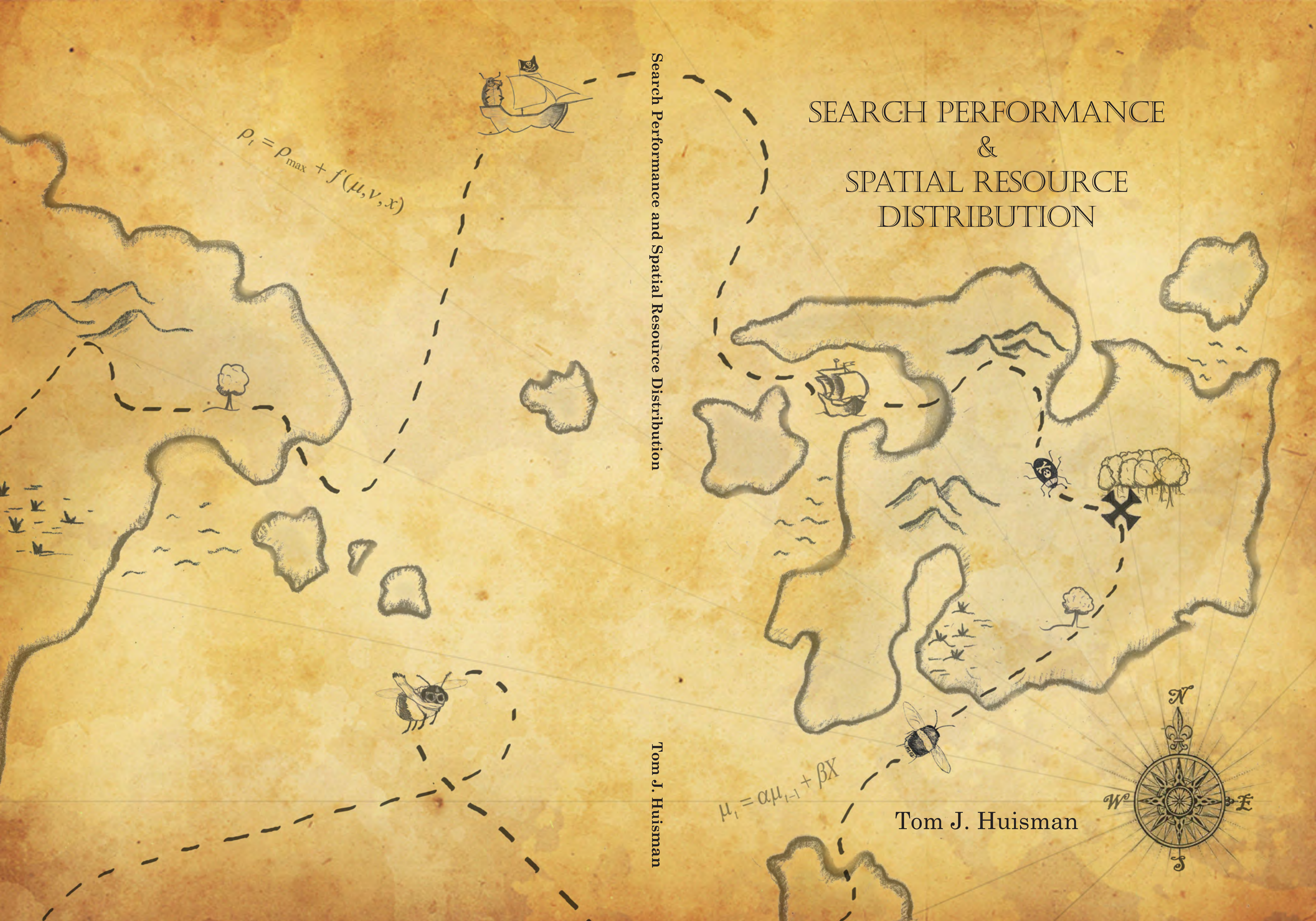

SEARCH PERFORMANCE
&
SPATIAL RESOURCE DISTRIBUTION

Tom J. Huisman

Search Performance and Spatial Resource Distribution

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Search performance and spatial resource distribution

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This research was conducted under the auspices of the C. T. de Wit Graduate School of Production Ecology and Resource Conservation

Search performance and the spatial resource distribution

Tom J. Huisman

Thesis
submitted in fulfilment of the requirements for the degree of doctor
at Wageningen University
by the authority of the Rector Magnificus
Prof. Dr M.J. Kropff,
in the presence of the
Thesis Committee appointed by the Academic Board
to be defended in public
on Tuesday 27 May 2014
at 11 a.m. in the Aula.

Tom J. Huisman
Search performance and the spatial resource distribution,
107 pages.

PhD thesis, Wageningen University, Wageningen, NL (2014)
With references, with summaries in Dutch and English

ISBN 978-94-6173-939-1

This thesis will be made available online through library.wur.nl/.
The cover was designed and illustrated by Atelier Rabbit (atelierrabbit.com

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Chapter 1 General Introduction

1.1 Movement and movement ecology

Animal movement is related to different causes, factors and behaviours. An animal may, for instance, be foraging (Stephens et al 2007; De Knegt et al 2007), provisioning (Ydenberg 2007), dispersing to different habitat or locations (Kot et al 1996), looking for mates (Ring et al 2011) or participating in seasonal migration (Wikelski et al 2003). Most interactions between animals and between animals and their environment involve movement, and through movement the various organisms are connected. In many cases animals have to search for their targets, be they water, twigs, flowers, prey or habitat patches (Ydenberg 2007; Chittka et al 2009). This searching behaviour can be an important part of movement, especially for foraging and searching for habitat during dispersal (Zollner and Lima 1999; Bartumeus et al 2005). Searches are necessary if the distance between targets is larger than the information horizon of the animal (Hengeveld 2007). Where an animal does not have information and needs to perform a search, it has been shown that the animal's movement behaviour or pattern determines the encounter-rate with targets (Bartumeus et al 2005; Zollner and Lima 1999; Viswanathan et al 1999; Benhamou 2007). More effective searches mean less energy expended, less time lost, more food found and consequently the fitness of animals is expected to depend on their search behaviour. The search for specific movement patterns and the continuing development, miniaturization and general availability of (animal) tracking technology has caused the study of movement to take flight (Turchin 1998; Bartumeus et al 2003; Holyoak et al 2008; Schick et al 2008; Giuggioli and Bartumeus 2010). So much so that it is possible to identify a new sub-discipline of movement ecology (Nathan 2008). If ecology is the study of the interactions between organisms and their environment, movement ecology is the study of how movement pertains to these interactions. Within the framework put forward for movement ecology (Nathan et al 2008; Holyoak et al 2008; Schick et al 2008) several more or less distinct approaches to animal movement were identified. These approaches are the cognitive, the optimal, the biomechanical and the random (referred to as paradigms see Nathan et al 2008; see figure 1). Cognitive approaches to animal movement focus on navigation and movement-related decision-making. The optimality approach on the other hand analyzes strategies and situations as an optimization problem. The hypothesis here is that animal behaviour will have come to reflect effective strategies through natural selection (Nathan et al 2008). The biomechanical and random approaches are both based on first principles. In the former case starting from the physical properties of animals and in the latter case starting with the idea of movement itself. The biomechanical approach is by its nature more specific and can provide definitive answers and analyses of animal movement, and is closest related to physics. Excellent examples are the analysis of the movement and wing shape of swifts (Lentink et al 2007) and the role of vertices in the aerodynamics of flies and seeds (Lentink and Dickinson 2009; Lentink et al 2009). Naturally there is a direct link between species traits, their movement, and actual dispersal distances; birds will disperse faster and further than, for instance, mice. Similarly, many parts of movement itself can be understood by looking at mechanics of species. Short term autocorrelations in movement, for instance, are caused by the orientation of legs, leading to an s-shaped, wobbly movement path (Turchin 1998). Such analysis gives specific explanations for movement patterns and behaviour of species. The random search approach, on the other hand, is more general and based on movement itself. Its basis lies in particle physics rather than mechanics. Since random walks play a central role in this thesis I will consider them at length in section 1.2.

Understanding animal movement is important since movement determines dispersal distances and speed, and hence (meta)population dynamics (Turchin 1998; Okubo and Levin 2001; Ovaskainen 2008). It governs the speed at which species may spread into new ranges (invasion biology), the spread of vector-borne diseases and the likelihood of infections. A thorough understanding is therefore crucial in order for ecologists to give sound advice to national health organizations dealing with vector-borne diseases and outbreaks such as the bird-flu or park and conservation management (Turchin 1998; Okubo and Levin 2001; Ovaskainen 2008). One of the main challenges to achieve such understanding is to understand how movement depends on the environment (Nathan et al 2008; Giuggioli and Bartumeus 2010). Furthermore to determine what constitutes likely behaviour and to make reliable predictions it is necessary to have a clear theoretical framework (Gurarie et al 2009; Giuggioli and Bartumeus 2010; Lewis et al 2013).

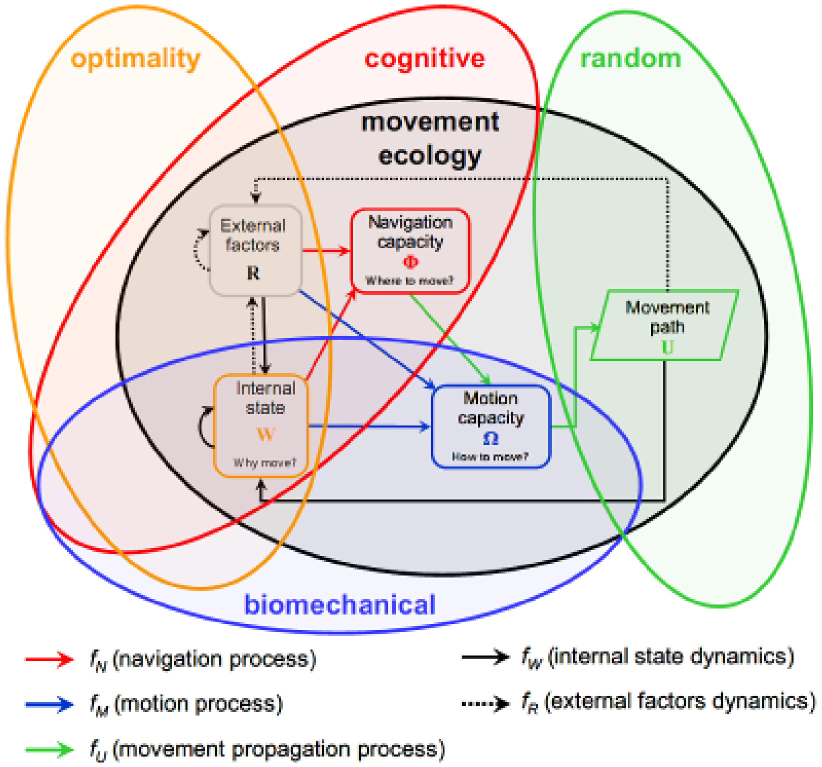

Figure 1. The various approaches in movement ecology as presented by Nathan et al (2008). Four main approaches, the optimality, the cognitive, the random and the biomechanical approach are distinguished.

1.2 Random walks in ecology

Random searches are based on random walks. Random walks are stochastic processes where the location *x(t)* varies with time *t* according to a set of probalistic rules (James et al 2011). Random walks were first used as models for the movement of pollen through collisions with atoms movement by Einstein, (1905) and have been used extensively to model animal movement (Codling et al 2008; Lewis et al 2013). The simplest of such walks, sometimes referred to as 'mere' or 'simple' random walks, result when it is assumed that discrete steps are taken at a fixed time interval, with fixed step length and completely random movement directions. This can be considered the basic random walk model and is used as a model for Brownian motion and diffusion processes (Turchin 1998). One of the advantages of using these random walks as models for movement is that their relative simplicity makes it possible to derive the time evolution of the probability density function of particles and get solutions for the mean squared displacement and invasion speeds (Skellam 1952). On the statistics and predictions derived from random walks and diffusion models much of the general theory on movement in invasion, metapopulation and dispersal biology has been build (Kot et al 1996; Van den Bosch et al 1992; Levin and Okubo 2001). While simple random walk and diffusion models yield valuable insight about the extent to which movement resembles diffusion (Holmes 1993; Turchin 1998) they have limitations. For instance, diffusion models of movement are not good at predicting the expansion speeds and leap-frog dispersal typical of many species (Kot et al 1996). Indeed, the problem is that animals do not behave like atoms and thus dispersal and invasion studies based on this approach lack the correct first principles approach (Hengeveld and Van den Bosch 1996). One clear way in which animal behaviour differs from a simple random walk is that they have some degree of directionality or ‘persistence’, where movement in successive steps is not completely random, but is more or less in the same direction (Patlak 1953; Kareiva and Shigesada 1983; Turchin 1998). This directionality and correlation is partly determined by the time-scale of observation, that is to say, if observations are further apart in time the positive autocorrelation in direction will decrease (Turchin 1998) and indeed at larger scales can be described again with simple random walks. Nevertheless at several spatial scales directionality is a non-trivial part of animal movement. It is possible to include this within random walks by generating a movement path with discrete steps and changing movement direction with a certain turning angle. Instead of moving in random directions at each step, there is correlation between the directions at two consecutive points in time. Such walks are aptly called correlated random walks (Kareiva and Shigesada 1986; Tuchin 1998). Within a correlated random walk model a simple random walk is the special case where the distribution of turning angles is uniform. Movement behaviour of many species has been compared to correlated random walks, and insects, in particular, appear to exhibit this type of behaviour (Skellam 1973; Holmes 1993; Turchin 1998). At larger scales, however, correlated random walk models predict behaviour similar to diffusion models (Holmes 1993; Codling et al 2008). As in the case of simple random walks, the most important discrepancy between predictions based on correlated random walk models and actual movement is that long-distance dispersal is more frequently observed in nature than is accounted for through diffusion-like behaviour. Thus, in models of dispersal in integro-difference and metatopulation models, where dispersal distances are reflected in dispersal kernels (e.g., Ovaskainen 2008), these kernels typically need to be leptokurtic, i.e. have fat tails, compared to diffusion modes, reflecting the higher frequencies of large displacement events (Kot et al 1996).

A way to include directionality while allowing for larger displacements in movement is to change the length of any given step in a random walk, combining directional phases in movement into a single step or ‘move’ (Turchin 1998). The leptokurtic dispersal kernels and long-distance displacement events thus have their counterpart in random walks whose move-lengths have similarly long-tailed distributions. The most common and discussed random walk of this type is the Lévy walk (Shlesinger et al 1987; Viswanathan et al 1999). After the scale-free, fractal Lévy walks were shown to be effective, even optimal, search patterns for certain distributions (Viswanathan et al 1999), a plethora of studies were published with evidence of Lévy walks in nature. Lévy walks were found in the movement of reindeer (Mårell et al 2002; Viswanathan et al 1999), spider monkeys (Ramos-Fernandez et al 2004), grey seals (Austin et al 2004), bees (Reynolds et al 2007) and marine predators (Sims et al 2008). However, there has been a reevaluation of methods and previous reports (e.g. Edwards et al 2007; Sims et al 2007; White et al 2008) and the debate over how common such patterns are still continues (Benhamou 2007; Sims et al 2008; James et al 2011; Reynolds et al 2012; Sims et al 2012). Meanwhile, various ways have been found in which Lévy patterns may originate based on other movement processes (e.g., Reynolds et al 2012).

Random walks are models for movement in ecology for various reasons. Firstly, random walks serve as a basis and benchmark for movement and movement models, since they are directly derived from the basics of movement itself. Furthermore, random searches are expected if animals perform true searches, with no information on the location of targets. Thus random movement models provide predictions and comparisons for observed movement patterns. As noted above, the advantage of random walks is that they can be linked directly to large-scale patterns, with specific predictions about the expected dispersal (Skellam 1952; Patlak 1953; Van den Bosch et al 1992), as movement and movement models become more complex the expected large-scale patterns are not straightforwardly derived (see figure 2). In this thesis I make extensive use of these models to study how animals may be expected to react to spatial heterogeneity in resource distributions.

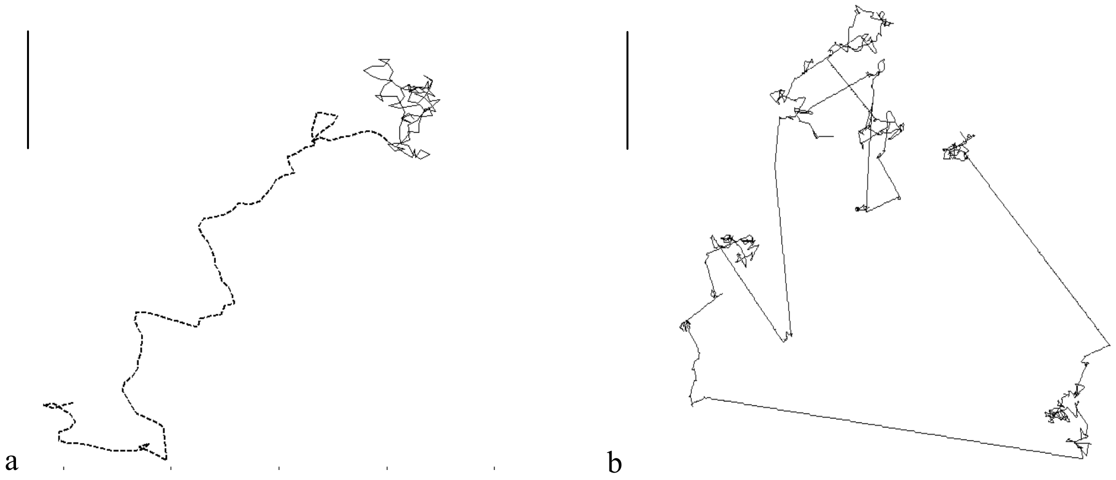

Figure 2. Examples of random walks, (a) a simple random walk (continuous line) and a correlated random walk (striped line) and (b) Lévy walks. The lines in the top left corner have equal length in each panel, showing that Lévy walks show a fractal pattern with similar movement patterns on several spatial scales.

1.3 Environmental heterogeneity and resource distributions

As noted, understanding the interaction between environment and movement is one of the key challenges in movement ecology (Morales and Ellner 2002; Schick et al 2008; Giuggioli and Bartumeus 2010). The environment part of this system includes abiotic factors such as topography (De Knegt et al 2008), as well as biotic factors such as the distribution of food and other resources and is consequently exceedingly complex. Theoretically it may be possible to combine these factors into a suitability-landscape describing the landscape as viewed from the needs of the animal (Hengeveld 1992), but practically a few focal resources such as water, cover or food are chosen as representative of the environment and as subject for study. The distribution of these resources, such as food, can determine dispersal rates, population survival and fertility in general (Hanski, and Simberlof 1996; Begon et al 2006). Generally the availability of food depends on factors such as climate, the food's life-cycle, and activity of other foragers - hence it varies over time (Pyke et al 1977; Prins and Van Langevelde 2008). While many resource distributions are highly aggregated, with items occurring in patches or clusters, others are more randomly distributed or, as in the case of agricultural crops, overdispersed or regular (figure 3). Resource aggregation is a reality for browsers (i.e. thickets and individual trees), grazers (i.e. grazing lawns, De Knegt et al 2007), and carnivorous fish (Sims et al 2007). On the other hand, habitat may be contiguous, such as a savannah or a forest, where, through competition, trees can be spaced out giving a uniform distribution. Indeed whether an animal's range is homogenous is strongly scale dependent and one animal's contigous cover may be another's forest patch. Spatial distributions change over time and space, are species specific, and in many cases hard to determine and harder to manipulate.

Given the importance of resource availability it is necessary to describe and understand the impact of changes in resources, however the mapping and describing of these resources can be difficult, although GIS data has enormously increased the available information (Gurarie et al 2009). Consequently, research trying to understand the influence of spatial structure on movement has focused on mathematical models and simulation in combination with simple experiments (Kareiva and Shigesada 1983; Zollner and Lima 1999; Viswanathan et al 2010; Bartumeus and Giugoli 2011) or natural experiments in the case of habitat destruction. In this thesis several different models are used to represent spatial heterogeneity and aggregation of resources, with the ultimate aim of understanding the influence that variation in these traits has on animal search efficiency.

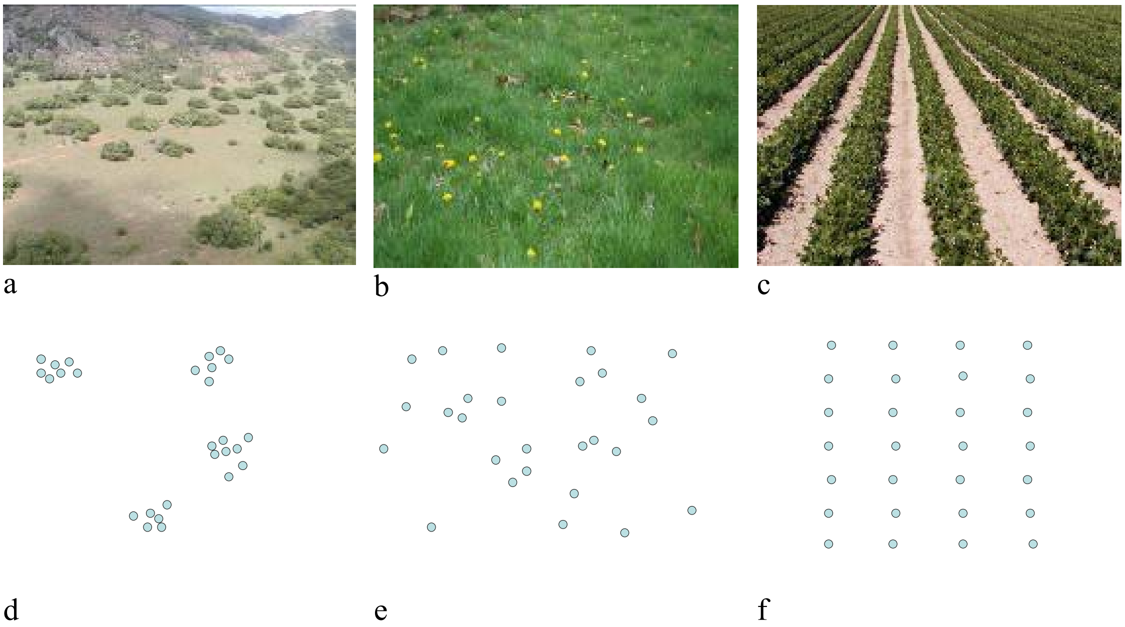

Figure 3. Examples of spatial distributions varying in aggregation (a-c) and examples of spatial distributions and their model representations (d-f).

1.4 Foraging, movement and information use

Foraging theory deals exclusively with animals and their use of resources (Stephens and Krebs 1986) and by its very definition has a significant overlap with the new discipline of movement ecology. Indeed the ‘optimality’ approach in movement ecology is based on the concepts derived from the optimal foraging theory. Interestingly, the classical optimal foraging models (Charnov 1979; Iwasa et al 1981) are, in a certain sense, the opposite to random search models. Whereas in random walks individuals are assumed to have no information, in optimal foraging individuals are assumed to have complete information. In later, more sophisticated models and studies, foraging theory has since dropped the assumption of perfect information and expanded into behavioural and cognitive parts with the ecology of fear, game theory, and community and population dynamics (Stephens et al 2007). Foraging theory now frequently studies available information-use and updating (Stephens 2007; Ollson and Brown 2006). Models of patch and resource exploitation, as used in optimal foraging studies, have thus moved into the study of behaviour. Conversely, random search models are used as the basis for more complex behavioural models, and one of the main challenges is to extend the random search approach to deal with environmental complexity (Nathan et al 2008).

Both foraging theory and random search approaches are concerned with the use of information in dealing with aggregated resources, and their integration is a logical step forwards for both fields. As a step in that direction in this thesis random walk models are combined with information use models and resource distribution models that were used and developed in foraging theory.

