the same area, returning to search the places where they have found food in the past. In these cases, landmarks and environmental cues help them navigate to particular sites. The situations described in this section are viable for organisms exploiting static resources in the same place, that are not depleted within a foraging bout or that can be regenerated within short periods of time.

There are numerous experimental reports that confirm the influence that memory has in shaping movement. One way to evaluate the effect of memory is to quantify the characteristics of movements occurring in the same location when resource quality changes. Noda *et al.* (1994) observed how planktivorous reef fish, *Chromis chrysurus* searched in a slow tortuous pattern when well within their normal feeding sites, that is, places where prey were abundant on previous occasions, but independently of the current presence or absence of prey, whereas their movement between foraging regions was quick and uneventful. On the other hand, some animals show a precise recollection of places that held resources and are able to travel in foraging paths that maximise collections by visiting only the locations where food was found. For instance, in an experimental setting, capuchin monkeys that have been exposed to a series of platforms of which some included food; when presented to the experimental setting again they visited only feeding platforms that included food on previous occasions (Janson and Di Bitetti, 1997)

The use of memory in organisms foraging inside patches, such as bumblebees, honey-

bees and hummingbirds has been the focus of a considerable amount of research. Many of the aspects we know about foraging choices and memory come from research on these species. This is the result of highly versatile experimental situations, in which a great number of the characteristics of the objects holding the food (color, quality and position) can be manipulated. For instance, to distinguish the roles of short and long term memory, Greggers and Menzel (1993) showed that the choices made by the bees depended on the short-term memory used for choosing the next feeder but on long-term memory when it came to visit feeders yielding a high reward. Also, memory in *B. terricola* contributes in avoiding previously visited flowers (Heinrich, 1978). The work by Saleh and Chittka (2007) on honeybees show that while experiencing a stable array of feeding sites, visits occur in a repeatable, stable order or traplining, in a near-neighbour sequence, while experimentally changing the positions of the feeding array increases the frequency of repeated visits to the same sites as well as the search times. Also, the bumblebee, *Bombus flavifrons*, uses resource distribution for direct foraging, performing nearest neighbours movements (Zimmerman, 1979).

Another interesting mechanism involved in foraging relates to cache recovery. On occasion, some animals obtain more food than it is possible to eat, and must save it for later. The hidden food must be later retrieved and thus, memory plays an important role. The precision with which cache is localised is outstandingly accurate and well documented. Accuracy depends on the time after which species retrieve: Some tits (of the Parus genus) can locate and consume the food within 24 hours while other species, like the nutcrackers birds of the Nucifraga genrus, can take months before retrieving food (reviewed in Kamil and Roitblat, 1985). Apparently, landmarks are crucial to success in locating caches, as Kamil, Balda and Good (1999) describe for the orientation movements used to infer the memory mechanisms associated with retrieval of hidden food.

Even in short sequences the calculation of all possible paths becomes a costly process memory-wise and thus, a futile exercise where energy is certainly better invested in other processes. Surprisingly, vervet monkeys that randomly visited locations of a feeding array where food was placed, have been shown to be able to compute the shortest path between

items (Cramer and Gallistel, 1997). Perhaps there are clever heuristics to compute an efficient solution, such as variations of the nearest neighbour strategy that guarantee to produce an efficient path and that once in a while hit the optimal path by chance alone, and save time and energy in the computation of more expensive solutions.

2.4.6 A word on identification of mechanisms

An interesting property of mechanisms is that they have strong individual and context-dependant components. In many occasions, a mechanism is determined by an interpretation of the relationship between inputs and outputs. The hypothesised mechanism may change depending on the internal state of a given individual at different moments: more risk-taking strategies can appear under stressful conditions. This is especially important in the case of experimental situations - organisms may find task-specific solutions to a problem under experimental conditions, but never have a chance to use it in the wild.

2.5 Summary

Given the availability of new methodologies that allow to record the movement and location of organisms, to know and understand how to use the tools, study, and analyse of movement paths of individual organisms is a priority for any researcher attempting to perform experimental work in this area. As can be observed from the scope of this chapter there is a vast framework in which movement paths can be interpreted. It has been shown that paths can be intuitively useful, given that their shape is intrinsically linked to the way in which organisms use their space. Also, paths have simple, easily quantifiable components, which are common to the movement of all organisms. This chapter reflects an effort to bring together methods, models and mechanisms related to path analysis and to use them as the background for constructing the experimental work. The organisation in the following chapters, including the methods used for pre-processing the records, the analysis of the performance based on path descriptors and the mechanistic interpretation, hold a clear resemblance to the structure of this chapter. The reason for this resemblance

is that this chapter was successfully used as a flow-diagram for the experimental work and may help guide future work.

Chapter 3

An experimental test on searching

behaviour

3.1 Introduction

The study and detailed description of search behaviour is an integral component for the understanding of how organisms interact with their environment and, more specifically, to infer the decision processes followed during searching (Bell, 1991). There are a large number of biological studies illustrating how various species search, which place most emphasis on the efficiency of the search strategies used (Pyke, Pulliam, and Charnov, 1977). Questions regarding the efficiency of a chosen search strategy are hard to formulate in conditions of unknown density and distribution of resources, as is often the case in real life search settings. Nevertheless, some findings make it possible to attribute an adaptive value to certain decision-making strategies, suggesting in turn the existence of an evolutionary pressure on searching efficiency (reviewed in Pyke, 1984). For modern humans searches usually have more relaxed constraints and reduced costs, less severe consequences and a more subjective benefit scale. However, many of the mechanisms that guide our search behaviour today may have been shaped during harsher times and therefore might reveal a tendency for efficiency (Kaplan, 1992).

In certain circumstances human movement appears to exhibit features of a random

process, as in the study of the displacements estimated by following the temporal records of the location of marked paper currency (Brockman et al., 2006) and by tracking cell phone use (González et al., 2008), which revealed a dispersive processes of Lévy characteristics combined with regular visits to the same place. Whether at finer length scales the diffusive properties of human movement continue to be an accurate description of the process, is an interesting question. Indeed, at finer scales one could anticipate that environmental features, cognitive components and short-term goals can induce systematic behaviours, which would deviate from the simple random processes that apply at larger scales. In fact, examples in nature, where systematic movements allow animals to increase the probability of finding their target, are few, but well documented such as the searching behaviour of Cataglyphis ants. When disorientated, these ants move in loops of increasing size in various directions that systematically cover the area, thereby increasing the probability of finding the nest (Wehner et al., 1981). Also, there is plentiful documentation on how organisms adjust their searching strategy to local resource conditions, especially density (Viswanathan et al., 1999; Zollner and Lima, 1999; Bartumeus et al., 2005). Adjusting tortuosity and speed (Fortin, 2003; Mårell et al., 2002; de Knegt et al., 2007; Haskell et al., 1997) or other searching strategies (Bartumeus et al., 2007; Thompson and Fedak, 2001) can increase the resource encounter rate, thus, improving the yield of the search.

Here, human search behaviour is studied in order to observe whether search paths were constructed through a systematic process sensitive enough to allow adjustment to the underlying resource distribution, (e.g. distance between targets), a topic for which there is far less documentation available (Gross *et al.*, 1995). The spatial structure reflects the characteristics of the distribution of resources in the physical landscape in which the search takes place (McIntyre and Wiens, 1999). For modern humans it is common to search in environments in which geometric regularities are present. These regularities may be exploited to give structure to a search and are often useful in predicting the location of a given target. However, we found that spatial regularity of the target distribution was largely ignored, or went unnoticed, and that searching appeared to be governed by

rather simple rules, influenced by a few physical constraints such as the arena size.

Due to the inherent problems in obtaining detailed recordings of search behaviour, few studies have focused on human movement in dimensions that allow a realistic representation of space and the cognitive processing involved. Also, the energetic costs of experimental situations usually differ considerably from real life. For instance, human foraging behaviour has been studied in virtual environments, where behavioural features are expressed in computer simulations (Goldstone and Ashpole, 2004). Multiple participants where simultaneously tested in a foraging task taking place in a virtual environment, consisting of a grid on a computer screen. Different experimental conditions were created by allowing the searcher to see the resource and the other searchers or by limiting the visibility of the searcher on the screen as well as temporal indicators of the collections it made. Testing conditions also varied the ratio of abundance of the two available patches. Researchers explained that each food point was equivalent to a lottery ticket to win a prize at the end of the test. Participants exhibited under-matching, that is the proportion of participants in every resource pool failed to match that pools' abundance of resources. Also, the participants exhibited migrations of participants from one pool to another when participants were failing to collect sufficient resources. Although experimentally accessible and hugely versatile, these approaches have the disadvantage that the representation of space, the cognitive processing involved, and the energetic costs differ considerably from real life situations.

Studies that require the participants to physically search are usually conservative regarding the spatial dimensions available, since they are conducted within the confines of laboratories, and provide little opportunity for efficient strategies to emerge. For example, pathways have been recorded for humans searching for a sensor hidden under a carpet, similar to rats searching for a hidden platform in a Morris water-maze (Bohbot *et al.*, 2001), or searching for a marble hidden inside one of many film containers distributed on the floor of a room (Gilchrist, North and Hood, 2001). Gilchrist and colleagues (2001) individually tested participants in a 3x3 m arena, where they had to locate a marble hidden inside a film canister. Individuals were tested twice for every display size (number of

canisters in the room); in one of the tests a marble was present and in another there was no marble. Participants were required to indicate when they had finished. They found that many of the aspects of the searchers' movements were similar to the aspects of the eye movement during visual searches, meaning that the amount of time doubles when there is no marble in the canister array and that search time grows linearly with the number of items.

Smith, Hood and Gilchrist (2005) individually tested children (5-8 years old) using a similar setup. Inside a 4x4m area surrounded and obscured by curtains, individuals were presented with a regular grid-like array of 49 (7x7) switches on the floor. Of these, only 16 switches were lit with a green light, and only one of them would, when turned, activate a red light. On one test, children had to turn the switches with their dominant hand, while on another they had to turn them with their non-dominant hand. Searchers with the non-dominant hand took longer and had more revisits than those with the dominant hand. The findings of such experiments confirm the relational increment between search time and the number of items, and suggest an important role for memory, as when participants return to review previously visited targets (Smith, Hood and Gilchrist, 2008).

In this chapter a new experimental approach is described, in which it is possible to study basic aspects of human search behaviour. In particular, the questions addressed are related to the decisions involved in the searching procedure, i.e., whether there are any systematic aspects and how does this change with conspicuity and the amount of information in the distribution. In this setup, an attempt is made to simulate a simple search situation reminiscent of childrens' games such as hide-and-seek or the Easter egg hunt, where constraints are few and relaxed, and the rewards are of no energetic or economic value. Rather than introducing an artificial reward for the searcher's performance (such as money or candy), this experiment aims to explore a basal condition which also occurs naturally since searching does not necessarily involve a monetary or energetic benefit. Furthermore, a large outdoor setting was used and, as in previous studies, the effect of target distribution and target conspicuity on participants search performance was tested. Paths were recorded using a common tracking device, such as the ones described in the previ-

ous chapter, more precisely Global Position Systems (GPS) technology, which already has been successfully applied to the study of human locomotion (Terrier and Schutlz, 2005; Shoval and Isaacson, 2006). Coarsening procedures described in chapter II were used to pre-process the data and deal with some of the resolution issues of the GPS. Finally, a comparison between the participants' behaviour and that of a simple statistical model was made, in order to gain further insights into the structure of the search process, and the role that cognitive aspects may play in this. In order to achieve this, traits of the probabilistic models were coupled with a mechanistic decision process, such as those described in chapter II.

Since the experimental task was reminiscent of a game, testing children was considered to be an adequate choice. A small group of children was used in a pilot study to determine the age at which children showed to perform well (finish the hardest version of the task in less than 8 minutes), locate the targets and understand the instructions. Amongst the benefits of testing 9-11 year old children are: 1) having participants with a positive attitude towards outdooractivities (Smith, 1984; 1986), 2) to ensure the task would be understood as a game, thus minimising the influence of possible speculation about the researchers' motives, and 3) to use an age group with well developed spatial abilities (Linn and Petersen, 1985). This opens the possibility to later explore younger and older age groups. Also, because of their developmental history or their reticence to participate in games, adults might have more varied strategies, while children of this age might still be developing their own. Very little work has been done in testing the search strategy of children, and even less so in dealing with the strategies through the analysis of searching paths, hence, the nature of this study was exploratory. The principal features of the search process at a certain length scale were mimicked using a simple computational model.

3.2 Methods

3.2.1 Searching experiments

Experimental setup

The test included 36 children (a total of 18 boys and 18 girls, three boys and three girls in each of the six test conditions described below) ranging from 9 to 11 years old and attending 5th grade of primary school in Mexico City. Search trials were carried out during school hours (9 am to 1 pm) with pauses during break-time. Fair weather and mild temperatures prevailed throughout the study. Experiments were carried out on one half of the grass soccer field of the childrens' school, a rectangle 60 x 80 m (4800 m^2) with clearly visible markers (orange fluorescent traffic cones) at each corner. Twenty golf balls were placed across the test area according to either the same random or to the same regular distribution (figure 3.1 a and b, respectively). These distributions were chosen as simple alternatives: a random distribution holds no structure while the regularity of the regular distribution holds information concerning how the targets are arranged. The two distributions were computationally determined using a 1x1 m lattice. The physical placement of the balls was aided by chalk marks at 1 m intervals along the arena perimeter, and the consistency of their location across trial was ensured by placing a small marker peg below each ball. Three levels of conspicuity were implemented but only one was used per trial: balls painted green to match the grass represented the cryptic level, unpainted white balls represented a semi-conspicuous level, and unpainted balls plus a 1 m pole with a flag marking their location, which was visible from every point in the arena, represented the maximum conspicuity level (figure 3.1 c-e). The height of the uncut grass covered the whole diameter of the balls, making them difficult to detect from a distance.

Each child was tested individually and brought directly from the classroom to the experimental field by one of the experimenters. To minimise participants communicating their experiences to classmates, children were taken from separate classrooms. Upon arrival the child was verbally instructed to find and collect, in a bag, as many balls as possible before the experimenters told the child to stop. A sample of the targets was

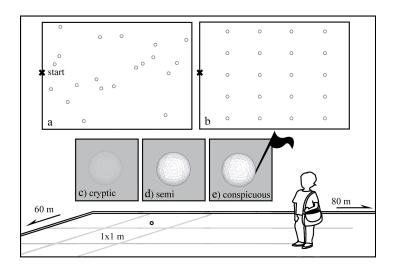


Figure 3.1: Summary of the experimental setup: (a) the random and (b) the regular distribution of the twenty balls, and (c-e) the three levels of their conspicuity.

shown, either a white or a green golf ball, and the role of the flags on the field was explained when appropriate. Children did not know the number of targets nor the 8 minute test time. Participants started to search from the midpoint of the fields southern short border, and two experimenters positioned at the starting point observed the search and recorded the time at which each ball was collected. Trials were ended after 8 mins or when all balls had been collected.

A GPS device (Garmin GPS V) set to record the child's position every second was placed on a belt around the child's waist and activated. The open test area ensured uninterrupted satellite reception. For a more extended discussion on the characteristics of the GPS please see appendix B.

Procedures conformed to the guidelines for human research of the Instituto de Investigaciones Biomédicas, Universidad Nacional Autónoma de México, and verbal or written consent was obtained from the children, parents, teachers and school authorities.

3.2.2 Path analysis

To reduce inherent error in the GPS recording of search paths and to help identify possible patterns, path records were coarsened using the procedure described in chapter II. The coarsening procedure involves joining path segments with small turning into one step by

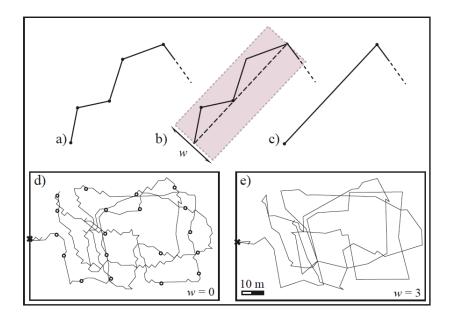


Figure 3.2

increasing the width around the line segments (figure 3.2 a-c) so that only main changes of direction remained. The width used to coarsen paths (3 m) was chosen based on the mean variance between individual collection records.

Searching was quantified using the following descriptors: *Total time spent* and *distance traveled*, which are indicators of the effort needed to perform the search; for example, for the cryptic targets we expected longer searches. These descriptors provide a transparent way to establish differences in the cost of the search process *Efficiency*, calculated as the distance traveled over the number of targets collected, providing an estimate of the cost per target collected *Total path self-crosses*, which is a gross estimator of performance; searchers who rarely cross their own path make better use of their effort. A *straightness index* (linear distance between collection points divided by actual distance traveled by the searcher between those points), which provides an indicator of the difficulty of the search, and an *optimality index* (linear distances between the actual sequence of collections divided by the linear distances between the shortest sequence of collections calculated by simulated annealing (Kirkpatrick *et al.*, 1983; Laarhoven and Aarts, 1987)), which relates to the global efficiency of the sequential collections made by the searcher. The above descriptors provide indirect information about the economics of de-

cision making during the search process. To estimate search success we also calculated the *collection rate* (balls per minute), and *total collections*. Collection rate reflects search efficiency, whereas total number of balls collected gives a global success measure.

Descriptor values across conditions were compared using the Matlab statistical tool-box (Mathworks Inc, 2008). As most data were not normally distributed (Lilliefors test for normality) non-parametric statistics were used throughout. Descriptor values were compared across conditions using Kruskal-Wallis tests followed by post hoc multiple comparisons with the Bonferroni correction.

As no difference was found on any measure between boys and girls, their data have been combined. Although this might appear controversial in light of the vast literature on gender differences in the use of space, it is worth remembering that the children in this study are young and few, so no conclusions should be drawn from this lack of difference between genders.

3.3 Collection of data

As can be seen from the analysis in appendix B, GPS technologies offers advantages and limitations. First, the length scales at which paths were recorded by GPS are to be analyzed and interpreted was rather coarse, so many of the details of the children's behaviour, such as head turns, did not appear on the records. Most outliers in path data were easy to detect and correct.

Precision, on the other hand, was problematic, since the coordinate values that the GPS assigned to a similar spot on different occasions could vary up to 15 meters. Therefore, measures were taken to rely minimally on the GPS for the match between spatial variables. For instance, the record the position of the targets was not recorded by GPS and then matched to their location to the path, since the two elements are likely to be severely de-phased in space. Instead, a more suitable for this technology was to allow the GPS to record the position of the searcher and then manually record the collection times while observing the experimental task.

