MOVING TO EAT

animal foraging movements in a heterogeneous environment

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Contents

1 Moving to Eat, optimal foraging and environmental heterogeneity

Geerten M. Hengeveld

For many animals, the food supply is heterogeneous in both the spatial distribution, the composition of (macro-nutrients) and the temporal availability. This heterogeneity provides animals the possibility to make choices on (1) what to eat, (2) where to eat and (3) when to eat (Schoener, 1971; Pyke *et al.*, 1977; Stephens & Krebs, 1986). These choices allow animals to influence the timing and location of foraging and the time that they can spent on non-foraging activities. In most natural conditions, food availability is limiting individual animals in their daily routines (Stephens & Krebs, 1986). This limitation is quantitative, qualitative, spatial and temporal. Quantitative because the requirements of the animal are so high that it has to eat a large part of the day to meet these requirements. Qualitative because the requirements of the animal for different (macro-)nutrients or for minimum quality are such that not all potential food is acceptable. The spatial distribution of potential food forces animals to move between different locations where food is available. Finally, the availability of food is mostly dependent on the timing of climate and the life-cycle of the food creating temporal variability in the availability of different types of food (Pulliam, 1974; Pyke *et al.*, 1977; Stephens & Krebs, 1986).

By strategically choosing what, where and when to eat, animals can increase the time that they have available for activities other than foraging, either at shorter or longer time scales, and plan activities at locations and times that are more suitable (Pyke *et al.*, 1977; Stephens & Krebs, 1986). It is therefore to be expected that foraging behaviour can create a fitness gradient within an animal population, *i.e.*, animals that make choices that increase their total intake of nutrients or have more time available for non-foraging activities like vigilance or courtship and mating behaviour, can increase their fitness relative to animals that made different choices (Stephens & Krebs, 1986). If fitness differences exist, transmitting the traits that cause these differences to offspring (either genetically or through learning or culture) can cause a selective advantage for animals exhibiting fitness increasing traits. In the course of evolution the foraging behaviour within a population should then become such that they anticipate and utilise the heterogeneity of forage in an optimal way (MacArthur & Pianka, 1966; Stephens & Krebs, 1986). Based on this assumption we can use mathematical models that describe (parts of) the foraging behaviour of animals and that capture the essence of the heterogeneity of food, we can predict which behavioural patterns 'optimal' animals should follow in a particular situation.

Foraging is a process that has many aspects and that takes place at various temporal and spatial scales (Schoener, 1971; Pyke *et al.*, 1977; Senft *et al.*, 1987; Bailey *et al.*, 1996). At most of these scales, choices about what and where to eat are being made by an animal. Different models of optimal foraging have thus focussed on different scales, ranging from the scale of the distribution of individuals over large areas (Fretwell & Lucas, 1970) to the scale of the timing of patch depletion (Charnov, 1976). At these different scales different decisions can be made and decisions will be based on different types of information, *e.g.*, within a pasture, the decision of a herbivore to eat at a specific location will depend on the quality of the food at that location relative to the quality in the pasture and not relative to the quality in a different pasture. However, the decision to forage in this pasture was made on the basis of the (expected) quality in this pasture relative to the (expected) quality in different pastures (Senft *et al.*, 1987; Bailey *et al.*, 1996). There are however few studies that integrate the different scales of foraging in a formal modelling approach.

As the density of food or patches of food declines from very abundant to very scarce, the rate at which an animal can consume that food is limited by different processes (Holling, 1959; Spalinger & Hobbs, 1992): at high density food is plenty and the processing of the food by the animal (*i.e.*, capturing, chewing) is limiting intake. As density decreases the distance between food patches of food will increase and movement between patches will limit the intake of the animal. Finally, at even lower density, the animal has to search for new patches of food while moving from one patch to another (Spalinger & Hobbs, 1992). The search for new patches can occur in informed and non-informed situations. When cues about the location of food are available, movements become directed towards these cues (Bell, 1991). In the absence of such cues, random movement rules provide a suitable movement model (Bell, 1991; Bartumeus *et al.*, 2005).

Foraging is a process that determines the behaviour of animals to a large extent. It is governed by decisions that can be taken at different spatial and temporal scales and limited by different processes at these different scales. Heterogeneity of food, in quantity, quality, space and time, limits the foraging behaviour of animals. In this thesis, I will focus on what decisions animals should take to cope with the limitations that especially spatial heterogeneity and heterogeneity in the quantity and quality of resources. The main focus of this thesis lies on exploratory movement at low food density (chapters 2 - 5). In the final chapters (chapters 6 & 7) the focus is shifted to the decisions on what to eat and how much of that to eat at two spatial scales, and how exploratory movements can influence these decisions.

1.1 Movement

When the information horizon of an animal is smaller than the distance between targets (λ), animals will not only have to move between targets, but they will have to search for them too (Bell, 1991; Spalinger & Hobbs, 1992; Bartumeus *et al.*, 2005). The pattern of moving during the search can result in different encounter rates with these targets (Pyke, 1984; Hogeweg, 1989; Viswanathan *et al.*, 1999; Zollner & Lima, 1999; Bartumeus *et al.*, 2005). For a forager, the choice of movement pattern can thus be an important choice within the foraging process.

The movement of animals is also important in mediating spatial processes in ecology (Turchin, 1996). By moving, animals connect places that could otherwise not have any interactions. During their movement, animals feed from the encountered resources, they take seeds, pollen and diseases from one location to another, they trample the soil, and they defecate. As such, the movement paths of animals are important for the locations and scales of interactions, connectivity and nutrient cycling in an ecosystem (Bovet & Benhamou, 1988; Turchin, 1991, 1996; Farnsworth & Beecham, 1999; Oom *et al.*, 2002; Cumming & Cumming, 2003; Morgan *et al.*, 2004; Mouissie, 2004; Oom *et al.*, 2004). Because different movement patterns result in different encounter rates, they can also change the locations and intensity of ecological processes (Turchin, 1996). In order to understand and predict ecological processes and patterns, it is thus important to understand and to be able to predict the movement patterns of animals.

1.1.1 Random walk models

Random walk models are often used to predict the large scale movement pattern of animals (Skellam, 1951; Kareiva & Shigesada, 1983; Bergman *et al.*, 2000; Zollner & Lima, 1999). The major advantage of random walk models, is that they do not need the assumption of any interaction between the animal and its environment, which makes it possible to derive analytical approximations of the displacement of an animal (Kareiva & Shigesada, 1983; Bovet & Benhamou, 1988; Benhamou, 2004).

Random walk movement can be modelled in various ways, but in general they assume that the movement path of an animal is a sequence of discrete steps and turning angles (Turchin, 1998). Simple random walks result from a uniform distribution of turning angles between $-\pi$ and π and step lengths of fixed length (Holmes, 1993) (Figure 1.1 a). The mean squared displacement (MSD) of animals moving with a random walk increases linearly with time (Holmes, 1993; Bartumeus *et al.*, 2005). For most animals, there is however some correlation between the direction of successive steps (Kareiva & Shigesada, 1983; Turchin, 1991). Various ways have therefore been proposed to relax the model assumptions of the simple random walk.

Two types of random walk models that are often used to describe animal movement are the correlated random walks (Kareiva & Shigesada, 1983) and the Lévy walks (Viswanathan *et al.*, 1999). Because these models will be used in this thesis, I will introduce the basic principles of these random walks here.

Correlated random walk (CRW) For the correlated random walk the simple assumption of a uniform distribution of turning angles is discarded and a unimodal distribution of turning angles is assumed. As a result, the directions of successive steps are correlated to each other (Figure 1.1 b). For generating the correlation between succesive steps several different distributions have been proposed (Cain, 1985; Zollner & Lima, 1999). Following Zollner & Lima (1999) and Bartumeus *et al.* (2005) I have used CRW simulations with a wrapped Caughy distribution (WCD). The

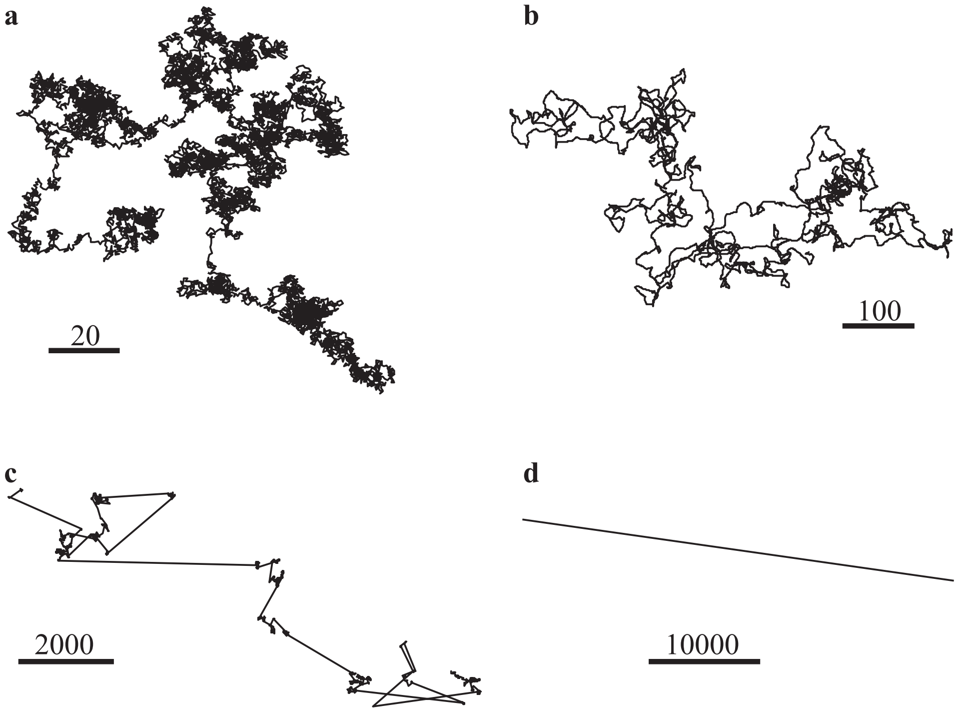

Figure 1.1: The movement patterns resulting from different movement models. Each panel shows a representative movement path. (a) Simple random walk (Brownian movement), (b) Correlated random walk (CRW) with $\rho = 0.9$, (c) Lévy walk (LW) with $\mu = 2$ and (d) ballistic (straight line) movement. *Note the different scales.*

parameter R that sets the level of directionality of the resulting movement path ($R = 0$ for highly tortuous movement (Brownian movement) and $R = 1$ for straight line movement (ballistic movement)) is equivalent to the length of the mean vector of the turning angles. This creates a straightforward link between observable properties of a movement path and the simulated movement paths. The MSD of a CRW can be approximated analytically (Bovet & Benhamou, 1988; Benhamou, 2004), but does not scale nicely with the length of the walk. In stead, with increasing length, the MSD of the walk becomes equivalent to the MSD of a simple random walk. The correlation between the direction of successive steps does not remain across scales (Bartumeus *et al.*, 2005).