1.5 Focus and thesis outline

In this thesis the central focus is on movement and more specifically the interplay between resource distribution and random or informed searches. The aim is to understand how variation and changes in the spatial resource distribution affect the performance of searches, and subsequently from this understanding derive expectations and hypotheses to test in experimental settings. In Chapter 2 I determine if and how variation in density and aggregation of resources determines search effectiveness of random searches. While the effect of density on search efficiency is well known (Koopman 1980; Bartumeus et al 2005; Hengeveld 2007), aggregation has so far not been studied in detail. Work on Lévy walk performance with varying regrowth rates (Raposo et al 2003) indicates that local resource density, and aggregation, is likely to affect search effectiveness. This chapter represents the first study varying both density and aggregation, enabling us to understand the interaction between the effects of these two key properties of the resource distribution.

In the third chapter the influence of another form of heterogeneity in resource abundance is considered. Previous work has considered patches to be interchangeable, that is to say, it was assumed that they all have either identical delay times (Viswanathan et al 1999; Raposo et al 2003; Bartumeus et al 2005; Hengeveld 2007) or identical numbers of local targets (Zollner and Lima 1999). There is, however, a significant amount of variation in the number of resources in patches (patch size) in nature (e.g., Prins and Van Langevelde 2008). This variation in patch size has previously been considered in optimal foraging theory by e.g. Iwasa and coworkers, who demonstrated that optimal use of patches requires different departure rules (Iwasa et al 1981). Using their approach to model variation in local resources I study how the effectiveness of random searches depends on such variation in patch size in terms of variance and skewness.

Having shown (Chapters 2 and 3) that effectiveness of random searches depends on resource distribution in terms of density and aggregation as well as in variation in patch-size, in the fourth chapter the focus shifts to the resource-searcher interaction. The model used to study this resource-searcher interaction constitutes a link between, and combination of, classical movement models (correlated random walks) and a classical information-use model from foraging theory (McNamara and Houston 1987). Here the central question is if optimal information use, or information updating, changes with variation in the resource distribution or whether a single type of behaviour may be optimal.

The fifth chapter is a report of experiments done on the movement behaviour of a carabid beetle (*Peucilus versicolor*) in resource distributions varying in aggregation and density. The hypothesis is that the carabid beetles will perform searches corresponding to optimal behaviour, thus showing correlated random walks in random distributions, while showing more area-restricted search or composite random walk type behaviour when resources are aggregated. The alternative hypothesis is that carabid beetles will have hard-wired behaviour, making movement independent from the resource distribution.

Finally, in the sixth chapter I review and synthesize the preceding chapters and link them to current and likely future developments in movement ecology. Based on the work in this thesis I emphasize that for movement ecology to build on the availability of data and go beyond species-specific analyses, it is necessary to study resource aggregation, and use models that incorporate the resource distribution (density and aggregation) and environment. In the development of such models I am convinced that the study of animal movement will converge with foraging theory and behavioural approaches, combining into an understanding of an animals' life from birth to inescapable death.

Chapter 2 Interactive effects of resource aggregation and density on search performance of Lévy, correlated random and composite random walks

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Submitted for publication

Abstract

So far, the performance of random walks has been analysed under varying resource densities, but a systematic analysis of the effect of variation in resource aggregation is lacking. To address this we simulated searches by three basic random search strategies: correlated random, composite random and Lévy walks. Our results show search performance is determined by resource density, resource aggregation, and the interaction between them. Random distributions favor correlated random walks with high directionality, but as resource aggregation increases the optimal random search strategy becomes a Lévy walk, and at highest resource aggregation levels a composite random walk becomes optimal. This means that there is no single optimal random search independent from the environment. This fact may provide an explanation for the variety of observed movement patterns, and the contradicting evidence for species ‘doing the Lévy walk’ may be explained by the limiting optimality of Lévy walks to specific levels of density and aggregation. We conclude that in order to understand which random search strategies are optimal for animals, it is necessary to consider both resource aggregation and density.

2.1 Introduction

An animal’s dispersal, foraging and mating success is to an important degree determined by its movement (Turchin 1998). Consequently, where, how and why an animal moves are topical questions in ecology (Turchin 1998, Okubo and Levin 2001). In recent years a wealth of data has become available on the movement patterns of a wide array of species

(Getz and Saltz 2008; Giuggioli and Bartumeus 2010). In tandem with this increase in available data, there has been an increase in studies dealing with various aspects of animal movement, such as those dealing with more sophisticated analysis of movement paths (Dalziel et al 2008; Edwards 2008, Gurarie et al 2009) and the search efficiency of random searches (Bartumeus et al 2005; Benhamou 2007) leading to the development of what is now called movement ecology (Nathan et al 2008; Giuggioli and Bartumeus 2010; Lewis et al 2013).

Random search behaviour is expected when no information is used or available to the searcher. This behaviour is modelled using random walk models taken from particle physics (Turchin 1998). Of these random walks, Lévy walks in particular have received considerable attention, as they can describe disparate movement patterns using a single shape parameter, and show scale-free patterns (Viswanathan et al 1999, Edwards et al 2007, Reynolds and Rhodes 2009). The movement patterns observed in field studies sometimes fit these patterns derived from theoretical expectations (Osborne et al 2000; Sims et al 2007), but in many cases the fit has been poor or lacking (Edwards et al 2007) which has ascribed to poor methods, sampling frequencies and behavioural changes (Gurarie et al 2009; Lewis et al 2013). There has been considerable debate whether organisms perform Lévy walks, and composite random walks (also called multi-scaled as well as combined random walks; e.g. Gautestad and Mysterud 2005) have been proposed as a more appropriate model for animal movement (Benhamou 2007). The composite random walk model describes an animal that combines short-term, local movements with less frequent but more far-ranging displacement (Gautestad and Mysterud 2005). Although Lévy walks were expected because they were found to be optimal in finding aggregated resources (Viswanathan et al 1999), composite random walks are able to outperform both Lévy and correlated random walks in finding resources (Benhamou 2007). One of the factors known to influence search efficiency, and optimality, of different random walks is resource density. Specifically, the efficiency edge of Lévy walks is present only in low density distributions (Bartumeus et al 2005). A recent study indicated that resource aggregation influences the efficiency of searches with longer and more ‘intensive’ or ‘extensive’ searches (Scharf et al 2009), but the interactive effect of resource density and aggregation on the search efficiency of Lévy, composite and correlated random walks has not been systematically investigated. This is surprising given the number of studies using random search strategies (Viswanathan et al 1999, Sims et al 2007, Holyoak et al 2008) and the fact that patchy resource distributions are ubiquitous (Prins and Van Langevelde 2008). In this paper therefore, we study the effect of resource density, resource aggregation and their interaction on search performance of random walks. To this end we simulate animals performing correlated random walks, Lévy walks and composite random walks searching for resources in distributions which vary both in density and aggregation.

Based on previous work (Bartumeus et al 2005, Benhamou 2007; Scharf et al 2009) we expect random walks to differ in their response to changes in resource density and aggregation. Aggregation is known to adversely affect the efficiency of correlated random walks (Bartumeus et al 2005). Consequently, a decrease in search efficiency is expected with increasing aggregation. Lévy walks and composite random walks, on the other hand, given their optimality in some aggregated and fractal resource distributions (Viswanathan et al 1999; Benhamou 2007), are expected to be efficient at least at several degrees of aggregation. Increases in resource density favour displacement or relocation behaviour, since the benefit of leaving the current resource grows with the augmented proximity of neighbouring resources. This thus leads to an increased effectiveness of high directionality correlated random walks and composite random walks with high displacement frequencies. So while Lévy and composite random walks are efficient at finding aggregated resources (Bartumeus et al 2005; Benhamou 2007) and correlated random walks in high density or random distributions, it is uncertain how the various searches compare at low or intermediate degrees of aggregation and density.

2.2 Methods

Searching Strategies

Searches are simulated in discrete time and in a continuous two dimensional space spanning 100x100 spatial units (SUs). We use torus boundaries, where an exit on one side means entrance on the other. Movement speed is assumed to be constant, so that a searcher moves one SU at each time step. Correlated random walks are modelled by drawing turning angle values from a wrapped Cauchy distribution (WCD) (Bartumeus et al 2005). These correlated random walk can be described by one parameter, ρ, which determines the directionality of the movement.

As opposed to correlated random walks, the movement direction before and after a change in direction is uncorrelated in Lévy walks. They derive their characteristic movement pattern from the distribution of move lengths, given by the Lévy distribution. We use the common approximation (Viswanathan et al 1999, Bartumeus et al 2005):

$$P(l) = l(0) \cdot l^{-\mu} \tag{1}$$

where $P(l)$ is the distribution of move lengths, $l(0)$ is the minimum step length and μ is the shape parameter. As in previous models (e.g. Viswanathan et al 1999) a move is stopped upon encounter with resources, and a new move length is drawn after resource consumption, which usually triggers a local search.

Composite random walks are random walks whose move lengths are drawn from different distributions (Benhamou 2007). Here, a simple two-level composite random walk is used with move lengths drawn from single values, being either 1 or 100 SU (Benhamou 2007) with respective probabilities of Z_1 and $Z_2=1-Z_1$. This represents a very basic local search or displacement strategy similar to the 'intensive' and 'extensive' search modes as used by Scharf et al (2009). For reasons of simplicity we limited the composite random walk to two step sizes to vary the proportion of area-intensive search to area-extensive search with one parameter. Similar to Lévy walks the composite random walks respond to resources by consuming the resource and drawing a new move length, thus a local search can start upon resource encounter.

Resource Distribution: Aggregation and Density

In theoretical studies used to study the efficiency of Lévy walks (Raposo et al 2003), resources are modelled through regrowing resource points (at least in non-depletion searches) to keep overall density constant. In this model the delay time determines the relative richness of the local resource and the optimality of Lévy searches is shown to be dependent on this delay time (Raposo et al 2003).

To explicitly include the additional moment (i.e. aggregation) of the spatial distribution of resources we model patches as aggregations of resource points (see also Zollner and Lima. 1999). Regrowth of the resource still occurs however, but at time scales (100 time steps) that allow temporary local depletion and longer term regeneration. Upon rediscovery of the aggregation it will have regenerated.

To model distributions with differing degrees of aggregation, centres are first placed randomly, and subsequently resource points are placed around them. The location of resource points around a seeding centre is created by randomly selecting x and y coordinates within a circle defined by a radius. Using this method there are two ways to control the degree of aggregation. The first is to change the radius within which resource points are seeded. The second is to change the number of resource points while keeping the radii constant. Since changing the number of resource points per aggregation would introduce differences in the amount of resource points per aggregation alongside increasing aggregation itself, we changed the degree of aggregation by changing the seeding radius.

Resource density is varied in a range from 0.001 to 0.101, which would in random distributions result in mean free paths ranging from 5 to 5 x 10^2. Resource clusters have a set number of resource points, so increases in density are modelled by increased numbers of resource clusters.

Quantitative measures of aggregation

A large number of methods have been used to detect and describe spatial structures or patterns (Dale et al 2002). Here we use variance:mean ratios to describe aggregation, mainly for their general familiarity within ecology. The variance:mean ratio is based on the fact that for a Poisson distribution the variance equals the mean. Therefore, a distribution created by a Poisson process, creating a random distribution of resource points, should have a variance:mean ratio of approximately 1. Higher variance:mean ratios are indicative of more aggregated distributions.

Searching efficiency

The detection rate of a searcher moving in a straight line in a random distribution is a linear function of resource density. The expected number of encounters is this detection rate multiplied by the search time (Koopman 1979; Hilborn and Mangel 1997) and is used to calculate an index for search performance (Bartumeus et al 2005). This search efficiency can be used to compare the performance of searches in distributions with widely varying densities, as it corrects for the effects of differences in resource densities.

Search parameter values

Each movement algorithm is simulated at different values of its respective parameter. Correlated random walks are simulated with ρ-values of 0.5, 0.8, 0.9 and 0.99 (figure 1). Brownian search is included as a special case with ρ=0.

Reported results on Lévy walks indicate μ-values between 1.4-2.7 (Edwards et al 2007; Sims et al 2007), which covers a variety of movement patterns. Here we simulate Lévy walks with μ-values of 1.3, 1.6, 2, 2.4 and 2.9.

Composite random walks can be modified using the relative frequency of their respective step sizes and by changing the move lengths that can be drawn, i.e. the size-distribution. We simulated the smallest step size at 1 SU, being the minimum spatial step size of the Lévy and correlated random walks, and the longest at 100 SU (Benhamou 2007). The parameter that is varied is the relative frequency of the two movement steps. The range is Z_1=0.99, 0.9, 0.8 and 0.5. At a frequency of 0.5 the dominating aspect is constant relocation and area-restricted searches rarely occur and are short, whereas area-restricted searches are dominant at Z_1=0.99.

2.3 Results

The number of encounters of a search increased approximately linearly with density (figure 1a-c). We found that this increase was, however, strongly dependent on the interaction with aggregation (figure 1). Furthermore, the encounter rate was also determined by the parameter values of each of the strategies.

The encounter rate of correlated random walks decreased with increasing aggregation at all densities (figure 1a). This is true irrespective of the value of the movement parameter ρ. We found that the correlated random searches with higher search performance at high resource density had a relatively larger decrease in their encounter rates as aggregation increased, whereas the already relatively inefficient searches with low encounter rates at low resource densities were minimally affected by the level of aggregation (figure 1a). Furthermore, as figure 1a shows, the resource density x aggregation interaction effect constitutes an important part of the total variation in encounter rates.

Rather than the general decline in efficiency for correlated random walks, the influence of aggregation on Lévy walk encounter rates varied for different μ-values and resource densities (figure 1b). Specifically, Lévy walks with parameter values of μ=1.6 and μ=2 increased in efficiency at moderate aggregation levels at low density (<0.001 resources SU^{-2}). At higher resource densities, all Lévy walks (i.e., irrespective of parameter values) were negatively affected by an increase in aggregation level, similar to correlated random walks.

Composite random walk search performance was also influenced by aggregation, density and their interaction (figure 1c). Composite random walks are an exception, however, in that some parameter values performed better (Z_I=0.99) with increased aggregation, irrespective of resource densities, whilst others performed worse (Z_I=0.5; figure 1c). This is in contrast to correlated random walks or Lévy walks that consistently performed worse with increasing aggregation. High search directionality (Z_I=0.5) leads to a decrease in encounter rates with increased aggregation at a given density, whereas the reverse is true for searches with more area-restricted search-like behaviour (Z_I=0.99; figure 1).

Looking at the best strategy and parameter value for any given resource distribution (figure 2), we see that correlated random walks were generally optimal at ρ=0.99. Only at high aggregation (variance:mean>6) and low density (<0.031 resources SU^{-2}) is there some uncertainty if lower ρ-values were actually better (figure 2a).

Lévy walks at densities higher than 0.03 resources SU^{-2} were optimal with high directional persistence and limited area-restricted search behaviour (μ=1.3; figure 2b). At lower densities, however, higher efficiencies were found when searching with less directionality (μ=1.6 and μ=2). Between low and high density there was a range (0.01-0.03 SU^{-2}) at which the optimal parameter value depended on both aggregation and density (figure 2b).

The optimality of composite random walks was sensitive to the degree of aggregation and relatively insensitive to changes in density (figure 2c), while the reverse was true for Lévy walks whose optimality was dependent on density more than aggregation (figure 2b). For composite random walks, the optimal parameter value always depended on aggregation, with high relocation frequencies optimal at low degrees of aggregation and high local search frequencies optimal at high degrees of aggregation (figure 2c). At low densities, parameter values associated with more relocation (Z_l=0.5) were optimal only in random distributions (variance:mean = 1), whereas at higher densities they were optimal at a wider range of aggregation (variance:mean between 1-4.6).

The optimal strategy in any given distribution of resource points is a clear function of both density and aggregation (figure 2d). In random and slightly aggregated distributions, correlated random walks had highest search efficiency, whereas highly aggregated distributions were best searched by composite random walks (figure 2d), and Lévy walks were optimal in a region in between these two (figure 2d). As density increased correlated random walks incrementally became the best search strategy, even at slightly higher levels of aggregation, increasing the range of their optimality (figure 2d). Decreases in density, conversely, increased the range of aggregation levels at which composite random walks were optimal. At lowest densities this amounts to composite random walk optimality at all aggregation levels.

2.4 Discussion

Our results show that search performance is significantly determined by the degree of resource aggregation (figures 1 and 2). Moreover, the extent of the influence of aggregation on search efficiency is proven to be dependent on both density and movement behaviour (figures 2 and 4). This interaction effect between aggregation and density rejects our hypothesis that searches are efficient at a given aggregation level, irrespective of density. This effect has not been demonstrated before since previous work has focused on single levels of aggregation at various densities (Bartumeus et al 2005, Benhamou 2007) and changes in aggregation by comparison of regular, clumped and random distributions with a focus on behavioural traits (Scharf et al 2011). The interaction between aggregation and density indicates that in order to understand the impact of changes in resource distribution, for instance through habitat destruction, it is necessary to have data on both resource density and degree of aggregation. Furthermore, since the effects of changes in density and aggregation vary between movement strategies (figure 2), species will respond differently to changes in their resource distributions depending on their movement pattern.

Regarding specific movement behaviour, our results confirm that random distributions favour higher directionality (figure 2) and this is in line with expectations for Lévy walks as well as for correlated random walks (Koopman 1979; Raposo et al 2003) and in general for behaviour resembling displacement and area-restricted search (Scharf et al 2009). Indeed, in general the results on search performance are in agreement with expectations. The optimality of correlated random walks, for instance, was highest at the highest directional persistence (ρ =0.99), which is in agreement with previous work (Bartumeus et al 2005). Also in accordance with previous work (Viswanathan et al 1999) we found optimality of Lévy walks with μ-values of around 2. Interestingly, however, this is conditional on the degree of aggregation and density: the range of resource density and aggregation at which Lévy walks are optimal is small (figure 2). This intermediate optimality of Lévy walks (figure 2b) could be caused by their included intermediate-sized move lengths, which could be optimal at only some specific distribution types, such as in fractal or hierarchical resource distributions (Sims et al 2007). The fact that random searches employed by animals have their own individual region of optimality (figure 2) provides an explanation for the variety of observed movement patterns. Contradicting evidence for species 'doing the Lévy walk' (Benhamou 2007, Reynolds 2008), while partly attributable to statistical errors and increasing sophistication of movement data analysis (Gurarie et al 2009; Codling and Plank 2010) can now be understood by our finding, which show that the optimality of Lévy walks is limited to specific levels of density and aggregation (figure 2). Additionally, the fact that many species are found to employ correlated random walks (Turchin 1998; Byers 2001; Johnson et al 2008) can be explained since despite inefficiency in highly aggregated distributions and the observed patchy nature of resource distributions (Prins and Van Langevelde 2008), such behaviour is actually optimal across a wide range of resource aggregation levels, especially at higher densities (figure 2). Similarly, species that use composite searches (Benhamou 2007) or simple displacement and intensive search (Scharf et al 2009), may primarily search for resources that are highly aggregated.

Understanding the interactions between animals and their environment remains one of the main challenges in movement ecology (Schick et al 2008; Giuggioli and Bartumeus 2010), and here we show that analysing resource aggregation as variable property of the environment may help us to understand observed movement patterns. Recent studies are increasingly dealing with aspects of movement in relation to both behaviour and the intricacies of the resource distribution and the landscape in general (Ring et al 2011; Giuggioli and Bartumeus 2012; de Jager et al 2011; Sims et al 2012; Reynolds 2012 Lewis et al 2013). Our study illustrates the influence that simple variation in resource distribution can have on search efficiency and consequently in what would be an optimal search strategy. This means that it is not possible to use a single movement model as null-model for animal movement based on effectiveness in a specific distribution. Rather than a single hypothesis for all non-informed searches these results show that specific distributions require specific movement behaviour in order to be optimally searched. The results from Viswanathan et al(1999) are valid only for the specific spatial landscape model used, and even down to the specific regrowth time (see Raposo et al 2003). Since such effects may be present in more sophisticated search strategies, variation in both density and aggregation should be included in investigation and evaluation of search behaviour.

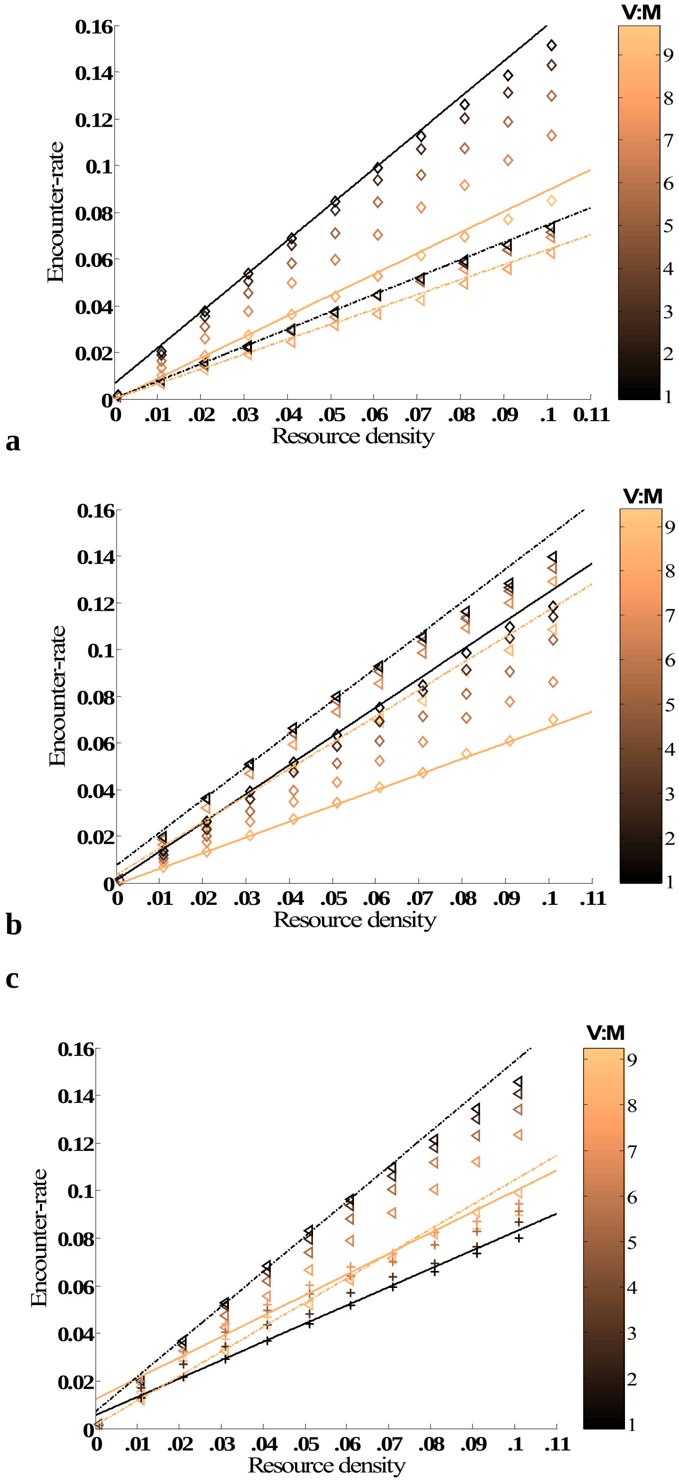
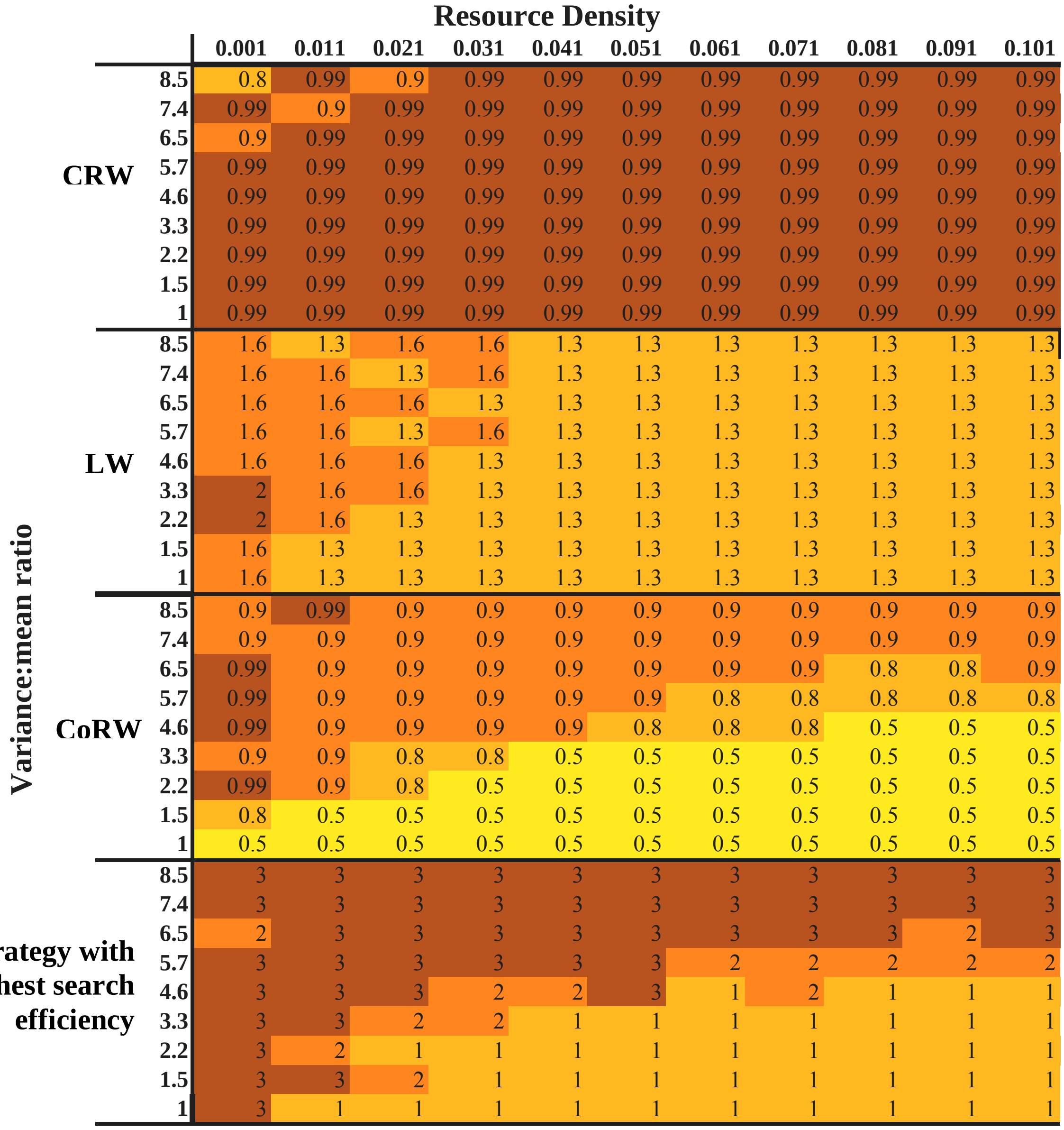