3.4 Searching performance of the children

In terms of participant interest and involvement, the task was a success. Children seemed eager to participate since the recruiting procedure. On the field, walking rapidly and continuously with an occasional sprint. Clearly, their determination and speed were faster on the conspicuous task. Even though they knew beforehand that no award or prize was given, on many occasions they asked for a score or the time in they had taken to complete the task and which was the fastest path so far. After the test, researchers attempted to engage in a chat about their impressions, whether they had noticed if the targets were placed in a certain pattern or if they had a particular way of moving about the arena, but their discourse proved to be very unspecific.

Visual inspection of the coarsened paths suggests that the children walked in essentially straight lines across the arena (e.g. figure 3.2 d and e), and that the factors accounting for the few changes in direction were (perhaps obviously) the arena boundaries or the detection of a nearby ball and its subsequent collection. Some spontaneous turns not associated with collections or collisions were also observed. However, the number of such turns decreased dramatically with the coarsening width, suggesting that they might contribute to the structure of search paths at fine spatiotemporal scales. Unfortunately, the resolution of the searchers' data was not adequate to explore such fine scale structures.

Admittedly, searching is a complex behaviour and the GPS records do not provide nearly enough detail to make out important aspects, such as head turns which children may have used to scan the field as they traveled. It is possible to see from the turning angle distribution of uncoarsened paths that they did have a large percentage of turns in small angles, thus, in many instances the full body displacements did occur forward in a semi straight line. This phenomena is captured by the coarsening procedure in the form of long steps. As mentioned above, quantification of the turning angles revealed that the children turned near the borders and near collection points, as well as in many other locations, but the number of turns near locations that were neither a collection points nor boundaries, diminished greatly after coarsening. However, it is impossible to say exactly if turns near collections took place before or after the collection was done.

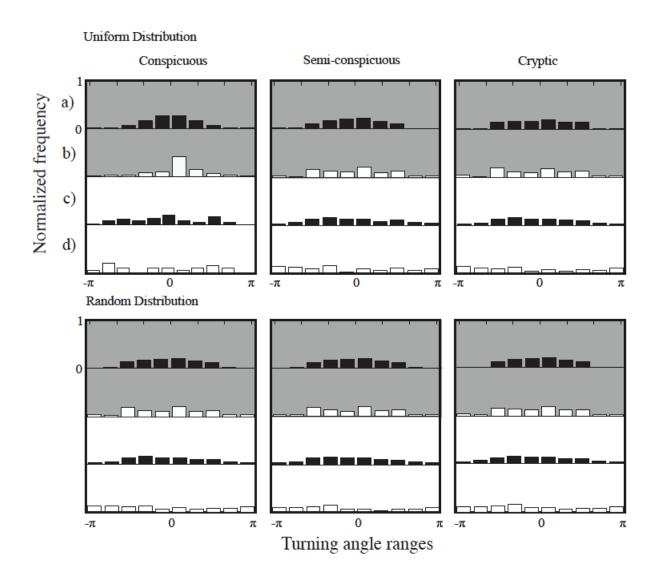


Figure 3.3: Normalized turning angle distribution for both uncoarsened (gray background) and coarsened paths (white background). Histograms show the distribution of internal turning angles (black bars) and the distribution of turns occurring within 3m of the boundary (white bars)

The distributions of turning angles for both coarsened and uncoarsened paths are shown in figure 3.3. While the turning angle distribution for the uncoarsened paths appeared to show some degree of persistence, i.e. a tendency to take steps roughly in the direction of the previous step, the details fall below the current spatial resolution. After coarsening, all the turning angle distributions flattened considerably, as expected.

The distributions of turning angles for both coarsened and uncoarsened paths are shown in gure 3.3. While the turning angle distribution for the uncoarsened paths appeared to show some degree of persistence, i.e. a tendency to take steps roughly in the direction of the previous step, the details fall below the current spatial resolution.

The self-correlations of turning angles and step lengths of coarsened and uncoarsened paths are shown in gure 3.4. While the turning angles appear to have a self-correlation value of around 0.3 in the case of uncoarsened path, this disappears with a small coarsening width. Step lengths, on the other hand, have very low correlation values even when uncoarsened and even lower when coarsened.

The flat (uniform) turning angle distribution and the uncorrelated turning angles provides clues as to the main decision processes involved in the searching path and greatly simplifies statistical modelling efforts.

Search performance varied slightly for some descriptors between the random and regular distribution of the targets (significance p < 0.05, Mann-Whitney test, but p < 0.05, multiple comparisons using a Bonferroni test), but the direction of difference was not consistent across descriptors and the degree of difference was generally not significant. On the other hand, performance descriptors varied consistently with conspicuity, with significant differences found mainly between the cryptic and the conspicuous conditions (figure 3.5).

In general, the lower the conspicuity of the targets, the longer the search paths (figure 3.5a), the more time spent searching (figure 3.5b), and the lower the efficiency of the searching process (figure 3.5c). Furthermore, participants crossed their own path more often (figure 3.5d) and had more tortuous paths (figure 3.5e) when searching for cryptic targets. Nevertheless, in all conditions the sequence of collections resulted in an optimal-

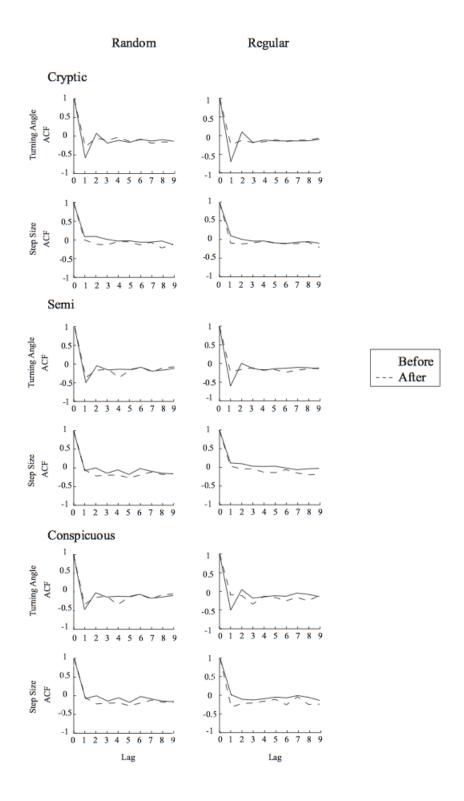


Figure 3.4: Autocorrelation functions for the turning angles and step sizes of the children paths. A small correlation can be percieved in the sequential turning angles of the uncoarsened paths. This autocorrelation is no longer noticeable after coarsening.

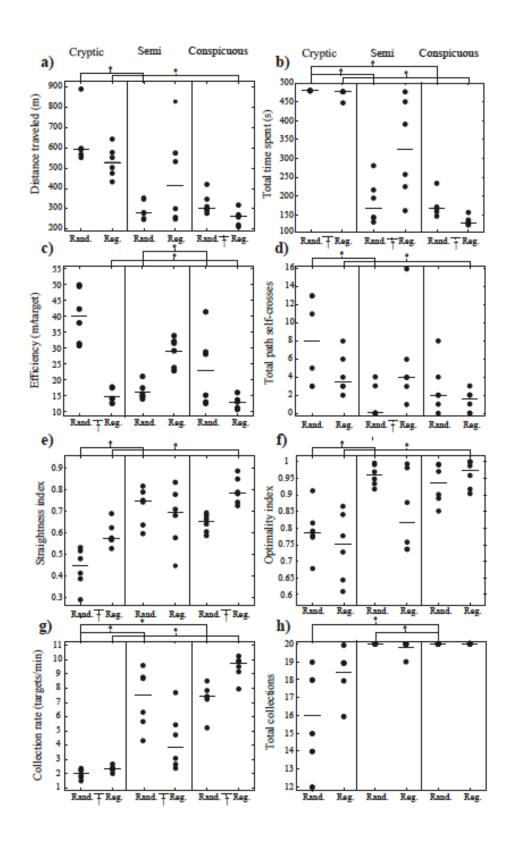


Figure 3.5: Comparison of path descriptors across conditions. *p>0.05 (See text for explanation of statistical tests)

ity index of 0.6 or larger (figure 3.5f). Finally, children collected fewer cryptic balls per minute (figure 3.5g) and often failed to collect all the balls (figure 3.5h). The percentage of times that participants collected the closest ball ranged from 50% in the random cryptic condition to 70% in the regular conspicuous condition, showing that the paths departed from a nearest neighbor search.

3.5 The bouncing search model

To model childrens search behaviour a numerical simulation was implemented following the main features of the children searching paths, such as the uniform turning angle distribution of the coarsened paths and the long steps, that reflect the persistent movement of the children when not interrupted by a collection or a boundary: Agents move in straight lines until they collide with a boundary or detect a target. After boundary detection or collection of the target, a new direction is assigned randomly from a uniform angular distribution, with the restriction that agents do not leave the arena (bouncing; figure 3.6a). Target conspicuity is represented in the model by a circle (of radius r_d) that allows detection of the target located at its center (figure 3.6b). Intersection of the circle's perimeter by the agent's path will result in target collection. To simplify calculation, when a collection occurs the path is redefined as the straight line between the previous bouncing point and the center of the detection circle.

While this barely changes the performance of the agent in conditions with very small r_d values, it is important for the large r_d values, where it introduces a false two step collection process: one step goes from the point of origin to perimeter of the circle of detection and a second step extends from the perimeter of to the center the circle of detection. Collected targets are removed from the target array. If several detection circles are intersected by the agents path, only the closest target is assumed to be collected, and information about other targets is discarded. Thus, as the simplest implementation of the process, the model assumes no memory or learning in the searching mechanism.

A total of 10,000 simulated paths were calculated for each r_d from 1 to 70 m in 1 m intervals. Arena dimensions, target distributions and test time were the same as in the

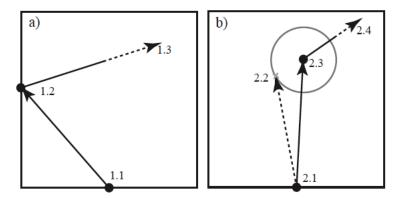


Figure 3.6: Main features of the bouncing search model (a) The agent moves in a straight line until intersecting a boundary (1.2), that produces an effective step between the last previous position (1.1) and the collision point (1.2), after which a new angle is chosen (1.3) (black line), and the next step is calculated (black and dashed line). (b) The agent moves in a straight line until intersecting a circle of detection (2.2), producing an effective step between the previous position (2.1) and the collection point (2.3) (black line), after which a new angle is again chosen (2.4) (black and dashed line). The original intersecting step (dashed line) is discarded. See explanation in text.

experiment. Search times were calculated from distance travelled, assuming a speed of v=1.7m/s, corresponding to the minimum mean velocity of all experimental conditions. By considering this velocity, we give the model the same time window as the slower children. Furthermore, the maximum difference between the average speeds was about 30 %, so results do not vary much from one case to another.

3.6 Behaviour of the bouncing search model

The model produced smooth curves showing a clear relation between the r_d values and the distance travelled, the main descriptor chosen for comparison with the experimental data (figure 3.7). In these curves, three broad regions may be identified: a region with $r_d=1-5m$, characterised by paths commonly composed of long, uninterrupted steps, and trials that finished before all targets were collected, a second region with $r_d=6-12m$, where small changes in r_d resulted in rapid shortening of the search paths and collection of all targets, and the third region with $r_d>12m$, where the distance travelled slowly reached a plateau as every step resulted in intersecting with a circle of detection and the collection of all targets in a nearest neighbour pattern. The model proved to be robust,

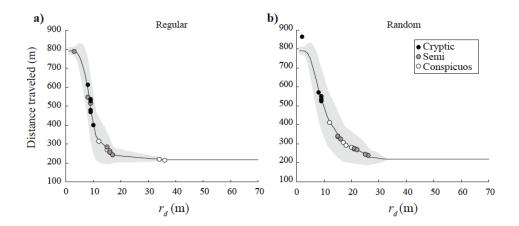


Figure 3.7: Matching of the experimental and model data: The continuous line represents the mean distance travelled (grey area s.d.) produced by the model, and each circle represents data from an individual participant in the corresponding experimental condition. The mean distance travelled by each participant was used to estimate an r_d value by matching it to the closest position on the curve generated by the model.

since changing the mean velocity of agents, the probability of collecting a detected target, or the probability of altering the direction without intersecting a boundary or a centre of detection resulted in curves with similar properties to the ones obtained with the original bouncing model.

3.7 Comparison between the model and the children's behavior

For this, the main descriptor of search behaviour considered was total distance travelled. It was possible to estimate each child's r_d value by matching its distance to the nearest value on the curve produced by the model (figure 3.7).

The values for the distance travelled by the search paths of the model was averaged for every r_d from 1 to 70m. Each average represents 10,000 runs of the model using a single r_d . This produced a curve in which the distance travelled is plotted against the r_d values. For the distance travelled by every child, a match was found amongst the average distances travelled by the model. This match indicated the r_d value that most likely corresponded to the conspicuity of the targets for the child. The r_d values resulting from matching all

the children values from a single condition were used to calculate a different subset of descriptors with which to compare the other descriptors of the children.

An illustration of the distributions of distance travelled by the children and the model agents can be obtained from figure 3.7, where the distances traveled by the children are matched to their corresponding r_d value using the results of the model (the grey area in the figure represents the standard deviation of the distribution of the distances travelled).

This allowed us to estimate the mean r_d for each of the six experimental conditions, giving a minimum r_d of 7 m for the cryptic condition and a maximum r_d of 16 m for the conspicuous condition. Children's turning rate did not differ significantly across conditions, but showed a tendency to decline with increasing conspicuity. In contrast, the model showed no such tendency with an overall constant turning rate for experimentally equivalent r_d values. This suggests that the children's turning rates were influenced by factors not represented in the model.

In order to compare the search behaviour of the children and the model, a subset of the descriptors was calculated for the model using pooled r_d values for which the total distance travelled matched the corresponding child's value for each experimental condition (figure 3.8).

The overlap of values that the pooled r_d s yielded is consistent (i.e. the children data points fall within the range of the values calculated for the model, which is of no statistical value but denotes an interesting trend) with the descriptors of the childrens search paths, which though there were a few instances in which single childrens path descriptors fell slightly outside the range predicted by the model.

3.8 Discussion

A simple behavioural model was implemented using what was identified as the constitutive events of the search process performed by the children, namely movement in straight lines with turns in random directions when close to the field boundaries or at collection points. We stress that the model was designed to mimic what appeared to be the individual events that gave rise to the search path, without recourse to memory or to other cognitive

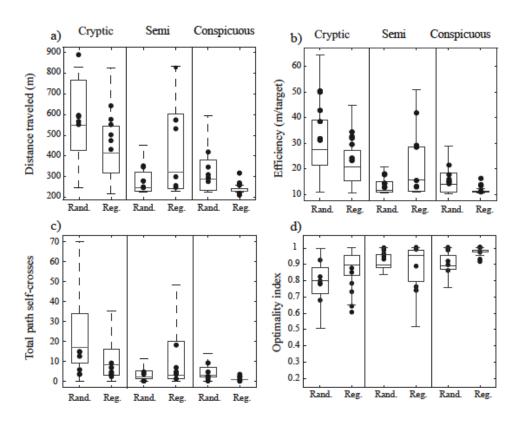


Figure 3.8: Boxplots of path descriptors generated by the model for the pooled r_d 's corresponding to the childrens matches of distance traveled (shown in Fig 3.7); horizontal bars give the median, horizontal borders of the box give the 25th and 75th percentiles, and the whiskers extend to the most extreme data points. Each black dot represents the score of a child for that particular descriptor. Given the inner workings of the model, only some of the performance descriptors are comparable to the childrens search paths. For clarity, outliers for the model data are not shown.

processes. A more detailed model could be implemented by including small departures from this coarse behaviour at small length scales. In spite of it's simplicity, the resulting displacement process is intrinsically non-Markovian (due to the collecting of targets), and thus not amenable to analysis using the usual tools of random walk theory. Further, while designed to reproduce the behaviour of the children at the level of individual events, the model was tested by comparing the descriptors of complete search paths generated by the model with those for the paths of the children. We found that these global descriptors already matched satisfactorily.

The children's paths suggest that they made little use of the underlying spatial distributions of targets to orient themselves, if at all. On the other hand, the manipulation of conspicuity yielded the expected effects, given that searching in the conspicuous conditions resulted in movement in essentially straight lines along the flags, while the cryptic condition provided a searching challenge reflected by longer paths, longer search times and lower collection rates. It was notable that most targets were collected in sequences with an optimality index above 0.6, even in the more difficult experimental conditions, possibly by using essentially the same searching behaviour, consisting mainly of locomotion in essentially straight lines combined with deflections from the boundary or to pick up balls. Our data resolution does not allow an accurate account of departures from this behaviour at finer length scales. Nevertheless, mechanisms operating at finer scales might exist, which may increase the efficiency of the search, especially in the cryptic condition. Recording and modelling this fine scale behaviour presents an technological challenge that may be useful to attempt to address in the future.

The distribution of step lengths suggests an exponential distribution in both the children's and the model's paths within the dimensions set by the strict borders of the search field (figure 3.9). It should be noted, however, that the process cannot be described as a simple random walk with exponential distribution of step lengths. The reason for this is that as the search progresses, the target distribution changes as targets are collected, giving rise to a non-Markovian process. Further, it is difficult to use the model to predict how children would search in larger areas without strict boundaries, although it does present a

testable hypothesis in which long uninterrupted steps should reflect the dimensions of the search field (a larger search field makes possible longer steps). While it is rare for foraging models to consider environmental boundaries, this is in most cases the search situation in the every day life of humans, particularly in urban areas where physical boundaries and obstacles commonly define the areas we search in.

The children did not appear to detect the structure of the regular distributions. A possible reason for this could be that the regular properties of these distributions were modified by the collection events, making the identification of the original structure difficult. An interesting modification could be to consider *patchy* distributions, where after visiting various patches subjects might detect a pattern and upon finding a target, search for others nearby. Unfortunately, patchy distributions were explicitly discarded as an experimental possibility in the present study because adequate patches could not be constructed without the numerical ranking of conspicuity levels.

The findings suggest that, at least in the current scenario, children may instead have mainly used the presence of boundaries or the visual detection of targets to turn while searching. Often, the places we search in are bounded spaces (e.g. parking lots, libraries, supermarkets) and contain information regarding the location of targets (e.g. codes on library shelves or in parking lots) that could make it less necessary to *bounce* around the search space before reaching the target. Still, the bouncing strategy appears to be a cheap, simple rule of thumb that does not require that one reads signs, memorizes codes or constructs spatial maps, and requires little or no information to function in unknown environments (Gigerenzer and Todd, 1999). Future work could focus on the information acquired during the search, for instance by asking the participants to draw a map of the location of the targets after completing the task to evaluate whether they are able to detect the shape of the underlying distribution through the collection of targets.