Lévy walk (LW) The Lévy walks are a class of fractal random walks. The directions of successive steps are uncorrelated, and the distribution of the lengths of the steps (called flights) is characterised by a long fat tail (Viswanathan *et al.*, 1999). The distribution $P(l)$ of lengths l of these flights can be described with a Lévy distribution, which is best approximated as $P(l) \sim l^{-\mu}$. μ can be estimated as the slope of the log-log regression of the frequency distribution of steps (Viswanathan *et al.*, 1999; Sims *et al.*, 2007). The value of μ can range between 1 (many long steps) to 3 (Brownian motion). For $\mu \approx 2$, the movement path shows a fractal alternation of short and long steps (Figure 1.1 c). The MSD of the LW scales to the duration of the walk with a power between 1 and 2, depending on μ. The LW thus produces scale free super-diffusive behaviour (Bartumeus *et al.*, 2005). The LW can be approximated by superimposing the Lévy distributed reorientations (turning angles $\in [-\pi, \pi]$) on a CRW with a high directionality (R), without losing the optimal efficiency of $\mu_{opt} \approx 2$ (Bartumeus *et al.*, 2005).

In the absence of information about the whereabouts of targets, a searcher should use a random movement strategy to search (Bell, 1991; Bartumeus *et al.*, 2005). By incorporating simple assumptions on behavior around the targets being sought (*i.e.*, stop at the location of the target and consume it), Viswanathan *et al.* (1999) found that two different classes of distributions of targets resulted in different optimal movement patterns for LW; with a homogeneous target distribution, $\mu_{opt} \rightarrow 1$, resulting in ballistic movement is optimal, while with a patchy target distributed (modelled through targets that are not consumed at encounter) $\mu_{opt} \approx 2$. The results for homogeneous target distributions correspond to earlier results with CRW's (Pyke, 1984; Hogeweg, 1989; Zollner & Lima, 1999). Bartumeus *et al.* (2005) show that the optimal LW for patchy target distributions cannot be rivalled by CRW's. Many studies have used CRW and LW models to explain or describe observed movements of animals (Root & Kareiva, 1984; Viswanathan *et al.*, 1996, 1999; Atkinson *et al.*, 2002; Mårell *et al.*, 2002; Bartumeus *et al.*, 2003; Austin *et al.*, 2004; Bowne & White, 2004; Ramos-Fernández *et al.*, 2004).

1.2 Thesis outline

This thesis consists of two parts. In the first part of this thesis (chapters 2 - 5) I have increased the understanding of the mechanisms generating optimal searching efficiency of the Lévy walks. Hereto I first give account of an experiment observing the foraging movement of goats (*Capra hircus*), that do show these Lévy walks under specified conditions (chapter 2). Then I report the results of two studies using computer simulations. These chapters deal with the influence of the basic assumptions of random walk models on model performance (chapter 3) and the influence of target encounters on the diffusive properties of the LW models (chapter 4). Finally I report the results of an experiment with laughing doves (*Streptopelia roseogrisea*), where we tested the predictions of Viswanathan *et al.* (1999); Bartumeus *et al.* (2005) and chapters 2, 3 and 4.

In the second part (chapters 6 & 7) of this thesis I focus on what foraging decisions animals should take when they require several (macro-) nutrients that are heterogeneously distributed over different food species. Based on the assumption that animals do not live to eat, but eat to live, we designed a modelling framework that can find nutrient balancing and intake maximising foraging choices using different decisions made at different scale levels (chapter 6). In the final chapter (chapter 7), I refer back to the results of chapters 3 and 4 on the efficiency of searching under different target densities and derive approximations for the perceived target density, based on different movement patterns. I integrate this perceived target density into the model presented in chapter 6 to come to a model formulation that addresses the three of the main questions in optimal foraging theory: what to eat, how much to eat and how to move to find it.

1.3 Disclaimer

The models presented in this thesis are focussed on animals searching for food resources. There is however no guarantee that the concepts of searching for targets and choosing between different types of resource cannot be applied to other situations within the biological sciences or in the economic or information sciences. The author would encourage the reader to do so.

2 Patch Density Determines Movement Patterns and Foraging Efficiency of Large Herbivores

**Henrik J. de Knegt, Geerten M. Hengeveld, Frank van Langevelde,
Willem F. de Boer & Kevin P. Kirkman**

Few experimental studies have tested theoretical predictions regarding the movement strategies of large herbivores and their consequences for the efficiency of foraging. We therefore analysed how the movement and foraging behavior of goats is related to patch density, by analysing their movement and behavior in a low and high patch density plot, with patches being trees and bushes. We show that their movement paths become more tortuous when patch density increases, resulting in shorter steps and larger turning angles at high patch density. We also found a switch from Lévy motion at low patch density to a movement strategy tending towards Brownian motion in high resource abundance. At low patch abundance these statistical properties were sufficient to explain the amount of food encountered by the goats. However, the goats foraging in high patch abundance encountered more food than would be expected on the basis of these statistical properties. Hence, at high patch density the sequence of steps and turns becomes an important determinant of the foraging efficiency. We argue that this originates from an increased amount of information cues available to the foragers to include in their decision making. While changing the movement behavior with increasing patch density, the goats raised the efficiency of their foraging behavior more than proportional to the increase in patch density. These findings provide support for theoretical expectations on the foraging behavior of large herbivores in relation to resource density.

2.1 Introduction

Spatial variation within landscapes results in a heterogeneous distribution of animals' food resources. To exploit these resources animals have to move. The movement strategy that animals use while foraging on spatially dispersed resources is crucial to their success in exploiting (Bell, 1991; Viswanathan *et al.*, 1999; Zollner & Lima, 1999; Bartumeus *et al.*, 2005). Since the interplay between environmental heterogeneity and movement of individual foragers is an extremely important aspect of ecological dynamics (Turchin, 1998), the movement strategies of foraging animals have been a central focus in ecology (Schoener, 1971; Pyke *et al.*, 1977; Stephens & Krebs, 1986; Bell, 1991; Turchin, 1998;

Viswanathan *et al.*, 1999; Zollner & Lima, 1999; Bartumeus *et al.*, 2005). Ecologists have therefore invested a lot of effort in quantifying movement patterns of organisms (Turchin, 1998). This is mostly done within the realm of microorganisms, insects, birds, and small mammals (Kareiva & Shigesada, 1983; Turchin, 1991; Crist *et al.*, 1992; Cole, 1995; Viswanathan *et al.*, 1996; Levandowsky *et al.*, 1997; Viswanathan *et al.*, 1999; Atkinson *et al.*, 2002; Bartumeus *et al.*, 2003; Austin *et al.*, 2004; Ramos-Fernández *et al.*, 2004). However, experimental studies of the movement strategy of large mammalian herbivores in relation to resource density, and the consequent influence on foraging efficiency are rare (but see Gross *et al.* (1995); Bergman *et al.* (2000); Mårell *et al.* (2002)). In order to increase our understanding of the movement and foraging behavior of large herbivores, experiments need to be carried out to test theoretical predictions. In this paper, we therefore analyse the movement behavior of a large mammalian herbivore species (the goat, *Capra hircus*) in relation to the density of resources and the effect of these movements on foraging efficiency.

Several foraging studies showed that animals adjust their decision-making in relation to the distribution and density of food resources (Benhamou & Bovet, 1989; Bell, 1991; Farnsworth & Beecham, 1999; Nolet & Mooij, 2002; Newlands *et al.*, 2004). Generally, it is hypothesised that foraging animals adjust movement path sinuosity to the density of resources encountered (Benhamou & Bovet, 1989; Bell, 1991; Turchin, 1998; Benhamou, 2004). Most key parameters in movement models for foraging animals therefore modulate the tortuosity of the movement paths. Considering animal movement as a discrete series of displacement events separated by successive reorientations provides a very powerful approach to modeling and analysing movement paths (Turchin, 1998). This approach allows for the characterisation of movement paths by few parameters and it provides a mathematically tractable way for both analysing and modeling them (Benhamou, 2004). Discretisation of movement paths can determine the statistical distributions of displacement lengths (*i.e.*, step lengths), and of changes of direction (*i.e.*, turn angles) (Bartumeus *et al.*, 2005). To shift movements from tortuous to straight, animals can decrease the frequency or magnitude of turning, increase the proportion of long steps, or do both (Bartumeus *et al.*, 2005).

A general hypothesis in foraging ecology is that animals, in order to increase the efficiency of foraging, increase the tortuosity of their movement paths and decrease the speed of movement when resource density increases (Kareiva & Odell, 1987; Bell, 1991; Turchin, 1991; Focardi *et al.*, 1996; Turchin, 1998; Viswanathan *et al.*, 1999; Bartumeus *et al.*, 2005). By doing so, animals foraging in an area with high food abundance have a lower net displacement and decrease the chance of leaving the high resource density area, thereby increasing the utilisation of resources (Kareiva & Odell, 1987; Turchin, 1991; Focardi *et al.*, 1996; Bartumeus *et al.*, 2005). On the other hand, when resources become scarce, straighter and faster movements become more efficient than highly tortuous ones, as they result in high net displacement, thereby minimizing the chance of revisiting an already visited resource and increasing the chance of finding new resources (Turchin, 1991; Crist *et al.*, 1992; McIntyre & Wiens, 1999; Viswanathan *et al.*, 1999; With *et al.*, 1999; Zollner & Lima, 1999; Bartumeus *et al.*, 2005). When resources are distributed in few patches, a special type of movement, known as Lévy walks (LW), is most efficient in exploiting them (Viswanathan *et al.*, 1999). These Lévy walks are scale-free movements that are characterized by an exponentially decreasing frequency distribution $P(l) \sim l^{-\mu}$ of flight lengths (l). These flights are episodes of approximately straight locomotion and can be interpreted as the aggregation of steps in more or less the same direction. If $\mu \approx 2$, movement is optimal for exploiting scarce resource patches, while $\mu \rightarrow 1$ results in straight line movements and $\mu \rightarrow 3$ results in highly tortuous movements that are optimal at high patch density (Viswanathan *et al.*, 1999; Bartumeus *et al.*, 2005).