Figure 1. Encounter rate as function of resource density and aggregation for correlated random walks (a), Lévy walks (b) and composite random walks (c). The lines indicate the

interaction effect between resource density and aggregation, illustrating the differences between the density effect at low (variance:mean ratio =1; bold line) and high (variance:mean ratio =9, thin line) aggregation levels for two (broken and continuous) parameter values for each of the three search strategies (respectively ρ=0.5 and ρ=0.99 for correlated random walks; μ=1.3 and μ=2.9 for Lévy walks; and Z_I=0.5 and Z_I=0.99 for composite random walks).



		Resource Density										
	Variance:mean ratio	0.001	0.011	0.021	0.031	0.041	0.051	0.061	0.071	0.081	0.091	0.101
CRW	8.5	0.8	0.99	0.9	0.99	0.99	0.99	0.99	0.99	0.99	0.99	0.99
	7.4	0.99	0.9	0.99	0.99	0.99	0.99	0.99	0.99	0.99	0.99	0.99
	6.5	0.9	0.99	0.99	0.99	0.99	0.99	0.99	0.99	0.99	0.99	0.99
	5.7	0.99	0.99	0.99	0.99	0.99	0.99	0.99	0.99	0.99	0.99	0.99
	4.6	0.99	0.99	0.99	0.99	0.99	0.99	0.99	0.99	0.99	0.99	0.99
	3.3	0.99	0.99	0.99	0.99	0.99	0.99	0.99	0.99	0.99	0.99	0.99
	2.2	0.99	0.99	0.99	0.99	0.99	0.99	0.99	0.99	0.99	0.99	0.99
	1.5	0.99	0.99	0.99	0.99	0.99	0.99	0.99	0.99	0.99	0.99	0.99
	1	0.99	0.99	0.99	0.99	0.99	0.99	0.99	0.99	0.99	0.99	0.99
LW	8.5	1.6	1.3	1.6	1.6	1.3	1.3	1.3	1.3	1.3	1.3	1.3
	7.4	1.6	1.6	1.3	1.6	1.3	1.3	1.3	1.3	1.3	1.3	1.3
	6.5	1.6	1.6	1.6	1.3	1.3	1.3	1.3	1.3	1.3	1.3	1.3
	5.7	1.6	1.6	1.3	1.6	1.3	1.3	1.3	1.3	1.3	1.3	1.3
	4.6	1.6	1.6	1.6	1.3	1.3	1.3	1.3	1.3	1.3	1.3	1.3
	3.3	2	1.6	1.6	1.3	1.3	1.3	1.3	1.3	1.3	1.3	1.3
	2.2	2	1.6	1.3	1.3	1.3	1.3	1.3	1.3	1.3	1.3	1.3
	1.5	1.6	1.3	1.3	1.3	1.3	1.3	1.3	1.3	1.3	1.3	1.3
	1	1.6	1.3	1.3	1.3	1.3	1.3	1.3	1.3	1.3	1.3	1.3
CoRW	8.5	0.9	0.99	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9
	7.4	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9
	6.5	0.99	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.8	0.8	0.9
	5.7	0.99	0.9	0.9	0.9	0.9	0.9	0.8	0.8	0.8	0.8	0.8
	4.6	0.99	0.9	0.9	0.9	0.9	0.8	0.8	0.8	0.5	0.5	0.5
	3.3	0.9	0.9	0.8	0.8	0.5	0.5	0.5	0.5	0.5	0.5	0.5
	2.2	0.99	0.9	0.8	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5
	1.5	0.8	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5
	1	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5
Strategy with highest search efficiency	8.5	3	3	3	3	3	3	3	3	3	3	3
	7.4	3	3	3	3	3	3	3	3	3	3	3
	6.5	2	3	3	3	3	3	3	3	3	2	3
	5.7	3	3	3	3	3	3	2	2	2	2	2
	4.6	3	3	3	2	2	3	1	2	1	1	1
	3.3	3	3	2	2	1	1	1	1	1	1	1
	2.2	3	2	1	1	1	1	1	1	1	1	1
	1.5	3	3	2	1	1	1	1	1	1	1	1
	1	3	1	1	1	1	1	1	1	1	1	1

Figure 2. Optimal parameter values for the three random walks and the optimal search strategies at varying resource densities (x-axis, in resources SU^{-2}) and degrees of aggregation (y-axis, variance:mean ratio). The top three panels give the optimal parameter value, yielding the highest search efficiency, for each combination of resource density and aggregation for, from top to bottom, correlated random walks (CRW), Lévy walks (LW), and composite random walks (CoRW). The bottom panel describes the search strategy with the highest search efficiency for a given resource density and aggregation level. Values in this bottom panel refer to (1) correlated random walks, (2) Lévy walks and (3) composite random walks.

Chapter 3 Variance and skewness of patch size distributions determine search efficiency of correlated random, Lévy and composite random walks

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Submitted for publication

Abstract

Previous work has shown that the efficiency of random walks in the search for resources depends on the spatial resource distribution in terms of both aggregation and density. However, most studies on the efficiency of random searches assume that the number of resources aggregated in patches is constant and no evaluation of the effect of changes in the patch-size distribution exists. Here, we studied how variation in local resource abundance, or patch size, affects the efficiency of random searches. To this end we modeled random searches, based on correlated random, Lévy and composite random walks, in resource distributions with increasing variation in patch size. This variation was modeled using negative binomial and discrete uniform distributions to determine whether the variance and skewness of the resource distribution that influencespatch-size distributions influence search efficiency. Our results show long-term random search performance is affected by increased skewness of the patch-size distribution, rather than variance. Furthermore composite random walks outperformed Lévy and mere random walks and were better able to deal with increased skewness. We conclude that our findings here stress the importance of including previously ignored aspects of the resource distribution into studies of optimal search behaviour. An accurate model of the interaction between an animal and its resource distribution, even in relatively simple cases, will require sophisticated descriptions of resources and their distributions as encountered in nature.

3.1 Introduction

Random searches are used in ecology as null models for simulation and analysis of animal movements and their foraging efficiencies (Nathan et al 2008). The introduction of Lévy walks into ecology (Viswanathan et al 1999) has sparked renewed efforts to test for the existence of random searches in movement patterns of species, ranging from bumblebees (Osborne et al 1999; Reynolds 2009), to flagellates (Bartumeus et al 2003), and goats (De Knegt et al 2007). Combined with the development of theory (Bartumeus et al 2005; Behamou 2007, Scharf et al 2009) and of technology and methods of tracking animals as well as movement data analysis (Gurarie et al 2009; Lewis et al 2013) this is the heart of what is now called movement ecology, within which various approaches have been identified, such as for instance biomechanical, optimal foraging and random search approaches (Nathan et al 2008). One of the focal points in the study of movement is the interaction between search and the environment (Nathan et al 2008; Giuggioli and Bartumeus 2010, 2012; Lewis et al 2013). Here we use the random search approach to study the interaction between animal and the environment in terms of the resource distribution.

Resources are often clustered in patches, such as apples in a tree, or leaves on a herb. The resource abundance at any given point in time and space is known to be dependent on competition, weather, and the history of resource exploitation, and consequently local resource abundances are highly unpredictable (Prins and Van Langevelde 2008). Similar variation follows from population models can be highly variable (van Teeffelen and Ovaskainen, 2007), and these are a resource to other species. So it is expected that there is variation in local resource abundance, or patch size, although the degree and type of variation will vary with resource as well as time, space and history of use (Prins and Van Langevelde 2008). However, the effect of changes in the variation in local abundance has hithertofore not been considered in studies on random walks (Viswanathan et al 1999; Bartumeus et al 2005; Lewis et al 2013). Indeed it has generally been assumed that upon encounter with a resource the local conditions are identical and consequently at that point a single behaviour is not effective.

To determine if this is indeed the case, here we investigate how variation in patch size, i.e. the number of resources in a local aggregation, influences the efficiency of composite random, correlated random and Lévy walks. To this end we use different patch size distribution to describe the variation in the number of resources per patch. Such variation in patch size has previously, in the context of foraging theory, been described using Poisson and negative binomial distributions (Iwasa et al 1981). Following their approach we modelled variation in patch size by drawing patch sizes, in terms of resource items, from discrete uniform and negative binomial distributions, with a Poisson distribution included as a special case of the negative binomial. This choice allows for an important distinction between the variation generated by the two methods to be made. The symmetrical discrete uniform distribution can have increased variance, while maintaining symmetry and hence having no or zero skewness. In the case of the negative binomial distribution, on the other hand, skewness increases with variance (figure 1).

3.2 Methods

3.2.1 Movement

Correlated random walks are modelled by drawing turning angle values from a wrapped Cauchy distribution (WCD; Bartumeus et al 2005):

$$\varphi = 2 \cdot \arctan\left(\left(\frac{1-\rho}{1+\rho} \right) \cdot \tan\left(\pi \cdot (\xi - 0.5) \right) \right) \tag{1}$$

where φ is the turning angle, ξ is uniform random [0,1] and ρ is the shape parameter or the net resultant vector, equal to the mean cosine of the turning angle.

The Lévy walks are modelled using the common approximation (Bartumeus et al 2005):

$$P(l) = l(0) \cdot l^{-\mu} \tag{2}$$

where $P(l)$ is the distribution of move lengths, $l(0)$ is the minimum step length, and μ is the shape parameter.

Composite random walks are random walks whose move lengths are drawn from different distributions (Benhamou 2007). Here, a simple two-level composite random walk is used with move lengths drawn from single values, being either 1 or 100 SU (Benhamou 2007) with respective probabilities of Z_1 and $Z_2=1-Z_1$. This represents a very basic local search or displacement strategy similar to the ‘intensive’ and ‘extensive’ search modes as used by Scharf et al (2009). For reasons of simplicity we limited the composite random walk to two step sizes to vary the proportion of area-intensive search to area-extensive search with one parameter.

Both Lévy walks and composite random walks responded to resources by consuming the resource and drawing a new move length, thus a local search can start upon resource encounter (Hengeveld et al 2007).

3.2.2 Resource distribution

The resource distribution is defined by a patch size distribution, determining the number of resource points in a patch, and an algorithm that results in a spatial distribution (i.e. the position in space of these resources). The patch-size distribution describes the variation in the number of resources across patches. In all simulations, the total number of resources was fixed at N=1000, distributed over an average of 40 patches. The patches were placed randomly in the landscape. Within these patches, the resources were again placed randomly, within a fixed radius (10 SU's) that gives the spatial patch size. For a given patch, the number of resources is determined by drawing random numbers from the selected patch size distribution. Here this distribution of patch sizes was modelled using a negative binomial and a discrete uniform distribution. In the uniform case, the variation in the patch size distribution is obtained by varying the number of resources per patch according to a discrete uniform distribution around the mean number of resources/patch (set at 25). In other words, the variance is increased by increasing the range, R, of the uniform distribution from which the number of resources per patch were drawn. This range was increased from 2 to 48, yielding uniform distributions with substantial variation in patch size. The variance, V, in local patch size is in this case given by:

$$V(X) = \frac{(b-a+1)^2 - 1}{12} \tag{3}$$

where a and b are the boundaries of the uniform distribution ($b - a = R$).

Following previous work (Iwasa et al 1981) we used a negative binomial distribution to model high variation in resource densities among patches (figure 2). The negative binomial represented cases with relatively high frequencies of patches with low resource abundances with occasional higher abundance patches, and has been used previously to model patchily distributed resources (Iwasa et al 1981; Hilborn and Mangel 1997). Increased variation was modelled by keeping the mean constant and increasing the variance. The mean value, $E(X_{NB})$, of the negative binomial is given by:

$$E(X_{NB}) = \frac{r \cdot (1-p)}{p} \tag{4}$$

and the variance, $V(X_{NB})$:

$$V(X_{NB}) = E(X_{NB}) + \frac{E(X_{NB})^2}{r} \tag{5}$$

where r and p are the negative binomial parameters used to adjust the shape of the distribution (usually these refer to the number of fails before a stop and the probability of success in each trial). From equation (5) it is clear that we can change the variance and keep the mean constant by varying r as long as we keep the ratio in equation (4) constant. Therefore the values of p are given by:

$$p = \frac{r}{r + E(X_{NB})} \tag{6}$$

Note that the Poisson distribution is included as the special case of the negative binomial distribution where the variance approaches the mean (i.e. for large values of r).

The important difference between the two distributions used to describe patch size variation is their degree of symmetry. The discrete uniform distribution is symmetrical and thus has zero or no skewness. The negative binomial distribution, on the other hand, can be highly skewed. Indeed, since the skewness of a negative binomial distribution is given by:

$$\gamma = \frac{1+p}{\sqrt{r \cdot p}} \tag{7}$$

and since increasing the variance requires decreasing r and p this skewness increases with variance. Thus the discrete uniform distribution varies only the variance, whereas the negative binomial increases variance and skewness simultaneously.

3.2.3 Simulations

Searches are simulated in discrete time and in a continuous two dimensional space spanning 316x316 SU’s with torus boundaries. This allowed us to model an infinitely large space with repeating patterns of resource distributions. In these landscapes, the exploitation efficiency is determined by searching. It was assumed that a searcher moves at a constant movement speed of one SU per time step. Simulation time was set at 10^5

time steps and simulations were repeated 20 times for each search-parameter set. The parameter values for which the movement strategies were run are as follows: ρ= [0 0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9 0.95 0.99 0.999], μ=[1.1 1.25 1.4 1.55 1.7 1.85 2 2.15 2.3 2.45 2.6 2.75 2.9] and Z_l=[0.1 0.5 0.8 0.9 0.935 0.95 0.97 0.98 0.985 0.99 0.992 0.994 0.996]. When multiple resources are within the detection radius (1 SU), each is consumed, taking a single time unit, before another step is taken.

3.2.4 Search efficiency

A simulated search yields a total number of resource encounters. To make these search results comparable a benchmark is used. A common benchmark for search efficiency is given by the expected number of encounters of a ballistic path of the searcher, which standardizes search results for density and search time. The detection rate of a simple ballistic search when searching in a random distribution is a linear function of resource density, N (Hilborn and Mangel 1997; Koopman 1979). The expected number of encounters is:

$$E(Enc) = \frac{2 \cdot d \cdot v \cdot N}{A} \cdot T \tag{8}$$

where A is the area in which is searched, T the search time, v is the searcher's velocity and d its detection radius (1 SU). The effect of density on searching performance is straightforward and if velocity is set to 1, directly related to the mean free path between targets (Bartumeus et al 2005). The expected number of encounters is used to calculate the search efficiency as an index for performance (Bartumeus et al 2005):

$$S_{eff} = \frac{Enc_{sim}}{E(Enc)} \tag{9}$$

where Enc_{sim} is the number of encounters in the simulation. This search efficiency can be used to compare the performance of searches in distributions with varying densities, as it corrects for the effects of differences in resource densities.

3.3 Results

3.3.1 Discrete uniform resource abundance distribution

Increasing the variance of the uniform resource abundance distribution had no discernable effect on search performance, regardless of the search strategy (figure 3a-c). Furthermore the optimal search parameter value was independent from the variance in local resource abundance for all three strategies (figure 3a-c). Correlated random walk searches were most effective with search parameter values>0.99 with the best results using $\rho=0.999$, which was the most straight and directional movement included. In the case of Lévy walks, general search performance was best between $\mu=1.7$ and $\mu=2.1$ with optimal value at $\mu=1.85$. Searches using composite random walks had most encounters with parameter values between $Z_1=0.7$ and $Z_1=0.95$ with best performance at $Z_1=0.8$.

Comparing the three strategies the most efficient strategy by far was the composite random walk, with maximum search efficiencies (S_{eff}) of 1.2. Lévy walks perform distinctly worse with highest efficiencies of 0.825, but better than correlated random walks with search efficiencies of 0.65 and lower.

3.3.2 Negative binomial resource abundance distribution

The negative binomial resource distribution results showed an entirely different picture with the efficiency of all three strategies being affected by the change in variance (figure 4). Interestingly both correlated random walks and Lévy walks performed better with increasing variance (figure 4a,b), whereas the search efficiency of the composite random walks decreased with increasing variance. Specifically, correlated random walks were most efficient at standard deviations>25 with best search performance at the highest variance, 35.7, at the highest search parameter value $\rho=0.999$. Levy walks performed best at standard deviations ranging from 18 to 36, with highest performance at a variance of 26.9 and $\mu=1.7$. Composite random walks performed best at standard deviations ranging from 5 to 10 with highest search performance at a variance of 5.9 and parameter value of $Z_1=0.985$. For correlated random walks and composite random walks the optimal search parameter values did not change clearly with increasing variance. In the case of Lévy walks, however, the optimal search parameter changed with a slight decrease, from $\mu=1.85$ to $\mu=1.7$ in the optimal value of μ with increasing variance. Again, as in the uniform cases, the most efficient searches were the composite random walks, with highest search efficiencies (S_{eff}) of 1.35, whereas Lévy walks had highest efficiencies of 0.75, and correlated random walk search efficiency was always below 0.6.

3.4 Discussion

Our results showed that the search efficiency of random searches is independent of the variance in local abundances when these abundances follow a uniform distribution (figure 3). When the local abundances follow a negative binomial distribution, however, search efficiency did vary with variance in local abundance. In this case both correlated random and Lévy walks perform best with high variance (figure 4a,b), whereas composite random walks have their optimal efficiency at lower variances. This discrepancy between the discrete uniform and negative binomial search results suggest that variance of the patch-size distribution is not the main factor influencing search effectiveness. As noted, the main difference between the discrete uniform and the negative binomial distribution is that increasing the variance of the negative binomial distribution increases skewness as well. Therefore it is the skewness in the patch-size distribution that is important for the effectiveness of searches rather than the presence of variation in patch size per se (figure 4). This is interesting since negative binomial and other asymmetrical distributions of local abundances are known to occur frequently in nature (Prins and Van Langevelde 2008). Fish catch data and populations, for instance, often have negative binomial distributions (Hilborn and Mangel 1997). Indeed within a species' range its numbers are well described by negative binomial distributions (Pielou 1977; Vos and Hemerik 2003) and the case has been made that foragers exploiting prey with such distributions are likely to be common in nature (Ollsen and Brown 2006). In summary, the results show that one of the key aspects of variation in the resource distribution found in nature has far-reaching effects on the efficiency of random searches.

In agreement with earlier work (Benhamou 2007; Chapter 2) composite random walks are by far the most efficient random searches. While it is known that Lévy walks are effective in low (0.0001 SU^{-2}) densities (Hengeveld et al 2007) it is striking that the search performance of simple composite random walks is nearly twice that of Lévy walks, especially since our modelled composite random walk behaviour is basically only switching between intensive and extensive search, or searches for and within patches (similar to e.g. Scharf et al 2012). Again (Chapter 2) simple composite random walks are a more effective search strategy than Lévy walks. While there has been debate on the methods used to detect Lévy walks (Sims et al 2007; White et al 2008; Plank and Codling 2009) there is substantial evidence that Lévy searches are performed by animals (Reynolds 2009, Viswanathan et al 2008; Reynolds and Rhodes 2009; James et al 2009). A possible explanation of this discrepancy may be that behaviour effective at finding resources within a preys' range, such as a composite random walk, is not effective at larger scales. In other words, the behaviour required to find a new area in which prey is present and the behaviour required to effectively find resources within such an area may be different (Benhamou 1992; Reynolds 2012). Another possibility is that observed Lévy walks are the result of composite random walks at various spatial scales (see also Reynolds 2012). In that case a behavioural framework such as the one propounded by Scharf et al(2009), which is similar to composite random walks and previous patch-use foraging models (Benhamou 2007; Iwasa et al 1981), could be responsible for search patterns with power-law properties over multiple spatial scales. Indeed not distinguishing between movement behaviors and misidentifying movement due to sampling (James et al 2011) have been suggested as an additional reasons for contradicting evidence on Lévy walks in nature (Scharf et al 2012). Based on their effectiveness in our results, as well as previous studies (Chapter 2), search behaviour similar to a composite random walk, or global/local search mechanism (Scharf et al 2009) is most likely to be encountered in nature. This seems the more plausible given the simplicity of composite random searches and the fact that search efficiency of local search behaviour may be straightforwardly improved using an exit-rule and/or adaptable local search times (Scharf et al 2009; Iwasa et al 1981; Benhamou 1992). On the other hand Lévy walks remain optimal in certain distributions (Chapter 2) and have been shown to effectively deal with certain distribution of patch sizes (Reynolds 2012) which is a case for Lévy walks as the more likely behaviour. It is impossible, it seems, to determine what is the expected movement behaviour without reference to the resource distribution.

Our findings here stress the importance of including previously ignored aspects of the resource distribution into studies of optimal search behaviour. An accurate model of the interaction between an animal and its resource distribution, even in relatively simple cases, will require more sophisticated descriptions of resources and their distributions as encountered in nature.