In conclusion, the behavioural experiment and model described here should prove useful for the investigation of social and cognitive processes in a variety of contexts. Even the very simple model employed here proved useful for mimicking basic aspects of the children's paths. Increasing the model's complexity should help identify the effect

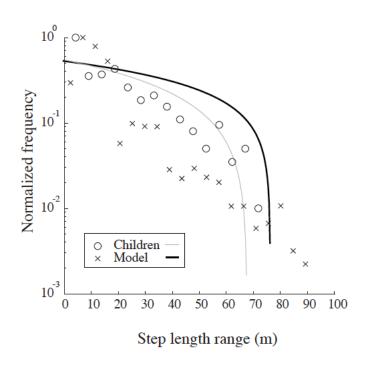


Figure 3.9: Semi-log plot of the normalized frequency of step sizes for the model and children's search paths: The frequent occurrence of small steps and the increasing decline in the frequency of larger step sizes suggest an exponential distribution. Slopes of linear fits are not significantly different (Children: -0.0065, Model = -0.0071)

of additional factors contributing to search behaviour under more challenging conditions. Further, changing the motivational context and/or the age group of the participants in the experiment may help test whether the structure of systematic target distributions can be detected during the search. Although only a first step, the present study already suggests that at least basic features of children's search behaviour can be simulated using very simple decision rules.

Chapter 4

Search Behaviour in Patchy

Distributions

4.1 Introduction

In the previous chapter, the planning and testing of an experimental task to record human searching behaviour in large, open areas was presented. The experimental design described in the previous chapter was aimed at finding the effect of changing the spatial distribution and the conspicuity of the targets on several descriptors related to searching performance. Afterwards, a simple model was built by incorporating what were considered the main features of the search paths of the subjects, namely, linear movement in a random direction after the collision with an arena boundary or the collection of a target. The *bouncing search model* replicated the searchers behaviour to a great extent and matched the subject's descriptors with considerable success.

The results presented in the previous chapter indicate that conspicuity of the targets has a strong effect on searching performance. Conspicuity, or the approximate distance at which the targets can be detected, was a property that was only qualitatively ranked for the experimental tests described in chapter III. However, the experiments and model described in the previous chapter allowed an approximation to a numeric quantification of conspicuity values through the match between the distance travelled calculated for every

 r_d of the model and the distance travelled by the children. This permitted the design of new tests to challenge the findings of the experimental task as well as the inner workings of the model, using distributions which presumably provide more information to the searcher. Such is the case of patchy distributions, where targets are found to be clumped together, leading to locations with higher density (or patches) surrounded by areas with lower (or zero) target density. When within a patch, a searcher may be able to estimate the higher density through measures such as the collection rate or the time interval between collections and thus, increase the chances of finding more targets by adjusting the searching movements accordingly. A finer search of the area surrounding a collection point may be achieved, for instance, by increasing the turning rate while reducing the step sizes.

One of the main questions derived from the previous chapter is whether subjects can detect cues from the underlying distribution or incorporate any cues acquired from their searching manner. The results and analysis presented in the previous chapter suggests that, at least in the limited conditions of the current experimental setup, children fail to detect or choose to ignore the information regarding the underlying structure of the target distribution. However, it could be argued that the spatial distributions of targets used in the experiments described in the previous chapter hold either no structure (random) or were based on regularities that are rarely exploited in normal situations (regular). It has been argued that patchy distributions are amongst the most frequent distributions found in natural conditions, thus making them an interesting candidate in which to test human search behaviour (Rougharden, 1977).

At the heart of the concept for searches in patchy environments lies the marginal value theorem, or the strategy that searchers should implement to maximise collection efficiency when in a patch by calculating an optimal patch-leaving time based on the collection rate (Charnov, 1976). Patch detection and exploitation mechanisms have been described for insects (Kohler, 1984), birds (Ydenberg, 1984), mammals (De Knegt *et al.*, 2007) and several other groups. In humans, experiments that try to elucidate the mechanisms of patch exploitation, via the development exercises, have shown to be interesting. For instance, in a searching exercise, subjects had to search for words using sets of random

letter sequences (Wilke *et al.*, 2009). Another test asked subjects to *fish* in simulated ponds, so the researchers could study the factors that subjects take into account when deciding to stay in one pond or to move on to a different one (Hutchinson, 2008). These studies support the idea that subjects decide to leave a patch by mechanisms other than the calculation of collection rates, they tend to spend more time than expected in a single patch, and choose to move away from a patch following a successful collection.

Few studies have attempted to elucidate the decisions involved in the searching behaviour of humans in semi-natural conditions, where searching involves the costs of displacement. There are, however, several examples of human searching for resources in patchy distributions in natural conditions. Rural communities search edible mushrooms (Pacheco-Cobos, 2010), firewood (Biran *et al.*, 2004) or other edible plants (Ladio and Lozada, 2000). In urban environments, many resources are arranged in conspicuously marked patches, such as supermarket aisles, and although searchers easily find their location and limits, they rarely deplete them. Since searchers of different backgrounds often experience patch distributions, the question posed here is whether they can actually detect a patchy distribution of resources based on the information gathered during their search procedure and consequently adjust their movements to achieve efficient collections. Also, if a searcher holds some knowledge about the nature of the distribution, can this result in a finer search and more efficient collections.

A semi-natural search situation, such as the one presented in the previous chapter, would not only allow to test whether subjects can detect a patchy distribution, but also give some indications as to how the exploitation of the patches occurs.

4.2 Methods

In order to expand on the experimental findings of the previous chapter, slight modifications were made to the experimental setup. On this occasion, the test included 42 children (21 boys and 21 girls, three boys and three girls in each of the seven test conditions described below) from ages 9 to 11 years and attending 5th grade of primary school in Mexico City. Search trials were carried out during school hours (9 a.m. to 1 p.m.) with

pauses during break-time. The dates of the experiment on this occasion also coincide with the end of the rainy season, so fair weather and mild temperatures prevailed throughout the experimental sessions.

The arena location and dimensions were identical to the ones used in the previous study. Again, visible markers (orange fluorescent traffic cones) marked the corners of the arena. Twenty golf balls were placed in the test area according to one of two different distributions (figure 4.1 a and b, respectively). A set of heterogeneous cluster patches (cluster distribution from here on) were constructed using a hexagon as a blueprint to insure that all targets in the patch were at least 10-12 m apart from each other. This distribution included 6 patches, with 2, 3, 4, 5 and 6 elements respectively. A second patchy distribution was constructed by placing two layers of targets (layer distribution from here on) parallel to each of the long limits of the experimental arena. The placement of the targets in every layer was also done so that targets were at least separated by 10-12 meters. The physical placement of balls was done by locating the position of one of the targets using chalk marks at 1 m intervals along the arena perimeter, and then placing the rest of the targets in the patch using a set of strings to insure that the distance between was kept constant. This point is particularly important, as explained below, when conspicuity comes into play, the targets should not be perceived visually as a patch, but inferred from the change in target density as collections are made. The consistency of their location across trials was ensured by placing a small marker peg below each ball.

This experimental setup used the same three conspicuity levels for every distribution used. For the cluster patchy distribution, a condition was added in which the children that would search for cryptic targets were instructed that targets are clumped, which means that once a target is found, it is probable that other targets are nearby. To insure that the instruction had been clear, they were also asked to explain, in their own words, the patchy nature of the distribution. This condition was introduced with the goal of having subjects know a central property of the distribution and see whether they could adjust their searching behaviour accordingly.

The main question of this work is whether children could detect the underlying proper-

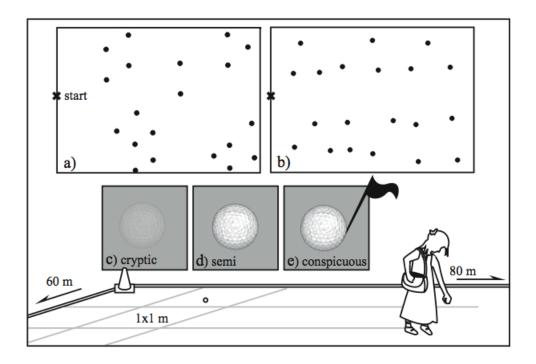


Figure 4.1: Summary of the experimental setup, showing of 20 targets with which a distribution of (a) cluster patches and (b) layer patches was constructed, as well as the three (c-d) conspicuity levels used.

ties of the target distribution. In both distributions, if subjects managed to detect the local increment in target density, a localized searching pattern should follow. The performance of a localized search should differ from the performance of the bouncing search. The presence of smaller steps and more frequent turns should be reflected in the descriptors and differences with the bouncing search model should be evident.

The cluster distribution tested the capacity to detect the presence of patches and items within the patch itself, but since patches were arranged randomly, the presence of a patch gave no cue as to the location of other patches. The patchy distribution tested the capacity to detect the presence of patches and items within the patch itself, and since the patches where almost symmetrical in their location, so patch location had an intrinsic structure. Conspicuity levels were conserved as in the experiment in chapter III for reasons of comparison as well as because they provide a gradient of intensity of the searching process. Cryptic targets could not be seen from inside the patch, so only density cues suggested the presence of a patch. The semi conspicuous targets, it is possible to see the layout of

the patch, but not the layout of other patches, while in the case of conspicuous targets the whole distribution was apparent from any place in the arena.

Each child was taken directly from the classroom to the experimental arena and tested individually. The method and manner in which the experiment was conducted was identical to the experiment described in chapter III. Again, procedures conformed to the guidelines for human research of the Instituto de Investigaciones Biomédicas, Universidad Nacional Autónoma de México, and informed consent was obtained from children, parents, teachers and school authorities.

Out of the 42 children tested, only the path of one girl searching for cryptic targets arranged in cluster patches was not included in the data set, due to GPS malfunctions.

4.3 Collection of data

Along with the advantages and limitation of GPS use discussed in chapter III, it is possible to expand on a few of the caveats derived from the tests in appendix B. While the GPS scores on coherence appear to be trustworthy for the comparison between subjects, at least at a coarse length scale, the precision scores can introduce errors in repeated testing. The GPS records of the spatial distribution should not be used to match collection points and searching paths. Also, GPS does not have enough precision to be used to construct and reconstruct the experimental distribution. Instead a more accurate and precise solution was to use fixed objects around the field that provide a stable landmark and strings of different measures to accommodate the targets and precisely measure the distance between them.

4.4 Path Analysis

In order to maximise comparability, the coarsening procedure applied in chapter III was also used for the paths of these children, the same descriptors calculated and the same statistical tools applied. Once again, no difference was found between boys and girls for any descriptor, so gender was ignored when pooling the data.

4.4.1 Searching Behaviour

Children were seemingly enthusiastic and involved in the task. Performance was visibly influenced by the conspicuity of the targets. Some of the children tested in the cryptic condition reported that searching was 'hard' because it was 'difficult to see the targets'. Also, when questioned about the distribution, responses were vague, but descriptions such as 'all over' were frequent and none responded with any adjective similar to 'clumped, aggregated or patchy'. In the experimental condition where they expected a patchy search, all children responded affirmatively to understanding the instructions and gave coherent explanations when asked to repeat the instructions in their own words.

The distributions of turning angles for both coarsened and uncoarsened paths are shown in figure 4.2. While the turning angle distribution for the uncoarsened paths appears to show some degree of persistence, i.e. a tendency to take steps roughly in the direction of the previous step, the details fall below our spatial resolution. As expected, coarsening makes all the turning angle distributions flattened considerably. No visible difference was found between the turning angle distribution of the children searching for cryptic targets and those who where briefed with information regarding the patches.

Also, as can be seen in figure 4.3, the values of the auto correlation function (ACF) show that turning angles were only slightly correlated with the turning angle of the previous immediate step. This slight correlation can be attributed to oversampling, which is common when the recording rate (1 sec intervals) is frequent and steps travelled in the same direction are recorded as separate events. The correlation values drop sharply after coarsening. The coarsening width (w=3m), taken from the previous chapter, although small, was sufficient to remove the jags in the paths caused by the limits of GPS resolution and oversampling. Step sizes showed no correlation either before or after coarsening.

The conspicuity level deeply affects the searching performance of the children, as shown by the descriptor values in figure 4.4. Subjects looking for cryptic targets travelled longer distances, spent more time and had an overall lower efficiency of collections, measured as meters travelled per target collected. They also crossed their own path more often, travelled in a more tortuous manner and collected the targets in a sequence measur-

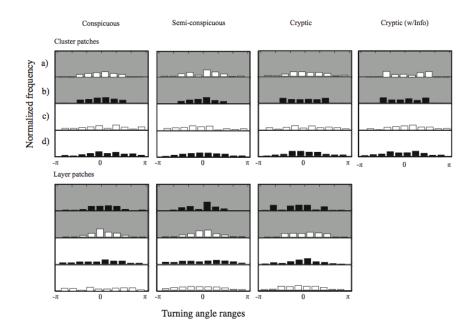


Figure 4.2: The normalised distribution of internal (white bars) and near-wall (black bars) bouncing angles, before (grey background) and after coarsening (white background). Notice the decrease in the number of steps and the flattening of the distributions after coarsening.

ing almost two times the distance travelled by the optimal sequence of target collections, determined by simulated annealing. Children in the cryptic condition had a lower collection rate and collection of the targets went on for the entire duration of the test. Also, no consistent differences where found between distributions.

The performance between the briefed subjects and their uninformed counterparts was practically identical for most descriptors. A slight variation resulting in a difference of statistical significance could be observed in the case of the collection rate and the total number of collections, although in both cases, performance is consistently poorer when subjects had information about the spatial arrangement of the targets.

4.4.2 Model Fit

The model was applied to the patchy target distributions, matching those used to test the children in the semi natural experimental conditions. Examples of the paths of the children and the model for the distributions used in the current and the previous chapter

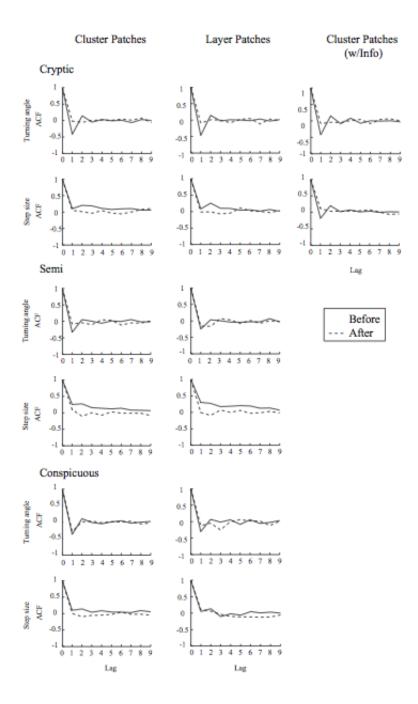


Figure 4.3: Mean autocorrelation values for the turning angles and step sizes before (continues line) and after coarsening (dashed line) for different shifted versions of the value sequence.

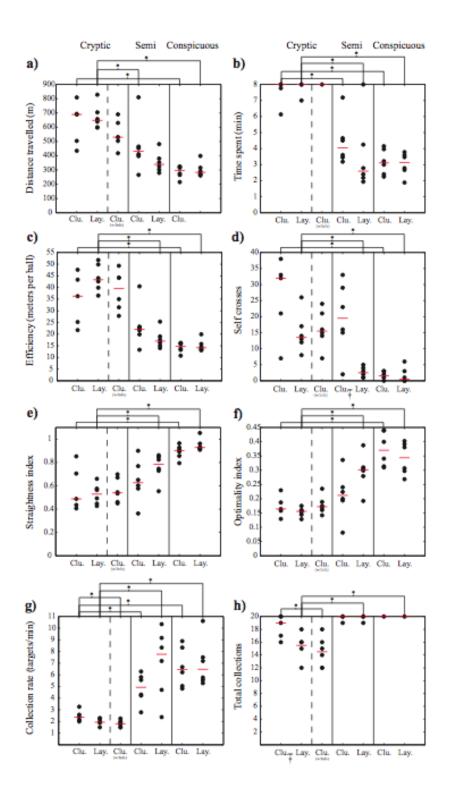


Figure 4.4: Children's descriptors of searching performance. Dots shown individual values for every child while lines show median values.* p_{i} 0.05.

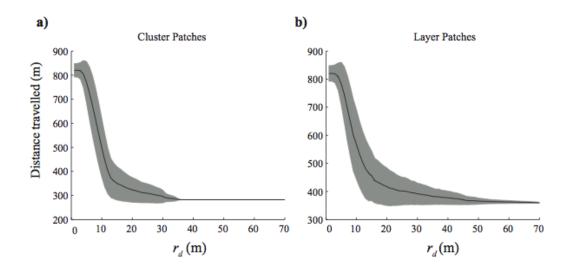


Figure 4.5: Mean distance travelled (black line, SD grey area) values produced by the output of 10,000 runs of the model for every r_d value.

(i.e random, regular, patchy clusters and patchy layers) is shown in appendix D.

Curves displaying the mean and standard deviation of the distance travelled by the 10,000 search paths generated by the bouncing search model for every integer r_d value from 1 to 70 m, are shown in figure 4.5. These curves show that, once again, there is a monotonic relation between the r_d values and the descriptor values.

Each of the values for distance travelled by the children were matched to the corresponding most similar value in the curve that displays the mean distance travelled by the model (curves in figure 4.5). The set of r_d values resulting from the match were in turn used to calculate the values yielded by other descriptors. The resulting comparison of both values is shown in figure 4.6. It is worth mentioning that the mean matched r_d values in the current chapter and chapter III, have a striking similarity, particularly for the cryptic conspicuity level (cluster \bar{r}_d = 8.3, layer \bar{r}_d =7.2, random \bar{r}_d =9.5, regular \bar{r}_d =8.2)

The model fit appears to be exceptionally good in most cases. In very few cases, such as the self-crosses (or number of times the trajectory of a searcher crosses itself) in the semi conspicuous cluster patches or the optimality index in the conspicuous layer patches, the model's prediction is smaller than the variation observed in the children.

Step size frequency for every target distribution was plotted separately (figure 4.7). The distribution of children and model step sizes appear to approach an exponential dis-

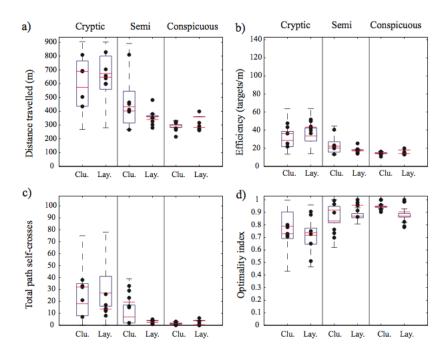


Figure 4.6: Overlap between the children's values of chosen descriptors (black dots) together with boxplots summarising the descriptor's values for the model for the r_d values resulting from matching the children's and models' behaviour. In each box, the central mark is the median, the edges of the box are the 25th and 75th percentiles, the whiskers extend to the most extreme data points. For clarity, outliers are not shown.