The shape of movement paths is a fundamental determinant of the efficiency of movement strategies (Bartumeus *et al.*, 2005). This research therefore focuses on the movement pattern and foraging efficiency of goats foraging on spatially dispersed resource patches. We analyse the movement and foraging behavior of goats in two different patch densities to address a set of consecutive hypotheses. We hypothesise that, as patch density increases, (1) the movement paths become more tortuous, resulting in shorter steps and larger turning angles. In accordance with results of LW models, movement paths are converted into flights and we hypothesise (2) a shift in the slope μ of the Lévy distribution of flight lengths from $\mu \approx 2$ at low patch density towards $\mu \approx 3$ at high patch density. To test whether the efficiency of movement of the foraging goats can reliably be characterized by the statistical distributions of turn angles and step lengths, or by the distributions of the aggregated flight lengths and their turn angles, we conduct a modeling exercise and compare observed movement paths with statistically equivalent bootstrapped pseudo paths. We hypothesise that (3) the goats encounter more browse while moving than simulated ones moving with the same statistical distributions of step lengths and turn angles. We then test our last hypothesis that, due to adaptations of their movement strategy to changes in patch density, (4) the efficiency of foraging increases more than proportional to an increase in patch density. We define foraging efficiency by means of both the sampling efficiency (number of visited patches per meter traversed) and the browsing efficiency (time spent browsing divided by time spent walking). We test these hypotheses in an experimental set-up by analysing the differences in movement and foraging behavior of goats between a high and a low resource density plot, and by comparing computer simulated pseudo paths with the observed paths. While testing these hypotheses, we aim at finding empirical evidence for theoretical predictions of the behavior of foraging animals and hence contributing to a better understanding of the foraging behavior of large mammalian herbivores.

2.2 Material and Methods

2.2.1 Study species and Study site

We selected goats (*Capra hircus*), because in our study area they mainly browse on easily recognisable Acacia trees and bushes (Breebaart *et al.*, 2002) and thus visit clearly delimited patches and thus visit clearly delimited patches, enabling us to avoid the common problem of herbivores that forage on patches that are very diffuse (Senft *et al.*, 1987; Bailey *et al.*, 1996). We used fifteen goats that had no previous exposure to the study sites.

We conducted fieldwork at Ukulinga Research Farm, Pietermaritzburg, South Africa (29°67'E, 30°40'S). Two adjacent plots with savanna vegetation were used. Both plots were similar regarding vegetation structure and composition, since both were influenced by the same management practices and abiotic conditions. Both plots were composed of a homogeneous grass layer with randomly scattered trees and bushes, which we will further refer to as patches.The dominant tree species was *Acacia nilotica*, making up more than 90% of the patches. *Acacia sieberiana*, *Lippia javannica*, *Lantana camara* and *Rhus pyroides* also occurred. Within each plot, three release areas (20x20 m) were selected in which the goats were released for observations. The two plots are called plot LPD (Low Patch Density) and plot HPD (High Patch Density). Plot LPD covered 1.3 ha and contained 239 patches, while plot HPD covered 2.0 ha and contained 594 patches, respectively 178 and 294 patches/ha.

With an aerial photograph and a GPS, we surveyed both plots and drew detailed maps (scale 1:500) showing all patches and plot boundaries. At each patch we recorded species, X and Y co-ordinates, patch height, canopy bottom height and average canopy radius. With these measurements, the browse availability per patch below the upper browse height of goats (1.5 m) was estimated following Camp & Hardy (1999).

There were no significant differences in patch characteristics between the plots (canopy height: Mann-Whitney, $U_{239,594} = 70058.5$, $P = 0.768$; canopy bottom height: Mann-Whitney, $U_{239,594} = 67882.5$, $P = 0.321$; canopy radius: Mann-Whitney, $U_{239,594} = 67642.5$, $P = 0.288$; browse availability: Mann-Whitney, $U_{239,594} = 69793.5$, $P = 0.705$). The distribution of the patches in both plots did not significantly deviate from a random distribution (LPD: nearest neighbor ratio= 0.935, $z = -1.930$, $P > 0.05$; HPD: nearest neighbor ratio= 0.982, $z = -0.855$, $P > 0.05$; calculated using ArcMap 9.1, ESRI inc., Redlands, California). Daily air temperature and rainfall were recorded during the fieldwork period, but no significant differences were found between observation weeks (rainfall: Anova, $F_{5,24} = 0.936$, $P > 0.05$; daily air temperature: Anova, $F_{5,24} = 2.392$, $P > 0.05$).

2.2.2 Observations

The goats were divided into three groups of five goats. For five consecutive days, one group of goats was selected and released at a random position in a randomly chosen release area of a plot. From this group, we randomly selected one goat that was observed at short distance for a period of 15 minutes. The behavior of the observed goat was recorded in space and time. At regular intervals (5 s) we recorded the location of the observed goat on the plot map. Our fine-scale maps and close focal observation allowed us to achieve mapping accuracy of 0.5 m. For the temporal measurements, we used a Psion Workabout portable computer and the program Observer (V3.0, Noldus Information Technology, Wageningen, The Netherlands) to record the activity of the goat at a 1-second resolution, simplified with the classes *browsing*, *grazing*, *walking*, *standing*, *lying* and *other*. Since the grass layer in both plots was visually homogeneous and did not differ between the plots, we cannot relate characteristics of movement paths or foraging behavior to grazing. In this paper we therefore focus on browsing and walking. On average, 8 observations were carried out per day. The observations per day were lumped to have a sufficient number of steps and turns to be able to determine the statistical characteristics of the movement paths. At night the goats were kept in a stable without access to food. We observed the goats for six weeks, each week with one group in one plot, so that after six weeks each group was observed in both plots.

2.2.3 Discretisation and Analyses of movement paths

To test our first hypothesis that the steps become shorter and the turn angles become larger when patch density increases, we calculated the distances between all successive positions (*i.e.*, step lengths) and the turn angles between successive steps, using all recorded positions. The turn angles were calculated as deviation angles from straight locomotion with the interval $\{-180°,180°\}$, where negative angles were turns to the left, positive angles turns to the right and 0° corresponded with straight locomotion. We then analysed the distributions of step lengths for differences between the plots. We analysed the turn angle distributions with Oriana, a circular statistics program (V2.0, Kovach Computing Services, Anglesey, Wales), based on the methods described by Fisher (1993). For both plots, we calculated the orientation and length (R) of the mean resultant vector. The orientation of the mean resultant vector expresses the angular mean (*i.e.*, the mean turn angle), and the length of the mean resultant vector expresses the concentration of the distribution around its mean, between $R = 0$ (uniform, fully dispersed circular distribution) and $R = 1$ (punctual distribution, all angles being equal) (Benhamou, 2004). Hence, the length of the mean resultant vector is a measure for the strength of directionality of the turn angles, *i.e.*, the tendency of the forager to maintain a similar heading from one time step to the next.

Based on the discretisized movement paths, we also calculated and analysed the total distance traversed per movement path, the average speed while traversing and the net displacement, i.e. the beeline distance between the first and last point of an observation. Furthermore, we calculated the ‘searching intensity’ index, expressing the searched area per distance unit traversed, *i.e.*, the ratio between the area of a movement path with width x (with $x = 0.5$ m, see below) divided by the total length of the movement path. This area:length ratio expresses the level of overlap in searched area. High values indicate that a large proportion of the searched area is scanned only once, whereas low values indicate a large overlap in searched area so that a larger proportion of the searched area is scanned more than once. Reversely, the area:length ratio can also be interpreted as a measure of the tortuosity of the movement paths, with high values indicating straighter movements and low values indicating a high level of tortuosity, since an increasing frequency or magnitude of turning results in an increase of the searched area that overlaps with each turn.

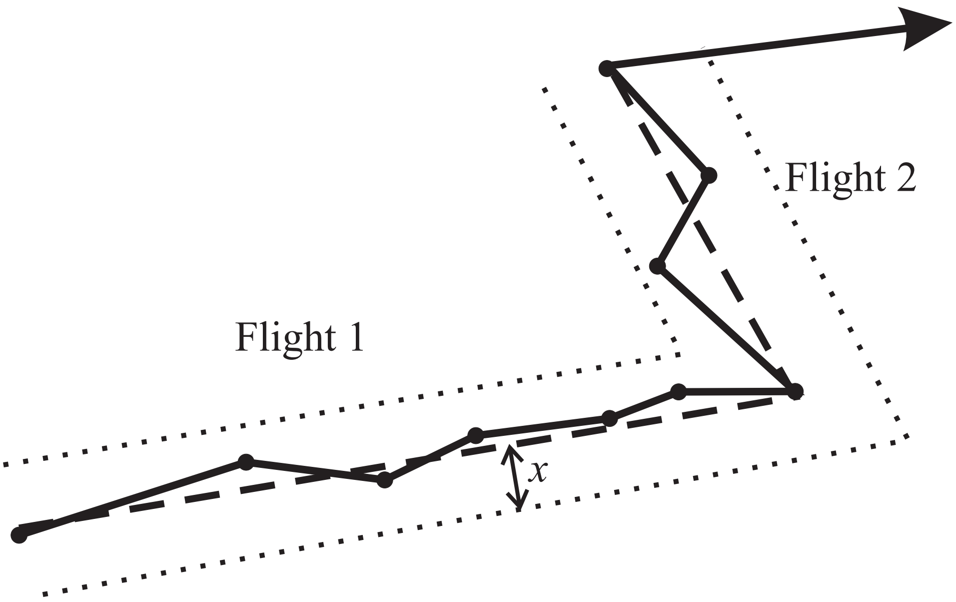

Figure 2.1: Aggregating N positions of an animal's movement path into one flight if all intermediate positions are no more than x m away from the line connecting the first point with point N (after Turchin (1998)). We used $x = 0.5$ m.

2.2.4 Path aggregation and Lévy flights

To be able to test the hypotheses from LW models that animals move with $\mu \approx 2$ in low patch density environments and towards $\mu \approx 3$ when resources are abundant, we converted the movement paths into flights. Following Bartumeus *et al.* (2005) the flights of the LW can be interpreted as an aggregation of steps in more or less the same direction, separated by acute turns. We aggregated a variable number of steps into flights using the approach suggested by Turchin (1998). N positions were aggregated into one flight if all intermediate positions were no more than x m away from the line connecting the first point with point N (Figure 2.1). For x we used 0.5 m, since this is the approximate step size of the goats and the accuracy of observation. Oversampling was avoided, since serial correlation of turn angles vanished (Pearson product-moment correlation coefficient; LPD: -0.019, HPD: -0.049). The Lévy index (μ) of the flight length distribution was subsequently described with a linear regression of the double logarithmic frequency distribution of flight lengths, where the regression coefficient is equivalent to $-\mu$. The slope μ was then tested for differences between the plots .