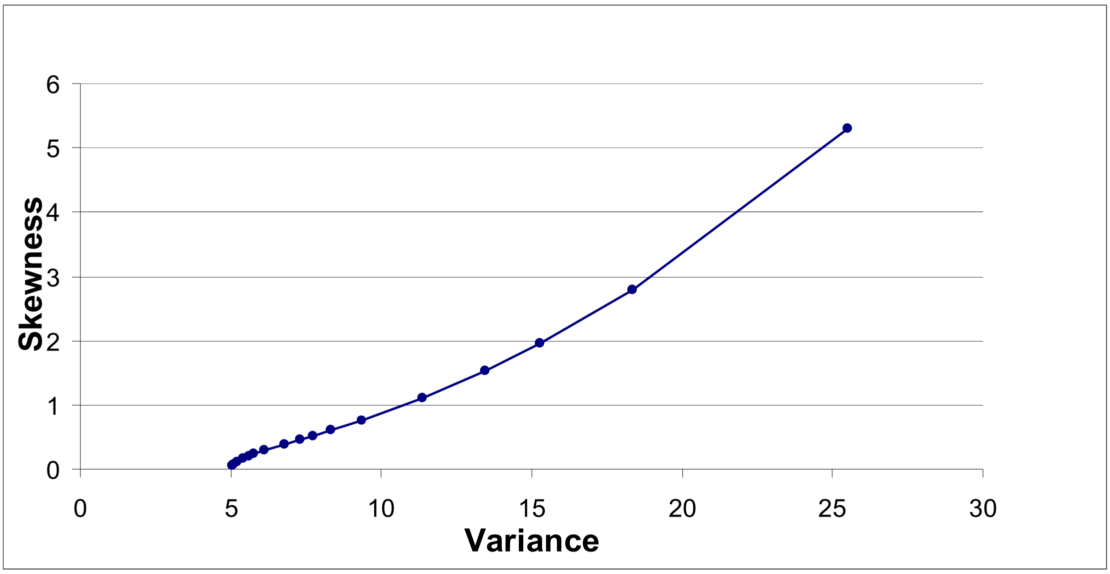

Figure 1. The skewness of the modelled negative binomial distribution against its variance.

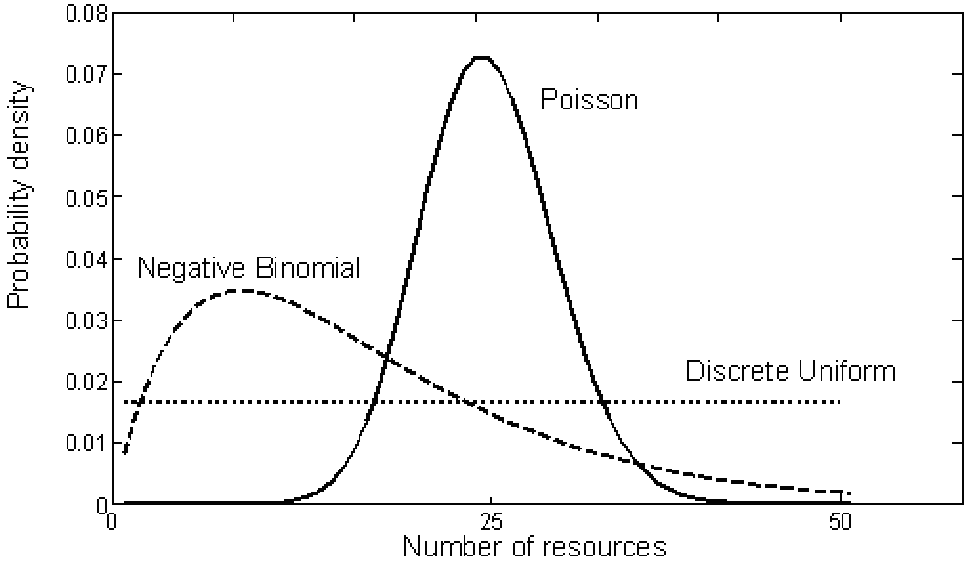

Figure 2. Continuous representations of the discrete probability density functions used to describe the distribution of the number of resources per patch. Shown are the uniform (dotted line) negative binomial (dashed) and the extreme case where the negative binomial approaches Poisson (continuous line) distribution.

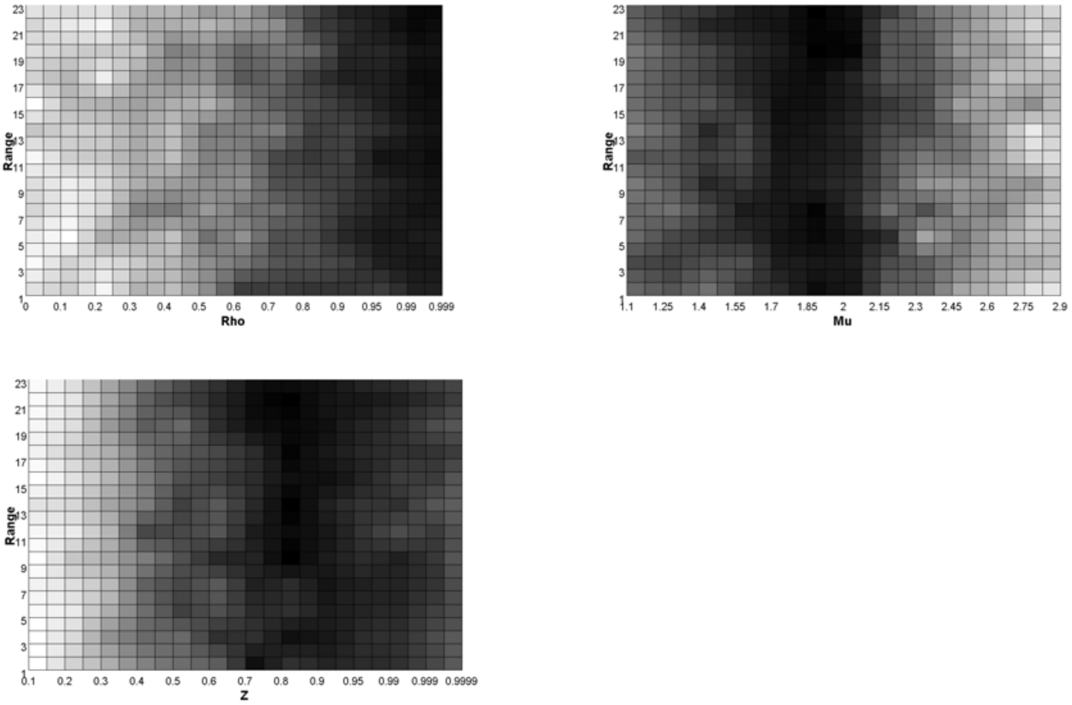

Figure 3. (a-c) Search efficiency (S_{eff}) of searches at various search parameter values of the specific random walks (x-axis: ρ, μ and Z for correlated, Lévy and composite random

walks respectively) in distributions with a discrete uniform distribution of local resource abundances with increasing variance (y-axis)

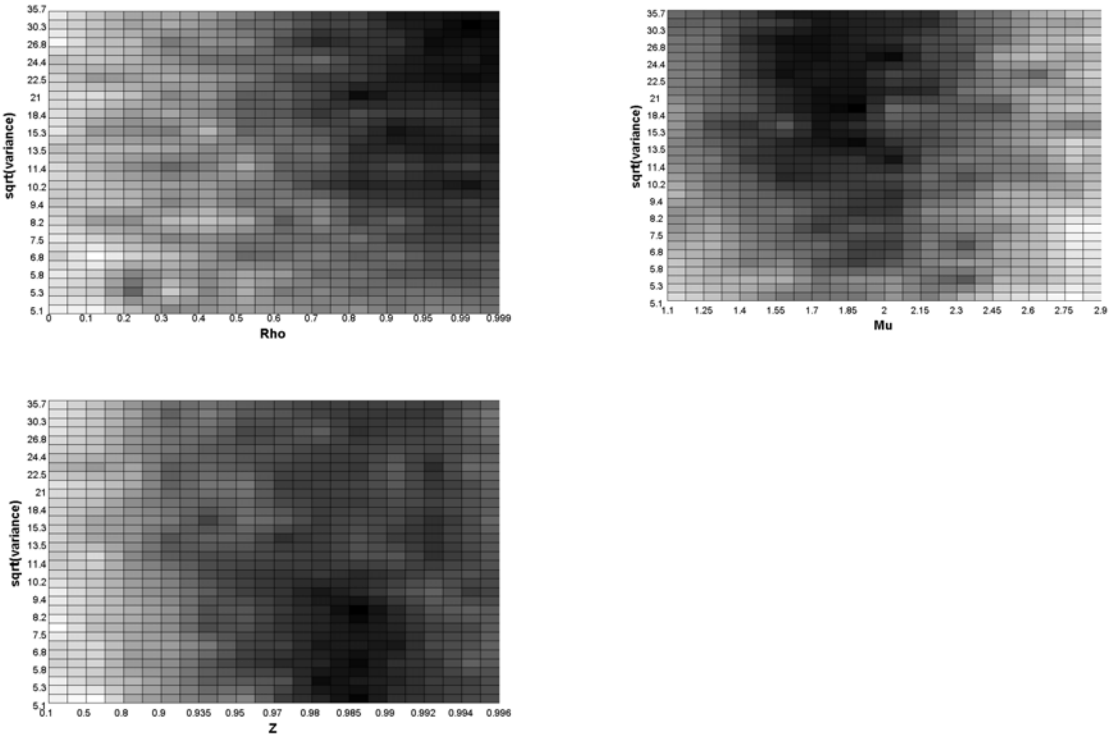

Figure 4. (a-c) Search efficiency (S_{eff}) of searches at various search parameter values (x-axis: ρ, μ and Z for correlated, Lévy and composite random walks respectively) in distributions with a negative binomial distribution of local abundances with increasing variance (y-axis). The values on the axes correspond to the performed simulations. Within each figure grayscale reflects search efficiency, with darker coloring for more effective searches.

Chapter 4 Resource density and aggregation determine value of new over old information in correlated random walks

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Submitted for publication

Abstract

The interaction between the environment and animal movement is central to movement ecology. So far, this interaction has been studied in the context of random walks, but this interaction requires extending the random movement paradigm into cognitive and even optimality approaches. The use of information and decision making is needed because it has been recognized that most resources and species are distributed in aggregations at several spatial scales and that search efforts need to be intensified in areas with higher densities. Furthermore, it has been shown that no single random search strategy is optimal at all degrees of aggregation. Our central question is how, if at all, the optimal value of past over present information changes with variation in resource aggregation and density. Here we integrated random and cognitive approaches by combining random walk and information use models. Specifically, we used a correlated random walk model together with an updating information use model to determine if the relative value of old and new information is dependent on the degree of resource aggregation and density. Therefore we simulated searches varying the number and size of patches. To mimic different types of resources we analysed four different local resource density gradients of patches. Our results showed that the optimal response to encountered resources depends on the resource distribution. Specifically, the value of old information relative to new information initially increases with increasing patch size. An intermediate to high sensitivity to information was found to be optimal in most of the resource distributions, regardless of the local resource density gradient, illustrating the value of behavioural flexibility. The variation in local gradients showed that optimal sensitivity to new information is dependent on the shape of the gradient. Long local resource gradients require a delayed response to new information. Our results show that optimally searching

animals should adapt their sensitivity to new information depending on the resource density and aggregation.

4.1 Introduction

One of the main challenges in movement ecology is to understand the movements of foragers and the interaction between movements, the state of the forager and the surrounding landscape (Schick et al 2008; Nathan et al 2008; Gurarie et al 2009). So far, this interaction has been studied in the context of random walks, but this interaction requires extending the random movement paradigm into cognitive and even optimality approaches (Nathan et al 2008). Recent work in movement ecology has squarely placed the searcher in its resource distribution and landscape in general (Scharf et al 2009; Giuggioli and Bartumeus 2011; De Jager et al 2011; Raposo et al 2012). There remains a challenge, however, to integrate theoretical random search models with behavioural aspects such as information use. The natural area to study when considering information use is how searchers can effectively deal with aggregation of resources (Chapter 2). Firstly because it has been recognized that most resources and species are distributed in aggregations at several spatial scales (Fryxell et al 2008; Prins and Van Langevelde 2008), and secondly, because effectively responding to aggregation requires the use of information and decision making, since search efforts need to be intensified in areas with higher densities. Indeed, random walks, such as Lévy walks (Viswanathan et al 1999) and composite random walks (Benhamou 2007), perform well in aggregated distributions because of well-timed information use. Stopping the current move is possibly the simplest of responses to new information and leads to efficient search behaviour as long as resources are patchily distributed and patches can be considered equal. This part of composite random and Lévy walks is captured in recently discussed long/short movement models (Scharf et al 2009). We argue that a logical area for expanding the random search approach in movement ecology (Nathan et al 2008) is exactly in the response of animals to such encounters; that is to say in the use of information after encounter.

Another reason to study information use is because performance of random searches is found to be dependent on resource aggregation and density, and hence employing a fixed random movement behaviour is inefficient (Bartumeus et al 2005;

Scharf et al 2009). When searching in varying distributions, either for different resource types or resources in temporal flux, searches are expected to change with the properties of the resources distributions (Chapter 2). The obvious solution would be to use information to adapt the random movement behaviour to increase the search efficiency.

When extending random searches with an information use component, one would like to stay close to known theoretical models and have a very general model to understand basic effects. We combined a classical model of movement in ecology, the correlated random walk (Kareiva and Shigesada 1983; Byers 2001; Bartumeus et al 2005), with the information use model of McNamara and Houston (1987). The correlated random walk model was chosen since it, as opposed to composite random and Lévy walks, does not have a local search that is triggered by resource encounters. Behavioural changes in the correlated random walk can be modelled directly by changing a single central parameter, changing the shape of the turning angle distribution and hence the tortuosity of the movement path (Benhamou 1992; Bartumeus et al 2005). The choice made here does not exclude other mechanisms and an equally valid approach would be to let the information to vary movement speed or move length distribution, both of which are relevant parameters in movement (Giuggioli and Bartumeus 2010).

The McNamara-Houston model is a classical model of information use and specifically the value of information over time (Stephens 2007). It assumes that the information available to the animal is summarised in a single value or state that reflects the animals' assessment of its environment, for instance in suitability, food availability, or predation risk. Each time the assessment is updated, the past value is updated with the current information (McNamara and Houston 1987; Stephens 2007). The relative importance allotted to past information and current information is set by its main parameter. Thus our central question is how, if at all, the optimal value of past over present information changes with variation in resource aggregation and density. If there is no advantage in the use of new information this would mean that an organism can effectively search for resources using a single memory rule, conversely if different distributions require specific responses an optimal searcher may be expected to display these.

We vary the density and aggregation of resources by varying the number and size of patches. Since updating information can take time, the transition from matrix to patch may become important. If for instance there is a sudden change in local resource density, information should be updated more quickly, whereas if there is a slow gradient it may be more effective not to respond to slight increases in resource density. The spatial distribution of a given resource depends on the type of the resource (e.g., water, nutrients, prey). Therefore we model various gradients that searching animals might encounter. Surface water, for instance, may follow a distribution with surface water being in pools and hence is either present or not. Wind dispersed seeds, on the other hand, a food resource for numerous species, may follow more closely ‘plumes’ changing shape with prevailing winds (Okubo 1980). The distribution of ants around their nest may resemble negative exponential density curves (Depickere et al 2008).

4.2 The resource distribution model

Here we assume that the local distribution can be described by a continuous function that is able to model the overall spatial distribution of resources in a patch. Assume, for instance, that a Gaussian function best represents the resource density from a resource patch centre to its edge. At the landscape level this means the resource abundance is the sum of all such local resource functions:

$$R(x,y) = \sum_{i=1}^{n} A_i \cdot \exp\left[\frac{(X_i - x)}{2\sigma_{xi}^{2}} + \frac{(Y_i - y)}{2\sigma_{yi}^{2}}\right] \qquad (1)$$

where (X_i, Y_i) are the coordinates of the centre of patch *i* and σ_{xi} and σ_{yi} the respective standard deviations in the *x* and *y* direction (figure 1a).

Alternatively, if the local resource abundance follows a negative exponential distribution, this is given by:

$$R(X,Y) = \sum_{i=1}^{n} A_i \cdot \exp - \left[\delta \cdot D_i\right] \qquad (2)$$

where D_i is the distance from the patch centre *i* and δ is the rate of decline in density with this distance (figure 1b).

If resources show a linear decrease in abundance with distance from the centre, the resource distribution can be modelled by the function:

$$R(X,Y)=\sum_{i=1}^{n}\begin{cases}A_i-\gamma\cdot D_i & if \quad A_i>\gamma\cdot D_i\\ 0 & otherwise\end{cases} \tag{3}$$

where γ sets the decrease in resource density with increasing distance (D_i) from patch centre *i*. The distribution generates cone shaped distributions (figure 1c).

In case the resources are either absent or present and follow a binary distribution without a spatial gradient, such as in the case of patches of water, this would be (figure 1d):

$$R(X,Y)=\sum_{i=1}^{n}\begin{cases}A_i & if\ D_i<radius\\ 0 & otherwise\end{cases} \tag{4}$$

For our analyses we compare the impact of the different resource distribution types and assume for each type that all patches are identical and symmetrical, although patches can partly overlap.

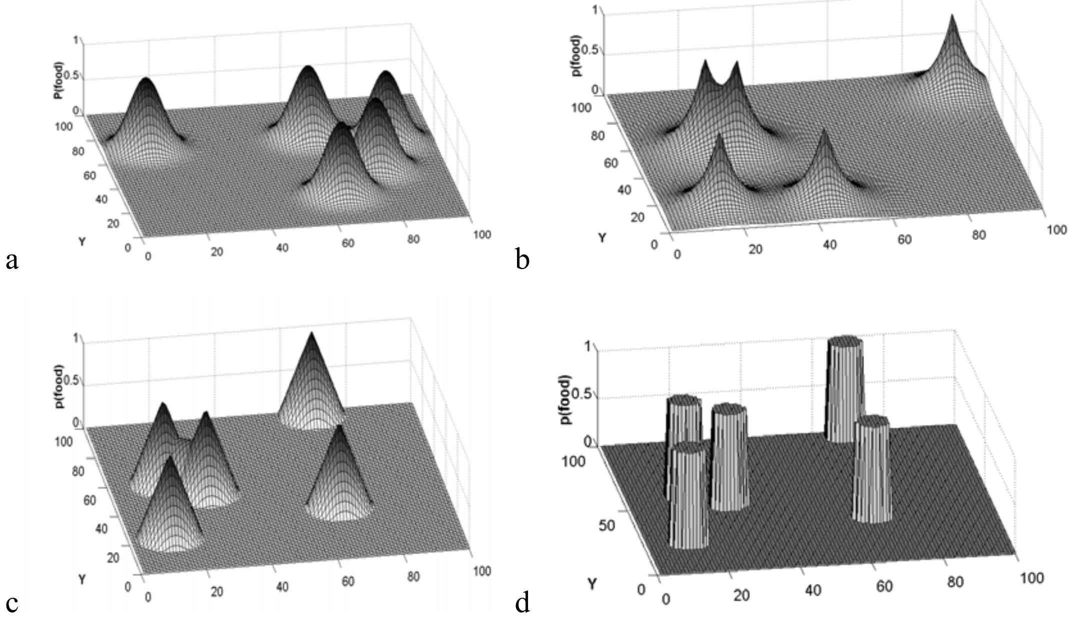


Figure 1. Examples of resource distributions generated using distribution functions defined by gradients given by a Gaussian (a), a negative exponential (b), and a linear (c) local resource function, and one function where resource patches follow a binomial distribution (d). The graphs show the probability of finding a resource point (z-axis) at any given position in space (X,Y).

4.3 Movement model

The correlated random walk model used in our study is based on turning angles drawn from a Wrapped Cauchy Distribution (Bartumeus et al 2005):

$$\varphi = 2 \cdot \arctan\left(\left(\frac{1-\rho}{1+\rho}\right) \cdot \tan\left(\pi \cdot (\xi - 0.5)\right)\right) \tag{4}$$

where φ is the turning angle, ξ is a random value drawn from an uniform distribution [0,1] and ρ is the shape parameter or the net resultant vector, equal to the mean cosine of the turning angle. We assume that the searcher has a fixed speed and moves at 1 spatial unit per time unit.

Modelling information use

Past experience can influence current behaviour through for instance physiological factors (e.g., satiation) or memory (Stephens 2007). The relative influence of past and present information on current behaviour is the updating rule given by McNamara and Houston (1987):

$$\mu_t = \alpha \cdot \mu_{t-1} + (1-\alpha) \cdot X \tag{5}$$

in which, in our case, μ_t is the animal's assessment of its environment at time t based on past and new information, α $(0 \le \alpha \le 1)$ sets the relative importance of past over current information and X is the new information obtained. If α is small the new information X is emphasized over the past information. Vice versa, if α is close to one the past information is more influential.

Influence of information on movement

To model the influence of information on movement we let the information state directly influence the value of the ρ parameter of the turning angle distribution (Eq. 4). In the field, animals searching for food show increased tortuosity with high availability of food (Benhamou 1992), for instance, dispersal of muskrats is faster in unsuitable habitats compared to dispersal in suitable habitats (Hengeveld and van den Bosch 1997). We assume, therefore, that a searcher has the highest degree of directionality, $\rho_{\max}$, when no resources are present. Assuming a linear relation between movement and the information state, the ρ at time t is given by:

$$\rho_t(\mu_t) = \rho_{\max} - \beta \cdot \mu_t \qquad (6)$$

where β is the slope between the animal's assessment of its environment and movement parameter ρ, and sets the effect of information on movement directionality. Minimum directionality, or maximum tortuosity, is given by $\rho_{\min} = \rho_{\max} - \beta$ and is the result of maximum sensitivity to information (figure 2). An increase in the effect of information increases the degree to which movement directionality is impacted, with only limited response, i.e. only a limited increase in tortuosity, at low β-values, and vice versa.

The movement behaviour is fully defined by the sensitivity to new information α, the effect information has on movement, β, and the innate movement in absence of food, $\rho_{\max}$. The special case of β=0 means there is no effect of information on movement and movement behaviour remains constant with directionality $\rho = \rho_{\max}$. Similarly, if α=1 the information state does not update and μ is a constant and thus movement behaviour remains constant with directionality $\rho = \rho_{\max} - \beta \cdot \mu$. Setting α=0 yields a model in which the information state is always set by the most recent information contained in the estimate for new information, *X*.

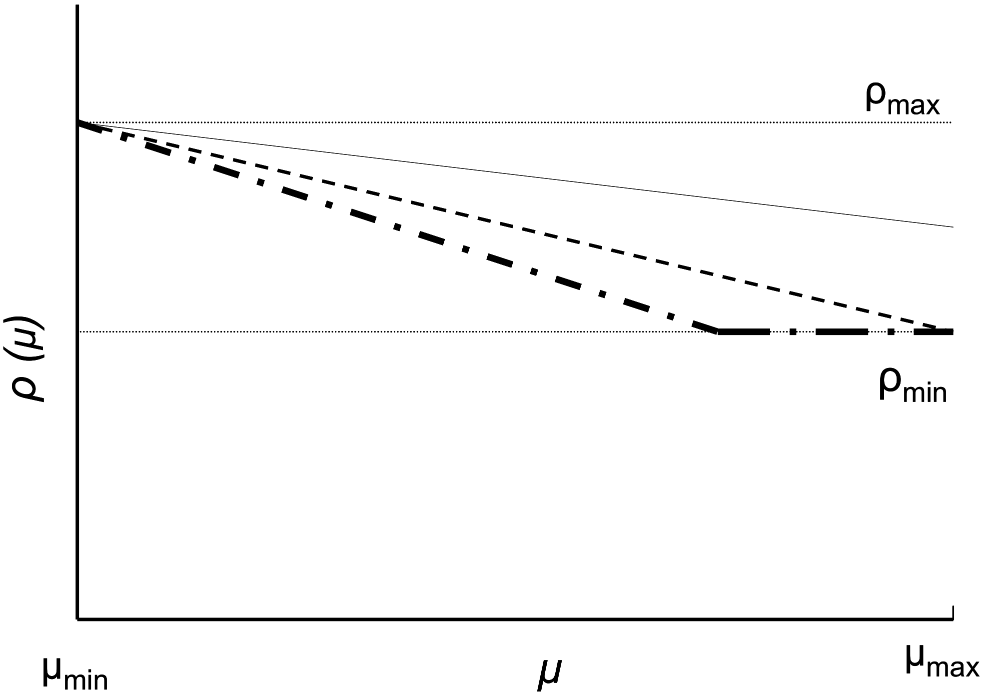


Figure 2. The modelled relation between the internal information state or the animal's assessment of its environment (μ) and the movement parameter ρ.