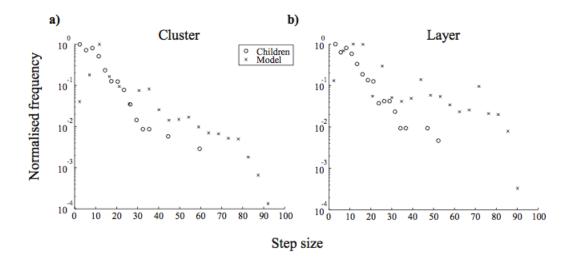


Figure 4.7: Normalised step size distribution for the coarsened children's paths and the model. tribution.

4.4.3 Patch Depletion

To explore the nature of the visits to patches, the collections of targets within the same patch were quantified as vertical increments in the step plots of figure 4.8. Using the linear interpolation of the first and last points of these step plots, it is possible to see that a higher slope is indicative of a large number of sequential collections while inside the same patch. For instance, it is possible that conspicuity had a strong effect on the number of collections made in the same patch. In general, the slope of the stair plot increases as targets become more conspicuous. The individual cases however, show that some of the children in the conspicuous conditions have a poor perception of the patchy structure, which results in an unexpected and uneven set of slope scores for the subjects in this condition. Also, information on the patchy structure, however, does not appear to modify the slope of the stair plot, and in fact, appears to actually make it make it smaller.

The slope values produced by the collection sequences of the model have considerably less dispersion than the slopes of the children, as illustrated by figure 4.9. The sequences of collections followed by the model do not include as much variability as the children.

On occasions, a subject may revisits patches (4.10). Searchers looking for cryptic tar-

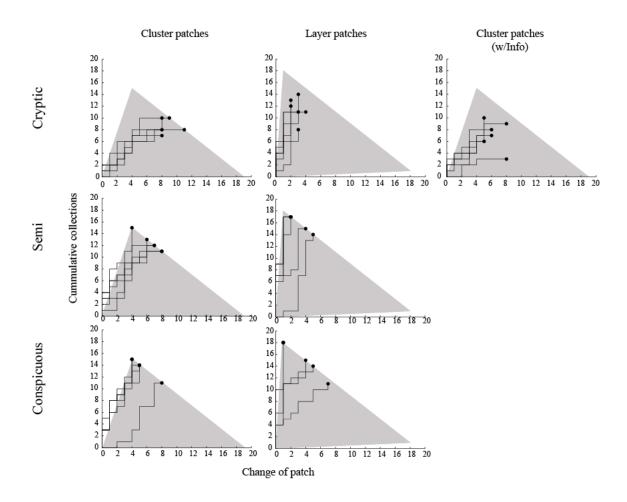


Figure 4.8: Stair plots showing the sequence of collections of targets for each subject. Vertical increments account for collections of targets belonging to the same patch, while horizontal increments occur when sequential collections involve targets from different patches. Grey triangles mark the limits for the optimal and the worst possible slopes for that the sequence of collections particular to that distribution.

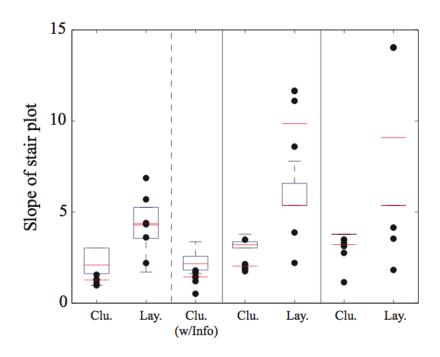


Figure 4.9: Slope values for the individual children's stair plots (dots) and the model (boxplots).

gets revisit the patches more often than in any other condition, while some of the searchers in the semi and conspicuous conditions manage to completely deplete the patches. Although the range of values is not very large, a large amount of individual variation can be observed. It is surprising, for instance, that some children in conspicuous conditions do not deplete the patches even-though they are evident. This is true even for the laminar patches, where revisits means crossing to the other side of the arena. Revisiting frequency is one of the few descriptors that show a statistical difference for the condition in which children were cued with information about the patches; in this case they show a lower revisiting frequency than the uninformed counterpart. The range of the model's revisiting frequency appears to be produce similar values for the cryptic and semi condition, but has very low variance for the conspicuous condition.

4.5 Discussion

The searching task and experimental setup proved, once again, to be useful for collecting paths of searching children, this time under a new set of spatial distributions. The distance

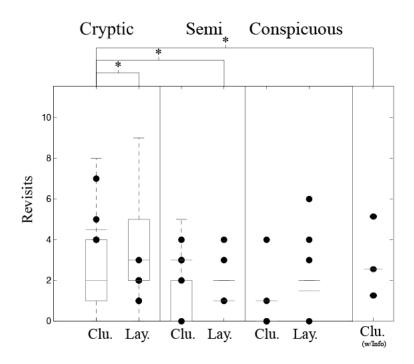


Figure 4.10: Revisiting frequency or the times of times the searcher makes a comes back to make a collection to an already visited patch. Boxplots show the revisiting frequency for the bouncing search model. *p > 0.05

between the targets in a patch, used in the construction of the patchy spatial distributions and derived from the matches of the r_d proved to be adequate, as shown by the performance of the subjects. GPS records showed a reasonably low amount of outliers, which were dealt with accordingly; for more information of GPS precision and a few ways with which to deal with outliers, see in appendix A.

The main results, regarding the capability of searchers to detect a more *natural* distribution represented by targets arranged in patches, suggests that searchers ignore or do not keep track of information regarding the spatial array of the targets. Not only do the children's descriptors fall within the same range as the values of the children searching in random and regular distributions, but also the model performance correctly matches the children's behaviour for this experimental setup. Other tasks in which human subjects are confronted with patches, suggest that they are not very good in using conventional information when exploiting the patch (Wilke *et al.*, 2009, Hutchinson, 2008). Detecting the spatial distribution requires a larger set of rules than simply bouncing, and does not necessarily lead to a larger number of collections.

The lack of an apparent response to the patches could be a particular choice of searching, but more likely the children did not pick up the cues as to the patchiness of the distribution. This could be for a number of reasons. First, it might not be an easy task to estimate distance or density, even for conspicuous elements. Estimation of parameters while searching, and specially during a first exposure, could be too large a cognitive burden. The density aspects could be tested in future setups, but it might require a different configuration of elements, since the green golf balls used here were already at their visual threshold that is, if the targets were placed any closer it they would be visible from other targets location, which would not lead to a search processes. In the case of the layered patch, the changes made a larger drop and the payoff given by a local search could be reflected in the performance. Also, if one of the sides was explored successfully, following the rules on the other one would have been fruitful. A necessary direction for the future is retesting the same subjects, since local searches and patchy environments are probably learned quickly and performance should improve dramatically within a few testing sessions.

The group of subjects that were given information as to how the targets were arranged, appear to have failed to properly execute a patchy search. Seeing that there is no evidence that subjects can identify the concept of a patch based solely on information gathered during the collection process, there are doubts about whether subjects of this age will be able execute a patchy search even if told that it could result in a larger number of collections. It is impossible to totally discard a patchy search, because head movements were not included in the path records. Then again, patchy searches, if executed, it did not over-perform in any aspect the search patterns of the uninformed children and were in fact slightly less profitable in terms of collection rate and total collections.

Given the popularity of patchy distributions in the searching and foraging literature, testing patchy distributions was a necessary addition to the current experimental setup and an interesting challenge for the bouncing search model. The performance of a bouncing search in a patchy distribution does not appear to differ from the performance of the children. It is possible to successfully make several sequential collections inside a

patch without the assistance of information. The probabilities of encountering a target belonging to the same patch after bouncing off a collection is large, specially if elements of a patch are spread away enough from each other so that the first collection is made close to the centroid of the patch. Thus, for some patch densities, the path followed by a patchy search could be remarkably similar to the path produced by a bouncing search. The bouncing search has a strong dependance on boundaries, which might increase the likelihood of collections, since the subject remains within the arena the whole time. In an environment where borders are less obvious or further away and targets are found in small but very dense patches, the performance of finer searches might prove more profitable.

4.6 Conclusion

The challenge posed by adding more or different types of information to the spatial distribution, in the form of targets arranged in patches, did not drastically alter the main characteristics of the children's searching paths, at least, given the current dimensions and the resolution of the recording methodology. Attention to the spatial array does not appear to be relevant to searching under the current motivational concerns and rewarding schema. A simple model replicates the performance descriptors and to a certain degree, the patterns of patch visits. The bouncing search, with its simple set of rules, manages to mimic the performance and statistical features of humans searching for targets in an enclosed space. There are however, many questions related to the capacity of humans to detect spatial distributions from the information derived from their searching behaviour, as well as the utility that this capacity may have in real life.

Chapter 5

Optimisation of a simple searching algorithm

Mobile organisms often face the problem of having to search for resources in unknown environments. In order to invest as little energy as possible, searching strategies aimed at maximising resource encounters are probably shaped through evolutionary history and previous experience (Hassell and Southwood, 1978; Milton, 1988). Some strategies attempt to match movement characteristics to those of the resource or the environment. Experience shows that in order to increase the intake when inside a resource patch, movement should be slower and more tortuous. Conversely, when resource density is poor, faster straight-line movement may be more beneficial (MacArthur and Pianka, 1966; Root and Kareiva, 1984; Bernstein, Kacelnik and Krebs, 1988). Environmental features may restrict the area in which a searcher moves, which helps in establishing the geometric properties needed for a systematic scanning, such as the turning angle of a zig-zag that bounces against parallel borders.

The bouncing search test follows the work of Rosetti et al., (2010) (also described in Chapter III) to model children's search behaviour inside a bounded arena. The model guidelines dictate that a searcher follows linear trajectories that either collect one of the circular targets or collides with the arena boundaries, from which an angle to bounce off is chosen. The searching continues until all targets are collected or until a time limit

is reached. The probability of the searcher's trajectory making a collection is greatly dependent on the radius of detection around the target, which is the main parameter explored along with the spatial distribution of the targets. In the current work, we aim to use optimisation strategies to shape the search paths and study the characteristics of the resulting solutions, to see whether they represent successful strategies. Another aim is to explore how the target distribution can qualitatively modify the performance of the solutions brought on by the optimisation task.

5.1 Experimental Setup

5.1.1 Environment

The bouncing search model was submitted to an evolutionary optimisation procedure. A computational version of the model was implemented in Matlab (Mathworks Inc, 2008). The simulated environment consisted of a rectangular arena ($60 \times 80 \, m$) with 20 randomly placed non-regenerating resources following one of four types of target distributions: random, regular, cluster patches and layered patches. The starting point of the searcher is fixed on one of the shorter sides of the rectangle. The main criteria for termination were the collection of all targets or reaching a given number of steps.

5.1.2 Genetic Algorithm

A series of tests using genetic algorithms (GA) were setup to investigate whether the turning angles in the bouncing search could be shaped into a systematic strategy capable of collecting all targets, and to determine whether their location could be predicted. The matlab code can be found in the following link ¹.

Genotype to phenotype mapping

The individual genomes consist of an array of 100 θ values distributed between $-\frac{2}{pi}$ and $\frac{2}{pi}$, which in turn codify the turning angles (Figure 5.1) and the total number of steps avail-

 $^{^{1}}http://docs.google.com/Doc?docid=0AXBqPCRUKfQHZGRnYnI0Z21fMjNtOXd6cGJnbQ\&hl=ender and the control of the$

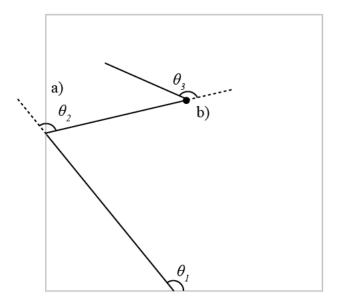


Figure 5.1: Representation of the turning angles of a search path. The turning angle, or the angle with which the searcher bounces off the boundaries or from a collection point is the only characteristic coded in the genome.

able. On the randomly generated population, the turning angles are randomly assigned a uniform distribution to each one of the steps. The step size is not assigned, since by the inner workings of the bouncing search, it will be determined by the direction of the turning angle and the presence of a boundary or a collection point. The total number of steps is determined by the size of the genome, although not all of the steps will necessarily show, since all targets could be collected before reaching the end of the genome or the time limit may be reached before all the turning angles in the genome are presented.

For each iteration of the bouncing search, a new step of the search path is calculated. The options for a step are to collide against a boundary, make a collection, or end up outside the arena. Another array keeps track of the bouncing angles that result in successful collections.

Distributed genetic algorithm

The first choice of algorithm was a *distributed genetic algorithm*, in which each solution is placed on a unique location over a toroidal grid (Husbands *et. al.*, 1998). After testing, each individual is assigned a fitness value according to it's performance. A random loca-

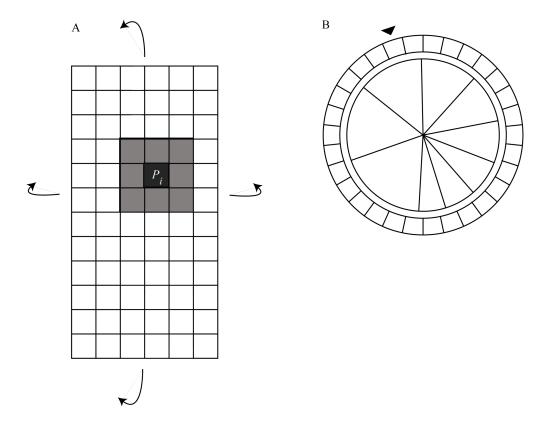


Figure 5.2: A graphic representation of a section of a toroidal grid (a). A selected individual (in grey) and the neighbourhood grid that surrounds it will participate in a process of roulette based selection. The roulette-based selection is illustrated in (b). The solutions in the neighbourhood are ranked and a probability of being selected for a parent in the generation is directly proportional to the proportion that their fitness contributes to the mating pool, illustrated here by the pie chart inside the roulette.

tion of the toroidal grid is taken along with the solutions in the surrounding neighbouring grid locations. This *mating pool* of solutions is ranked in descending order, after which, the parent solution is chosen by a rank-based roulette explained below (Figure 5.2)

Rank-Based Roulette In the rank-based roulette (Figure 5.2), the ith solution (ranked from 0 to N1, with N1 being the fittest) of the mating pool has a chance of passing on to the next generation proportional to i or:

$$P(i) = \frac{2i}{N(N+1)}$$
 (5.1)

This gives the lowest rank solution no probability of becoming a parent, while giving the highest rank solution no probability of being replaced by the newly formed child.

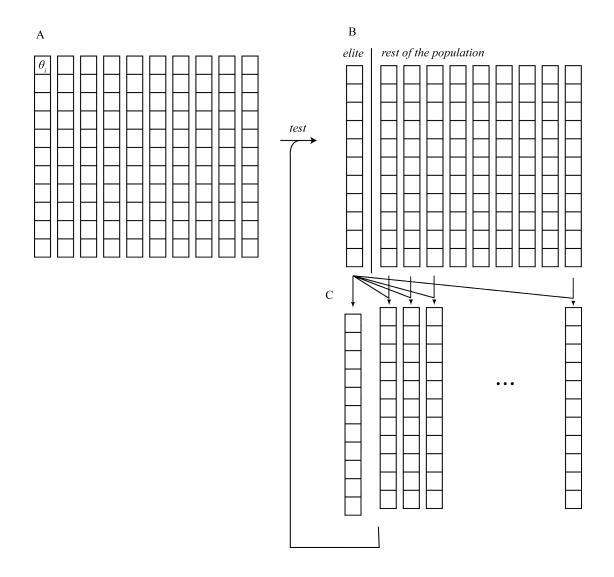


Figure 5.3: An illustration of the population (a), consisting of linear arrays of θ values. The population is tested and their performance quantified through a fitness value. The top scoring values (10%) of the population is separated from the rest. This elite is used to generate the next population and a copy passes unchanged (c). The process continues until a solution is found.

Elitist genetic algorithm

The second choice of algorithm explored, consisted of an *elitist genetic algorithm*. After solutions are tested and a fitness value is assigned to their performance, the population is ranked in descending order. A percentage of the population with the top fitness scores is chosen to be the parents with each solution contributing to an equal percentage of the new population. Also, the top scoring solutions are reinstated to the next generation with no modification (Figure 5.3).

Elitism The elitist reproduction guarantees the *survival of the fittest* solutions, while introducing new variants by mating a member of the elite with several random solutions of lesser fitness. Since each member of the elite produces an equal percentage of the next generation this guarantees that no single solution dominates the gene pool, which would stagnate the evolutionary process.

Mutation and Reproduction

Both asexual and sexual reproduction were tested.

Creep and complete mutation During asexual reproduction, a parent genome was passed on to the next generation changed only by mutation operators. Two different mutation types operate over the genome: a creep mutation would produce slight changes to a gene (the value of a single bouncing angle) by replacing it with a random value normally distributed around the value previously occupying that gene. A complete mutation would change the θ value completely by assigning a new one randomly chosen from a regular distribution of -2π to 2π .

Tests were done for different frequencies in which a mutation occurred. The complete mutation occurred during the generation of a new population on 1, 5 or 10 percent of the population, while the creep mutation happened to 10, 20 or 30 percent of the population.

Cross over Cross over occurred only if sexual reproduction was allowed. By crossing over, genes from the selected parent (the result from the roulette or a member of the elite, depending on the type of generic algorithm used) and non-selected member of the mating pool combine their genomes into an offspring. The percentage that parents contribute to the genome can vary. Once an element of the next generation is produced, sexual reproduction contemplates the possibility of a mutation occurring to it's genome.

5.1.3 Evaluation

In every algorithm, the original setup involved a population (PopN=100) of paths that were subjected to the bouncing search test on separate occasions (TestNum=10) and

then their mean success was quantified and ranked. A new population was created by the different methods and parameters described above. This process was iterated for a given number of generations (GenN=100) or until a satisfactory solution was found. Velocity and time were not taken into account. Instead, large numbers of steps were available prior to termination of the task, thus, only the genes coding the turning angle of the successful sequence of collections were passed on. This was done to ensure most solutions would be successful collectors and thus, introducing plasticity in the pool of solutions.