2.2.5 Simulation of pseudo paths

We simulated movement paths that are statistically equivalent to the observed movement paths, and compared their performance to that of the observed paths. They were generated using the bootstrap procedure as described by Turchin (1998), in which each step consists of a random draw from the observed step length and turn angle distributions for that plot. Pseudo paths were generated for both the short range turn angles

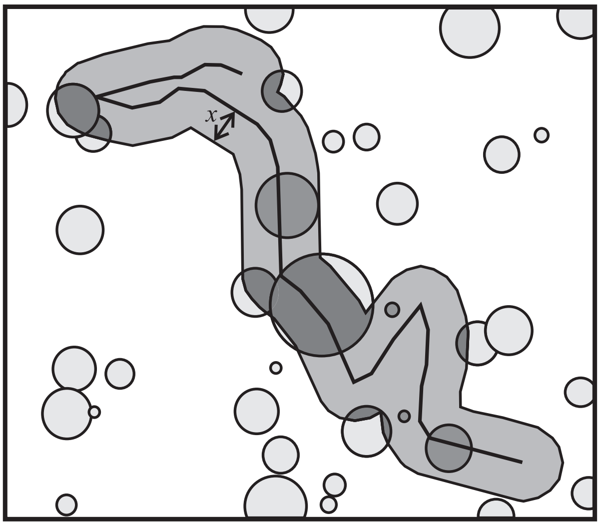

Figure 2.2: Calculating the performance of the observed and simulated movement paths: available browse encountered (dark) divided by the area of the movement paths with width x. The area of the dark circles represents the amount of browse available to the goats. The performance of the movement paths thus expresses the fraction (or percentage) of the searched area that contains available forage.

and step lengths and for the aggregated flight lengths and accompanying turn angles. As was the case for the observed paths, we let the pseudo paths begin at a random point within one of the release areas of a plot. The performance of a path was defined as the amount of available browse encountered within a distance x from the path, divided by the area of the movement path with radius x (Figure 2.2). The performance was calculated for all observed movement paths and simulated pseudo paths for $x = 0.5$ m. On average, the browse availability per square meter was 7% in plot LPD and 12% in plot HPD. Per plot the performance of the observed movements were compared with the plot average using a t-test and to both types of simulated pseudo paths using Anova followed by Dunnett's post-hoc test for comparison to a control.

2.2.6 Analysing foraging efficiency

To analyse the foraging efficiency of the observed goats, the efficiency of their foraging behavior was defined by means of their sampling and browsing efficiency. The sampling efficiency was calculated as the number of visited patches per observation divided by the total distance traversed. The browsing efficiency was calculated as the time spent browsing divided by the time spent walking. The sampling and browsing efficiencies were subsequently tested for differences between the plots.

Table 2.1: Summary of the results

	Plot LPD	Plot HPD
Patch density (patches/ha)	178	294
Median step length (m)	2.24	2.00
Mean turn angle (°)	0	0
R (length of the mean resultant vector)	0.75	0.6
Trend of R over time	increasing	decreasing
Average length of movement path (m)	63.0	53.6
Net displacement per observation (m)	30.7	24.6
Speed during locomotion (ms)	1.4	1.1
Area:length ratio	1.3	1.0
μ (slope flight length distribution)	2.1	2.9
Tortuosity of movement paths	Lower	Higher
Sampling efficiency (patchesm)	0.020	0.040
Browsing efficiency	0.7	2.6
Foraging efficiency	Lower	Higher

2.3 Results

2.3.1 Analyses of discretisized movement paths

The distributions of the short range step lengths of both plots differed significantly (Mann-Whitney, $U_{2938,2939} = 3190954.0$, $P < 0.001$), with shorter steps in plot HPD than in plot LPD: median 2.00 m in plot HPD and 2.24 m in plot LPD (see table 2.1 and Figure 2.3). The distributions of short range turn angles of both plots deviated significantly from a uniform circular distribution (plot LPD: Rayleigh's Uniformity test, $Z = 1565.686$, $\nu = 2826$, $P < 0.001$; plot HPD: Rayleigh's Uniformity test, $Z = 1019.276$, $\nu = 2827$, $P < 0.001$) and from each other (Chi-Square test, $\chi^2 = 273.025$, $\nu = 71$, $P < 0.001$) (Figure 2.4). The angular mean of the turn angle distributions of both plots was 0° (t-test, $t = -1.435$, $\nu = 2826$, $P = 0.151$ for LPD and t-test, $t = 0.30$, $\nu = 2827$, $P = 0.976$ for HPD) and the distributions were symmetrical around the angular mean (plot LPD : Mann-Whitney, $U_{1469,1358} = 993130.0$, $P = 0.842$; plot HPD: Mann-Whitney, $U_{1395,1433} = 974302.0$, $P = 0.245$). The length of the mean resultant vector (R), as measure of the strength of directionality, was significantly lower in plot HPD (Anova, $F_{1,28} = 58.673$, $P < 0.001$): 0.60 compared with 0.75 in plot LPD. We also found a significant decrease of R over time (*i.e.*, observation days) in plot HPD, but there was a significant increase over time in plot LPD (Anova, $F_{9,20} = 9.203$, $P < 0.001$) (see Figure 2.5).

The movement paths in plot HPD were significantly shorter than in plot LPD(Mann-Whitney, $U_{111,111} = 4849.5$, $P = 0.006$), as was the net displacement (Anova, $F_{1,220} = 8.405$, $P = 0.004$). While traversing, the goats moved with a significantly lower speed in plot HPD (Mann-Whitney, $U_{111,111} = 4739.5$, $P = 0.003$). No significant difference

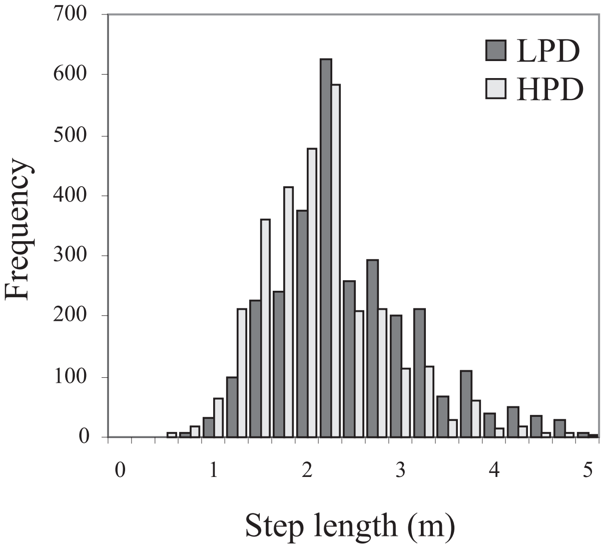

Figure 2.3: Frequency distribution of step lengths for both plots, using all recorded positions. Since the sampling intervals for all the moves are equal (5 s), the frequency distributions also represent the frequency distributions of speeds of each plot.

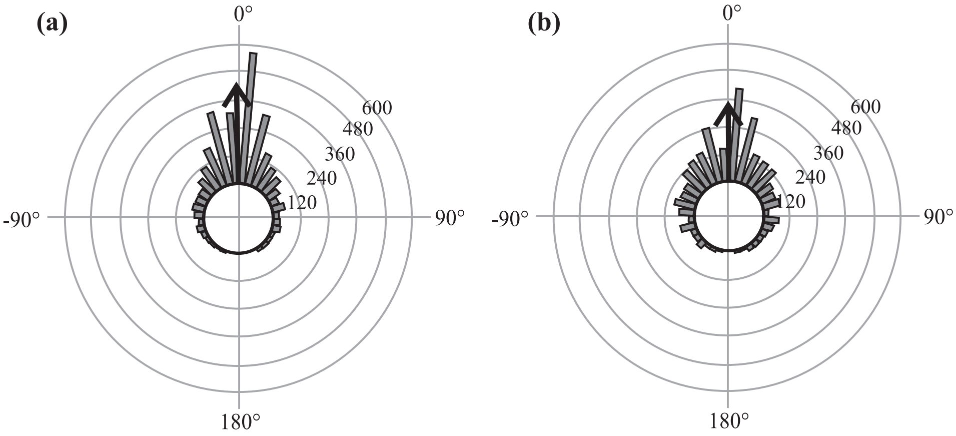

Figure 2.4: Circular frequency distribution of turn angles in (a) plot LPD ($n = 2827$) and (b) plot HPD ($n = 2828$). The concentric circles represent frequency increments of 120 and the numbers at the outer circle represent degrees. The direction of the arrows represents the mean turn angle (0° for both plots) and their lengths the strength of directionality ($R = 0.75$ for plot LPD and 0.60 for plot HPD, with $R = 1$ at the outer circle). See text for statistics.

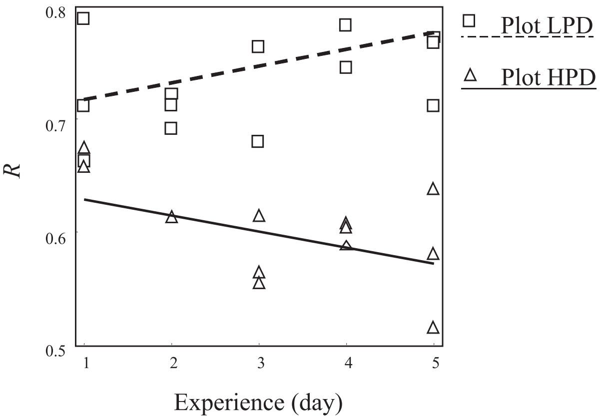

Figure 2.5: The strength of directionality (R) of the turn angle distributions in relation to increasing experience with the plots, here the number of days of exposure to the plots.

in time spent walking was found between the plots. Analyses of the searching intensity index showed that the goats foraging in plot LPD had a significantly higher area:length ratio than foraging in plot HPD(Mann-Whitney, $U_{111,111} = 4759.0$, $P = 0.003$): 1.3 in plot LPD compared with 1.0 in plot HPD.

2.3.2 Flight lengths

The distributions of the aggregated flight lengths could be well described with Lévy distributions ($R^2 = 0.90$ on average). The average value of μ in plot LPD was 2.1, compared to 2.9 in plot HPD. The values of μ were significantly higher in plot HPD than in plot LPD (Anova, $F_{1,28} = 11.168$, $P = 0.002$). See Figure 2.6.