Shown here are three sensitivities to information state (β): high (thick, dash-dot), intermediate (medium, dash) and low (thin, continuous). The dotted lines give the maximum and minimum ρ values.

Simulations

Resource distributions are modelled at 6 patch sizes (PS), varying from PS = 4, 10, 30, 60, 100, to PS = 200 units, yielding patches a few spatial units in diameter, to patches spanning a hundred spatial units. Number of patches (N) was varied over 3 orders of magnitude, with N = 1, 10 and 100 patches respectively. The search area was 400x400 spatial units, with continuous (torus) boundary conditions. In each of the resulting 18 distribution types, searches were simulated at values from α=0 to α=1 at increments of 0.025, and for each of these at values from β =0 to β=4 at increments of 0.1. Searches were simulated for 10^5 time steps and 10 searches were performed per distribution. Search success, or search efficiency, was calculated as the sum of all encountered resources per unit time, yielding the mean probability to find food.

4.4 Results

In general both the optimal value of old over new information, α, and the sensitivity of the correlated random walk to this information, β, vary with patch size and density irrespective of the exact shape of the local resource density function (figure 3a-d). In most cases searches are effective with high (α>0.8) values of old information over new, and show intermediate to high sensitivity of movement behaviour to this information (β>2.5). Irrespective of local gradients, at the largest patch sizes search performance is independent of both α and β.

Gaussian gradient

In the case of a distribution with a single small Gaussian patch (PS=4) the optimal α ranges from 0.75-0.95. As patch size increases, high values of α remain optimal (α >0.95). This increase in optimal α with increasing patch size from 4 to 8 is seen at all three patch densities, but at the highest patch density this increase of optimal α continues to patch size 12 (figure 3a). While high values of α remain optimal, increasing patch density makes searches at more values of α effective, as can be seen from the increasing region of effective searches (figure 3a).

Given a single patch, the optimal value-range for β increases with patch size between PS=4 to PS=12, and then decreases when patch size increases from 30 to 60 (figure 3a). At higher patch densities search effectiveness becomes independent from α and β. This occurs earlier, i.e. at lower patch sizes, when patch density is higher. Indeed in distributions with 100 patches the search results are nearly independent from either parameter at patch size 20 and higher.

Linear gradient

Searches in distributions with linear gradients yield similar results to those with Gaussian distributions (figure 3). Again the optimal α-value range shifts from 0.75-0.95 with small patch size to 0.9-1.0 with an increase in patch size (figure 3b). Also, again similar to the Gaussian results, an increase in patch density at any given degree of aggregation widens the range of optimal α-values. At diameter 12 and 1 patch, for instance, the optimal region for α is 0.85-0.95, whereas at the same diameter with 100 patches the optimal region is less clearly defined and is slightly lower (0.65-0.95). Finally, as in the Gaussian case, search results become independent from α and β when patch density increases and when patch size increases (figure 3b).

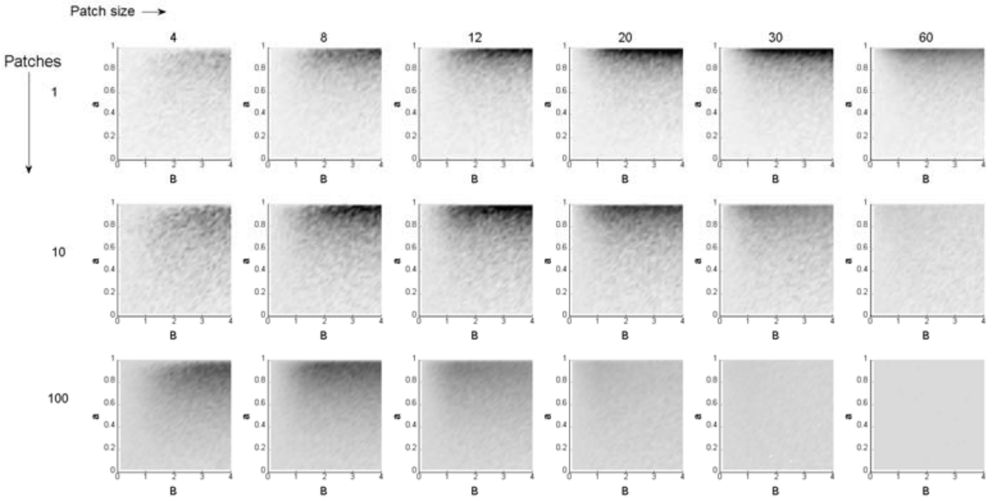
Negative exponential gradient

In a distribution with a single small (PS=4) patch with a local negative exponential gradient it is hard to determine which parameters yield the best search results. Some high search efficiencies are visible around $\beta \geq 3$ and $\alpha=0.6$. As patch size increase, these values increase to $\beta=2.5\text{-}3.5$ and $\alpha=0.6$ and continue to move up until at the highest patch size (60) α values of >0.95 are optimal. This pattern is mirrored at higher densities. The main difference is that at higher densities the pattern is more clearly defined. As in previous results, in distributions with large patch sizes and density search results are independent of α and β.

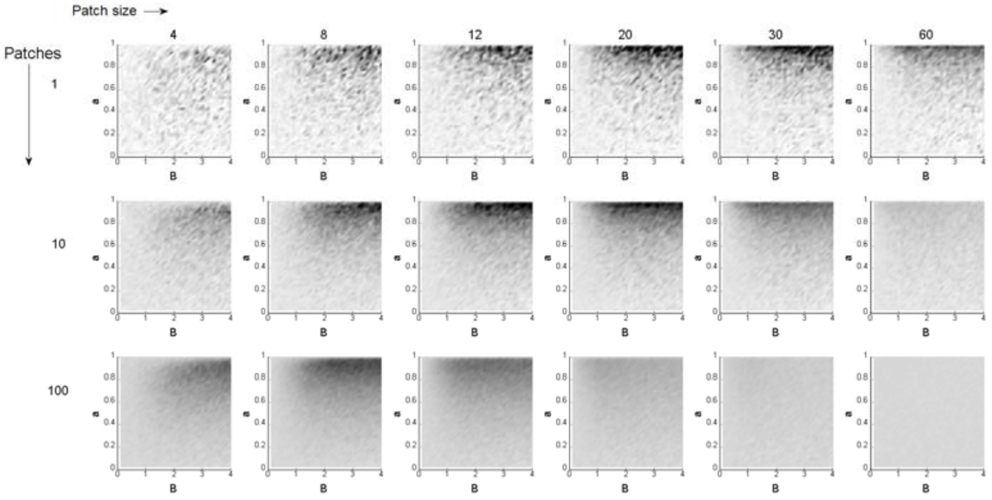
Presence-absence

The results for the presence-absence case are similar to previous results in that at high densities and large patch sizes search results are independent from the search parameters *α* and *β*. In the single patch distributions (N = 1) effective searches are strongly linked to α values of >0.95 and the region of optimality is small. Another difference is the wider range of values of β for which searches are effective, with β values between 1 and 4 leading to relatively efficient search behaviour (figure 3a).

(a)



(b)



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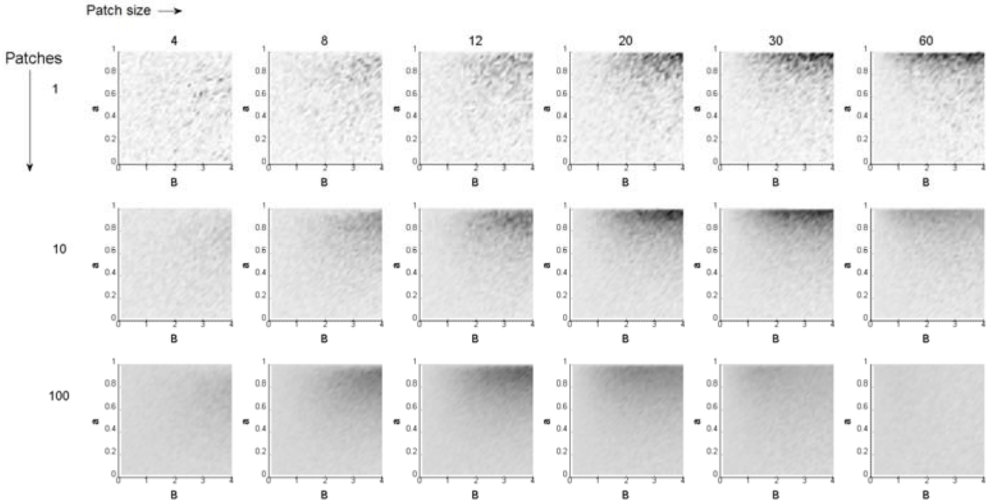

(d)

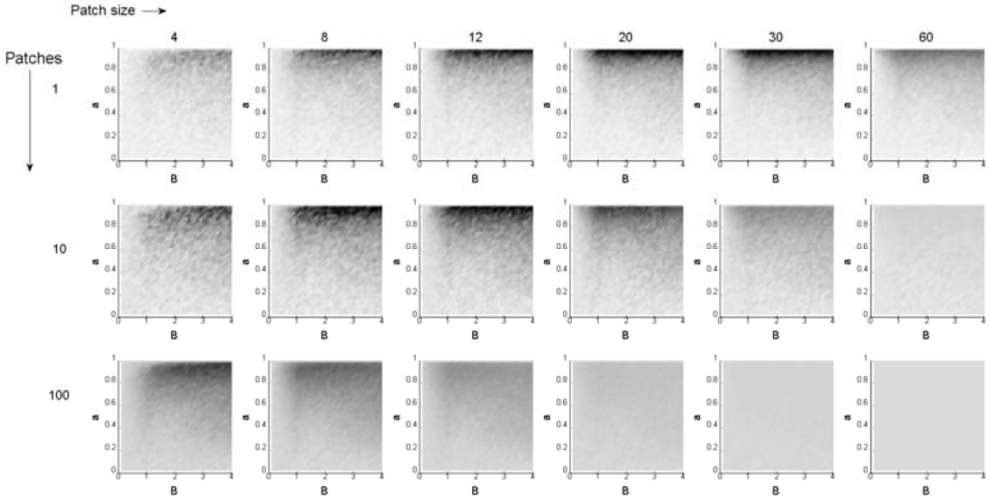

Figure 3. Search efficiency (the darker the cell the higher the number of resources that was encountered) at different values for the effect of information (*β*, x-axis) and the relative value of old over new information (*α*, y-axis). The range of search efficiency is dependent on patch number. With a single patch it ranges from 0 to 1.5, with 10 patches from 0 to 0.6 and with 100 patches from 0 to 0.4. The results are given for searches in (a) Gaussian, (b) linear, (c) negative exponential and (d) binary distributions. The patch

size increases over the columns from left to right and is given at the top of each column. The patch density increases as indicated from top to bottom.

4.5 Discussion

In resource distributions with a continuous local density gradient the optimal value of old over new information is dependent on both patch density and patch size (figure 3a-c). These results alone indicate that an optimal searcher using information on past encounters will have to change its memory strategy to fit the distribution of its resources. In conjunction with previous results (Bartumeus et al 2005; Chapter 2) this means that an efficient searcher should adapt and change its search behaviour to fit the spatial resource distribution, both when using purely random searches like composite random or Lévy walks and when using information on past encounters.

In most of the distributions, regardless of the local resource density gradient, an intermediate to high sensitivity to information was found to be optimal (figure 3). This implies that behavioural flexibility is optimal for searching animals. Since having a relatively high sensitivity to information does not appear to be detrimental in any case, a general rule of thumb strategy for searchers is to be highly sensitive to any resource encounter, which indeed is a behaviour that is frequently observed (Heinrich 1979; Stephens et al 2007).

One of the most important results is that in most distributions it is an advantage to use information on past encounters (figure 3). The only cases in which this was not the case are those where both aggregation is low (patch size is large) and density is high. The results show that there is an increase in the importance of old information (α approaches one) going from small to intermediate patch sizes. The increased importance of old information in cases with intermediate patch size may reflect the need to ignore the lower densities found in the periphery of patches. This is supported by the fact that with patches that follow a negative exponential local resource distribution and therefore have a larger 'periphery', the increase in the value of old information is continuous over the full range from small to intermediate and large patch sizes.

Interestingly, at smaller patch sizes, while it is important to retain a memory of previous results, the response to new information is more important. This leads to a quicker transition into an area restricted search, as well as to an earlier switch from local searches back to long-distance searches. Under both small and intermediate patch sizes the patches may be readily left and retaining information may be understood as a mechanism to increase the probability of revisiting a small patch, similar to how Lévy and composite random walks are efficient because of increased probabilities of revisiting a local resource (Viswanathan et al 1999; Hengeveld 2007). Indeed, observed Lévy and composite random walk movement patterns (e.g., Viswanathan et al 1999; Sims et al 2007) may be the result of a memory updating mechanism similar to the one modelled here.

As density increases search effectiveness became increasingly independent of the relative value of old over new information and sensitivity to information (figure 3). This independence of search results from memory dynamics is caused by the fact that resource distributions with a high patch density start to resemble two-dimensional uniform distributions, in which it indeed does not matter whether movement is straight or tortuous.

The specificity of the interaction between the search and memory strategies on the one hand and the resource distribution on the other hand has certain implications. For instance, if animals search in strongly aggregated and locally high density resources, using optimal behaviour (De Knegt et al 2007), this behaviour may prevent them from effectively finding low local density resources even when they use information on recent encounters. Interestingly, such an effect may have a protective effect on resources, through a type of Allee-effect, since at low densities the prey will be less efficiently found. On the other hand, prey and predators may be likely to adjust their behaviour to their internal state (e.g., hunger or satiation; Stephens 2007) and increase their sensitivity. Thus it is possible that search pattern and information use are dependent on their internal state.

Conclusion

By combining a random search and an information use model we have shown that the specifics of the resource distribution in terms of aggregation and density determine not only which random search is optimal (Chapter 2), but also how information on resource encounters should be valued and responded to. Furthermore, the preferred memory dynamics suggest a possible mechanism for observed Lévy and composite random walks patterns. This study provides a natural expansion of the random movement approach and is simultaneously a step towards integration between optimal and random approaches to foraging and movement.

Chapter 5: Movement characteristics of *Peucilus versicolor* in resource distributions varying in aggregation and density

Huisman, T.J., W.F. De Boer, , H.H.T. Prins, F. Van Langevelde

Abstract

Understanding the interaction between the environment and a forager is one of the main challenges in movement ecology. Theoretical studies indicate that the optimal random search strategy in a given resource distribution is dependent on both the density and the degree of aggregation of resources. Here we tested this hypothesis using an experiment where carabid beetles (*Peucilus versicolor*) forage in distributions varying in degree of resource density and aggregation, whilst their movement is tracked using digital video.

The main hypothesis was that movement patterns of *P. versicolor* change with changing spatial resource distributions to reflect optimal behaviour in any given experimentally manipulated resource distribution. More specifically we hypothesized that with increasing aggregations *P. versicolor* would switch from correlated random walk to composite random walks behaviour. The alternative hypothesis is that movement behaviour of *P. versicolor* is not affected by the specifics of the spatial distribution of resources, reflecting the case where searching animals have fixed behaviour and movement patterns and are unable to modify their behaviour.

P. versicolor movement patterns showed slight variation with resource distributions. However, while statistically significant the differences are not meaningful with similar movement patterns and statistics regardless of the resource distributions. Therefore, based on these results we rejected our main hypothesis that *P. versicolor* movement patterns reflect optimal behaviour and concluded that, at small spatial scales, *P. versicolor* performs a correlated random walk regardless of the spatial resource distributions. This implies that, at least at small spatial scales as in this experiment, the targets or resources for which *P. versilor* is searching are more or less randomly distributed, with very low levels of aggregation. To be able to make more accurate predictions about the influence of the resource distributions on movement characteristics

of a forager it may be necessary to study in more detail the spatial distribution of its resources.

5.1 Introduction

Animal movement determines dispersal speed (Turchin 1998), the spread of invasive species, the size of home-ranges (Osborne et al 1999; Reynolds and Rhodes 2009), the spatial scale of ecological interactions (De Knegt et al 2008; Fryxell et al 2007) and the migration routes of numerous species (Bowlin 2010). There is an increase in data on movements of many species (Sims et al 2007; Getz and Saltz 2008), and together with theoretical developments (Viswanathan et al 1999; Gautestad and Mysterud 2005; Benhamou 2007) this has led to what has been dubbed movement ecology (Nathan et al 2008). Movement ecology deals with the role of movement in ecological interactions and ecosystem functioning as a whole (Nathan et al 2008). Within movement ecology the main challenge is to increase our understanding of the underlying processes that drive animal movements (Gurarie et al 2009; Nathan et al 2008); going from data on movement to understanding of the decisions and causes underlying them. This is especially challenging since extracting the impacts of separate environmental effects on movement from field data is difficult or even impossible. Experiments and theoretical models are needed to determining which factors are likely to be important and how these factors are likely to influence movement characteristics (Gurarie et al 2009).

One aspect of the environment that influences movement patterns is the spatial distribution of resources. Since species' resources are generally aggregated (Prins and Van Langevelde 2008), species are expected to have movement patterns that allow them to efficiently find these resources (Viswanathan et al 1999; Chapter 2). Hence, the movement algorithm generating the highest search efficiency when searching for aggregated resources is a suitable null-model for animal movement (Viswanathan et al 1999; Bartumeus et al 2005; Benhamou 2007; Chapter 2). The popularity of Lévy walks as a model for animal movement was based on their optimality in locating aggregated resources. The movement patterns observed in field studies sometimes fit these patterns derived from theoretical expectations (Osborne et al 2000; Sims et al 2007), but in many cases the fit has been poor or lacking (Edwards et al 2007) which has ascribed to poor methods, sampling frequencies and behavioural changes (Gurarie et al 2009; Lewis et al 2013). In previous work we showed that the effectiveness of random searches depends on the specifics of the spatial distribution of resources (Chapter 2). This casts doubt on the use of a single movement strategy as a null model for movement independent from the environment and hence is an additional explanation for the varying evidence for and against Lévy movement. Here we use these theoretical results to derive a new set of hypotheses for animal movement and test these using experiment with carabid beetles.

Given that the effectiveness of random searches varies with the degree of aggregation and density of resources, the most effective strategy is to change the search movement to suit the current distribution of resources (Chapter 2). However, animals searching only for resources following one specific distribution may not need to, nor be able to, change their movement behaviour. Any given animal may thus be able to change movement behaviour with changes in the resource distribution or perform the same movement pattern regardless of the resource distribution

Our main hypothesis therefore is that movement patterns will reflect the resource distribution. More specifically we hypothesize that in random distributions searches are expected to resemble correlated random walks (Bartumeus et al 2005), and with increasing aggregation, movement is expected to resemble composite random walks or Lévy walks (Chapter 2). Furthermore, since at higher density correlated random walks remain optimal at higher degrees of aggregation (Chapter 2) we expect the hypothesized transition from correlated random walks to composite random or Lévy walk behaviour to occur at higher degrees of aggregation. At higher resource density the transition may not occur at all, since correlated random walk are efficient in higher resource densities.

We test this at two different resource densities and three levels of aggregation. The expectation is that when Lévy or composite random walk behaviour occurs, there will be higher frequencies of longer-distance moves indicative of displacement phases in Lévy and composite random walks (i.e. fatter tails, figure 1; Benhamou 2007). Similarly the turning angle distribution in composite random or Lévy walks, composed as they are of directional and non-directional movement, is expected to result in higher variation in turning angles (figure 2). In the case of a change of behaviour from correlated random walk to composite random or Lévy walk we therefore expect an increase in longer moves and an increase in the variation in turning angles.

In summary, the aim is to determine whether movement of *P. versicolor* the movement changes from a correlated random walk to a composite random walk or Lévy type of movement as the level of resource aggregation is increased from random to aggregated.

5.2 Materials and methods

Experiment

We tested the effect of resource distribution by offering resources at three different degrees of aggregation and two levels of density, yielding a total of six different distribution types. Densities are 20 resources and 80 per 9m^2, or 2.22 and 8.88 resources m^{-2}. Aggregation levels were created by using distributions that corresponded to computer-generated distributions. In these distributions variation in aggregation was created by varying the spatial extend of aggregations. An aggregation has a centre and individual resource points were created by randomly distributing resources in a fixed circle around this point. Changing the diameter of these circles determined the degree of aggregation (Chapter 2). Distributions were random, or aggregated with a diameter of 10 or 20 cm around the centre. In each case the local aggregations had 10 resource points.

P. versicolor

Beetles were caught using pitfall traps in Wageningen, the Netherlands. Traps were set all through spring and summer 2009. Beetles (n=253) were first fed at least three days on mealworms. Before use in the experiment beetles were starved for three days. The individual resource points were 2mm pieces of mealworms. After use beetles were replaced and not used for at least 4 days.

Experimental setup

The setup consisted of a camera, a 60 W light bulb, strip lighting and reflective foil. Strip lighting was located above the entire setup to prevent directional bias based on light-sources. The camera (manufacturer: U-eye, model: LE) was positioned above an experimental arena of 3x3m, filled with a 0.5 cm thick layer of river sand. The camera was used to record the position of beetles with a 2x2 mm strip of reflective foil on their carapace as they walked across the arena. Videos were recorded at 2 frames per second. The video-input was recorded using software included with the camera. The stored video-files were extracted into jpeg picture files using VirtualDub (v. 1.9.6). In every picture the beetle's location was taken as the centre of the reflective foil.

Beetles were released in the centre of the arena. Runs were stopped after 10 minutes or when beetles showed long periods of inactivity (3 minutes). Resource distributions were replaced, but arena sand remained. Ambient temperatures were between 21-23˚C, with an average of 21.4˚C.

Movement data analysis

Movements along and near (within 15 cm) the edge of the arena were not included in the analysis to prevent edge-effects. Movement paths were checked for over-sampling using path-discretization (Turchin 1998; De Knegt et al 2008), with an analysis width set at 1 cm, removing the noise due to over-sampling while leaving the observed movement path close to the continuous path traced by the searcher.

Pair-wise Kuiper-tests were used to test for general differences between the turning angle distributions. These tests and descriptive statistics, such as the mean and standard deviation of the turning angles, were calculated using the circular statistics toolbox for Matlab (Berens 2009). The mean absolute turning angle and the mean cosine of the turning angle were used to determine the directionality in the different treatments. To test if there is an increase in variance of the average turning angle, we calculated the mean cosine of the turning angle and its deviation.

Differences in move length distributions were tested using pair-wise Kolmogorov-Smirnov tests. The distribution of the move length data was analysed by fitting Pareto and exponential distributions, using maximum likelihood methods (Edwards et al 2007; White et al 2008). Variation in move-frequencies was determined by comparison of the complementary cumulative density function (survival function) of the move lengths in the respective treatments.

5.3 Results

Move lengths

Results from pair-wise Kolmogorov-Smirnov tests between the move-length distributions showed significantly different distributions for all comparisons ($p<0.001$ for all treatments; Bonferroni corrected $\alpha=0.003$).