The regular as well as both of the patchy target distributions used for testing were fixed, while the random distribution was generated for every test. The fixed distributions were used to test the capacity of the algorithm to study the performance of the evolved search paths for different target configurations, while the random distribution provided the challenge of producing a systematic strategy. Tests were done for radii of detection of (r_d) 2, 5 and 10 m.

Fitness

The main fitness criteria included the collection of all targets with the minimum number of steps. Fitness (f) was calculated using the following formula:

$$f = (\frac{n_c}{N}) * 10 + (\frac{1}{i}) * 100$$
 (5.2)

where n_c is the number of targets collected, N is the total number of targets in the arena and i is the number of steps taken to solve the task.

In the case of testing the regular distribution of targets a single value for the fitness was used. For the random distribution of targets a ranked fitness was used. When scores are ranked the fitness F is the weighted sum of the N scores with a weight proportional to the inverse ranking i (ranking is from 1 to N, with N as the lowest score):

$$F = \left(\frac{2}{N(N-1)}\right) * \sum_{i=1}^{N} i f_i$$
 (5.3)

Ranking fitness provides pressure for the algorithm to do well on every test and diminishes the effect of tests in which the solution is quickly found by fortuitous circumstances. It evens the scores out so that a solution doing moderately well on every test has a better fitness than one that succeeds in an isolated incident.

At first glance, it may seem that the algorithm could find an optimal solution by not moving at all. However this possibility is non-existent since the only conditions ending the task are the collection of all targets or exhausting all the available steps. Also, notice that the fitness is calculated with the number of steps, not the distance travelled, favouring the paths that find solutions and not merely the shortest paths. Therefore, the greatest percentage of the fitness value is given by the number of targets collected (maximum value = 10), and it is progressively increased by solutions that use fewer steps (maximum value 5). The fitness was calculated for every individual as an average of fitness obtained in each test. With this, we attempted to give the better fitness to search paths that were consistently successful, and to avoid favouring rare events producing high fitness by chance alone.

5.2 Results

5.2.1 Exploration of the parameter space

Only paths searching in a regular distribution managed to be completely successful (20 targets in 20 steps) although often the evolutionary procedure will produce suboptimal solutions of 21-25 steps. It is clear that the few final targets are considerably hard to collect than the first ones. In the case of the random distribution, evolution would not yield an optimal solution, having reached search paths that could collect all targets using 35-50 steps.

The different algorithms were tested using various parameters. There were no great differences in the evolutionary performance measured in the capacity to reach a successful solution and the number of generations needed to do so. All algorithms could produce a search path that collected all regularly distributed targets and none could yield a search

path that guaranteed the collection of all the targets in the random distribution. Larger generations did not improve the evolutionary process.

As mentioned before, the creep mutation produces slight changes to the turning angle based on a normal distribution. Given that this is the main driving force behind change during asexual reproduction, larger probabilities were tested (0.10, 0.20 and 0.30). In the case of the random distribution, different creep mutation settings appear to have no effect on the chance to obtain a satisfactory solution. The mean population fitness oscillates around the same value. For the fixed distributions, steady increments were observed in the maximum fitness in the case of the elitist GA, and although more fluctuations in the mean fitness were produced, the distributed GA also manages to reach a steady maximum fitness. The creep mutation probability of occurring on only 10% of the population appears to be the best choice, since it introduces enough variability to find better solutions while larger values appear to somewhat disrupt the evolutionary process.

The complete mutation replaced the value of the chosen gene with a new θ value chosen from a regular distribution. This was done to avoid stagnation and to introduce new values that could provide a sudden solution, rather than the much more subtle creep mutation operator. Given that this operator can be as disruptive as it is productive, it was introduced with less probability than the creep operator (0.01, 0.05 and 0.1). Changing the probability of the occurrence of complete mutations did not visibly modify the evolutionary process for the random distribution or any of the fixed distributions.

Cross over rates were needed when sexual reproduction was allowed. The cross over procedure places complete parts of a parent onto the offspring genome (75, 50 or 25 %). The combination of path segments might be faster in producing new solutions, although the disruptive effect might be considerable. Changing the proportion that the parent contributes to the next generation did not change the general pattern of the fitness growth in the GAs. For the random distribution, oscillations in the fitness are observed along with the inability of the algorithms to find a solution. In the fixed distribution, the elitist GA maintains the top fitness value across generations or increases it, while heavier oscillations are observed for the distributed GA when sexual reproduction is introduced.

Based on the maximum fitness achieved by the GAs, the algorithm chosen was the sexual and elitist reproduction and a cross rate of 50%, a creep mutation of 0.20% and complete mutation of 0.01%.

5.2.2 Performance of solutions

Turning angle

The evolution procedure began by using angles drawn from a regular distribution ranging from $-\pi$ to $-\pi$. The distribution of the turning angles after the evolutionary process is reminiscent of a bimodal distribution with peaks around $\frac{-\pi}{2}$ and $\frac{\pi}{2}$ (Figure 5.4). This modification of the turning angle distribution suggests that, upon reaching the border, angles that allow the searcher to bounce off the arena walls in a perpendicular manner tend to maximise the collection of targets. The bimodal shape of the turning angle distribution is gradually lost as the r_d values increase, since for large r_d 's the step do not reflect bounces from the wall but from previous collection points and when collections occur often. Also, in the case of the turning angle histograms of the fixed distributions of targets, the bimodal shape is not as smooth. This is due to the bounces from the wall being overall less frequent than in the paths that evolve under a random distribution of targets.

The turning angle distributions for the random, cluster and laminar target distributions appear also to be of bimodal nature. However, the shape of the distribution is not nearly as smooth as that of the regular distribution. For small r_d s, small turning angles were not present. Small turning angles may only occur after a collection point, whereas only large angles occur when bouncing off boundaries. As the r_d increases, the turning angle distributions show a tendency to be either more one-sided (regular target distribution) or the frequency of few turning angles to dominate the distribution. It is possible that, as r_d increases, the number of solutions that the bouncing search can provide become very limited, thus always recurring to the same set of angles with the same frequencies. Also, for a less structured target distribution (random target distribution), more contrast is shown between the frequency of appearance of a given range of turning angles.

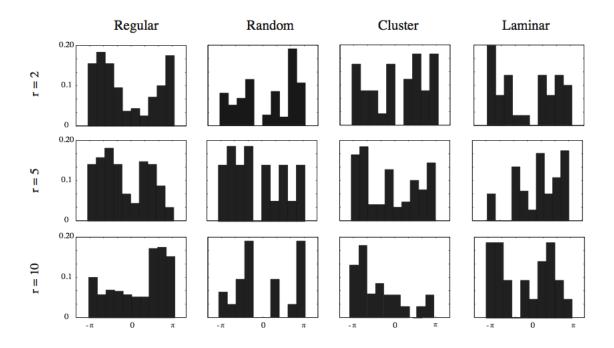


Figure 5.4: Turning angle distribution of the paths found as solutions to the optimisation procedure occurring under the bouncing search constraints. Turning angles are shown for the different distributions used as well as for different r_d values.

Step size

The step size distribution of the population of solutions found by the GAs resembles an exponential distribution in the case of the random distribution (Figure 5.5). The shape of the step size distributions of the fixed target distributions does not appear to have an obvious pattern. The distribution of step sizes of the search paths evolved in the random (dynamic) distribution suggests that the distribution contains a great proportion of bounces against the boundaries, thus the smooth distribution. On the other hand, the length of the steps shown in the distribution of step sizes for the paths evolved on fixed distributions are strongly marked by the distances between collections.

Performance descriptors

The performance descriptors calculated for the search paths show the difference between the challenge posed by dynamic or static distributions. The distance travelled by the paths searching for random, dynamic targets of $r_d=2$ was about $\bar{d}=3000$ m, decreasing by half ($\bar{d}=1480$ m) for $r_d=5$ and even further ($\bar{d}=1000$ m) for $r_d=10$. The distance

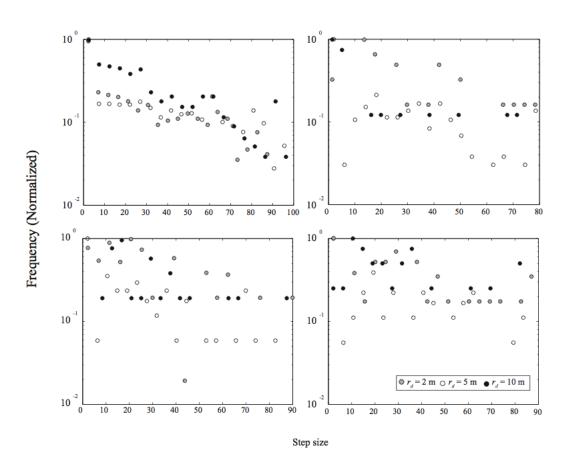


Figure 5.5: Step size distribution of the paths found as solutions to the optimisation procedure.

travelled in the fixed solutions was always considerably less (regular $\bar{d}=1645,\,520,\,330\mathrm{m}$, patchy cluster $\bar{d}=1381,\,840,\,426\mathrm{m}$, patchy layered, $\bar{d}=1518,\,555,\,560\mathrm{m},\,r_d=2,\,5,\,10$ respectively). The efficiency (number of meters travelled per target collected) follows a similar pattern, with the random targets proving challenging to collect: $r_d=2$, $\bar{e}=165$ m/target, $r_d=5$, $\bar{e}=75$ m/target, $r_d=10$, $\bar{e}=50$ m/target. Again, the fixed targets more than halves this amounts (regular $\bar{e}=80,\,26,\,16$ m/target, patchy cluster $\bar{e}=70,\,42,\,33$ m/target, patchy layered, $\bar{e}=75,\,28,\,28$ m/target, $r_d=2,\,5,\,10$ respectively). The number of crosses in the paths shows an even larger drop between the condition with random dynamic targets () $r_d=2$, $\bar{c}=500$, $r_d=5$, $\bar{c}=120$, $r_d=10$, $\bar{c}=50$) and the static ones (regular $\bar{e}=145,\,12,\,2$, patchy cluster $\bar{e}=114,\,32,\,4$, patchy layered, $\bar{e}=128,\,13,\,16,\,r_d=2,5,\,10$ respectively). In general terms, the solutions follow the expected pattern.

5.3 Discussion

While the optimisation techniques seem to be able to produce optimal results for fixed, static distributions, it cannot to do so for dynamic, random distributions. The reason behind this is not immediately clear. It could be an intrinsic limitation of the optimisation process to be unable to produce a systematic strategy, given that it should be completely efficient and use the fewest steps possible. On the other hand, the inability to produce systematic searching paths that guarantee the collection of all targets could be related to the rules of the bouncing search model. Thus, the constraints set by the conditions of the bouncing search are extremely harsh, since missing a single target would break up the possibility of constructing a systematic strategy, moving the solutions away from the optimal fitness goal. In short, the model may have the possibility of constructing a systematic strategy, but as yet it does not have enough flexibility to shape the turning angles in a way they could exploit it productively.

An important point to make regarding the random distributions is that even though a strategy may prove to be efficient in collecting random targets through a systematic sweeping of the arena, it may prove an enormously costly effort. As collections occur, the density decreases, producing more and more steps that would not collect a target by mere chance. If a systematic search discovers all the targets but one, yet the elusive target requires a complete re-scanning of the arena, this might severely hinder the overall fitness value. This could be a clue as to why systematic movements are so rarely found in nature, relating closely to the optimal foraging principle described by Charnov (1974) relating to the time at which it is best for an organism to leave the current patch and start foraging in a new one. In both cases, the current and the original experiments, the whole arena can be considered as a single patch. Also, in both experiments success was measured by collections, ending either when there were no more targets in the arena or when the time limit expired, denying the searcher possibility of giving up.

A random distribution of targets does not allow the paths to establish steps that are consistently successful. Converging directionality in the turning angle is one of the signs of a systematic search strategy. For small r_d values, the turning angles that produce a collection hold little chance of being successful under other random distributions of targets while for high conspicuities, any step will find a target at the start of the test. However, with less targets in the arena the possibility to miss one increases, ruining the chances that a searcher can get a perfect fitness score.

5.4 Conclusion

Genetic algorithms, and other computerised optimisation techniques, provide an excellent framework with which to explore the searching strategies. The optimisation process can be moulded to particular searching of environmental peculiarities and the most varied fitness constraints. In this particular case, the algorithm that produced solutions for the bouncing search of fixed targets could not produce a suitable systematic solution that would solve the problem of searching for randomly distributed targets. This illustrates that producing these solutions is not trivial and can rarely guarantee giving a searcher one-hundred percent accuracy. Also, they are uncommon in nature because the search for resources works in a non-exhaustitive way. Further directions of testing systematic searches could include the seeding of possible solutions, and observing the solutions that

generic algorithms produce with them.

Chapter 6

Conclusion

6.1 A brief recapitulation

This work provides an effort to manage the theoretical and experimental tools needed to research search behaviour, a classic topic related both to behavioural biology and computer science. A brief recapitulation can be made following the thesis structure.

On the methodological side, the thesis showed the main difficulties linked to recording movement, the different methods involved and the consequences link to every choice. Also, some of the most popular ways of preprocessing data were explained with examples. While on theoretical side, the thesis introduced some of the main concepts related to path analysis and the measurement of descriptors to evaluate performance or to explain the statistical characteristics of the paths. With the use of examples, mainly from behavioral ecology, the main questions related to the topic of searching behavior were illustrated.

On the experimental side, the experimental setting proved to be versatile enough to accommodate several different distributions, the subjects seem to be involved and enjoy the task, while the recording apparatus proved to be accurate enough to allow recordings and interpretation, at least at one choice of a length scale. Experimental conditions manipulated the distribution and conspicuity of the targets. A straightforward conclusion of the experimental work centered around how the visual conspicuity of targets (resources) is closely related to the characteristics of the success of a search effort. Even more interestingly, is how changes in spatial distribution did not affect performance and that sub-

jects appear not to be able to detect the underlying structure of the spatial distributions. The bouncing search model seems to be a good platform for comparing search behaviour which is bounded. The simple workings of the model allow for quick adjustment to a different variety of experimental conditions as well as the manipulation of the parameters under which it operates. Amongst the conclusion that the model allowed this research to reach, is the similarity between the model and the children, in both the performance and the statistical features of the searching paths. The simple rules of operation of the model appear to closely mimic the behaviour of the children.

On the computational side, the optimisation procedure provided clues regarding the difficulties of optimal searches of randomly distributed targets under the movement criteria dictated by the bouncing search model. Even though it may manage to learn the location of fixed targets, the number of steps needed to guarantee a solution that will collect all the targets is so large that it is compensated by failing to collect all targets with a smaller number of steps. What appears at first glance to be a sub-optimal solution could be related to the patch leaving time, or the point at which searching for a target becomes increasingly expensive. Further optimisations in both computational terms and human experiments could be seeded by suggesting a systematic solution and observing the modifications obtained from the test trails and the evolutionary process. The main results produced by this work can be summarised by showing how seemingly complex behaviour can have simple underlying mechanisms.

Applications of this research may be limited because of the basic nature of this research. Many of the findings described here are derived from a particular lengthscale and are therefore limited to these specific choices. However, others can be extrapolated to any scenario in which search is used in a context of spatial movement and is tied to a temporal or energetic constraint. The current findings can be applied to any number of situations where search movements are bound and conspicuity is a crucial aspect of the finding process. For instance, it could be used to understand the movements of subjects attempting to exit a building, searching on a supermarket or an airport parking lot, or even reading a book or browsing a web page can be an homologous process of searching, where the path

is constrained by the margins of the page or of those of the browser. Links or relevant information can be made more or less conspicuous using colors, font attributes or sizes. The current experiments and model provide a simple platform to explore the movement in many of these examples.

6.2 Further efforts

Searching is a basic aspect of the life and behaviour of any organism. In humans this becomes even more interesting due to the diversity of activities, scenarios and constraints that technological innovation has created. During these activities it may be relevant and original to study the validity of old mechanisms, the strategies to adapt them to new situations or the creation of entirely new ones. Although the methodology used in this case study of search behaviour was quite largely exploratory, it is complex enough to derive a rich set of variations.

In future experiments, the developmental questions can be pursued by involving younger and older participants. Cooperation and competition can be introduced by keeping scores and involving several simultaneous participants in the task. Other cognitive questions can be pursued by changing the conspicuity and distribution and the score array. Further testing should also include a test to measure the impact of area, number of targets and testing time to calibrate the search effort to a certain standard and to be able to manipulate these variables in relation to the tests. The main aspect to maintain in the new set of experiments, and any other experiments involving search, is ecological validity. Although it's true that kids normally do not search for balls on a football field on their own accord, the activity was treated as a game and children enjoyed the challenge.

Searching can be explored in other everyday situations such as the parallel project (abstracts can be found in the Appendix B) which involves searchers of Nahua communities looking for mushrooms in the Malinche Volcano in the state of Tlaxcala, a few hours away from Mexico City. This group of foragers search for mushrooms on weekends and studying their searching pattern can provide insight into several questions ranging from ecological matters to highly cognitive explanations. Following a similar tendency, in ur-

ban environments, further directions of this work involve the analysis of the routes people take in supermarkets and large buildings of several types. All these studies should be complemented with statistical simulations and computer models, such as the bouncing search model.

6.3 Conclusion

In conclusion, the experimental work shown here is highly useful and is the beginning of an exploration into a very long line of research. Along with the experimental setup, a set of analytic tools were put to the test, including preprocessing and parameters of probabilistic model. Also, interpretation frameworks were shown including a simple computational model and the testing of conventional optimisation techniques. The use of this toolbox can only improve with further experimentation and testing, starting with the many questions suggested by this work and with the experience and wisdom gained by this experience. Future studies should provide interesting observations about the different search patterns of humans in order to enrich our understanding of one of the most basic behavioural activities.

6.4 Thesis Achievements

Again, in recapitulation of the main contributions of this work we can mention:

- First, the understanding of the vast framework of analysis and interpretations that can be applied to movement data that can be seen in chapter II. This chapter provides a good frame of references on the methods and the difficulties to be encountered when dealing with path analysis.
- Chapter III successfully attempts an experimental semi natural setting in which children search for targets arranged in a regular and a random distribution. The main findings include, how the performance is affected by conspicuity of the targets,

whereas the distribution does not appear to affect at all. Also, the performance of the children, as evaluated by several descriptors and statistical properties of the searching paths, does not appear to differ from the performance of a model in which an agent traveling in straight lines bounces of boundaries and collection points in random directions.