2.3.3 Simulated pseudo paths

In both plots, the performance of the observed movement paths was not different from the plot average available canopy per square meter. In plot LPD the performance of the observed movement paths was not different from the performance of the random sequences of either the short range or the aggregated step lengths and turn angles (ANOVA, $F_{2,330} = 1.72$, $P = 0.181$). In plot HPD the observed movement paths had a significantly higher performance than the pseudo path of aggregated flight lengths, and tended towards a higher performance than the short range pseudo path (Anova, $F_{2,330} = 3.219$, $P = 0.041$, Dunnett's test observed-short-range $P = 0.066$, observed-aggregated $P = 0.043$). See Figure 2.7.

2.3.4 Foraging efficiency

The goats foraging in plot HPD had a significantly higher sampling efficiency (Mann-Whitney, $U_{111,111} = 3701.5$, $P < 0.001$) and browsing efficiency (Mann-Whitney, $U_{111,111} =$

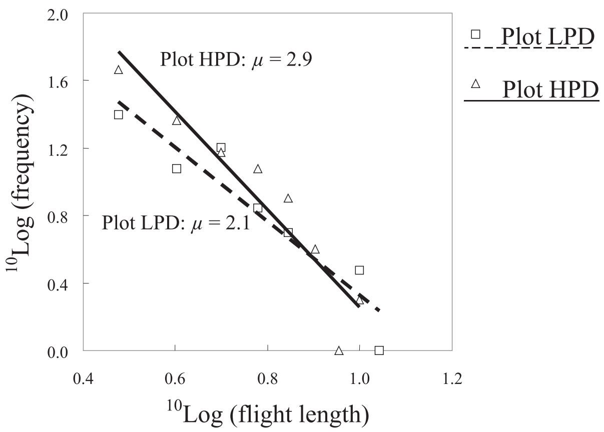

Figure 2.6: Frequency distribution of flight lengths for both plots, with μ from the Lévy distribution $P(l) \sim l^{-\mu}$ of flight lengths (l) being the regression coefficient of a linear regression between $^{10}\log$ (frequency) and $^{10}\log$(flight length).

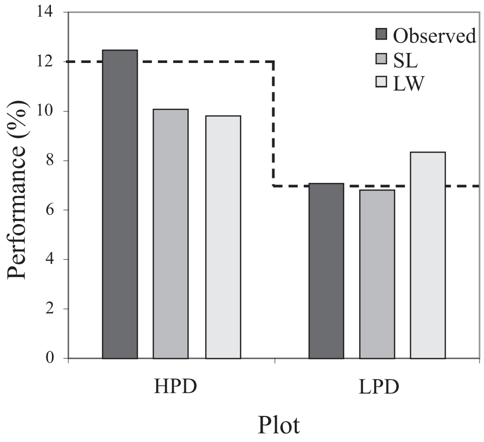

Figure 2.7: Performance of the observed and simulated movement paths in both plots, for $x = 0.5$m. The movement paths are simulated for both the short range step lengths and corresponding turning angles (SL), as well as for the aggregated flight lengths (LW) and angles. The performance can be expressed as the percentage of the searched area that contains available forage. The dotted line represents the plot average (plot LPD: 7% and plot HPD: 12%). Within plot LPD, there were no significant differences in the performance between the observed paths and both simulated pseudo paths, whereas in plot HPD both simulated pseudo paths had a significantly lower performance than the observed paths, see text for statistics.

3095.5, $P < 0.001$). They visited more patches per movement path (Mann-Whitney, $U_{111,111} = 4010.0$ $P < 0.001$) and spent more time browsing per observation (Anova, $F_{1,158} = 34.881$, $P < 0.001$). All these measures showed a larger difference between the plots than the difference in patch density would indicate (Table 2.1).

2.4 Discussion

In this paper, we experimentally analysed several key aspects of animal movement and foraging behavior in relation to the density of resource patches. Our main focus is the shape of the movement paths as a fundamental determinant of the efficiency of movement strategies. Our first hypothesis that the movement paths become more tortuous resulting in shorter steps and larger turning angles when patch density increases was supported by our data. The steps were significantly shorter in plot HPD, while the level of directionality in turn angles was lower. Hence, more large turns occurred in the movement paths of the goats in plot HPD. The goats did not exhibit a preference for either right or left turning, which corresponds with research on angora goats Ganskopp (1995), goldenrod beetle Goodwin & Fahrig (2002) and reindeer Mårell *et al.* (2002). However, they showed a higher tendency to maintain a similar heading from one time step to the next in the low patch density plot. These results agree with predictions generated by correlated random walk models (Kareiva & Shigesada, 1983; Bovet & Benhamou, 1988; Turchin, 1991; Crist *et al.*, 1992; Johnson *et al.*, 1992; Bergman *et al.*, 2000). Also our other measures for the tortuosity of the movement paths (e.g. net displacement and searching intensity index) confirmed our hypothesis that the tortuosity of the paths increased with increasing patch density. In the high patch density plot, the goats thus exhibited highly tortuous movement paths, resulting in a lower net displacement. In the low patch density plot, however, the goats exhibited straighter movements, resulting in a higher net displacement. Straight paths increase the chance of finding areas with high food density (Crist *et al.*, 1992; McIntyre & Wiens, 1999; Viswanathan *et al.*, 1999; With *et al.*, 1999; Zollner & Lima, 1999; Bartumeus *et al.*, 2005). Combining this with a lower speed and distance traversed in the high patch density plot results in intensive foraging on a small area in a high patch density environment, but extensive foraging on a larger area in a low patch density environment. These findings correspond to the concept of area restricted search (*e.g.*, Haskell (1997)), stating that foragers increase the frequency or magnitude of turning and decrease the speed of locomotion following encounters with food resources.

Our second hypothesis that the goats moved with $\mu \approx 2$ of the Lévy distribution of flight lengths in the low patch density plot, but with $\mu \approx 3$ in the high patch density plot was also supported by the data. As in other studies (Levandowsky *et al.*, 1988; Cole, 1995; Schuster & Levandowsky, 1996; Viswanathan *et al.*, 1996, 1999; Atkinson *et al.*, 2002; Mårell *et al.*, 2002; Bartumeus *et al.*, 2003; Ramos-Fernández *et al.*, 2004), the observed flight length distributions could be well explained by Lévy distributions. The goats followed movements with a Lévy distribution of flight lengths with $\mu = 2.1$ in plot LPD, but with $\mu = 2.9$ in plot HPD. These results correspond with findings of authors studying the movement of other species (Focardi *et al.*, 1996; Viswanathan *et al.*, 1996, 1999; Atkinson *et al.*, 2002; Mårell *et al.*, 2002; Bartumeus *et al.*, 2003; Ramos-Fernández *et al.*, 2004). These results provide empirical evidence for theoretical expectations that Lévy walks with $\mu \approx 2$ are optimal when resources are scarce, but that the principal advantage of a flight length distribution with $\mu \approx 2$ becomes negligible when there are ample patches, since then a Brownian strategy (*i.e.*, $\mu \geq 3$) becomes an optimal solution (*e.g.*, Viswanathan *et al.* (1999); Bartumeus *et al.* (2003, 2005)). In the low patch density plot, the goats approached this predicted optimal strategy with $\mu = 2.1$, whereas in the high patch density plot the goats indeed tended to move according to Brownian motion by moving with $\mu = 2.9$. Hence, we agree with the conclusions from Bartumeus *et al.* (2003) that Brownian motion should not be considered as a null model, but rather as another movement strategy that is optimal under high resource levels, and to expect a switching behavior between Lévy and Brownian strategies as optimal solutions when resource levels increase.

In addition to the findings that patch density influences the statistical characteristics of the movement paths, we compared the performance of the observed movement paths with statistically equivalent pseudo paths, both for the short range step lengths and turn angles and for the aggregated flights and turns, to test whether the statistical properties of the discretisized movement paths do reliably predict the efficiency of the movement strategies. In the low patch density plot the observed paths did not perform significantly better than the pseudo paths. In the high patch density plot however, the performance of the observed paths was significantly better than the pseudo paths generated from the aggregated flights and tended to be better than the pseudo paths generated from the short range steps and turns. Hence, the sequence of steps and turns did not significantly matter in the low patch density environment, whereas is did matter in the high patch density plot. Consequently, the statistical distributions of step lengths and turn angles are sufficient to characterise the efficiency of movement behaviour in a low patch density environment, while these properties are insufficient when patches are more abundant. Since animals use information cues from the surrounding environment to increase the efficiency of their foraging process (Kohler, 1984; Gross *et al.*, 1995; Bailey *et al.*, 1996; Laca, 1998) and these cues are more abundant when resource density increases, these cues are probably at the basis of the higher observed performance in the high patch density plot. Hence, the statistical properties of the movement paths become relatively less important when resource levels increase and the sequence of steps and turns becomes important due to the use of these cues. On the other hand, in low patch abundance the relative importance of information cues and thus the sequence of steps and turns becomes negligible and the statistical distributions of step lengths and turn angles can be used to predict the performance of movement strategies. This might explain why we could not find a significant difference in performance between the observed and simulated movement paths in the low patch density plot.

To test our fourth and last hypothesis, namely that, due to adaptations in their movement strategy to the density of patches, the goats were able to increase their foraging efficiency disproportional to an increase in patch density, we analysed the sampling and browsing efficiencies of the goats. Both indices for foraging efficiency showed a significant increase with increasing patch density. The sampling and browsing efficiencies even showed a larger difference between the plots than would be expected from the difference in patch densities between both plots (see table 2.1). This increase in foraging efficiency agrees with studies on other animals (Crist *et al.*, 1992; Viswanathan *et al.*, 1996; Stapp & van Horne, 1997; Gillis & Nams, 1998; Schultz, 1998; Schultz & Crone, 2001; Fortin, 2002; Nolet & Mooij, 2002). We argue that this disproportional increase in foraging efficiency results from behavioural adaptations in movement strategy as shown in previous sections of this paper and the use of environmental cues that are more abundant when resource density increases. Hence, the efficiency of foraging depends upon the strategy of movement, the amount of information available to use in decision making and the density of food patches.

The goats used in this research had no previous experience with the plots and therefore did not have prior knowledge regarding the distribution of the food patches. With more experience in the plots, they would be presumed to increase their expectation of the patch density in the plots (Bailey *et al.*, 1996). The observed decrease in time of the strength of directionality in plot HPD and its increase in time in plot LPD could indicate that the goats used this experience to adjust their movement paths to the experienced density. It is possible that the goats, when first confronted with the plots, moved following a naive distribution of turn angles but adjusted this distribution in response to the experienced resource density. No other differences due to experience were found (μ, sampling efficiency and browsing efficiency remained constant), which contradict the results of Gillingham & Bunnell (1989); Johnson (1991); Noda *et al.* (1994); Laca (1998), who showed that foragers increase their foraging efficiency with increasing experience.