Direct comparison of the complementary cumulative density functions, however, indicated that at lower density the degree of aggregation had little effect on the relative frequency of various move lengths (figure 3), and that the lower density treatments all have similar frequency distributions. The move-length distribution of the searches in the high density, the random distribution treatment was similar to the low density move length distribution. In the high aggregation and high density case, however, there were fewer short moves (1-10 mm, figure 3) coupled with an increased frequency of intermediate moves (10-100 mm). The moderate aggregation, high density treatment showed another distinct pattern with more move lengths in the 20 to 60 mm range, fewer in the 100-500 mm range and then again a higher frequency of longer 800-2000 mm moves.

Turning angles

Pair-wise comparisons showed that the turning angle distributions differed ($p<0.001$ for all comparisons; Bonferroni corrected $\alpha=0.003$). In all cases turning angles were centralized around zero for all resource distributions, each with a small positive deviation from zero.

As opposed to the move lengths, the turning angles distributions were statistically significantly different, but did not have meaningful treatment effects. At both densities and all three degrees of aggregation the turning angles distributions were similar. The lack of effect was confirmed by the mean resultant vectors which all range between 0.72 and 0.76, indicating there is little change in the overall directionality.

5.4 Discussion

We found significant differences between move length distributions of *P. versicolor* in distributions varying in aggregation and density. Variation in aggregation at low density did not, however, influence the move lengths and only at higher density, there were differences between observed movement in low, intermediate and high aggregation (figure 3). More specifically, at high aggregation *P. versicolor* performed fewer short and more intermediate moves than in the random distribution. In the moderately aggregated resource distribution, there were more short-intermediate (20-60mm) then fewer long-intermediate (100-500) and then again more long (800>) moves. These results partly confirm our hypothesized (figure 1) increase in longer moves with aggregation, even though there are longer moves in the moderately aggregated distribution. The variation in the move-length distribution with aggregation might indicate behavioural flexibility. We conclude that the results on *P. versicolor's* move lengths were in part in agreement with our hypothesis, since the overall effect of aggregation is increased move lengths compared to results in random distributions. However, the lack of clear differences at the lower densities is contrary to our null-hypothesis that an eventual switch in behaviour with increased aggregation would occur more readily at lower densities. The contrary evidence here indicates that the effect may be a result of direct sensory interaction between the resources and the searcher (Chittka et al 2009).

The lack of response in the turning angle distributions is in contradiction to our hypothesized increase in fatness of the tails with increased aggregation (figure 2). Aside from our hypothesized effect we might expect a treatment effect in parallel with the found changes in the move length distributions. The absence of such changes indicates that *P. versicolor* can modify behaviour separately through move-length and turning-angle distributions.

Overall we conclude that our results support the alternative hypothesis that *P. versicolor* does not change its search strategy in response to changes in the distribution of resources. Especially the reversal in the role of density and the lack of effect in lower density makes the partial prediction of increased move lengths seem to be tentative. It seems likely that the observed changes in the move length distribution have their root cause in the direct interaction between resource and searcher. Furthermore, the similarity of the low density results to the resulting move length distribution in the high density random distribution suggests that these results represent a lack of a treatment effect, indicating that movement pattern is independent of the resource distribution. If the movement behaviour is indeed innate and fixed, we can then hypothesize that the movement patterns, which resemble correlated random walks, are optimal in the spatial distribution of resources utilized by *P. versicolor*. The correlated random walks may therefore indicate that this distribution is either random or lightly aggregated or highly abundant (e.g., Bartumeus et al 2005; Chapter 2).

Searches that are independent of the resource distribution or aggregation are unexpected however, since this can lead to loss of efficiency by not intensifying searches in aggregations and by spending too much time walking through empty areas (Turchin 1998; Chapter 2). Indeed, previous studies and field data showed that movement patterns change depending on local conditions, with increased search effort in rich or suitable environments (Turchin 1998; Reynolds and Rhodes 2009). Therefore our results may instead provide indication that *P. versicolor* reacts to factors correlated with resource presence rather than resource presence or encounter itself. Reacting to humidity levels may, for instance, allow *P. versicolor* to more readily find little insect prey, without the need for reacting to or tracking the encounter-rate.

An alternate explanation of our results is that the scale of the experiment and the spatial scale at which the beetles respond to stimuli do not correspond. Previous coarse-grained movement studies on radioactively labelled *P. versicolor* revealed that these beetles have a directional persistence and locally search on time scales in the order of days (Brunsting 1985). Combined with the lack of variation in the experimental data, this may indicate that an analysis on scales of hundreds rather than several meters may reveal the expected interactions between searcher and resource distributions. To test whether this is the case requires movement measurement on larger scales, such as done with harmonic radar on bumblebees (e.g., Osborne et al 1999).

A problem with experimental testing is the extent to which the results reflect actual natural conditions and behaviour. In our experiment beetles were allowed to forage for food and indeed did find and eat it, still it is possible that the experiment did not offer the required environment to study responses to differences in resource distributions. Considering the lack of shelter most of the measured behaviour may, for instance, have consisted of displacement behaviour in search of more suitable habitat instead of habitat selection or resource searching behaviour (Van den Bosch 1992; Brown 1999). Careful testing of the influence of cover may reveal the extent to which the ecology of fear applies to movement patterns of carabid beetles.

Concluding, our results indicate that on small spatial scales *P. versicolor* movement behaviour is hard-wired as a correlated random walk type, which leads to the hypothesis that their food resources (small seeds, insects) are randomly distributed at such spatial scales.

Acknowledgements

The authors would like to thanks B. Allema and W. Rossing for their help in setting up the experiment, use of equipment and field captures.

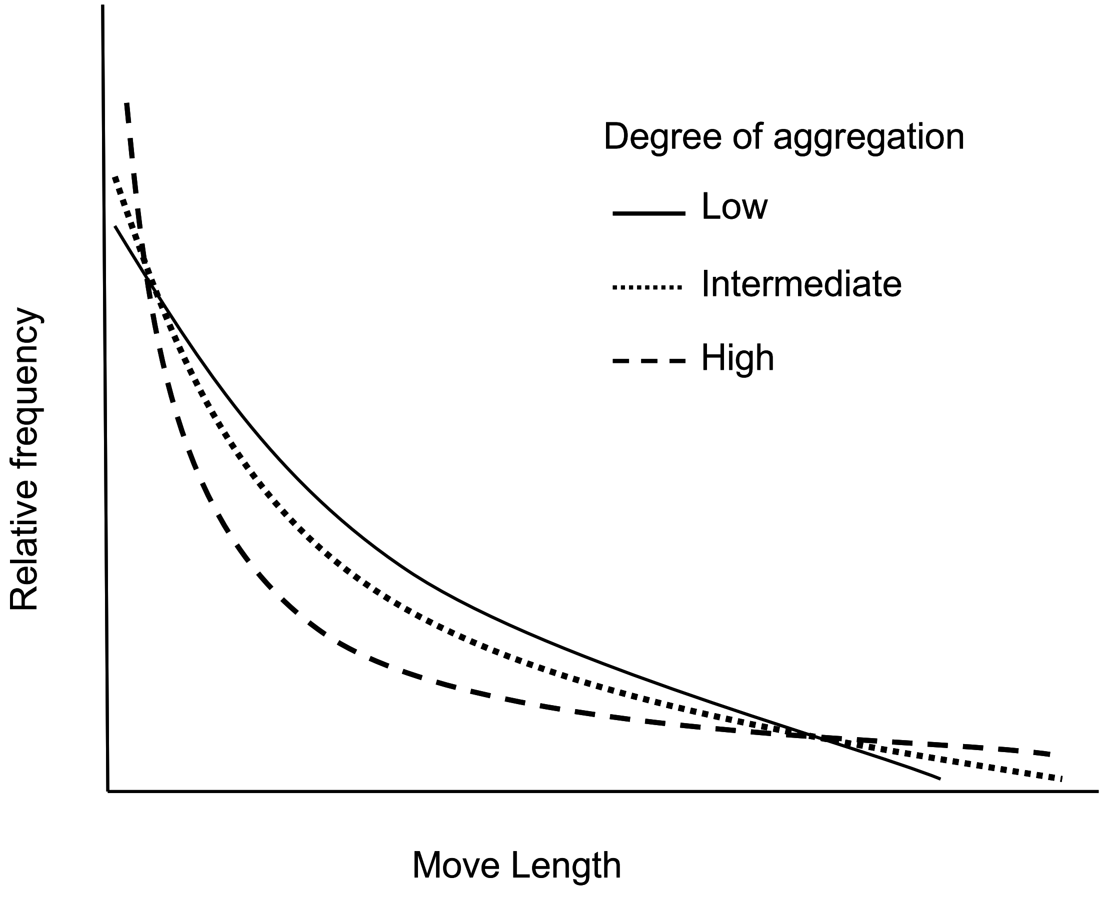

Figure 1. Schematic overview of the expected effects of aggregation on move length distributions. Increased resource aggregation (from random, to intermediate to high levels of aggregations) is expected to lead to increased frequencies of short moves as

well as higher frequencies of longer distance moves, i.e. fatter tails.

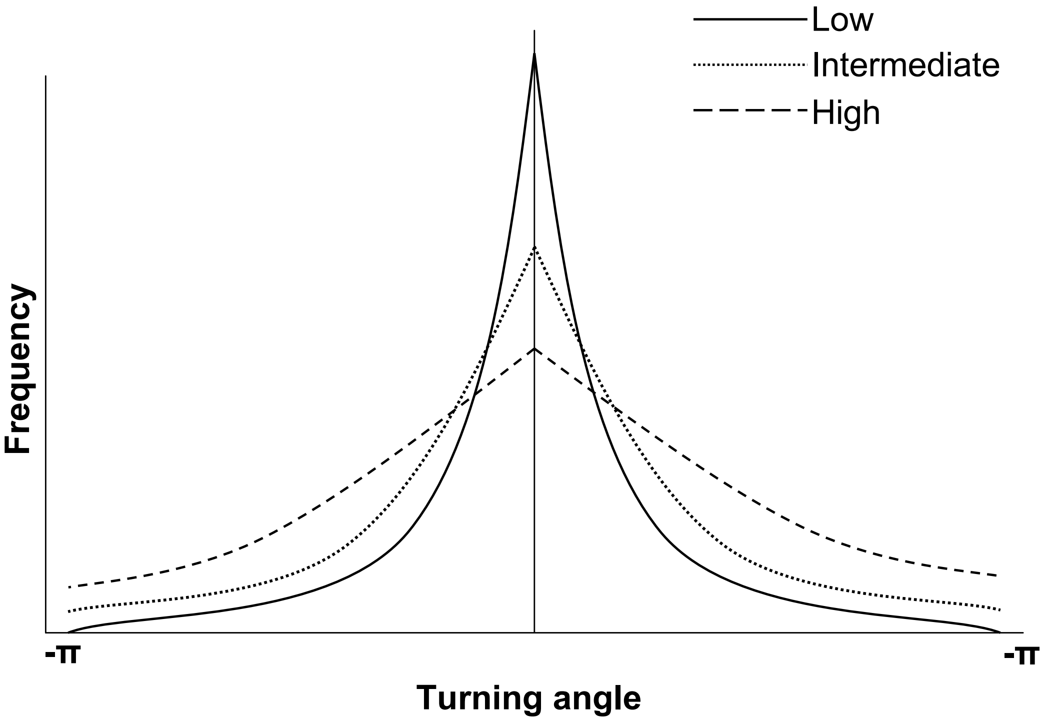

Figure 2. Schematic overview of expected turning angle distributions. The general expectation is a change from concentrated around zero to a wider distribution of turning angles with increasing level of aggregation. This results in decreased frequency of near-zero turning angles and higher frequency of larger turning angles. The increase in larger turning angles at higher levels of aggregations is expected to be more pronounced at lower density than at higher density.

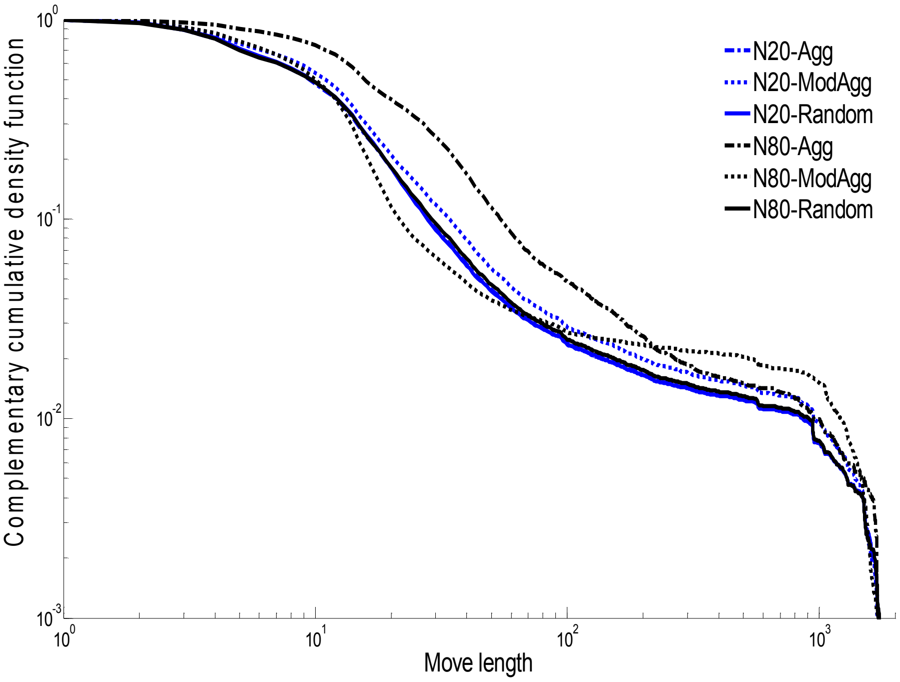

Figure 3. The complementary cumulative density function (CCDF; survival function, tail-function) of the move lengths. This gives the fraction of observed move lengths larger than the move length on the x-axis. Changes in frequency over a trajectory indicate a high frequency of moves with these lengths. The low density treatments are in blue, higher density in black. Aggregation level is indicated by linestyle; continuous denotes aggregated, dotted moderately aggregated and striped random distributions.

Chapter 6 Animal movement in ecology

6.1 Introduction

Animal movement connects ecosystems on scales ranging from the microscopic movement of flagellates (Bartumeus et al 2003) to migrating birds traversing whole continents (Wikelksi 2000). Movement connects the flower and the bee, the predator and its prey, sexual partners with each other and mosquitoes with their pond. On the other hand, movement is also what connects an agricultural pest with its favoured host and the group of elephants with the farmer’s crop (Osborn and Parker 2002). Through movement a mosquito is not only connected with the pond, but also with the unfortunate animal or human that is its intended meal. Indeed movement is what spreads vector-borne diseases such as malaria, dengue and Lyme across a landscape (Gratz 1999; Gubler 2002; Mardulyn et al 2013), and movement determines how the invasive species spreads into a new territory (Holway and Suarez 1999; Davis 2009). Movement, in short, is a fundamental part of ecology and of direct relevance to public health, nature conservation and wildlife management as well as scientific understanding of population dynamics, dispersal and indeed any ecological interactions that requires the actors to come into contact (Tilman and Kareiva 1997; Schick et al 2008; Nathan 2008; Gurarie et al 2009).

6.1.1 Spatial ecology and movement ecology

Despite the fact that movement plays a central role in ecology it has been a focus for research only in the last decades (Kareiva and Shigesada 1983; Patterson et al 2008), with a surge of studies in recent years (Giuggioli and Bartumeus 2010; Lewis et al 2013). We see that early ecology and biogeography has mainly been concerned with the connection between occurrence and abiotic factors (Begon et al 2006). Movement and space are completely absent from many classical models for population dynamics, which assume movement and spatial dynamics can be ignored by making the ‘well mixed’ assumption common in elementary physics. Despite or because of their simplicity such models are still in use, for instance in the illustration of possible catastrophic shifts (Scheffer et al 2001) and modeling of population dynamics (Turchin 2003; Abrams 2005).

Even with the development of spatial ecology (e.g., Tilman and Kareiva 1997) and spatially explicit models, movement itself was often subsumed by population level redistribution through kernels and migration rates (Kot et al 1996). The analysis of spatial processes using aggregated distributions has provided essential insights into the importance of spatial structure and migration speeds (Van den Bosch 1990; Kot et al 1996; Hanski 1992). However, the absence of the actual (spatial) process by which various ecological interactions occur is unsatisfactory since it yields explanations on the explanatory level itself (DeWit 1968; Hengeveld and Walter 1999). To extend knowledge beyond the observation stage into projections and even actual predictions, it is necessary to have an understanding of the processes at a lower explanatory level (De Wit 1968). In the case of dispersal, migration and indeed foraging this requires studying the actual movement process as part of ecological processes, shifting from the population point of view to the individual (or from an Eulerian to a Lagrangian perspective respectively; see also Turchin 1998).

While some early studies used telemetry data or radioactive marking (e.g., Dixon and Chapman 1980; Brunsting 1982), acquiring movement data was difficult and frequently research had to rely on repeated sightings and, for instance, marking and recapturing animals (Kareiva 1983). The last decade's surge of interest in individual movement (see e.g., Schick et al 2008; Sims et al 2007; Mandel et al 2008; Avgar et al 2013; Van Moorter et al 2013) is thus partly triggered by the availability and use of new lightweight tracking devices (Wilson et al 2006). The whirlwind of new technology and data in combination with new hypotheses and framework from theoretical studies have occasioned this new field of inquiry to be dubbed movement ecology (Nathan et al 2008). The central subject of inquiry in movement ecology is the interaction between movement and environment (Nathan et al 2008), which is also the central subject of this thesis.

6.1.2 Interaction between movement and environment

The interactions between resources and movement have been studied before in various disciplines, for instance, in invasion and dispersal studies (Van den Bosch et al 1992; Kot et al 1996), biogeography (Lomolino 2000), metapopulation theory (Ovaskainen 2008), conservation biology (Hanski and Simberloff 1997) and optimal foraging theory (Stephens et al 2007). From these studies we know, for instance, that the spatial arrangement of habitat patches can influence the survival probability of populations (Van Langevelde 2000; Hanski 2002), the rate of spread of populations (Hengeveld and Van den Bosch 1997) as well the reproduction of ovipositioning parasitic wasps (Vos and Hemerik 2003). As noted, the main difference between these approaches and the one adopted in movement ecology and in the current thesis is that the previous approaches all used an Eulerian perspective, and that current movement ecology is more concerned with individual movement, and uses the so-called Lagrangian approach (Turchin 1998).

6.1.3 Central focus and themes/subjects in this thesis

In this thesis the central focus is on movement and more specifically the interplay between resource distribution and random or informed searches. The aim is to understand how variation and changes in the spatial resource distribution affect the performance of searches, and subsequently from this understanding derive expectations and hypotheses to be tested in experimental settings.

To this end I have taken basic models of the random search paradigm (Nathan et el 2008) both as pertaining to the movement (Turchin 1998; Viswanathan et al 1999; Bartumeus et al 2003) and the distributions of resources (Zollner and Lima 1999; Raposo et al 2003), and used them to study the effects of variation in both density and aggregation of resources on search performance (Chapter 2). After having established the importance of the spatial properties of the resource distribution I followed the call to expand the random search paradigm to include other approaches from ecology (Nathan et al 2008). Using methods from foraging theory (Iwasa et al 1981) I studied the effect of variation in patch size on random search effectiveness (Chapter 3). Finally I combined a foraging theory based information use model and random movement model to study the importance of information on search performance in resource distributions varying in aggregation and density (Chapter 4). Experiments were performed in which carabid beetles were faced with variation in resource density and aggregation, highlighting the various expectations and hypotheses following from the previous results (Chapter 5).

In the following sections I will first review the results and findings of this thesis by subject, highlighting the most important consequences for further research. Subsequently, I address landscape- and resource distribution models in movement ecology and stress their importance in movement ecology and its extension and integration with other fields of ecology.

6.2 Effectiveness of random searches in structured spatial distributions

6.2.1 Background and model formulation

Random searches have received considerable attention in the last decade as possible models to understand the new wealth of movement data (Schick et al 2008). Lévy walks, in particular, have received considerable attention (Edwards et al 2007, Sims et al 2007,Reynolds and Rhodes 2009), since they were shown to be optimal search patterns in patchy distributions (Viswanathan et al 1999). Additionally, Lévy walks can generate various different movement patterns using a single shape parameter, some of which are scale-free (Viswanathan et al 1999). There has been considerable debate whether organisms perform Lévy walks (Benhamou 2007, Edwards et al 2007, Sims et al 2007; Reynolds and Rhodes 2009), and composite random walks have been proposed as a more appropriate model for animal movement (Gautestad and Mysterud 2005, Benhamou 2007). In this thesis it has been shown that optimality of random searches changes and depends on the spatial resource distribution in terms of density and aggregation (Chapter 2) as well as on variation in patch size (Chapter 3). This places previous arguments for Lévy walks as the most efficient random search pattern into context, with the set of resource distributions in which Lévy walks are optimal forming a subset of all relevant resource distributions (Viswanathan et al 1999; Benhamou 2005). This means that it is not possible to use a single movement model as null-model for animal movement based on effectiveness in a specific distribution. Rather than a single hypothesis for all non-informed searches these results show that specific distributions require specific movement behaviour in order to be optimally searched (figure 1). The results from Viswanathan et al (1999) are valid only for the specific spatial landscape model used, and even down to the specific regrowth time (see Raposo et al 2003).

The link demonstrated between distribution properties and movement also has possible implications for herbivores and predator search behaviour and the spatial distribution of their respective foods, allowing for suitable evolutionary strategies for both predator and prey (Scharf et al 2012). Searching predators that use, for example, a composite random walk pattern, make it attractive for prey to disperse. Conversely, if predators search with a correlated random walk it becomes attractive for prey to aggregate. Naturally this logic can be reversed from the predator's point of view.

Alternatively in a dynamic system with relatively high predator or herbivore pressure the spatial distributions may change, through over-predation to ones in which the previously employed movement behaviour becomes inefficient. A previously contiguous and relatively dense area of forage may, for instance, turn into fragmented patches of remaining forage. Animals searching for this resource using their, previously effective, correlated random walk would suffer from decreasing search efficiency on top off declining overall resource density. Naturally this would have a stabilizing effect on predator-prey dynamics.

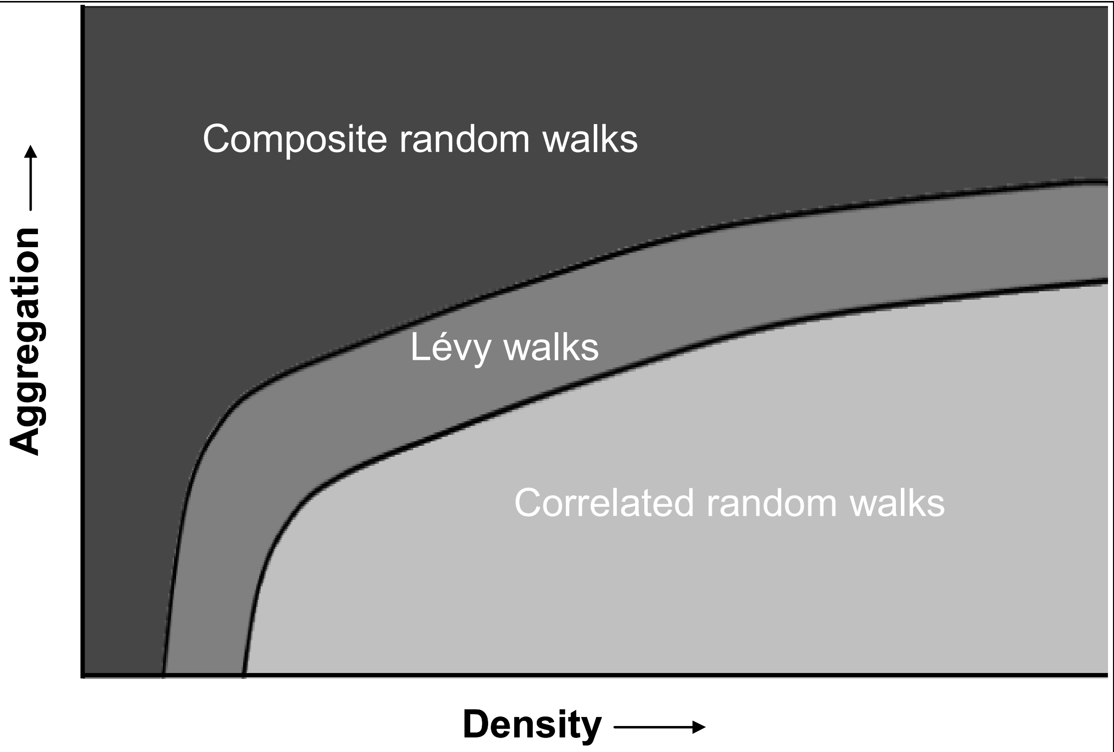

Figure 1. A schematic overview of the interactive effect between moments of the

resource distribution in terms of resource density and aggregation on the effective random movement strategies (Chapter 2). Aggregation and density increase over their respective axes.