- Chapter IV expands the findings of chapter III, and uses them to create two different patchy distributions. Children were tested in the same conditions of conspicuity. An important addition is, however, a condition in which children were given hints about the distribution of the targets. The main finding includes the effect of the conspicuity of performance and more interestingly, the lack of reaction to the patchy distribution of targets. Again, the bouncing search model, performs in a similar way to the children, suggesting that the searching strategy of the children is produced by simple rules and effective behaviour (rushing after collections) rather that attempts at deciphering the characteristics of the target distribution.
- It is worth noting that the experimental series described here constitutes one of the first examples of the evaluation of searching performance through the study of search paths. The use of GPS recordings for human behaviour has a recent history, but was never used in an experimental task.
- Finally, chapter V, describes an attempt to incorporate the characteristics of a bouncing search into an optimisation procedure, which resulted in paths with a bimodal distribution of turning angles with the two distinct peaks centered around ^{-π}/₂ and ^π/₂. Also, performance of the solutions suggested by the optimization procedure proved to be similar to the performance of the children in previous chapters, while the optimisation procedure failed to provide solutions for dynamic targets.

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Appendix A

Tests of GPS tracking

Introduction

The ability to search for and locate resources is one of the most basic and vital attributes of animals, and one where several interesting aspects of their behaviour intersect (Bell, 1991). And yet, until recently the study of search behaviour in humans has proved difficult as the everyday spaces we move in are often too large and complex for direct behavioural observation or video recording. Traditionally, studies of human search behaviour have largely relied on pencil-and-paper tests (Silverman, Choi and Peters, 2007) and laboratory simulations. Although ingenious, such experimental set-ups do not accurately reflect real life situations in which the energetic and other costs of searching over larger areas are likely to affect search decisions and strategies. Furthermore, descriptions of mobility in real life scales such as those illustrated in the work of Brockmann, Hufnagel and Geisel (2006) or Gonzaléz, Hidalgo and Barabási (2008), rarely provide the possibility of introducing experimental conditions. In the last decade, however, there has been considerable improvement in the recording of human search behaviour in larger, more naturalistic contexts, while introducing experimental manipulations.

In this thesis, a low-cost and easily implemented method of recording human search behaviour over larger areas outside the laboratory is described, which is readily open to experimental manipulation and control. Our method, based on the popular game of the Easter egg or peanut hunt requires participants to search for small objects (targets) distributed across a large outdoor area such as a sports field (Rosetti, 2010). Participants

wear GPS devices, which automatically record their pathways. Experimenters note the time at which each target is collected, and at the end of testing, the information from the GPS is downloaded on to a computer together with the information on the time of collections, and analysed using readily available commercial software. However, some concerns have been raised regarding precision and accuracy of the GPS apparatus used in this work. These concerns are addressed in the experiments throughout this appendix.

GPS tracking

Automated tracking of search paths was performed using available and affordable GPS devices (in the example below, Garmin GPS V personal Navigator). The small size and weight of the GPS device (12.7 x 5.9 x 4.1 cm, 255 g with batteries) allowed participants to carry it in the back of a modified belt. In this position the antenna is maximally exposed and not obstructed when targets are picked up from the ground. Participant movement is not hindered by use of the modified belt. GPS offer a variety of geographical units with which to record position, but one of the most widely used and easily implemented employs Universal Transverse Mercator (UTM) units drawn from a planar grid onto which a global map has been superimposed. These units are expressed in a metric system of distance, making behavioural descriptors of paths easy to calculate and interpret (Langley, 1998). The computerised recording procedure can be set to record in fixed intervals of either time or distance. Technical aspects, such as memory storage or battery life might limit the duration of individual experiments to less than 10 to 12 consecutive hours. Commercial and open source programs are available to download and interpret GPS data.

Constant good reception is needed to obtain a reliable record of the positions of participants during the search. Furthermore, the accuracy error reported by the manual and previous studies can be greatly reduced by conducting experiments in an open area (Hulbert and French, 2001). For our particular apparatus, the reported accuracy of the GPS device is 0-15 m, 95 % C.I. (Garmin Reference Manual; Tougaw, 2002). It should be noted that there is a considerable and important difference between the accuracy and the precision of a GPS. In the present context accuracy is the difference between a position

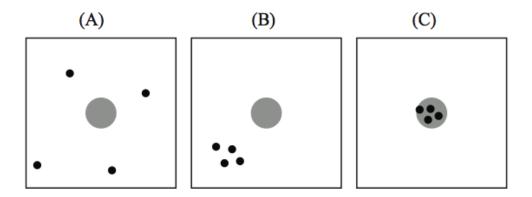


Figure 6.1: A visual representation of a real world location (grey, large dot in the centre) and a set of attempts to record it that are (a) neither accurate nor precise, (b) precise but not accurate and (c) accurate and precise.

recorded by the GPS and the true location, while precision stands for the dispersion of repeated measures of the same location (Figure 6.1).

The accuracy of a GPS is extremely hard to quantify but is of no consequence to the current study, since the true location is irrelevant to the characteristics of path records and behavioural descriptors. Precision, on the other hand, could be considered important since the location of the targets on the field and the movement of the children was recorded separately. In an ideal situation small dispersion values would make it possible to match the target distributions to the children's paths and also, it would be possible to replicate the distributions based on the locations given by the GPS. However, to reduce possible errors reliance on the GPS was kept to a minimum. The times at which subjects made a collection were recorded by the experiments during the tests and distributions were constructed daily using marks on the arena boundaries.

Outliers

Concerning the children's search paths the most important aspect was to reduce possible erroneous records from occurring along a search path, that is, to ensure that the characteristics derived from the sequential co-ordinate points forming a path display credible values. In the work of Pacheco-Cobos et al. (2009) the researchers tracking mushroom foragers under the forest canopy considered extremely harsh conditions for GPS record-

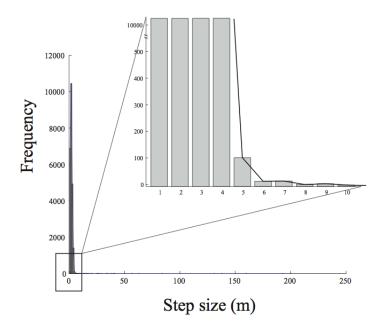


Figure 6.2: Step size distribution of the pooled, uncoarsened paths records of the experiments described in chapter III and IV. The detail of the histogram shows the drop in frequency after 5m

ings, and using the same apparatus as in the present study obtained only 1.8 % of outliers for over 21,00 recorded points, while sporadic events where satellite connection was temporarily lost accounted for 9.4 % of the 190 hours of continuous recording (personal communication).

Constructing an experimental setting in a football field or any other open, clear and flat area can reduce the size of this error by at least one order of magnitude. For example, the number of outliers was quantified for the movement records of all the children in the experiments described in chapter 3 and 4. Outliers were considered to be sequential points that were more than 5m apart from each other. The percentage of outliers in all the paths of the children combined accounted only for 1 minute from almost 3 hours of recording. The complete distribution of uncoarsened step sizes can be observed in figure 6.2. Clearly outliers exist, but the small number can be easily identified and replaced by linearly interpolating new co-ordinates inbetween the neighbouring records.

Precision

Nevertheless, taking into consideration that the performance of the GPS may need to be checked for a particular experimental setting, an estimation of precision can be obtained at the planned experimental site by placing a GPS apparatus in a fixed location and setting it to record it's position, for example, every second until the GPS memory is full (aprox. 3000 pts in the case of the Garmin GPS V). The dispersion from the mean reflects the precision of each coordinate (Serr, Windholz and Weber, 2006), calculated as the amount that each individual recording (x_i, y_i) varies from the mean:

$$CI_x = 1.96\sqrt{\frac{\sum_{i=0}^{n}(x_i - \bar{x})^2}{\sum_{i=0}^{n-1}, CI_y = 1.96\sqrt{\frac{\sum_{i=0}^{n}(y_i - \bar{y})^2}{\sum_{i=0}^{n-1}}}}$$
 (6.1)

Here, n is the number of recordings, and and are the mean values taken, calculated as:

$$\bar{x} = \frac{\sum_{i=0}^{n} x_i}{n}, \bar{y} = \frac{\sum_{i=0}^{n} y_i}{n}$$
 (6.2)

Precision was calculated for the 3000 records generated by the GPS while measuring the same location. Calculations of precision following the formulas described above returned a precision of 3.4 m on the x axis and a precision of 2.7 on the y axis. The location of measurements around the mean, including the amount of points falling at a given distance from the mean are illustrated in figure 6.3.

Coherence

To produce an estimate of the sequential recording coherence, which is, to show that GPSs can, on some scale, produce reliable behavioural measures, we recorded a set of laps around the football field. Two researchers, each holding a GPS, travelled 5 laps around the 403m soccer field depicted in the satellite picture shown in figure 6.4.

The perimeter length, calculated as the distance travelled during a lap was about 470m, that is, approximately 20% more than the amount measured using the satellite images. The difference is produced by the kinks in the path, efficiently removed by coarsening

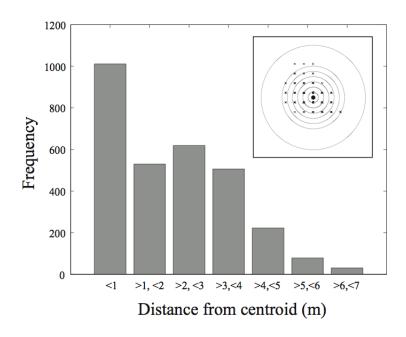


Figure 6.3: The GPS produced 3000 records of the same spot. Plot shows the number of records falling at a given at every meter from the average of all records while the detail on the top-right corner shows the location of the records.



Figure 6.4: Satellite view of the soccer-field used in the experiments.

(w=1.5) the paths (418m, or a 5% overestimation). The turning angle distributions before and after coarsening show consistency between laps as well as between travellers (Figure 6.5).

Conclusion

GPS's are valuable instruments in behavioural research, particularly, to record human behaviour in open, large spaces. Performing tests on precision and coherence gives us a better understanding of GPS capabilities as well as the limitations, and helps to plan experimental tasks that rely minimally on their precision. As recording technology develops and GPS apparatus shrink in size, in might be possible in the future to have several GPSs on a single subject and to average the paths to increase precision, if desired.

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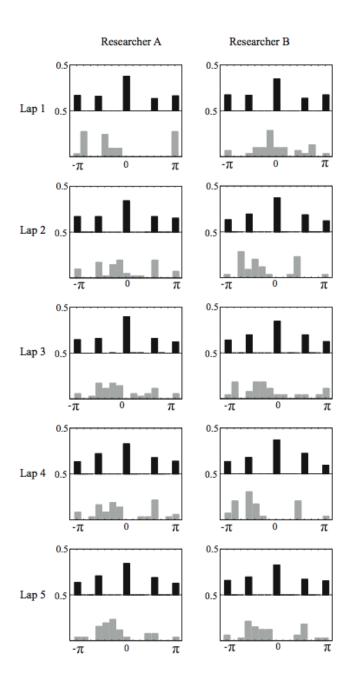


Figure 6.5: A pair of researchers, each carrying a different GPS, travelled 6 laps around the soccer-field. Plots show the normalised turning angle distribution for each lap of each researcher, before (black column) and after (grey columns) coarsening.

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Appendix B

Projects in collaboration

Spatial Distribution of *Taenia solium* Porcine Cysticercosis within a Rural Area of Mexico

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Abstract: Cysticercosis is caused by Taenia solium, a parasitic disease that affects humans and rurally bred pigs in developing countries. The cysticercus may localise in the central nervous system of the human, causing neurocysticercosis, the most severe and frequent form of the disease. There appears to be an association between the prevalence of porcine cysticercosis and domestic pigs that wander freely and have access to human feces. In order to assess whether

the risk of cysticercosis infection is clustered or widely dispersed in a limited rural area, a spatial analysis of rural porcine cysticercosis was applied to 13 villages of the Sierra de Huautla in Central Mexico. Clustering of cases in specific households would indicate tapeworm carriers in the vicinity, whereas their dispersal would suggest that the ambulatory habits of both humans and pigs contribute to the spread of cysticercosis. A total of 562 pigs were included in this study (AugustDecember 2003). A global positioning system was employed in order to plot the geographic distribution of both cysticercotic pigs and risk factors for infection within the villages. Prevalence of pig tongue cysticercosis varied significantly in sampled villages (p = 0.003), ranging from 0% to 33.3% and averaging 13.3%. Pigs were clustered in households, but no differences in the clustering of cysticercotic and healthy pigs were found. In contrast, the presence of pigs roaming freely and drinking stagnant water correlated significantly with porcine cysticercosis (p = 0.07), as did the absence of latrines (p = 0.0008). High prevalence of porcine cysticercosis proves that transmission is still quite common in rural Mexico. The lack of significant differentiation in the geographical clustering of healthy and cysticercotic pigs weakens the argument that focal factors (e.g., household location of putative tapeworm carriers) play an important role in increasing the risk of cysticercosis transmission in pigs. Instead, it would appear that other wide-ranging biological, physical, and cultural factors determine the geographic spread of the disease. Extensive geographic dispersal of the risk of cysticercosis makes it imperative that control measures be applied indiscriminately to all pigs and humans living in this endemic area.

Citation: Morales J, Martí}nez JJ, Rosetti M, Fleury A, Maza V, et al. (2008) Spatial Distribution of *Taenia solium* Porcine Cysticercosis within a Rural Area of Mexico. PLoS Negl Trop Dis 2(9): e284. doi:10.1371/journal.pntd.0000284

A new method for tracking Pathways of humans searching for wild, edible fungi

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Abstract: The study of human foraging behavior is relevant for social anthropology and behavioral ecology, because it makes it possible to study directly the relationship between human communities and the forest resources they use and manage. The recording of individual search pathways in the field has improved, in recent years, due to the availability of satellite technologies like the Global Positioning System (GPS). The present study was carried out in a Nahua community in Tlaxcala, Mexico, where wild fungi constitute an important source of food and income. We discuss different methods used to record foraging paths in humans as well as the spatial location of fungi gathered. Likewise, we mention the difficulties and procedures we have found useful in overcoming them. The best recordings were obtained when the GPS device was: 1) Programmed to record geo- graphical position by time rather than distance intervals; 2) Carried by the researcher; and 3) Used to mark the sites in the forest where fungi were collected. Although the sample size explored was small, we believe that the analysis of the paths obtained using this method can provide insights into the decisions that underlie the foraging patterns of humans, as well as the possible relation between these and the spatial distribution of fungi.

Citation: L. Pacheco-Cobos, M. Rosetti and R. Hudson. A new method for tracking Pathways of humans searching for wild, edible fungi. Micologìa Aplicada International, 21(2), 2009, pp. 77-87.

Sex differences in mushroom gathering: women forage more efficiently than men

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Abstract: Some of the strongest evidence for sex differences in human cognition relate to spatial abilities, with men traditionally reported to outperform women. Recently, however, such differences have been shown to be task dependent. Supporting the argument that a critical factor selecting for sex differences in spatial abilities during human evolution is likely to have been the division of labor during the Pleistocene, evidence is accumulating that women excel on tasks

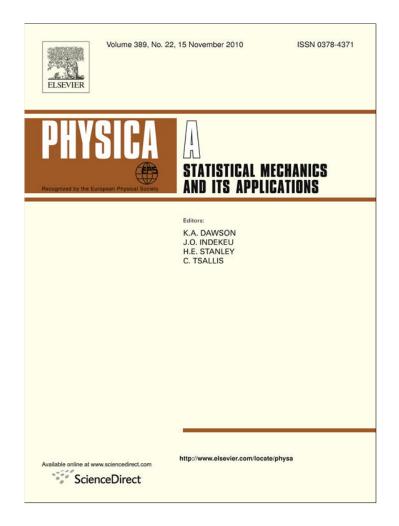
appropriate to gathering immobile plant resources, while men excel on tasks appropriate to hunting mobile, unpredictable prey. Most research, with the exception of some recent experimental field studies, has been conducted in the laboratory, with little information available on how men and women actually forage under natural conditions. In a first study, we GPS-tracked the foraging pathways of 21 pairs of men and women from an indigenous Mexican community searching for mushrooms in a natural environment. Measures of costs, benefits and general search efficiency were analyzed and related to differences between the two sexes in foraging patterns. Although men and women collected similar quantities of mushrooms, men did so at significantly higher cost. They traveled further, to greater altitudes, and had higher mean heart rates and energy expenditure (kcal). They also collected fewer species and visited fewer collection sites. These findings are consistent with arguments in the literature that differences in spatial ability between the sexes are domain dependent, with women performing better and more readily adopting search strategies appropriate to a gathering lifestyle than men.

Citation: Pacheco-Cobos L., Rosetti M., Cuatianquiz C., Hudson R. (2010) Sex differences in mushroom gathering: men expend more energy to obtain equivalent benefits. Evolution and Human Behavior, 31(4), 289-297.

Appendix C

Paper as first author

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An experimental and theoretical model of children's search behavior in relation to target conspicuity and spatial distribution

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ABSTRACT

This work explores search trajectories of children attempting to find targets distributed on a playing field. This task, of ludic nature, was developed to test the effect of conspicuity and spatial distribution of targets on the searcher's performance. The searcher's path was recorded by a Global Positioning System (GPS) device attached to the child's waist. Participants were not rewarded nor their performance rated. Variation in the conspicuity of the targets influenced search performance as expected; cryptic targets resulted in slower searches and longer, more tortuous paths. Extracting the main features of the paths showed that the children: (1) paid little attention to the spatial distribution and at least in the conspicuous condition approximately followed a nearest neighbor pattern of target collection, (2) were strongly influenced by the conspicuity of the targets. We implemented a simple statistical model for the search rules mimicking the children's behavior at the level of individual (coarsened) steps. The model reproduced the main features of the children's paths without the participation of memory or planning.

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1. Introduction

The study and detailed description of search behavior is important to understand how organisms interact with their environment and, more specifically, to infer the decision processes followed during searching [1]. There have been a large number of biological studies illustrating how various species search, in which emphasis is mostly placed on the efficiency of the search strategies (reviewed in Refs. [2–4]). Questions regarding the efficacy of the decisions underlying a search process are hard to formulate in conditions of unknown density and distribution of resources, as is often the case in realistic search settings. Nevertheless, some findings make it possible to attribute an adaptive value to certain decision-making strategies, suggesting in turn the existence of an evolutionary pressure on searching efficiency [5]. For modern humans, searches have in general more relaxed constraints and reduced costs, less severe consequences and a more subjective benefit scale. However, many of the mechanisms that guide our search behavior today may have taken shape during harsher times and therefore might reveal a tendency for efficiency [6].