In this paper, we show a positive correlation between patch density, movement path sinuosity and foraging efficiency of large mammalian herbivores. It provides further evidence that foragers often adjust their decision-making in relation to the density of food resources and by doing so are able to increase the efficiency of their foraging behavior. The novelty of our analysis is that we are able to relate statistical properties of discretisized movement paths with empirical measures of foraging activity and efficiency. Furthermore, we provide empirical evidence for several theoretical predictions on movement and foraging behavior in relation to the density of food patches. We show that many characteristic properties of animal movement and foraging behavior are influenced by the patch density of the environment. These characteristic properties include the shape of the step length and turn angle distributions, the exponent μ of the flight length distribution, the length, speed and net displacement of the movement paths and indices regarding the foraging efficiency of herbivores. The data show a switch from Lévy motion with $\mu \approx 2$ in a low resource density environment to a tortuous movement strategy with $\mu = 2.9$ at high resource abundance, thereby tending towards Brownian motion. Moreover, the sequence of steps and turns becomes important when resources are abundant and we argue that this originates from an increased amount of information cues available to the foragers to include in their decision making. With a change in movement behavior with increasing patch density, the goats were able to raise the efficiency of their foraging behavior more than proportional to the increase in resource abundance. These findings provide further experimental evidence for theoretical expectations and we hope this will contribute to the development of theory on foraging animals by investigating mechanisms behind foraging behavior.

Acknowledgement

Our gratitude goes to the University of KwaZulu-Natal, Discipline of Grassland Science, which made it possible to conduct the fieldwork for this research at Ukulinga Research Farm. Furthermore we would like to thank Thomas Groen, Chippy du Toit, Craig Morris, Gerry Naiken and Richard Fynn for their help and support during this research. We also thank Herbert Prins, Emilio Laca and Chris Loggers for their valuable comments on the manuscript.

3 Search Efficiency and General Assumptions in Random Search Models

Geerten M. Hengeveld, Frederic Bartumeus, Frank van Langevelde & Herbert H.T. Prins

Random searches are employed when searching for targets (*e.g.*, resources or mates) with little information available in the environment. Some random searches are more efficient than others in locating targets. Here, we explore which are the essentials that provide the basis for this success by relaxing some general assumptions of random search models. Following previous work, we use two types of random walk models; Lévy walks and correlated random walks. We relax three assumptions related to the target encounter and dynamics. First, we assume that the searcher needs to go to the exact location of the target for consumption. Second, we assume that the searcher does not start a new search in a new direction after resource encounter. Third, we assume permanent depletion of targets in the environment due to consumption. Three main results are obtained: without the start of a new search after target encounter (1) the Lévy walk looses the super-efficiency if targets are not depleted and (2) straight-line (ballistic) search movements become even more efficient if targets are depleted, finally (3) moving to the location of the target increases the efficiency of correlated random walks if targets are not depleted. We attribute the super-efficiency of Lévy walks to their ability to generate 'area-restricted search'-like patterns; a fractal combination of local searches that are anchored at the location of a target and occasional long range exploratory moves. We conclude from these results that the interactions with resources are important for random search models. In particular, with target depletion interactions with targets diminish the efficiency, while with fast recovery of targets these interactions anchor the movement to the location of the targets and increase efficiency.

3.1 Introduction

For most animals, the search for food takes a large part of their time (Schoener, 1971; Jander, 1975; Pyke, 1984). Although random searching rules are less efficient than searches based on feedbacks between experience and behaviour (Bell, 1991), there are many situations where animals are forced to use random searches (Bartumeus *et al.*, 2005). Random searches are most likely to occur in areas with unknown distributions of targets, variable environments or a large number of competitors (Bell, 1991). As such, the best movement rule for random searching should be efficient over a wide range of conditions.

For a searching animal, the environment can be divided into a known, recently searched area and an unknown area. Visiting unknown areas is only rewarding if recovery of recently visited targets is slow or all known targets are depleted. In the case of recovery of targets, the searched area will be depleted only for a limited time, but after that, the animal faces the choice of searching in new, unexplored and thus uncertain areas or returning to a known area. Even for random search models this local depletion effect is important (Raposo *et al.*, 2003).

Random search models range between two extreme types of movement: ballistic search characterised by straight line movement and Brownian search, characterised by short movements in random directions. The spectrum of possible movement types between Brownian and ballisic movements can be filled in by two different types of random walks that have been proposed to model animal movements; correlated random walks (CRW) and Lévy walks (LW) (Bartumeus *et al.*, 2005). In the CRW the direction of movement is correlated to the direction of the previous step. In the LW the length of movements is taken from a power-law distribution. Both models have one parameter that controls the shape of the movement path. For CRW this parameter is ρ, a parameter that controls the correlation of successive movements. For LW this parameter is μ, the negative exponent of the power-law distribution of movement lengths, that controls the relative importance of long movements in the movement path . For both models, the parameters can change the shape of the movement path from Brownian ($\mu = 3$ and $\rho = 0$) to ballistic ($\mu = 1$ and $\rho = 1$) movement (Bartumeus *et al.*, 2005).

Both models have been intensely studied for their efficiency in finding targets (Pyke, 1984; Cain, 1985; Hogeweg, 1989; Viswanathan *et al.*, 1999; Zollner & Lima, 1999; Bartumeus *et al.*, 2005). For situations where new targets should be found (because the targets that are found are depleted) these studies show that both CRW and LW should approach ballistic (straight line) movement. If targets are not depleted, the search efficiency of the LW is greatly increased for values of the parameter $\mu \approx 2.0$. This results in a fractal movement pattern consisting of periods of large range movement alternated with periods of short range local movements, that cannot be produced by a CRW (Bartumeus *et al.*, 2005).

The specific assumptions on how searchers change movement at or after target encounter could have a great influence on the exploration of the environment at the landscape-level, and thus, on the efficiency of the random search. Therefore we explore, in much more detail, some general assumptions of random search models (Bartumeus *et al.*, 2005). In particular, in the present paper, we focus on two assumptions regarding target encounter and one assumption regarding target dynamics; (1) that the target can be consumed from the location were it is detected, (2) that there is a random reorientation after target consumption and (3) that target depletion does not change the target density (Bartumeus *et al.*, 2005). Because we will simulate the depletion of the global target density, we cannot simulate with periodic boundary conditions (as is done in Viswanathan *et al.* (1999); Bartumeus *et al.* (2005)). Therefore we can also check for the effect of the assumption of periodic boundary conditions on the efficiency of the search movements.

These assumptions are not typical for the proposed random search models, but can have a profound influence on the path properties and the searching efficiency of these random searches. Furthermore these assumptions can conflict with the behaviour of different species, e.g., for tactile foraging animals resources can usually be taken and consumed at the same distance at which they are detected. This will not be the case for animals that detect their targets visually or by smell. In such cases animals will need to change their movement direction and move towards the detected target before they can consume it.

We change these assumptions by: (1) the introduction of explicit movement to approach a target, (2) no change in behaviour after target encounters and (3) a permanent depletion of targets and depression of target density. These changes in assumptions, may affect the displacement caused by the movement path (1 and 2) and the likelihood of finding new targets when returning to previously searched areas (3). With these changes in assumptions, we can investigate the effect of changes in the path properties, due to different behaviours at target encounter, on the overall search efficiency. In general, our results strengthen the findings of Viswanathan *et al.* (1999); Bartumeus *et al.* (2005) and give insight into the effect that these basic model assumptions have on the realised search efficiency.

3.2 Methods

To explore the differences between LW and CRW searches, we used a basic random walk simulation; each random walk consists of a sequence of moves separated by turns. Whenever a target is encountered it is consumed from the location where it is detected and the search is continued in a random direction. Search efficiency is expressed as $\lambda\eta$; the quotient of the encounter rate (η, the number of targets found divided by the distance moved) and the expected encounter rate ($\frac{1}{\lambda}$).

In the LW, the movement pattern is determined by the distribution of move lengths (also called flights (Viswanathan *et al.*, 1999)). This distribution of move lengths (l) is characterised by the distribution $P(l) \sim l^{-\mu}$, where $1 < \mu < 3$. Lower values of μ result in more long moves. The turns between successive moves are uniformly distributed. Because the search is continued in a random direction after target encounter, the move that resulted in the encounter is truncated.

In the CRW the steps are of fixed length and the movement pattern is determined by the distribution of turning angles. The turning angles are distributed according to a Wrapped Caughy distribution (WCD). The shape of this distribution, and thus the shape of the resulting movement path, is determined by the parameter ρ. Thus for both models there is one characteristic parameter (μ for LW and ρ for CRW). This parameter can scale the movement pattern from Brownian motion ($\mu \rightarrow 3$ and $\rho = 0$), to ballistic motion ($\mu \rightarrow 1$ and $\rho = 1$) (Bartumeus *et al.*, 2005).

We investigate the effect of two general assumptions on movement behaviour on the

Table 3.1: differences between the movement models. The movement models differ in the distribution of turning angles (TA) (either a Wrapped Caughy distribution (WCD) or uniform in $[-\pi, \pi]$), the distribution of move lengths (ML) (either Lévy distributed or fixed at 0.5), they can have to move to the target in order to consume it or not, and they can have a reorientation after target encounter according to a specified distribution ((WCD) or uniform in $[-\pi, \pi]$) or none at all.

Model	TA	ML	Approach target	reorientation
LW	$[-\pi, \pi]$	Lévy($_\mu$)	No	$[-\pi, \pi]$
CRW	WC(ρ)	0.5	No	$[-\pi, \pi]$
LW$_P$	$[-\pi, \pi]$	Lévy($_\mu$)	No	None
CRW$_P$	WCD(ρ)	0.5	No	WCD(ρ)
LW$_A$	$[-\pi, \pi]$	Lévy($_\mu$)	Yes	$[-\pi, \pi]$
CRW$_A$	WCD(ρ)	0.5	Yes	$[-\pi, \pi]$

searching efficiency of these random searches. These assumptions are (1) the consumption of the target from the location were it is detected, and (2) the random reorientation after target consumption. We alter these two assumptions by including movement towards a target and by excluding a change in behaviour after target encounter.

We explore the effect of a possible orientation and movement towards a detected target by modelling both the standard situation without approach to the target *i.e.*, the target is consumed from the location where it is detected, and the situation where the target should be approached before they can be consumed (suffixed A). To approach the target the searcher changes its direction towards the closest detected target and incrementally moves towards this target.