6.2.2 Search results dependent on interaction between density and aggregation

Aside from the general result that searches are effective in particular spatial distributions it has also been shown that search effectiveness is determined by the *interaction* between resource density and aggregation (Chapter 2). This means that changes in the spatial distribution through e.g., habitat destruction or eutrophication (Britton 2013) may have effects that are not predictable by only considering the fraction of habitat destroyed. Depending on the type of movement species will experience a drop in the availability of resources that is higher or lower than the fraction of habitat actually destroyed. A distinct difference will be between those animals that are able to change movement patterns and those that are not. An animal able to do so, based on direct or past experience, could optimize their foraging results through modifying their movement to reflect the habitat changes. The influence of changes in habitat distribution will thus depend on the flexibility of the animal in terms of search behaviour, the type of change in spatial structure in terms of aggregation and the total amount of habitat. This means that the ubiquitous ongoing habitat destruction and fragmentation (Laurence 2010; Krauss et al 2010) will have higher impact on species unable to modify their movement pattern. On the other hand, species that are able to successfully modify their behaviour may persist longer than would be expected based solely on fraction of habitat destroyed.

6.3 Experimental testing and movement data

The development of new tracking methods and technology has resulted in an enormous increase in field movement data (e.g. Cooke et al 2004 Sims et al 2007; Schick et al 2008; Cagnacci et al 2010). Analysis of such tracking data can reveal interesting behaviours. It can, for example, show us that elephants have daily patterns in relation to topography (De Knegt et al 2008), or that bumblebees travel substantial distances with possibly scale-free circular patterns (Osborne et al 1999; Reynolds 2009). Similarly GPS and telemetry data allows the mapping of migration routes and potentially even the collection of the entire life's movement path (Wikelski et al 2007). It is clear that GPS tracking is a magnificent tool for studying and analyzing animal behaviour, habitat use and migration. It is a challenge, however, to connect such movement data to a theoretical framework in a meaningful way (Morales and Ellner 2002; Gioguli and Bartumeus et al 2010). Manipulation of landscape level factors is possible (e.g., Osborne et al 1999), yet exceedingly difficult. To provide a connection between theory and the field data it is, therefore, necessary to do small-scale experiments to test theoretical studies and provide a bridge between field data and theoretical studies (Turchin 1998). In Chapter 5 we therefore tested the link between resource distribution and consumer movement patterns established in Chapter 2 with such an experiment. The main question being whether changes in the resource distribution affects the movement patterns of a carabid beetle (*Peucilus versicolor;* Chapter 5). If observed movement patterns changed with and reflected resource distribution this would be indicative of behavioural flexibility in response to disparate demands on search behaviour. There was, however no congruent influence found, and movement patterns closely resembled correlated random walks in all cases. Based on these results *P. versicolor* movement behaviour is thought to be inflexible. Within the framework set up with the results from Chapter 2 (see also Bartumeus et al 2003) this implies that the resources for which *P. versicolor* is searching have a more or less random distribution.

It should be noted that experimental tests of movement patterns suffer from scale-issues as well as possible behavioural problems. The necessarily small-scale nature of such experiments can be problematic since it is unclear at what scale what kind of behaviour will take place, and if results are readily transferable to larger spatial scales (Morales and Ellner 2002; De Knegt et al 2010). Furthermore results of such experiments do not readily transfer to field-systems since searching animals may be responding to abiotic factors corresponding with the presence of food-items (Lewis et al 2013), or other factors such as safety (Brown et al 1999).

In conclusion, the results from this experiment demonstrate that organisms employing random walks have several possible strategies to follow, none of which is optimal in all conditions. This leads to several behavioural options and associated hypotheses for movement paths of animals.

Path discretization and turning-angle and move-length distributions

As noted above, ecologists can track more and more species, greater numbers of animals, for longer periods of time and with higher sampling rates and accuracy (Schick et al 2008; Holyoak et al 2008). Given that turning angles reflect the rate of change in direction, measurement at higher temporal resolutions will yield smaller turning angles. An important consequence is, however, that in order for move-length and turning-angle data to be comparable across species, locations and even across different soft- and hardwares, ecologists need to be able to convert distances between sampling locations into some form of biologically relevant ‘moves’ (Turchin 1998). Ideally these moves represent the navigational decisions of the animal and are biological properties which should not be affected by the measuring equipment used. Previous studies suggested several ways to go from movement paths to biological moves, such as using the computational power of the human brain, correlation tables, and discretization until higher order autocorrelation disappears (Turchin 1998; De Knegt et al 2008). While this last method has also been used in the analysis of movement data for this research (Chapter 5) it does not provide an entirely satisfactory solution to the problem of identifying movement path properties that are independent from the temporal resolution used for tracking. This is because the discretization width (figure 2a) is chosen to yield ‘acceptable’ outcomes. This is not ideal and indeed Turchin (1996) recommends testing for higher-order auto-correlation to determine the appropriate discretization width. It is not, however, clear how this will reduce time-series to a series of navigational decisions. This is not a trivial point, since the differences between various move-length and turning-angle distributions based on what are considered ‘moves’ can be substantial (figure 3).Recently, analysis and identification of behavioural stages (e.g., Gurarie et al 2009) has been developed and such an approach may provide a better construct for deriving navigational decisions, which after all are behavioural, from movement data. Such an analysis could change existing move-length distributions substantially.

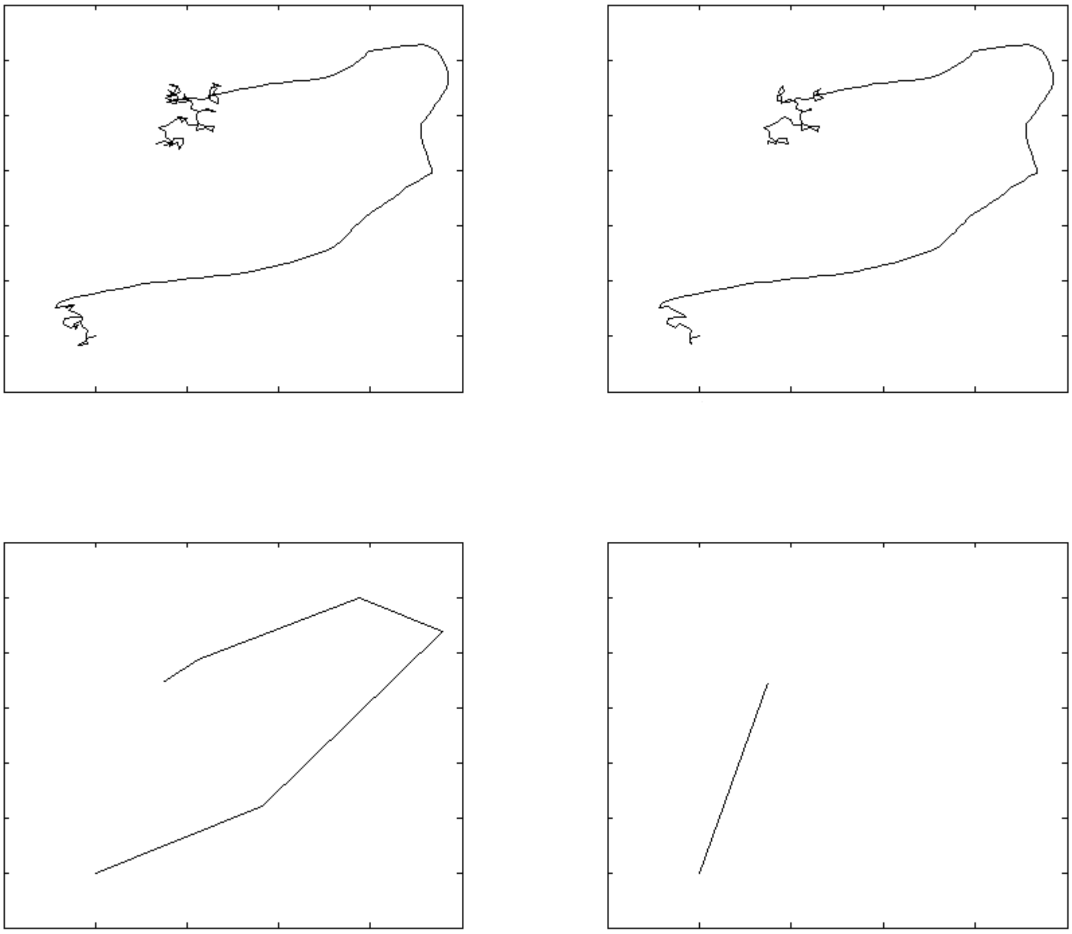

Figure 2. Illustration of the effect of discretization on a simulated path that combines correlated random and composite random walks. The original path (top left panel) clearly shows the displacement and local search phases. As discretization width *(dw)* increases, some movement in the area-restricted searches is removed (top right, *dw=1*), then the area-restricted searches themselves (bottom left, *dw=8*) and finally all movement detail except for the single displacement from starting point to end point (bottom right, *dw=50*).

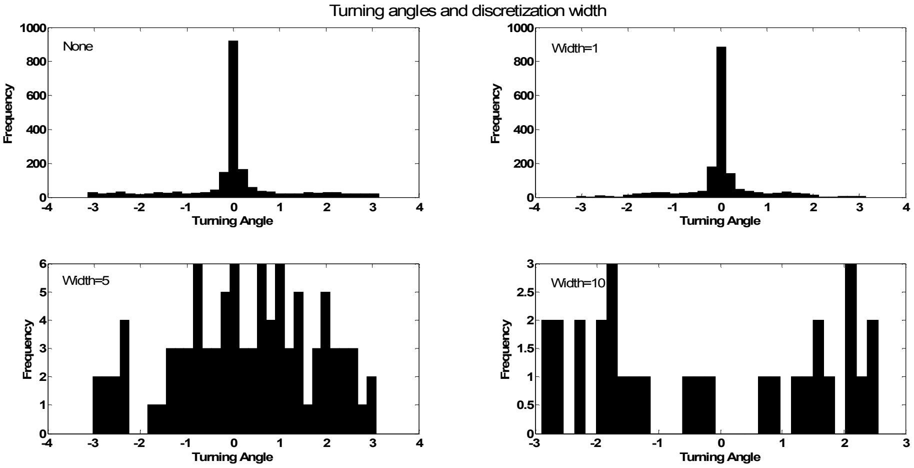

Figure 3. Turning angle distributions of the same movement path as given in figure 2 for different values of the discretization width (*dw*). The top left panel shows the distribution if there is no discretization. The top right panel shows the turning angle distribution for *dw*=1, the lower left for *dw*=5 and lower right for *dw*=10. As discretization width increases the turning-angle distribution moves from centered around zero to uniform, congruent with the effect of decrease in sampling rates.

6.4 Variation in patch size and random searches

In order to expand on previous work on patches in movement ecology, methods were taken from foraging theory, which has worked with and within the patch framework for decades (Iwasa et al 1981; Stephens et al 2007). Interestingly, the result showed that it is not the variance in patch size that influences search efficiency, but the skewness of distribution of patch sizes (Chapter 3). In other words, if variation in patch size is symmetrical across the mean searches can effectively employ a single strategy, whereas this is relatively inefficient when patches are often very low and occasionally very high in abundance (Chapter 3).

This finding is important because negative binomial and other asymmetrical distributions of local abundances are known to occur frequently in nature; fish catch data and populations, for instance, often have negative binomial distributions (Hilborn and Mangel 1997). Indeed within a species' range, its numbers are well described by negative binomial distributions (Pielou 1977; Vos and Hemerik 2003; Ollson and Brown 2006) and foragers exploiting prey with such distributions are likely to be common in nature (Ollson and Brown 2006).

Another significant result of introducing variation in patch size is that composite random walks are nearly twice as effective as Lévy walks. This is all the more interesting since composite random walk behaviour is basically switching between intensive and extensive searches, or searches for and within patches (e.g., Scharf et al 2009). Once again (Benhamou 2007; Chapter 2), simple composite random walks are a more effective search strategy than Lévy walks. There should be however an explanation for the evidence that Lévy searches are performed by animals (Viswanathan et al 2008). A possible explanation for this discrepancy may be that observed Lévy walks are the result of composite random walks at various spatial scales (Viswanathan et al 1999; Sims et al 2007). In that case a behavioural framework such as the one propounded by Scharf et al(2012), which is similar to composite random walks and previous patch-use foraging models (e.g., Iwasa et al 1981), could be responsible for search patterns with power-law properties over multiple spatial scales.

6.5 Information use and searcher-resource interaction

6.5.1 Background of model formulation

The use of information is the basis for optimal foraging theory (Stephens et al 2007) in which optimal solutions to foraging problems are derived from assumptions of perfect information (Charnov 1979; Iwasa et al 1981; Stephens and Krebs 1986). More recent studies in foraging theory have, however, moved from models in which animals have complete information to models dealing with imperfect and updated information (Olsson 2006; Stephens 2007; Ollson and Brown 2010).

Random walk approaches, on the other hand, use no information whatsoever and in that sense are the antitheses of optimal foraging models. Indeed in the simplest of search models there is no interaction between resources and searcher and the search result is merely a count of passed-over resource-points (Hengeveld 2007). This ‘passing-over’ is the most consistent random search model since it does not make any assumptions about the interaction between the targets and the searcher, nor about the behaviour of either after their encounter. Interestingly, in such cases Lévy walks are not optimal since their long-distance search phases are not interrupted (Hengeveld 2007; Bartumeus et al 2005). This last point is crucial since the search models stop the current displacement upon encounter with a target. This is a very natural assumption, but also crucial to the efficiency of Lévy walks and indeed any search pattern with long displacement phases (Hengeveld 2008). In many ways it is this response to encounters that lies at the heart of biological searches and in this interaction that biological searches will diverge from models from particle physics (de Jager et al 2013).

In a recently proposed framework, animal movement was divided into several parts, the animal's motion capacity, the navigation and the internal state (Nathan et al 2008; Giogguli and Bartumeus 2010). Using this terminology Lévy walks (not Lévy flight) and composite random walks actually have a very simple internal state model, namely a linearly-decreasing time counter, which is reset upon encounter with resources. The efficiency of composite random and Lévy walks compared to correlated random walks is partly due to the use of information that is possible due to this internal state (Hengeveld 2007). Stopping the current move is possibly the simplest of responses to new information and leads to efficient search behaviour as long as resources are patchily distributed and patches can be considered equal (Chapter 4). This part of composite random and Lévy walks is perfectly captured in recently discussed long/short movement models (Scharf et al 2009).

I argue that a logical area for expanding the random search approach in movement ecology (Nathan et al 2008) is exactly in the response of animals to such encounters; that is to say in the use of information after encounter. As was the case with variation in patches (Chapter 4), the use of information has been studied and modeled in foraging theory (Stephens 2007) and provides a fitting theoretical model for use in this context. The study shown in Chapter 4 is thus a natural expansion of the random movement approach and is simultaneously a step towards integration between optimal and random approaches to foraging and movement.

6.5.2 Sensitivity to new information and spatial patch size, density and distribution type

Just as the effectiveness of random searches was shown to depend on both resource aggregation and density and the interaction between them (Chapter 2), it was found that the optimal response to encountered resources is a function of resource density, the patch size, and the resource distribution type (Chapter 3). There is not, therefore, a single response to encountered resources that allows animals to efficiently search all resource distributions. Nevertheless it was shown that in all distributions it is an advantage to use information on/from past encounters, which makes this quite a likely trait to have evolved. Taking it a step further, our results also suggest that an animal able to actually modify its sensitivity to new information *will* be able to effectively use quite a variety of resource distributions. It is entirely possible that a simple link exists between, for example, hunger and sensitivity to information regarding the presence of food; indeed foraging theory shows that previous experience and satiation have pronounced effects on food selection (Stephens et al 2007).

Another interesting result in this context is that the most effective behaviour when patches are small involves high sensitivity and long retention leading to slightly prolonged local search. The longer retention increases the probability of visiting a local resource aggregation, an approach identical to local searches of Lévy walks and composite random walks which generally have a fixed expected local search time (Viswanathan et al 1999; Hengeveld 2007). Indeed, observed Lévy and composite random walk movement patterns (e.g., Viswanathan et al 1999; Sims et al 2007) could result from a memory updating mechanism similar to the one modelled here. It should be noted that the information-use model actually functions to model both the reaction to encounter new resources and the reaction to the absence of new findings (i.e. leading to the departure from this patch). In foraging theory the latter function is usually performed by a patch-departure rule (Iwasa et al 1981; Stephens and Krebs 1986). The explicit movement and information model from this chapter can be compared with implicit models from foraging theory.

6.6 Landscape and resource distribution models

The particulars of models used to represent the spatial resource distribution plays a pivotal role throughout this thesis. Indeed throughout the thesis the properties of the resource distribution are the independent variables. The way in which these properties were varied depends on the model used to describe them, Chapters 2-5). It is in this emphasis on the properties of the resource distribution that is the central contribution made in this thesis. This attention to the landscape is wholly justified since many if not all animals are faced with spatial variation in abundance and quality of resources (Prins and Van Langevelde 2008) and this heterogeneity is a fundamental part of the study of ecology (Begon et al 1996; Elith and Leathwick 2009). Understanding the effects of this variation is therefore one of the premier tasks for movement ecology (Nathan et al 2008). This is the more pressing since ongoing habitat destruction, fragmentation and degradation causes profound changes in the spatial distribution and again understanding and predicting the effects of such changes requires and understanding of the effect of the spatial resource distribution. In each chapter, the results show that the properties of the resource distribution affect which movement strategy is effective, demonstrating the importance of the spatial resource distribution when considering movement and search models. Despite this importance most frameworks dealing with movement are focused on the actual movement of the animal and the relation of this movement to their decisions, abilities and internal state (Nathan 2008; Schick et al 2008; Gurarie et al 2009). These properties cannot, however, exists separately from the medium in which animals move. It is especially pertinent for moving animals, where the structure of the landscape in terms of substrate, topography and vegetation will have direct effects on the motion capacity as well as on perception and navigation, and on its internal state (see giving-up densities Brown et al 1999). No framework for movement ecology is complete without explicit and due consideration of the landscape. Therefore in the following section I review the models used to represent the resource distribution both in this thesis and in movement ecology generally.

6.6.1 Patch-based resource distribution models

There are numerous ways in which landscapes can be translated to more, or less, abstract maps and distributions (Dale et al 2002) and the development of GIS has vastly expanded the possibilities of working within detailed maps and datasets (De Knegt et al 2008). In theoretical and experimental studies this heterogeneity is often reduced to ‘patches’ of habitat in a matrix of non-habitat or low-resource density. The patch-concept and model is used in dispersal and biogeography (McArthur and Wilson 1986; Lomolino 2000), metapopulation theory (Hanksi 1992; Ovaskainen et al 2008) and is central to optimal foraging theory (Charnov 1979; Stephens and Krebs 1986; Stephens et al 2007). The concept of a 'patch' is one that is widely used and well-known, and understood by all ecologists, and is also used in movement ecology. Yet, even where the simplification of a landscape into matrix and patches is accepted, there is variation in the specific way in which a patch is modeled or represented. In movement ecology the patch model has been used in the form of either simple 'regrowing' point resources (Viswanathan et al 1999; Bartumeus et al 2005) or equal circular patches (Zollner and Lima 1999). More importantly, it has been assumed that all patches are equal (Bartumeus et al 2005; Benhamou 2007), an assumption which is not borne out by spatial resource patterns (Fryxell et al 2007; Prins and Van Langevelde 2008). The study in Chapter 4 is the first model in movement ecology (using foraging theory; Iwasa et al 1981) to include variation in patches, including uniform and negative binomial variation. Again the results indicate that neglecting this type of variation yields results that will have limited bearing on animals in the field. When using a patch model to study movement and search efficiency it is necessary to specify precisely how the patches are modeled, and indeed how and if they respond to the visits (see e.g., Raposo et al 2003).

6.6.2 Quo vadis; a whole array of possible representations

Models of landscapes and the subset that is the resource distribution are not limited to the patch-concept. Distribution may be modeled using grids which are assigned various densities following a certain distribution, even on different scales (Van Langevelde 2000). Other models are fractal landscape distributions, generated using among others Lévy distributions (Sims et al 2007). Yet another type is based on gradients (Talley 2007), a type that includes the landscape model used in Chapter 3 which is my attempt at providing a flexible and powerful method of representing landscape variables. There are many landscape elements that potentially influence movement, including topography (De Knegt et al 2008), abiotic conditions (e.g., temperature), and the distribution of resources (Schick et al 2008; Bailey and Provenza 2008; Gurarie et al 2009), and the challenge is to select those elements most relevant to the research and species in question. In a sense the variation in the models (see figure 4) reflects the complexity of landscapes, and the challenge for theoretical studies will be to develop insight into the consequences of the landscape aspects on the movement process so that proper simplification is possible.

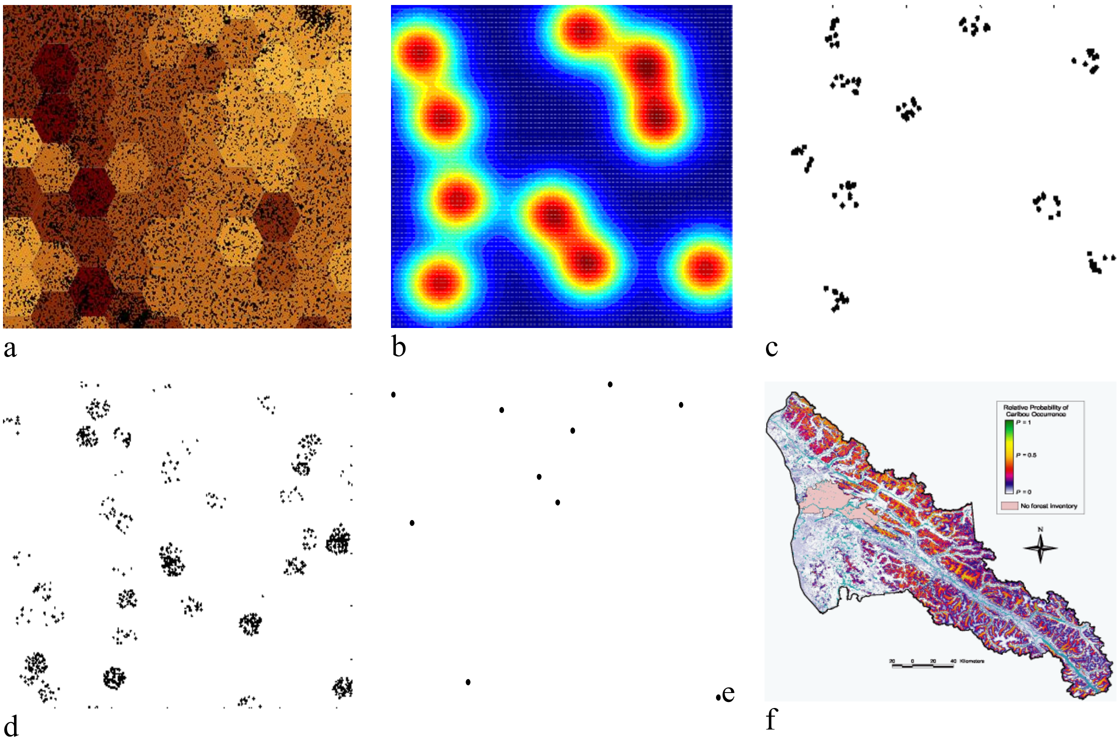

Figure 4. An illustration of the variation in models that can be used for resource distributions. They are (a) Juniper Patches with landscape shape index (Hugh Stimson 2008), (b) Gaussian patches (Chapter 3), (c) equal explicit patches of 10 resource points (Chapter 2), (d) Negative binomial patches (Chapter 3), (e) (f) Relative probability of Caribou occurrence (Johnson, UNBC).