In certain circumstances human movement appears to exhibit features of a random process, as in the study of the displacements estimated by following the temporal records of the location of paper currency [7] and by tracking cell phone use [8], which revealed a dispersive processes of Lévy characteristics combined with regular visits to the same place. Whether at finer scales the diffusive properties continue to be an accurate description of the process is an interesting question. Indeed, at finer scales one could anticipate that environment features, cognitive components and short-term goals

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can induce systematic behaviors, which would deviate from the simple random processes that apply at large scales. Actually, examples in nature where systematic movements allow animals to increase the probability of finding their target are few but well documented, such as the searching behavior of *Cataglyphis* ants: when lost, these ants move in loops of increasing size and varying orientation, systematically covering the area where there is a greater chance to find the nest [9]. Also, there is abundant documentation on how organisms adjust their searching strategy to local resource conditions, especially density [1,10–12]. Adjusting tortuosity and speed [13–16] or other searching values [17,18] can increase the resource encounter rate, improving the yield of the search.

Here, we studied human search behavior to observe if search paths were constructed through a systematic process sensitive enough to allow adjustment to the underlying resource distribution (e.g. distance between targets), a topic for which there is far less documentation available [19]. The spatial structure reflects the characteristics of the distribution of resources in the physical landscape in which the search takes place, elements that may be used by animals and humans to perform their search [20]. For modern humans it is common to search in environments in which geometric regularities are present. These regularities may be exploited to give structure to a search and are often useful in predicting the location of a given target. We found instead that spatial regularity of the target distribution was largely ignored, or went unnoticed, and that searching appeared to be governed by rather simple rules, influenced by a few physical constraints, such as the arena size.

Due to the inherent problems in obtaining detailed recordings of search behavior, few studies have focused on human movement in dimensions that allow a realistic representation of space and the cognitive processing involved, and the energetic costs of experimental situations usually differ considerably from real life. For example, paths have been recorded for humans searching for a sensor hidden under a carpet, similar to rats searching for a hidden platform in a Morris watermaze [21], or searching for a marble hidden inside one of many film containers distributed on the floor of a room [22]. Such studies, however, require the participants to physically search within areas that are usually rather small, given that they are conducted within the confines of laboratories, and provide little opportunity for spatial strategies that consider the costs of movement to emerge.

Here we describe a simple experimental and statistical model of search behavior based on the paths resulting from a search situation reminiscent of children's games such as the Easter egg hunt, where constraints are few and relaxed, and the rewards are of little value. Furthermore, we used a large outdoor setting and explored the effect of target distribution, and also of target conspicuity on the participants' search performance. To monitor and later analyze participants' search behavior we used the Global Positioning System (GPS) technology that has been successfully applied to the study of human locomotion [23–25]. Finally, we discuss the principal features of the search process, and the role that cognitive aspects might have played.

2. Search experiments

We tested 36 children (18 boys and 18 girls, three boys and three girls in each of the six test conditions described below) aged from 9 to 11 years and attending 5th grade of primary school in Mexico City. We chose children of this age (1) to have participants with a positive attitude towards outdoor activities [26,27], (2) to ensure the task would be understood as a game, thus minimizing the influence of possible speculation about the researchers' motives, and (3) to use an age group with well developed spatial abilities [28]. Search trials were carried out during school hours (9 a.m. to 1 p.m.) with pauses during recess. Fair weather and mild temperatures prevailed throughout the study.

Experiments were carried out on one half of the grass soccer field of the children's school, a rectangle $60 \times 80 \,\mathrm{m}$ ($4800 \,\mathrm{m}^2$) with clearly visible markers at each corner. Twenty golf balls were placed across the test area according either to the same random or to the same regular distribution (Fig. 1(a) and (b), respectively). To avoid effects of human bias, the random distribution was computer generated. The physical placement of balls was aided by chalk marks at 1 m intervals along the arena perimeter, and the consistency of their location across trials was ensured by placing a small marker peg below each ball. Three levels of conspicuity were implemented but only one was used per trial: balls painted green to match the grass represented the cryptic level, unpainted white balls represented a semi-conspicuous level, and unpainted balls plus a 1 m pole with a flag marking their location and visible from every point in the arena represented the maximum conspicuity level (Fig. 1(c)–(e)). The height of the uncut grass covered the whole diameter of the balls, making them difficult to detect from a distance.

Each child was tested individually and brought directly from the classroom to the experimental field by one of the experimenters. To minimize participants communicating their experiences to classmates, children searching under the same experimental conditions were taken from different classrooms. Upon arrival the child was verbally instructed to find and collect in a bag as many balls as possible before a stop was announced by the experimenters. A sample of the target was shown, either a white or a green golf ball, and the role of flags on the field was explained, when appropriate. Children did not know the number of targets nor the eight minute test time. A GPS device (Garmin GPS V) set to record the child's position every second was placed on a belt around the child's waist and activated. The open test area ensured uninterrupted satellite reception. Participants were started at the midpoint of the field's southern short border, and two experimenters positioned at the starting point observed the search and recorded the time each ball was collected. Trials were ended after 8 minutes or when all balls had been collected. The experimental time window was based on pilot studies showing that eight minutes was roughly the minimum time needed for a child to collect all the cryptic targets. In this experiment this was confirmed; in the

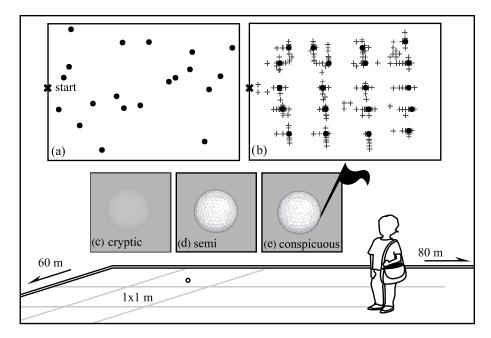


Fig. 1. Summary of the experimental setup showing (a) the random and (b) the regular distribution of the twenty balls (black) and their position as recorded as collection points along the search paths (gray crosses), and (c)–(e) the three levels of the balls' conspicuity.

cryptic condition only one child managed to collect all targets, while in the semi conspicuous condition only one child failed to collect all the targets. Procedures conformed to the guidelines for human research of the Instituto de Investigaciones Biomédicas, Universidad Nacional Autónoma de México, and informed consent was obtained from parents, teachers and school authorities.

Due to inherent fluctuations in the accuracy of the GPS device (0–15 m, 95% C.I. Garmin Reference Manual [29]), there were differences between the path records of each trial and the records of the balls' distribution. We therefore took the position of each ball to be the average of all the children's collection coordinates for that particular ball, resulting in a set of effective target coordinates that sometimes fell somewhat away from particular paths (0–6.9 m, 95% C.I., e.g. Fig. 1(b)).

To quantify searching we calculated the following descriptors: *total time spent* and *distance traveled*, which are indicators of the effort needed to perform the search; for example, for the cryptic targets we expected longer searches. These descriptors provide a transparent way to establish differences in the cost of the search process. *Efficiency*, calculated as the distance traveled over the number of targets collected, which provides an estimate of the cost per target collected. *Total path self-crosses*, which is a gross estimator of performance; searchers who rarely cross their own path make better use of their effort. *A straightness index* (linear distance between collection points divided by actual distance traveled by the searcher between those points) which provides an indicator of the difficulty of the search, and an *optimality index* (linear distances between the actual sequence of collections divided by the linear distances between the shortest sequence of collections calculated by simulated annealing) which relates to the global efficiency of the sequential collections made by the searcher [30,31]. The above descriptors provide indirect information about the economics of decision making during the search process. To estimate search success we also calculated the *collection rate* (balls per min), and *total collections*. The collection rate reflects search efficiency, whereas the total number of balls collected gives a global success measure.

To reduce inherent error in the GPS recording of search paths and to help identify possible patterns, path records were coarsened [32,33]. For this, path segments with small turning angles were combined into one step by increasing the width around the line segments (Fig. 2(a)–(c)) so that only main changes of direction remained. The coarsening width (3 m) used was equivalent to the mean variance in individual collection records resulting from the fluctuations in the GPS accuracy, as mentioned above.

Descriptor values across conditions were compared using the Matlab[®] statistical toolbox (Mathworks Inc. 2008). As most of the children's data were not normally distributed (Lilliefors test for normality [34]) we have used non-parametric statistical tests throughout. Descriptor values were compared across the six conditions using Kruskal–Wallis tests [35] followed by a *post hoc* multiple comparison procedure with the Bonferroni correction [36]. Performance scores between the regular and random target distributions within each conspicuity condition were further compared using Mann–Whitney tests [35]. As no difference was found on any measure between boys and girls, their data have been combined.

2.1. Path analysis of children's search

Visual inspection of the coarsened paths suggested that the children walked in essentially straight lines across the arena (e.g. Fig. 2(d) and (e)), and that the factors accounting for the few changes in direction were (perhaps obviously) the arena boundaries or the detection of a nearby ball and its subsequent collection. Some spontaneous turns not associated with

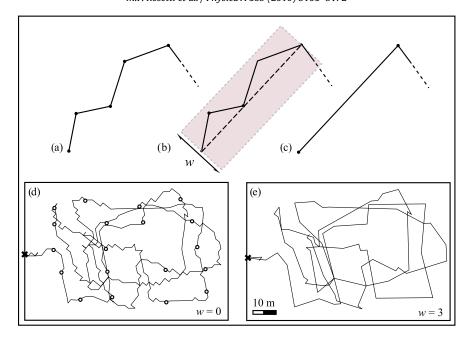


Fig. 2. Path coarsening. (a) An original path, where several segments move in the same general direction. (b) A rectangle of width (w) is then drawn (dotted line) from the first to every successive segment until one segment within the sequence falls outside the rectangle's area. The immediately previous interval is merged to form a single step (dashed line). (c) The coarsened path displays in general longer step lengths and sharper turning angles. Example showing the difference between (d) an uncoarsened path (regular distribution of cryptic balls) and (e) the same path after the coarsening procedure. The irregularity in the distribution of balls is due to the intrinsic error in the GPS recording of positions.

collections or collisions were also observed. However, the number of such turns decreased dramatically with the coarsening width, suggesting that they might contribute to the structure of search paths at fine spatiotemporal scales. Unfortunately, the resolution of our data was not adequate to explore such fine scale structures.

The distributions of turning angles for both coarsened and uncoarsened paths are shown in Fig. 3. While the turning angle distribution for the uncoarsened paths appeared to show some degree of persistence, i.e. a tendency to take steps roughly in the direction of the previous step, the details fall below our spatial resolution. After coarsening, all the turning angle distributions flattened considerably, as expected.

Search performance varied slightly for some descriptors between the random and regular distribution of the targets (significance p < 0.05, Mann–Whitney test, but p > 0.05, multiple comparisons), but the direction of difference was not consistent across descriptors and the degree of difference was generally not strong. On the other hand, performance descriptors varied consistently with conspicuity, with significant differences found mainly between the cryptic and the conspicuous conditions (Fig. 4).

In general, the lower the conspicuity of the targets, the longer the search paths (Fig. 4(a)), the more time spent searching (Fig. 4(b)), and the lower the efficiency of the searching process (Fig. 4(c)). Furthermore, participants crossed their own path more often (Fig. 4(d)) and had more tortuous paths (Fig. 4(e)) when searching for cryptic targets. Nevertheless, in all conditions the sequence of collections resulted in an optimality index of 0.6 or larger (Fig. 4(f)). Finally, children collected fewer cryptic balls per minute (Fig. 4(g)) and often failed to collect all the balls (Fig. 4(h)). The percentage of times that participants collected the closest ball ranged from 50% in the random cryptic condition to 70% in the regular conspicuous condition, showing that the paths departed from a nearest neighbor search.

3. The bouncing search model

To model children's search behavior a numerical simulation was implemented applying the following simple search rules: agents move in straight lines until they collide with a boundary or detect a target. After boundary detection or collection of the target, a new direction is assigned randomly from a uniform angular distribution, with the restriction that agents do not leave the arena ("bouncing"; Fig. 5(a)). Target conspicuity is represented in the model by a circle (of radius r_d) that allows detection of the target located at its center (Fig. 5(b)). Intersection of the circle's perimeter by the agent's path will result in target collection. To simplify calculation, when a collection occurs the path is redefined as the straight line between the previous bouncing point and the center of the detection circle. Collected targets are removed from the target array. If several detection circles are intersected by the agent's path, only the closest target is assumed to be collected, and information about other targets is discarded. Thus, as the simplest implementation of the process, the model assumes no memory or learning for the search strategy.

A total of 10,000 simulated paths were calculated for each r_d from 1 to 70 m in 1 m intervals. Arena dimensions, target distributions and test time were the same as in the field experiment. Search times were calculated from distance traveled, assuming a constant speed of v = 1.7 m/s, corresponding to the slowest mean velocity among the different conditions.

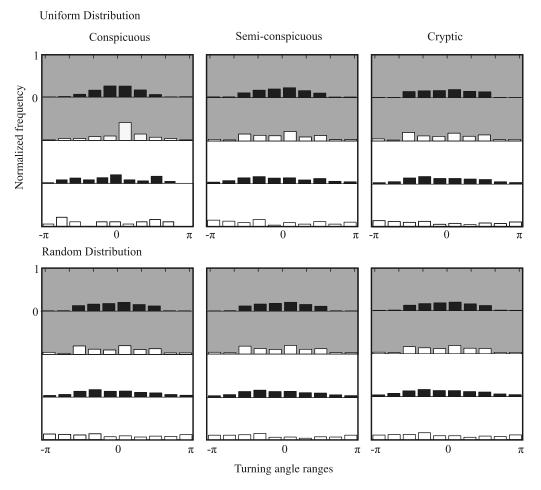


Fig. 3. Normalized turning angle distribution for both uncoarsened (gray background) and coarsened paths (white background). Histograms show the distribution of internal turning angles (black bars) and the distribution of turns occurring within 3 m of the boundary (white bars).

3.1. Path analysis of the bouncing search model

The model exhibited a clear monotonic relation between the r_d values and the distance traveled, the first descriptor chosen for comparison with the experimental data (Fig. 6). In these curves, three broad regions could be identified: a region with $r_d=1$ –5 m, characterized by paths commonly composed of uninterrupted steps, and trials that finished before all targets were collected. A second region with $r_d=6$ –12 m, where small changes in r_d resulted in rapid shortening of the search paths and collection of all targets. And a third region with $r_d>12$ m, where the distance traveled reached a plateau as every step resulted in an intersection with a circle of detection and the collection of all targets in a nearest neighbor pattern. The model proved to be robust; for example, assuming a probability of collecting a detected target or considering a small rate of making spontaneous turns without intersecting a boundary or a circle of detection, resulted in qualitatively similar curves to the ones obtained using the simple bouncing search model. In the latter case, departures from the model's behavior are expected to occur when the distance between spontaneous turns becomes comparable with the length scales in the system.

4. Comparison between the model and the children's behavior

To compare the model's results with the children's search behavior, we took what could be considered the main descriptor of search behavior, the total distance traveled. It was possible to estimate each child's r_d value by matching its distance to the nearest value on the curve produced by the model (Fig. 6). This allowed us to estimate the mean r_d for each of the six experimental conditions, giving r_d 's of 3–8 m for the cryptic condition and an r_d 's of 12–36 m for the conspicuous condition. However, variation in the r_d 's obtained from the matching process for different participants suggested that conspicuity was not only a property of the experimental conditions, but also arose from individual differences among the searchers, such as height, visual acuity or vigilance (cf. Fig. 6).

In order to compare the search behavior of the children and the model, we calculated a subset of the descriptors for the model using pooled r_d values for which the total distance traveled matched the corresponding child's value for each experimental condition (Fig. 7; cf. Fig. 4). The overlap of values that the pooled r_d 's yielded is consistent with the descriptors

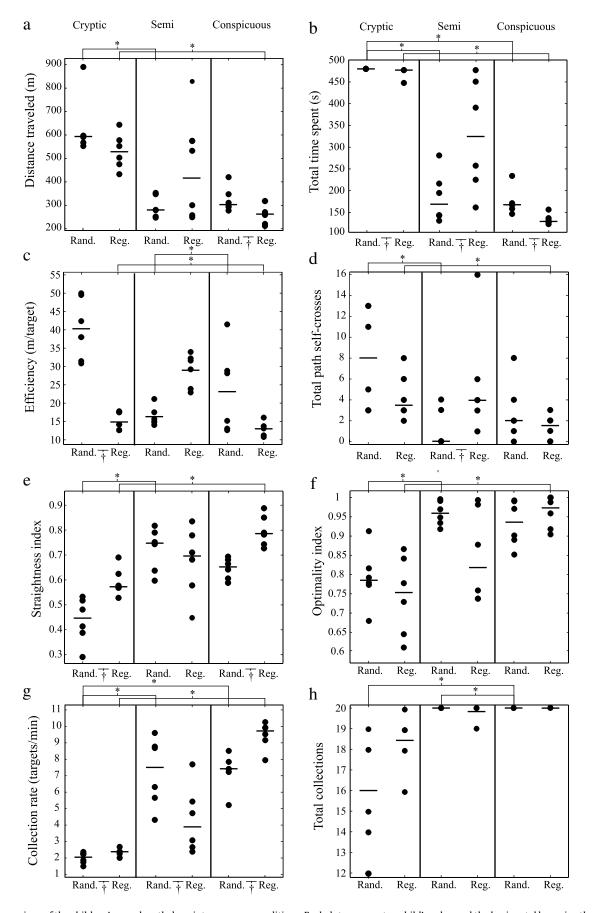


Fig. 4. Comparison of the children's search path descriptors among conditions. Each dot represents a child's value and the horizontal bars give the medians. All conditions were compared: * above columns for multiple comparisons, † below columns for Mann–Whitney U tests, p < 0.05 (see text for explanation of statistical tests).

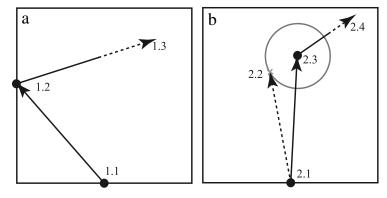


Fig. 5. Main features of the bouncing search model. (a) The agent moves in a straight line until intersecting a boundary (1.2), that produces an effective step between the last previous position (1.1) and the collision point (1.2), after which a new angle is randomly chosen (1.3). (b) The agent moves in a straight line until intersecting a circle of detection (2.2), producing an effective step between the previous position (2.1) and the collection point (2.3), after which a new angle is again randomly chosen (2.4).

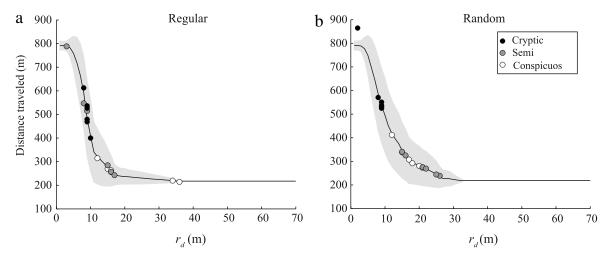


Fig. 6. Matching of the experimental and model data. The continuous line represents the mean distance traveled (gray area s.d.) produced by the model, and each circle represents data from an individual participant in the corresponding experimental condition. The mean distance traveled by each participant was used to estimate an r_d value by matching it to the closest position on the curve generated by the model.

of the children's search paths, though there were a few instances in which single children's path descriptors fell slightly outside the range predicted by the model.