The standard models of both LW and CRW assume random reorientation after encounter with a target. This assumption breaks the directional persistence of the movements. To relax this assumption we simulate a LW without the truncation of the movement at target encounter and a CRW where the reorientation after target encounter is not uniform but taken from the corresponding WCD (suffixed P).

Searching for targets has been categorised as destructive or nondestructive (Viswanathan *et al.*, 1999; Raposo *et al.*, 2003; Bartumeus *et al.*, 2005). In the destructive search, targets that are found are depleted and removed from the field, while in the nondestructive search targets remain attractive to the searcher after being found. To keep the target density the same, destructive searching is usually simulated by placing a new target in the search area whenever a target is found (Bartumeus *et al.*, 2005). Here we also include a type of destructive search where the global target density is declining, *i.e.*, where no replacement is taking place. This last search involves non-stationary dynamics, *i.e.*, the density of targets is not constant, and is referred to as the globally depleting search. The destructive search with replacement is referred to as the locally depleting search. For consistency, the non-destructive search will be referred to as the non-depleting search.

To avoid looping in the original path in the globally destructive search, which could

Table 3.2: parameter values used for the simulations.

Parameter	Model	Units	Values
detection radius	all	unit length	1
scan interval	all	unit time	0.5
duration	all	unit time	10^6
replicates	all	-	84

occur with periodic boundary conditions, all simulations take place in an expanding environment. Initially a region containing 10 targets is created. Whenever the searcher scans over the boundaries of this region, a new region containing 10 targets is added. For the locally depleting search, targets are replaced within the region where they are found to keep the target distribution homogeneous. After target encounter a refraction time of four steps is taken into account to allow for the searcher to move away from the target location (*cf.* Bartumeus *et al.* (2005)). The expanding environment allows us to check the existence of potential artifacts introduced by periodic boundary conditions in previous simulations (Viswanathan *et al.*, 1999; Bartumeus *et al.*, 2005).

To test the robustness of the movement rules to changes in the target density each movement rule was tested at four different target densities. Conform Viswanathan *et al.* (1999); Raposo *et al.* (2003); Bartumeus *et al.* (2005), we use the mean free path (λ) as a measure of the target density (see Bartumeus *et al.* (2005, Appendix 1) for the relationship between λ and the density). Searching success (η) is defined as the number of targets encountered divided by the total distance searched. To compare searching success across target densities, η is multiplied with λ. The searching efficiency ($\lambda\eta$) is a measure that standardises the searching success. If the average $\lambda\eta = 1$, the searching was as efficient as would be expected on the basis of the initial mean free path, *i.e.*, a target was encountered on average every λ steps.

Simulations were run with one searcher in the environment. Within each simulation the searcher would use one of the movement models (Table 3.1). Movement paths are simulated for five values for each parameter (μ and ρ) of the LW and CRW (Table 3.2).

3.3 Results

In general, the results support the findings of Bartumeus *et al.* (2005), in that:

1. Straighter movement paths ($\mu \to 1, \rho \to 1$) are more efficient in finding targets if targets are depleted.

2. LW with $\mu \approx 2$ are most efficient in finding non-depleting targets.

3. Intermediate values of μ result in more efficient movement paths than intermediate values of ρ.

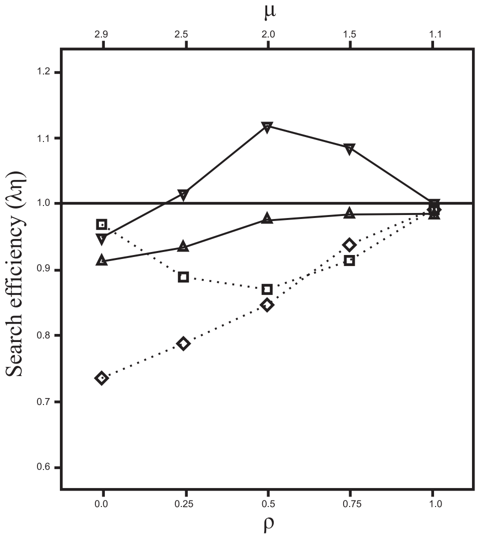

Figure 3.1: Searching efficiency while searching for non-depleting targets with $\lambda = 1000$. Shown are the efficiencies of the standard LW (▽) and CRW (◇) models and for the LW without truncation at target encounter (LW$_P$, △) and the CRW where the searcher moves to the exact location of the target before consumption (CRW$_A$, □). The horizontal axis represents an increase in ρ for the CRW models (lower axis) and a decrease in μ for the LW models (top axis). $\rho = 0$ and $\mu - > 3$ correspond to Brownian movement, $\rho = 1$ and $\mu - > 1$ correspond to ballistic movement. Results show averages for 84 simulations. Lines connecting symbols are drawn to guide the eye.

4. The efficiency of the optimal LW in a non-depleting search increases with increasing λ (decreasing density).

Our simulations extend these patterns to larger and smaller values of λ. With non-depleting targets, however, the difference in efficiency of the movement rules decreases for $\lambda = 10$. In contrast to the result presented in Bartumeus *et al.* (2005) that changes in ρ do not affect the efficiency in a non-depleting CRW, we find that an increase in ρ, results in an increase in the search efficiency in a non-depleting CRW (Figure 3.1).

The changes in model assumptions on target encounter and target dynamics did influence the efficiency of the searching patterns in some cases:

1. LW$_P$ (without truncation at target encounter) does not show the increased efficiency for intermediate values of μ in the non-depleting search compared to the standard LW (Figure 3.1). There is only a slight difference between the different values of μ for LW$_P$.

2. CRW$_A$ (with an explicit approach of the target) shows an increase in the efficiency of more Brownian motion ($\rho < 0.5$) in the non-depleting search compared to the standard CRW (Figure 3.1).

3. Both LW$_P$ and CRW$_P$ (without truncation and reorientation at target encounter)

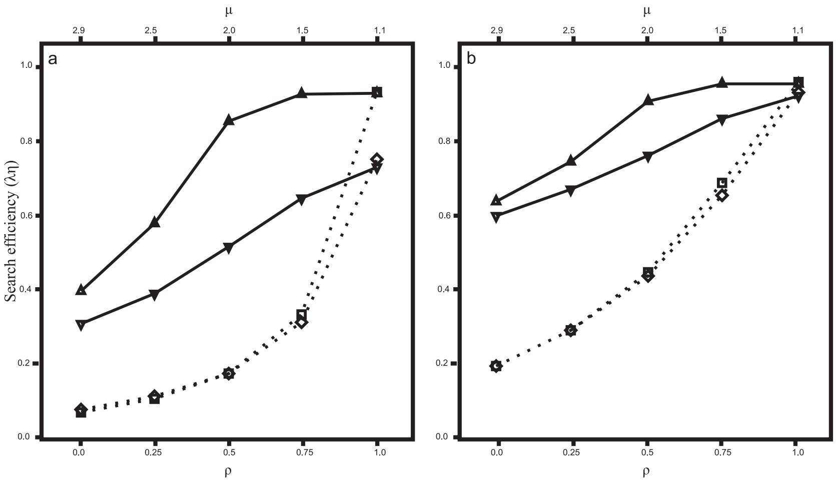

Figure 3.2: Searching efficiency while searching for depleting targets with $\lambda = 10$. Shown are the efficiencies of the standard LW ($\triangledown$) and CRW ($\diamond$) models and for the persistent variation of the LW (LW$_P$, $\triangle$) and the CRW (CRW$_P$, $\square$). Panel a shows the efficiency of the movement models for the globally depleting targets, while the panel b show the results for the local depleting targets. The horizontal axis represents an increase in ρ for the CRW models (lower axis) and a decrease in μ for the LW models (top axis). $\rho = 0$ and $\mu- > 3$ correspond to Brownian movement, $\rho = 1$ and $\mu- > 1$ correspond to ballistic movement. Results show averages for 84 simulations. Lines connecting symbols are drawn to guide the eye.

show an increased efficiency compared to the standard models at low λ (high target density) within the globally depleting search. The optimal movement regime is still ballistic ($\rho = 1$, $\mu \rightarrow 1$), but these variants without reorientation are more efficient than the standard models in finding the globally depleting targets (Figure 3.2). With local depleting targets and at larger values of λ, the standard models are as efficient as the variants without reorientation for $\mu = 1.1$ and $\rho = 1$, but LW$_P$ is more efficient than LW at $\mu = 2.0$ and $\mu = 2.5$.

4. Globally depleting searches have a lower efficiency than locally depleting searches. Apart from this quantitative effect of the non-stationary dynamics, the global depletion made little difference compared to the local depletion. The LW$_P$ suffered less from these non-stationary dynamics, especially with $\mu \leq 2$ (Figure 3.2).

3.4 Discussion

Because random searches are employed whenever there is uncertainty about the distribution of targets (Bell, 1991; Bartumeus *et al.*, 2005), optimal random searches should be efficient in finding targets in a wide range of target distributions. Moreover, the patterns found in the efficiency of random movement models should be robust to changes in the non-typical model assumptions.

Therefore we analysed the efficiency of different movement rules at target densities spanning four orders of magnitude and with three different types of target dynamics. The movement rules were based on Lévy walk and correlated random walk models following Bartumeus *et al.* (2005). To assess the robustness of these models to changes in model assumptions, we investigated the effect of changes in three general assumptions made by Bartumeus *et al.* (2005) on the efficiency of LW and CRW (see Table 3.1 for the notations). These changes are

1. The introduction of explicit movement towards the target after detection (suffixed A), resulting in less directional persistence and an anchoring of the movement path to the exact location of the target.

2. No reorientation or truncation of the move at target encounter (suffixed P), resulting in more directional persistence and less anchoring of the movement path to the location of the target.

3. Permanent depletion of the target after encounter, resulting a depression of the target density and the formation of a depleted search path.

The results of these analyses are in general agreement with Bartumeus *et al.* (2005) and earlier work on optimal movement patterns: LW searches with $\mu \approx 2.0$ are the best search if targets are not depleted. If the searcher is depleting the targets, ballistic searches ($\rho \to 1$ and $\mu \to 1$) are better than Brownian searches ($\rho \to 0$ and $\mu \to 3$). In contrast to Bartumeus *et al.* (2005), who find no effect of changes on ρ on non-depleting CRW, we find a positive effect of increasing ρ on the efficiency of non-depleting CRW searches.