This is research field in which empirical data of movement paths, aided by GIS and remote sensing data will have a distinct role, yielding insights into many interesting connections and observations (De Knegt et al 2008).

For theoretical movement ecology and especially the random movement approach to expand to other disciplines (Nathan 2008), the landscape model will require a more systematic approach to landscape modeling than has been practice in movement ecology. Landscape and animal movement are two sides of the same coin (figure 5).

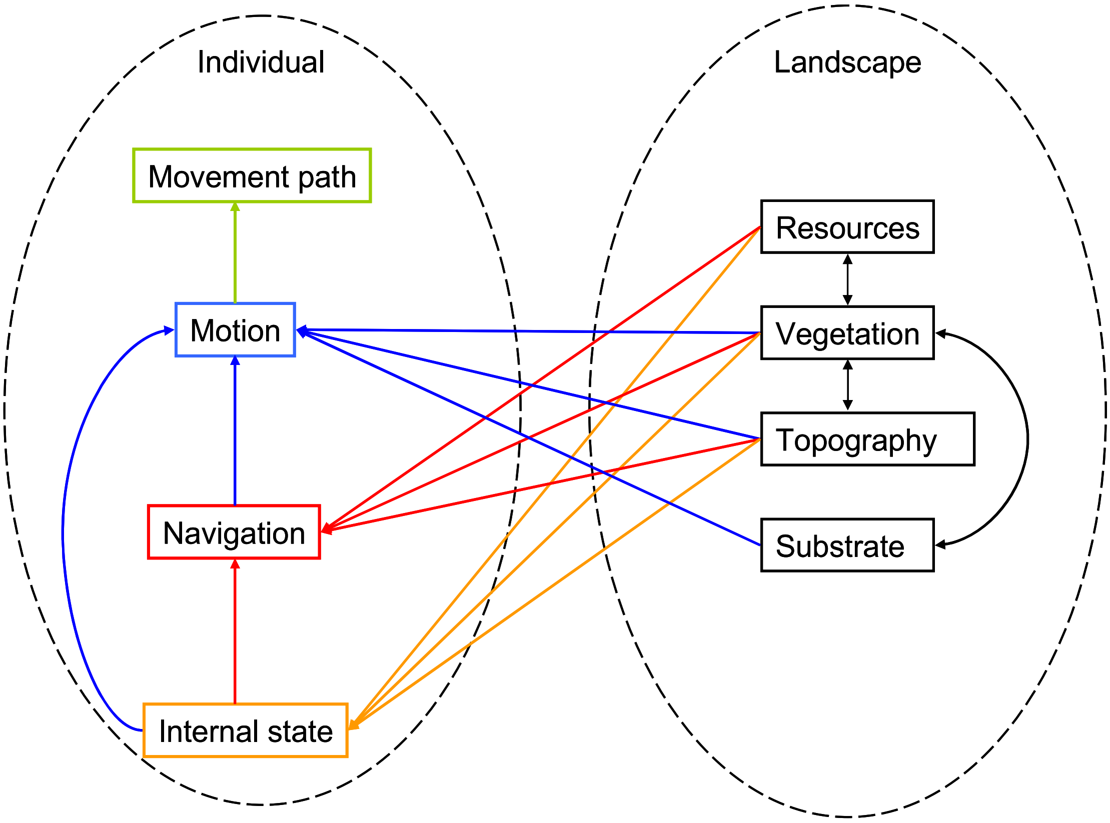

Figure 5. The landscape model is as important as the model for the moving individual. Various aspects of the landscape are shown to illustrate likely influences. The task for movement ecology is to determine which factors are most important (Based on Nathan 2008)

6.7 Conclusion

The overall aim of this thesis was '*to understand how variation and changes in the spatial resource distribution affect the performance of searches, and subsequently derive from this some expectations regarding field observations and hypotheses to test in experimental settings'*. This has been achieved for both random and density-dependent searches in various models for the spatial resource distribution, both continuous and point-resource based. It is clear that variation in the spatial resource distribution affects the various random searches disparately, with each random search performing optimally in a certain set of resource densities and degrees of aggregation (Chapters 2 and 4). Thus expectations for movement patterns in the field depend in turn on the expected resource distributions, and vice-versa observed patterns may be linked to the distribution of the sought-for resources (Chapter 5).

More generally, the findings in this thesis further stress the importance of including previously ignored aspects of the resource distribution into studies of optimal search behaviour. Aggregation (Chapter 2) and variation in patch size (Chapter 3) all have been shown to determine effectiveness of searches, even when taking into account recent experience (Chapter 4). An optimally searching animal will have to use information to try and change its movement and adapt it to the current resource distribution. This stresses that while the interaction between landscape and searcher is central to movement ecology (Getz and Saltz 2008; Lewis et al 2013), theoretical models have placed too much focus on movement. An accurate model of the interaction between an animal and its resource distribution, even in relatively simple cases, will require both to have their due place.

Interestingly this attention to landscape and its role in movement ecology provides a natural area in which the random movement approach can be extended (Chapters 3 and 4), namely with the specifics of how movement should change upon encounter with a sought-for resource. The studies in Chapters 3 and 4 are examples of how the different ‘fields’ of movement ecology and foraging theory share similar problems and can cross-pollinate. Indeed important elements of foraging theory such as patch residence times, patch departure as well as expected travel times (Charnov 1979; Stephens and Krebs. 1986) may be revisited using movement models (see also Bartumeus et al 2013).

Ultimately, by including landscape elements more rigorously and integrating movement ecology with existing fields such as invasion biology (Zhou and Kot 2013) and foraging theory I believe it will be possible to truly include the movement process into ecological explanations and understanding, finally enabling researchers to provide clear first principle explanations and predictions not only for ecology, but also for the benefit of epidemiologists, nature conservation and wildlife management and thus for society as a whole.

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Summary

In the last decades research into movement has taken flight in ecology. The development and miniaturization of tracking devices has enabled ecologists to collect and store the movement data of a large and increasing number of animals and species. Next to this increase in available data new theoretical models have been developed and discussed at length in the ecological literature. These developments together form what has been called “movement ecology”. The research in this thesis falls squarely within this new field.

In movement ecology there has been a lot of attention for the analysis of movement paths and the comparison of these paths with random walks, which were first used for describing the random movement of particles in physics. These random walks were compared with respect to their ability to encounter resources (e.g. food items); the idea being that those random walks that are more efficient will have more encounters and will through natural selection be more likely to occur in nature. In the analysis of their search efficiency there was, however, relatively little attention for the spatial resource distribution. Especially when my PhD-research started only some basic models were used to describe the spatial resource distribution and used to test the effect on the search performance of random walks. For my research I therefore set myself the aim of determining how the spatial context influences the search efficiency of the main random walks used in ecology through simulation and to test this using experiments.

The first analysis of search efficiency with varying resource density and aggregation as described in chapter 2, shows that search efficiencies are dependent on both the resource aggregation and density as well as on their interaction. These results show that any analysis of search efficiency requires specification of both density and degree of aggregation. Furthermore, the effect of changes in either density or aggregation on the availability of resources may not be straightforward (e.g. linear with density). An optimally searching animal will have to switch between different random searches, depending on the resource distribution.

The next step (chapter 3) was to determine the influence of the spatial resource distribution when it was described and approached from the “patch” framework that is

ubiquitous in ecology. In this framework it is the distribution of patch sizes (number of resources) that creates variation in the spatial distribution of resources.. The results show that it is not the variance in patch sizes, but the skewness of the patch-size distribution that determines the long-term search results of random walks. This is highly relevant since such skewed distributions are often seen in the distribution of plants, animals and resources. In addition the results indicate yet again that different distributions are best exploited by different random walks, and an efficient searcher would thus change movement depending on the spatial resource distribution.

Random walks are used for particles in physics and do not use information. Many animals do, however, use additional information in their search for food or resources. The use of information in foraging has been mainly studied in foraging theory. In chapter 4 I again studied the influence of the spatial resource distribution, but now with the searcher using information on past encounters. For this model I combined a random walk model with an information-use model from foraging theory. The results show that even when a searcher uses information on recent encounters an optimally searching animal will have to change its sensitivity depending on the spatial resource distribution.

On the basis of the simulations in the preceding chapters, for chapter 5 I conducted an experiment with carabid beetles. The beetles were allowed to forage in distributions varying in density and aggregation. The main hypothesis was that their movement patterns would change to be optimal in the respective distributions. The results showed, however, that the beetles did not change their movement behaviour with changes in the offered distribution. Based on this we expect the beetles' main resource to have a distribution that is efficiently searched using their movement pattern, which means that their resources are expected to have a random spatial distribution, with relatively high density.

Finally in the 6th chapter I review the results from the previous chapters and conclude that optimal searchers need to adapt to the resource distribution when they use random searches or information on past encounter. I argue for more emphasis on and explicit study of the spatial distribution in movement ecology, and for integration of movement ecology and foraging theory to study the how foragers should deal with aggregation which is the fundamental challenge for both foraging theory and movement ecology .

Ultimately, by including landscape elements more rigorously and integrating movement ecology with existing fields such as invasion biology and foraging theory I believe it will be possible to truly include the movement process into ecological explanations and understanding, finally enabling researchers to provide clear first principle explanations and predictions not only for ecology, but also for the benefit of epidemiologists, nature conservation and wildlife management and thus for society as a whole.

Samenvatting

In de afgelopen decennia heeft het onderzoek naar bewegingspatronen in de ecologie een vlucht genomen. Door de ontwikkeling van alsmaar kleinere gps-transmitters en chips worden tegenwoordig de bewegingsgegevens van een enorm aantal dieren en soorten opgeslagen. Naast deze enorme toename in beschikbare gegevens is er een ontwikkeling geweest in de theoretische modellen die besproken en gebruikt worden in de ecologische literatuur. Al deze ontwikkelingen tezamen vormen de nieuwe subdiscipline van de zogenaamde bewegingsecologie en het onderzoek in dit proefschrift valt precies onder deze noemer.

Nu is in de bewegingsecologie veel aandacht gegeven aan analyse van bewegingspaden en de vergelijking van die paden met de paden van zogenaamde ‘random walks’ ofwel toevalsbewegingen, afkomstig uit de natuurkunde. Deze toevalsbewegingen worden dan onderling vergeleken op hun vermogen om hulpbronnen (bijvoorbeeld eten) te vinden, met het idee dat toevalsbewegingen die daarin efficiënt zijn, door natuurlijke selectie een hogere kans hebben om voor te komen in bewegingspaden van dieren. Bij de analyse van deze efficiëntie werd er echter weinig aandacht gegeven aan de ruimtelijke context waarin de paden voorkwamen. Vooral aan het begin van het promotie-onderzoek was dit beperkt tot een aantal simpele modellen van verspreiding van hulpbronnen. Voor mijn promotie-onderzoek stelde ik mijzelf dan ook als taak om de invloed van de ruimtelijke context, met name zoals uitgedrukt in de hoeveelheid en mate van clustering van ‘hulpbronnen’, op de zoek-efficiëntie van de belangrijkste toevalsbewegingen te bepalen. Dit aan de hand van modellen en getoetst door middel van experiment.

In hoofdstuk 2 beschrijf ik de eerste analyse van de zoek-efficiëntie van theoretische bewegingsmodellen waarbij zowel de dichtheid als de mate van clustering (aggregatie) variëren. Het blijkt dat de invloeden van dichtheid en aggregatie op de zoek-efficiëntie van toevalsbewegingen niet onafhankelijk zijn van elkaar en ook nog eens sterk verschillen afhankelijk van het precieze bewegingsmodel. Dit laat zien dat het nodig is zowel dichtheid en aggregatie te specificeren voor elke analyse van zoek-efficiëntie. Daarnaast betekent het dat veranderingen in de verspreiding van hulpbronnen complexe effecten kan hebben op de beschikbaarheid van hulpbronnen (d.w.z. niet-lineair met dichtheid). Een optimaal zoekend dier zal afhankelijk van de verspreiding van hulpbronnen een andere toevalsbeweging moeten gebruiken.

De volgende stap was een onderzoek naar de invloed van ruimtelijke verspreiding wanneer die beschreven en bekeken wordt vanuit het alom gebruikte ‘patch’ concept in de ecologie. De verdeling van patch-groottes kan dan verschillende vormen aannemen. In dit hoofdstuk laat ik zien dat op de lange termijn alleen sterk scheve verdelingen een invloed hebben op de te verwachtten zoekresultaten van toevalsbewegingen. Dit is hoogst relevant aangezien zulke scheve verdelingen de norm zijn als het gaat over verspreiding van dieren, planten en hulpbronnen in de ecologie. Opnieuw blijkt ook dat efficiënt zoeken in verschillende ruimtelijke verspreidingen verschillende zoekpatronen vergt.

Toevalsbewegingen worden gebruikt als model voor deeltjes in de natuurkunde en zijn compleet willekeurig en maken geen gebruik van informatie. Voor veel dieren is het gebruik van informatie juist een onderdeel van het zoeken naar voedsel. Het gebruik van informatie bij foerageren is voornamelijk onderzocht in de foerageertheorie. In hoofdstuk 4 kijk ik opnieuw naar het effect van de ruimtelijke verspreiding van hulpbronnen, maar nu als er informatie gebruikt wordt bij het bepalen van de daadwerkelijke beweging. Om dit te bestuderen heb ik de toevalsmodellen voor beweging gecombineerd met één van de informatie-gebruik modellen bekend uit de foerageertheorie. Opnieuw blijkt hoe belangrijk de ruimtelijke verspreiding van hulpbronnen is voor effectiviteit van de zoekpatronen. Zelfs als een zoeker gebruik maakt van de recente geschiedenis zal het nodig zijn om de gevoeligheid voor die informatie aan te passen ten einde optimaal te zoeken.

Op basis van de modelstudies in voorgaande hoofstukken, met name hoofdstuk 2, heb ik een experiment uitgevoerd waarin loopkevers in verschillende distributies konden foerageren. De centrale hypothese was hierbij dat een optimaal zoekend organisme de bewegingspatronen zal aanpassen aan de verspreiding van hulpbronnen. Zoals in hoofdstuk 5 te lezen is, blijkt dat loopkevers hun gedrag niet aanpassen aan de aangeboden verspreiding van hulpbronnen. Daarom is de verwachting dat de belangrijkste hulpbronnen van de kevers in de natuur een verspreiding hebben die efficiënt doorzocht kan worden met hun zoekpatroon, wat in dit geval betekent dat de verwachting is dat die hulpbronnen willekeurig verspreid zullen zijn, met een relatief hoge dichtheid.

Tenslotte breng ik in hoofdstuk 6 de verschillende resultaten en inzichten samen en concludeer ik dat optimaal zoekende dieren zich aan moeten passen aan de verspreiding van hulpbronnen. Dit geldt als ze pure toevalsbewegingen gebruiken alsmede bij het gebruik van informatie van recente gebeurtenissen. Ik benadruk de behoefte aan het expliciet bestuderen van de ruimtelijke verdeling van hulpbronnen en naar een combinatie en integratie van bewegingsecologie en foerageertheorie, welke zich beide bezig houden met het fundamentele probleem van hoe dieren om kunnen gaan met aggregatie.

Uiteindelijk geloof ik dat, door het landschap grondiger mee te nemen en door bewegingsecologie te integreren en combineren met bestaande subdiscplines zoals de “invasion biology” en foerageertheorie het mogelijk zal zijn om het bewegingsprocessen daadwerkelijk in de ecologische bewijsvoering en verklaring op te nemen. Hierdoor zullen onderzoekers eindelijk in staat zijn om verklarende modellen te maken en daar voorspellingen uit af te leiden, wat niet alleen de ecologie zal helpen, maar ook epidemiologen, natuurbescherming en wildbeheer en uiteindelijk de maatschappij in zijn geheel.

Acknowledgements

Het schrijven van een proefschrift is een persoonlijke proeve van bekwaamheid en kan een lange en soms eenzame aangelegenheid wezen. Uiteindelijk echter gebeurd niks in compleet vacuüm en in de woorden van John Donne:

"*No man is an island entire of itself...*"

Voor het (kunnen) doen van mijn onderzoek ben ik dan ook velen dank verschuldigd voor hun bijdrage, hulp, bemoedigende woorden en steun.

Ten eerste en in het bijzonder geldt dit voor mijn copromotoren Frank en Fred; zonder jullie was die proefschrift er niet geweest.

Frank jij bent door de jaren heen altijd een klankbord en sparringspartner geweest en ik heb altijd met veel plezier met je gesproken over van alles en nog wat. Naast (tijdens?) werk was er ook tijd voor squash hoewel ik er in al die tijd nooit in geslaagd ben om een fatsoenlijke overwinning te boeken. Eens komt de dag dat ik je nog eens ga verslaan, maar afgezien van daarvan nogmaals bedankt voor alles.

Fred, jij was net als Frank er altijd met goede feedback en commentaar. Je combinatie van professionaliteit enerzijds en persoonlijk contact anderzijds maakt je de beste copromotor die een promovendus kan wensen. Ondanks de ongetwijfeld soms frustrerende tijden heb je nooit opgegeven en toch altijd weer die extra stap gedaan. Nog afgezien van de rest zal ik je hiervoor altijd dankbaar zijn!

Herbert, zoals je tijden geleden aangaf is de verdediging van oudsher een retorische opgave, of proeve, waarin de kennis, logica en het retorisch vermogen van de kandidaat getoetst worden. Meer dan alle anderen gaf jij leven aan deze kant van de wetenschap waar het plezier in redeneren, denken, verhalen en anekdotes, en een zekere mentale lichtvoetigheid de boventoon voert. Bedankt daarvoor alsmede voor de kans, de inzichten en de discussies!

My time at the REG has been a great one mainly because of all the great people I met there, thanks Ignas, Herman, Pim, Sip, Tom, Milena, Anne-Marie, Farshid, Priya, Eduardo, Namgail, Anil and all others for making it a magical time. Bedankt ook Gerda, dankzij jou was papierwerk regelen gezellig en dat deed je dan meestal met een lach (ok soms misschien een grimas). Bedankt Patricia voor je hulp en vriendelijkheid. Special thanks go to the initial group I started with, Ralf, Robert, Rudy, Mariaan and Jasper. It was a great time to start off with you all sharing a love for nature, science and life.

Jasper, tijdens de promotie was jij mijn REG-roomie, wetenschappelijke partner-in-crime en bovenal vriend. Bedankt voor alle mooie tijden. Ik wil je slechts één ding vragen: doe alsjeblieft nooit meer onderzoek waarbij het noodzakelijk is dat we muizen een nieuw kapsel geven in de vrieskou om 4 uur 's nachts!

Kyle, thanks for good company, that squashball and generally for being genuine. Vincent, I never did manage to come close to beating you at squash (only because of Kyle's ball of course) so I still owe you a cake!

De experimenten met kevers zouden onmogelijk zijn geweest zonder de hulp van Bas en de Farming Systems Ecology Group, het facilitair bedrijf en de proefboerderij, waarvoor dank! Ook bij mijn werk aan/met hommels, wat helaas niet meer terug te vinden is in dit proefschrift, heb ik van verschillende mensen en groepen hulp gehad. Hierbij wil ik graag Tim en Koppert bedanken voor zijn en hun (hulp met de) hommels. My thanks to the researchers at Rothamsted for their interest and willingness to discuss movement and bumblebees. Verder ook dank aan de Wageningse Bijengroep voor hun raad toen mijn hommels ietwat recalcitrant bleken.

Tijdens mijn onderzoek heb ik met verschillende mensen in groepen gewerkt aan uit elkaar lopende onderwerpen. Dankzij jullie, Wopke, Lia, Bas, Lennart, Joel waren die groepsessies éen van de beste ervaringen van mijn promotie-tijd, bedankt!

Tenslotte wil ik graag mijn familie en vrienden bedanken voor hun steun en het draaglijk houden van het bestaan. Aan mijn ouders: Een goed begin is het halve werk en in die zin was en is mijn werk altijd al half af, bedankt voor alles! Bedankt Patrick, Hellen, Marc, Joeri, Vincent, Tim, Egil, Noortje, Annemarie en al mijn vrienden hierboven voor jullie steun, inzicht en gezelschap. Het leek soms een eeuwigheid te duren, maar het is nu dan toch klaar en nu het eindelijk af is kan ik hopelijk vaker langskomen zonder het gevoel te hebben dat ik aan het werk zou moeten zijn.

Fiona, you were there throughout and have seen the good and the bad, the highs and the lows. Thanks for being there during both, keeping me grounded either which way.

"No man is an Iland, intire of itselfe; every man is a peece of the Continent, a part of the maine; if a Clod bee washed away by the Sea, Europe is the lesse, as well as if a Promontorie were, as well as if a Manor of thy friends or of thine owne were; any mans death diminishes me, because I am involved in Mankinde; and therefore never send to know for whom the bell tolls; it tolls for thee."

John Donne, Devotions upon Emergent Occasions, Meditation XVII

About the author

Tom Jesse Huisman was born on the 6th of February 1981 in Oosterhout, the Netherlands. He grew up in the north of the Netherlands, and headed south to study Biology at Wageningen University, as well as a brief period of studying philosophy at Nijmegen University. Biology won out over philosophy and within his studies he mainly focused on modelling population dynamics and spatial ecology. He researched dispersal models, invasive species, and the population dynamics of mangrove forests to obtain his Msc.

The PhD-research described in this thesis started at the Resource Ecology Group in 2007 and was a continuation of his work on spatial and population dynamics. Since 2011 he has been working on an enterprise to develop win-win approaches to spatial planning and land use. His interests in ecology and biology have developed into a love for horticulture and gardening and he continues to do small-scale experiments in mixed cropping in the tradition of C.T. de Wit.

Publications

Huisman, T.J. 2011. Universities: challenges to the last guild in a new information age. Volume 59, Issues 1–2, March 2012, Pages 3–5

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PE&RC Training and Education Statement

With the training and education activities listed below the PhD candidate has complied with the requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 32 ECTS (= 22 weeks of activities)

Review of literature (6 ECTS)

- Optimal foraging theory, animal search and foraging efficiency

Writing of project proposal (4.5 ECTS)

- Spatial resource distribution and search efficiency

Post-graduate courses (3 ECTS)

- Introduction to bumblebee research (2007)
- Consumer-resource interactions; PE&RC (2010)

Laboratory training and working visits (0.5 ECTS)

- Bumblebee rearing; Koppert, the Netherlands (2007)

Deficiency, refresh, brush-up courses (3 ECTS)

- Complex population dynamics (2008)
- Ecological detective (2009)
- Introduction to ecological design (2010)

Competence strengthening / skills courses (1.5 ECTS)

- Sollicitatiecursus (2013)

PE&RC Annual meetings, seminars and the PE&RC weekend (0.9 ECTS)

- PE&RC Meeting (2007
- NERN; oral presentation (2011)

Discussion groups / local seminars / other scientific meetings (5.5 ECTS)

- Ecological theory and application (2007)
- Quantitative analysis of movement (2007-2010)

International symposia, workshops and conferences (3.2 ECTS)

- Workshop Carabid tracking; the Netherlands (2008)
- GTO; Germany (2012)

Lecturing / supervision of practical's / tutorials (3 ECTS)

- Wildlife resource management (2010)
- Animal ecology (2007-2011)