5. Discussion

We implemented in a simple behavioral model what we identified as the constitutive events of the search process performed by the children, namely movement in straight lines with turns in random directions when close to the field boundaries or at collection points. We stress that the model was designed to mimic what appeared to be the individual events that gave rise to the search path, without recourse to memory or to other cognitive processes. A more detailed model could be implemented by including small departures from this coarse behavior at small length scales. In spite of its simplicity, the resulting displacement process is intrinsically non-Markovian (due to the collecting of targets), and thus not amenable to analysis using the usual tools of random walk theory. Further, while designed to reproduce the behavior of the children at the level of individual events, the model was tested by comparing the descriptors of complete search paths generated by the model with those for the paths followed by the children. We found that these *global* descriptors already matched satisfactorily.

The children's paths suggest that they made little use, if at all, of the underlying spatial distributions of targets to orient themselves. On the other hand, the manipulation of conspicuity yielded the expected effects, given that searching in the conspicuous conditions resulted in movement in essentially straight lines along the flags, while the cryptic conditions provided a searching challenge reflected by longer paths, longer search times and lower collection rates. It was notable that most targets were collected in sequences with an optimality index above 0.6, even in the more difficult experimental conditions, possibly by using essentially the same searching behavior, consisting mainly of locomotion in essentially straight lines combined with deflections from the boundary or to pick up balls. Our data resolution does not allow an accurate account of departures from this behavior at finer length scales. Nevertheless, mechanisms operating at finer scales might exist, which

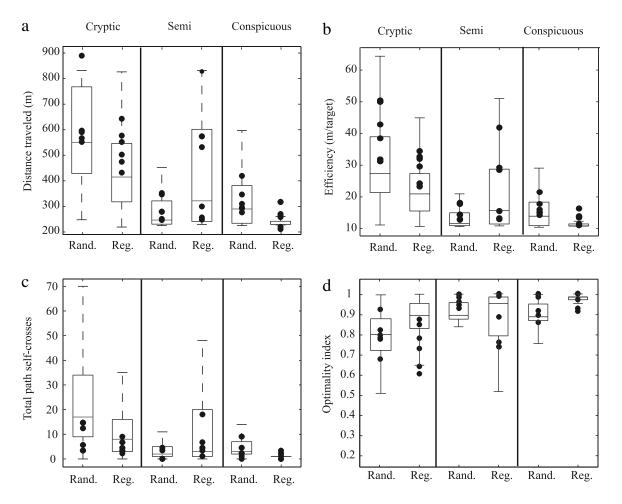


Fig. 7. Box plots of path descriptors generated by the model for the pooled r'_ds corresponding to the children's matches of distance traveled (shown in Fig. 6); horizontal bars give the median, horizontal borders of the box give the 25th and 75th percentiles, and the whiskers extend to the most extreme data points. Each black dot represents the score of a child for that particular descriptor. Given the inner workings of the model, only some of the performance descriptors are comparable to the children's search paths. For clarity, outliers for the model data are not shown.

may increase the efficiency of the search, especially in the cryptic condition. Recording and modeling this fine scale behavior presents an interesting challenge.

The distribution of step lengths suggests an exponential distribution in both the children's and the model's paths within the dimensions set by the strict borders of the search field (Fig. 8). It should be noted, however, that the process cannot be described as a "simple" random walk with exponential distribution of step lengths. The reason for this is that as the search progresses, the target distribution changes as targets are collected, giving rise to a non-Markovian process. Further, it is difficult to use the model to predict how children would search in larger areas without strict boundaries, although it does present a testable hypothesis in which long uninterrupted steps should reflect the dimensions of the search field (a larger search field makes possible longer steps). While it is rare for foraging models to consider environmental boundaries, this is in most cases the search situation in the everyday life of humans, particularly in urban areas where physical boundaries and obstacles commonly define the areas we search in.

The children did not appear to detect the structure of the systematic regular distributions. A possible reason for this could be that the regular properties of these distributions were modified by the collection events, making the identification of the original structure difficult. An interesting modification could be to consider "patchy" distributions, where after visiting various patches subjects might detect a pattern and upon finding a target, search for others nearby. Unfortunately, patchy distributions were explicitly discarded as an experimental possibility in the present study because adequate patches could not be placed without overlap in the arena we had at our disposal.

The findings suggest that, at least in the current scenario, children may instead have mainly used the presence of boundaries or the visual detection of targets to turn while searching. Often, the places we search in are bounded spaces (e.g. parking lots, libraries, supermarkets) and contain information regarding the location of targets (e.g. codes on library shelves or in parking lots) that could make it less necessary to "bounce" around the search space before reaching the target. Still, the bouncing strategy appears to be a cheap, simple rule of thumb that does not require that we read signs, memorize codes or construct spatial maps, and requires little or no information to function in unknown environments [37]. Future work could focus on the information acquired during the search, for instance by asking the participants to draw a map of

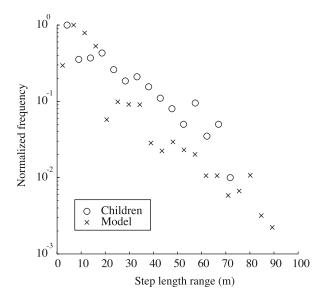


Fig. 8. Semi-log plot of the normalized frequency of step lengths for the model and children's search paths.

the location of the targets after completing the task to evaluate whether they are able to detect the shape of the underlying distribution through the collection of targets.

In conclusion, the behavioral experiment and model described here should be useful for investigating social and cognitive processes in a variety of contexts. Even the very simple model employed here proved useful for mimicking basic aspects of the children's paths. Increasing the model's complexity should help identify the effect of additional factors contributing to search behavior under more challenging conditions. Further, changing the motivational context and/or the age group of the participants in the experiment may help test whether the structure of systematic target distributions can be detected during the search. Although only a first step, the present study already suggests that at least basic features of children's search behavior can be simulated using very simple decision rules.

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Appendix D

Children's search paths

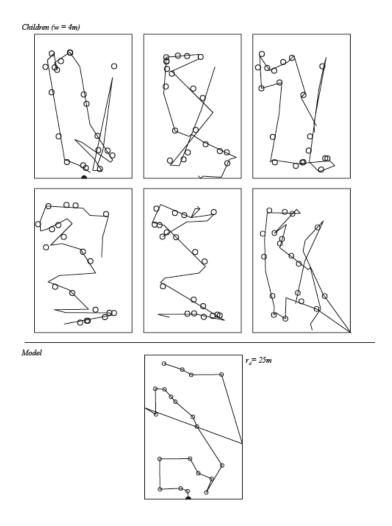


Figure 6.6: **Random distribution, conspicuous targets**. Search paths of children and an example of the a path generated by the bouncing search model. Children paths are coarsened with w = 4m. Starting points (black half dot) and collection points (white circles) are also plotted.

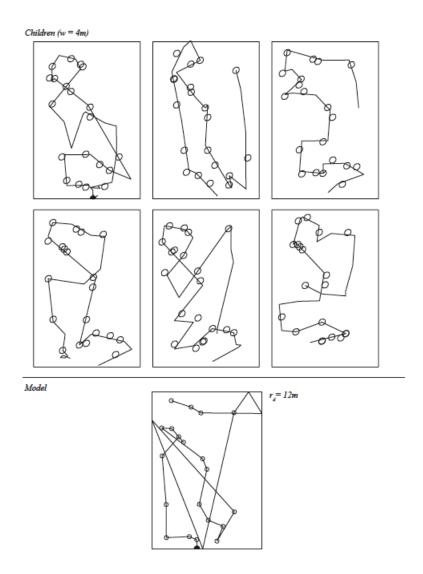


Figure 6.7: **Random distribution, semiconspicuous targets.** Search paths of children and an example of the a path generated by the bouncing search model. Children paths are coarsened with w = 4m. Starting points (black half dot) and collection points (white circles) are also plotted.

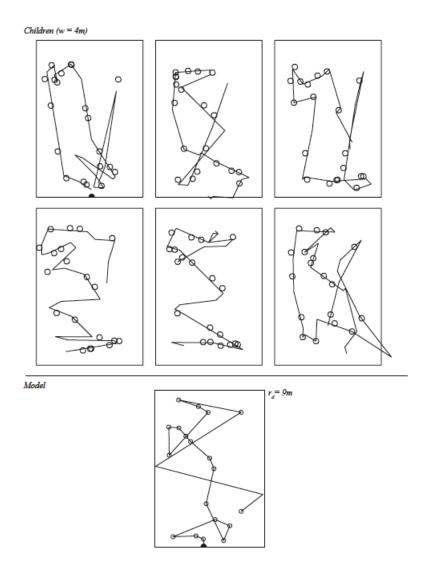


Figure 6.8: **Random distribution, cryptic targets.** Search paths of children and an example of the a path generated by the bouncing search model. Children paths are coarsened with w = 4m. Starting points (black half dot) and collection points (white circles) are also plotted.

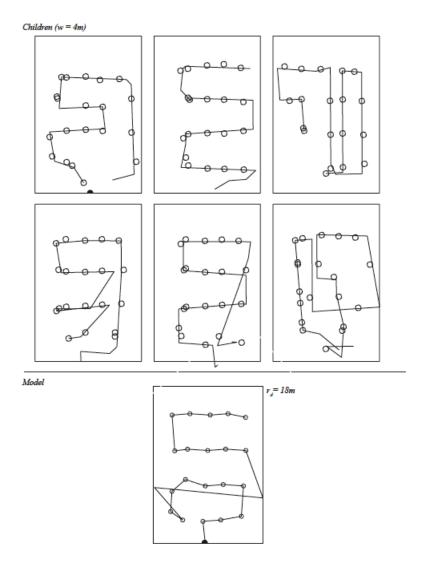


Figure 6.9: **Regular distribution, conspicuous targets.** Search paths of children and an example of the a path generated by the bouncing search model. Children paths are coarsened with w = 4m. Starting points (black half dot) and collection points (white circles) are also plotted.

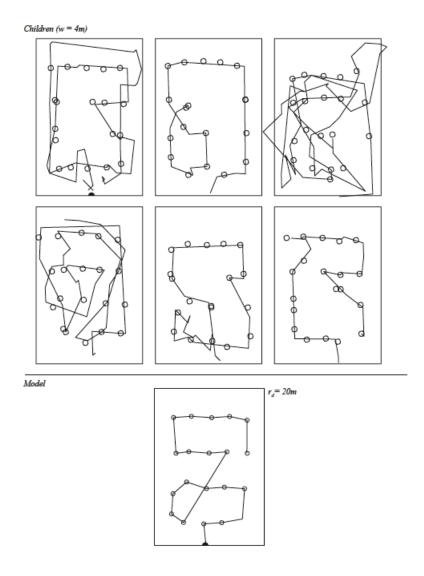


Figure 6.10: **Regular distribution, semiconspicuous targets.**Search paths of children and an example of the a path generated by the bouncing search model. Children paths are coarsened with w = 4m. Starting points (black half dot) and collection points (white circles) are also plotted.

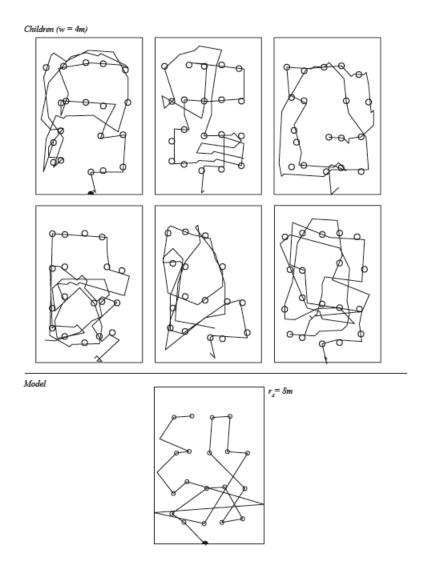


Figure 6.11: **Regular distribution, cryptic targets.** Search paths of children and an example of the a path generated by the bouncing search model. Children paths are coarsened with w = 4m. Starting points (black half dot) and collection points (white circles) are also plotted.

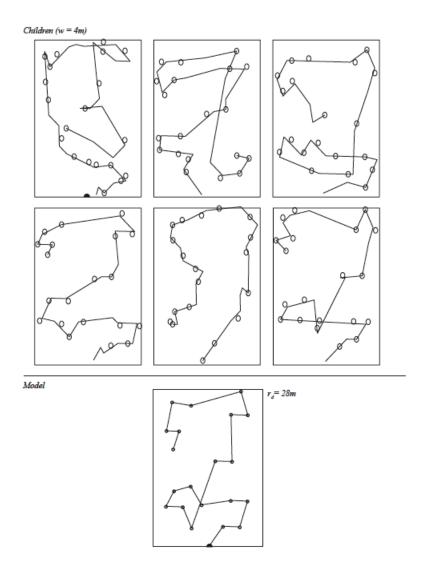


Figure 6.12: Cluster distribution, conspicuous targets. Search paths of children and an example of the a path generated by the bouncing search model. Children paths are coarsened with w = 4m. Starting points (black half dot) and collection points (white circles) are also plotted.

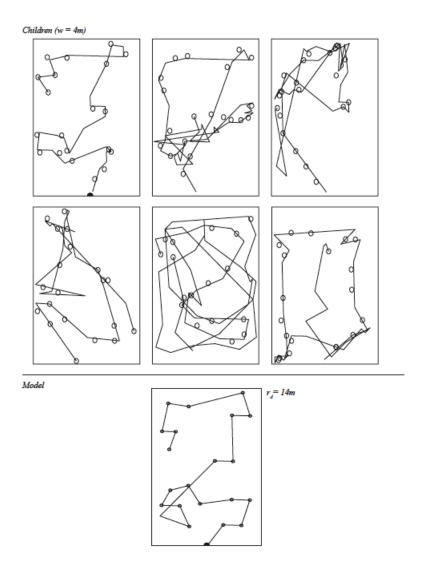


Figure 6.13: **Cluster distribution, semiconspicuous targets.** Search paths of children and an example of the a path generated by the bouncing search model. Children paths are coarsened with w = 4m. Starting points (black half dot) and collection points (white circles) are also plotted.

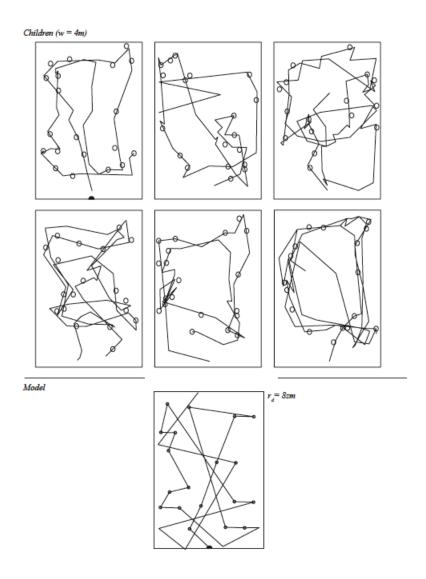


Figure 6.14: **Cluster distribution, cryptic targets.** Search paths of children and an example of the a path generated by the bouncing search model. Children paths are coarsened with w = 4m. Starting points (black half dot) and collection points (white circles) are also plotted.

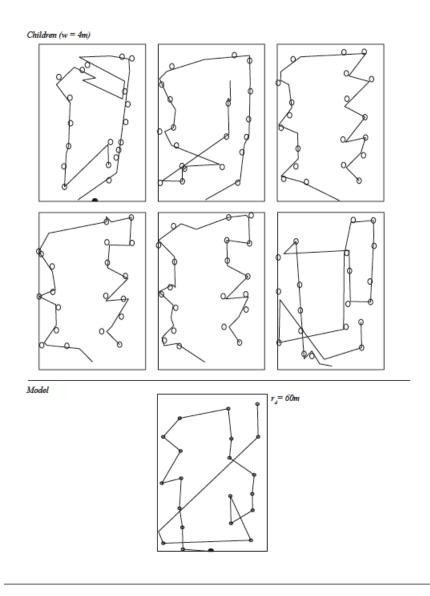


Figure 6.15: Layer distribution, conspicuous targets. Search paths of children and an example of the a path generated by the bouncing search model. Children paths are coarsened with w = 4m. Starting points (black half dot) and collection points (white circles) are also plotted.

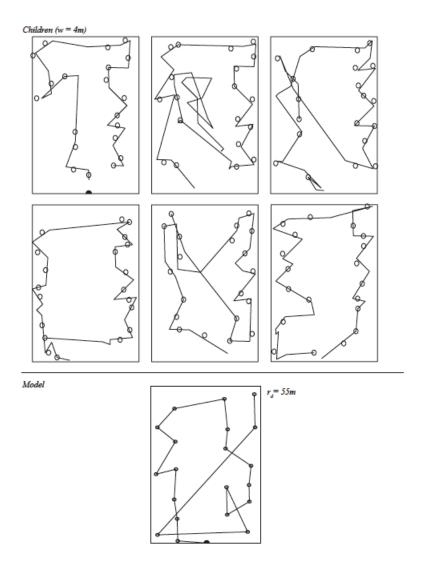


Figure 6.16: **Layer distribution, semiconspicuous targets.** Search paths of children and an example of the a path generated by the bouncing search model. Children paths are coarsened with w = 4m. Starting points (black half dot) and collection points (white circles) are also plotted.

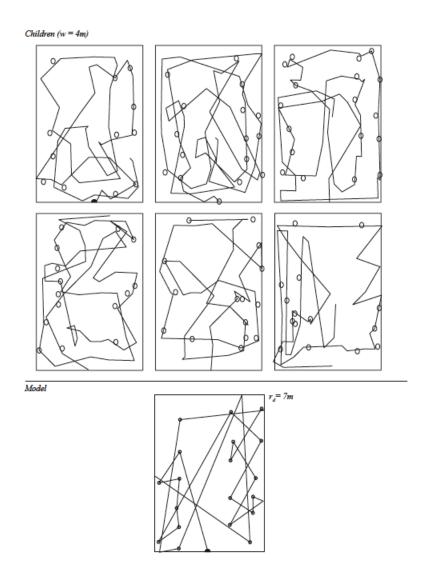


Figure 6.17: **Layer distribution, cryptic targets.** Search paths of children and an example of the a path generated by the bouncing search model. Children paths are coarsened with w = 4m. Starting points (black half dot) and collection points (white circles) are also plotted.