The changes in assumptions regarding target encounter effected the results only in three ways: (1) the explicit movement towards the target after detection increased the efficiency of the CRW with $\rho < 0.5$ in a non-depleting search, (2) in the non-depleting search the exclusion of the truncation of the movement at target encounter removed the increased efficiency of the LW with $\mu \approx 2$, and (3) the exclusion of the truncation of the movement and the reorientation at target encounter increased the efficiency of LW with $\mu \geq 2$ in all depleting searches with $\lambda < 1000$ and of CRW with $\rho = 1$ in the globally depleting search with $\lambda = 10$.

The changes in assumptions regarding the target dynamics only had a quantitative effect on the efficiency of the standard models; the globally depleting search resulted in less targets found. This is the effect of non-stationary target dynamics as a result of the depletion of the target density. The expanding environment used in this study did not affect the general results as they were also found by Bartumeus *et al.* (2005). This is to be expected because Bartumeus *et al.* (2005) simultaneously use multiple (non-interacting) searchers that generate a dynamic target distribution. This dynamic distribution will also negate any effects of periodic boundaries.

These results show that in a depleting search, directional persistence is most important, hence the increase in efficiency towards ballistic movements ($\mu \to 1$ and $\rho \to 1$) and the higher efficiency for movement rules that do not change direction after target encounter (LW$_P$ and CRW$_P$). Thus when targets become useless after the first encounter, re-sampling the same area greatly decreases the efficiency of the search and ballistic movement is the best exploration strategy (Pyke, 1984; Hogeweg, 1989; Viswanathan *et al.*, 1999; Zollner & Lima, 1999; Bartumeus *et al.*, 2005).

With non-depleting searches, the best movement rule would be to find a target and then to stop moving. However, the LW and CRW movement rules used in this study do not allow for such behaviour. Therefore we find that ballistic searches ($\mu \rightarrow 1$, $\rho \rightarrow 1$) are slightly better than Brownian searches ($\mu \rightarrow 3$, $\rho \rightarrow 0$). These ballistic searches are best at finding new targets, while Brownian searches have got a relatively slow displacement, but cannot be fixed to one location (Bartumeus *et al.*, 2005). By explicitly moving the searcher to the location of the target, as in CRW_A, CRW with $\rho < 0.5$ can be anchored to this location and the efficiency of the search can be greatly increased.

The best random search movement for non-depleting targets is a LW with $\mu \approx 2$. The LW produces a fractal movement path. With $\mu \approx 2$ this movement path is a fractal alternation of local movement clusters and long range connections (see Figure 1.1c. or (Bartumeus *et al.*, 2005, Fig 1d.) for an impression of LW movement paths). This alternating pattern does not result in the increased efficiency *per se*. By truncation of movements at the location of a target, the local movement clusters are anchored to this location and enable the searcher to repeatedly find the same target. Whenever the searcher wanders away from the target, the relatively large chance to make an extremely long movement enables the searcher to efficiently find a new target to exploit. When the truncation at the target location is removed from the model (LW_P) the efficiency gain of $\mu \approx 2$ disappears.

Empirical studies have often described animal movements exhibiting optimal LW searches with $\mu \approx 2.0$ (Viswanathan *et al.*, 1996, 1999; Mårell *et al.*, 2002; Bartumeus *et al.*, 2003; Ramos-Fernández *et al.*, 2004) (chapter 2). However, without considering the dynamics and the spatial configuration of the targets, no conclusions can be drawn about the mechanism generating these movement patterns (Ramos-Fernández *et al.*, 2004; Boyer *et al.*, 2006). Scale-free movement patterns resulting from a LW could also reflect a scale-free distribution of resources (Boyer *et al.*, 2006). Furthermore several data-based models have been formulated that combine different movement rules for different situations or behavioural states (Bell, 1991; Walsh, 1996; Fortin, 2002; Nolet & Mooij, 2002; Morales *et al.*, 2004). These models use feedback from past experience to combine local and a long range movements into an area-restricted search. Because of the truncation of movements at the location of the target, the LW model with $\mu \approx 2.0$ is the best way to generate this type of movement path without considering the underlying state of the searching animal.

Our results confirm earlier results that ballistic movement is most efficient in finding new targets (Pyke, 1984; Cain, 1985; Hogeweg, 1989; Viswanathan *et al.*, 1999; Zollner & Lima, 1999; Bartumeus *et al.*, 2005), and that a Lévy walk with $\mu \approx 2$ is most efficient for the combination of exploration and exploitation whenever targets are not depleted or have a patchy distribution (Viswanathan *et al.*, 1999; Bartumeus *et al.*, 2005). By relaxing some of the general model assumptions we show that these results are robust to a changing target density and to changes in boundary conditions. Assumptions that can anchor the movement path to the location of a non-depleting target, or that retain directional persistence over target encounter can increase the efficiency of the movement path. We find that the super-efficiency of the Lévy walk with $\mu \approx 2$ in finding non-depleting targets (as found by Viswanathan *et al.* (1999); Bartumeus *et al.* (2005)) is sensitive to the assumption that movement is truncated at target encounter.

Acknowledgements

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4 Target Encounters alter Lévy Search Characteristics

Geerten M. Hengeveld, Frank van Langevelde & Herbert H.T. Prins

Lévy flight random walks have two interesting features that separate them from other random walk models: (1) The scale free properties of the Lévy walks enable a linkage between local movements and landscape level processes. (2) Lévy walks are shown to be more efficient in finding targets than other random walk models. The efficiency in finding targets is dependent on the truncation of long movements at the target location. We investigate the effect of finding targets on the displacement of the movement path. We find that finding targets decreases the displacement of the Lévy walk and links the scale of the movement to the scale of the target distribution. By examining the distribution of observed movements we find that with an decrease in the mean free path between targets (λ) the slope ($-\mu$) of this distribution is systematically underestimated. Truncating movements at target locations, which is an assumption crucial to the success of Lévy walks, thus leads to a systematic error in both the estimation of the model parameter μ from local movements and the scale-free extrapolation from these local movements to landscape level processes. The linkage between the scale of the target distribution and the scale of movement will not be limited to interactions with targets in Lévy walks but will also be occur as a result of interactions with other landscape features in fractal-like movement patterns. Changes in the scale at which landscape features are expressed can thus change animal distribution patterns.

4.1 Introduction

Animal movement is a key element of many ecosystem processes (Bell, 1991; Turchin, 1991, 1996; Viswanathan *et al.*, 1999). Because movement determines the rates of encounters with resources, predators and habitats, the movements of individual animals will have a profound influence on their fitness (Pyke, 1984; Turchin, 1998; Viswanathan *et al.*, 1999; Zollner & Lima, 1999; Prasad & Borges, 2006). Individual movements determine in the distribution of a population, interactions with the environment and connections between sub-populations at the ecosystem scale (Turchin, 1991, 1996; Hanski, 1999). Therefore there is a lot of interest in using movement models that can describe movements at the level of the individual, and that can be used to predict large scale distributions of populations (Turchin, 1996). Random walk models can provide such a link between individual and local movement behaviour to population and large scale distributions (Kareiva & Shigesada, 1983; Turchin, 1991, 1998; Bartumeus *et al.*, 2005). Especially for fractal-like movement models, it is assumed that the statistical properties remain constant when scaling up from local movement paths to larger scales (Dicke & Burrough, 1988; Turchin, 1996). Based on this assumption rates of individual displacement and population diffusion can be calculated over larger scales than the scales on which parameter estimates were based (Turchin, 1996; Bartumeus *et al.*, 2005).

One important class of fractal-like random walks is that of the Lévy walks (Viswanathan *et al.*, 1999). Lévy walks consist of straight line movements (called flights) with a length drawn from a power-law distribution, and uniformly distributed turning angles. The resulting movement path is typically a fractal combination of frequent local movements with occasional long range movements (Viswanathan *et al.*, 1999; Bartumeus *et al.*, 2005). The exponent $-\mu$ of the power-law distribution is the parameter that determines the relative amount of those long movements. The power-law distribution of flights ensures scale-free properties of the movement path, potentially allowing for the extrapolation of results across scales. The parameter μ can be estimated relatively easily from animal movement data by estimating the slope of the downward part of the log-log frequency distribution (Viswanathan *et al.*, 1999; Sims *et al.*, 2007). This approach has resulted in many observations of Lévy walks in animal movements, *e.g.*, albatross (Viswanathan *et al.*, 1996), deer and bumblebees (Viswanathan *et al.*, 1999), jackals (Atkinson *et al.*, 2002), reindeer (Mårell *et al.*, 2002), micro-organisms (Bartumeus *et al.*, 2003), seals (Austin *et al.*, 2004), spider-monkeys (Ramos-Fernández *et al.*, 2004) and goats chapter 2.

The scaling of the mean squared displacement (MSD) to the duration of searching, is an important macroscopic property of movement behaviour (Kareiva & Shigesada, 1983; Bell, 1991; Turchin, 1991). Lévy walk paths result in a MSD that scales with a factor α between 1 and 2 (Bartumeus *et al.*, 2005). For Brownian motion, MSD scales with $\alpha = 1$ with duration, while for ballistic (straight line) motion $\alpha = 2$ (Bartumeus *et al.*, 2005). Fixed scaling allows for the extrapolation of path properties from small to large scale movements. Correlated random walks, often used to model animal movements, do not have constant scaling factor for the MSD, but rather converge to Brownian motion at the long term limit and thus α eventually converges to 1 (Bartumeus *et al.*, 2005).

The Lévy walk with $\mu \approx 2$ has been shown to be extremely successful in finding scarce patches of targets (Viswanathan *et al.*, 1999; Bartumeus *et al.*, 2005). Further investigations have shown that the crucial assumption determining the efficiency of the Lévy flight model is the truncation of flights at target encounter chapter 3. This truncation allows for repeated rediscovery of the same patch of targets, while the relative large frequency of long movements ensure high efficiency in locating new patches. The frequency of encounters is determined by the density of patches of targets or, inversely, the mean free path between two patches targets (λ) (Viswanathan *et al.*, 1999).

Thus Lévy walks show scale-free macroscopic properties and have the highest searching efficiency. These properties of Lévy walks can however be conflicting if the truncation of a flight at target encounter would change the shape of the frequency distribution of performed flights (da Luz *et al.*, 2001), chapter 3. This would be the case if these encounters occur often and proportional to the length of a flight. While the scale-free increase of the MSD depends on the scale-free distribution of flight lengths, the truncated flight is shorter than the original flight, increasing the frequency of the smaller flight classes at the expense of the larger flight classes and possibly changes the distribution of flights. da Luz *et al.* (2001) have quantified the effect this truncation has on the distribution of the short flights, but the formula they provide does not allow for changes in the frequency of long flights in the distribution. Furthermore a change in the distribution of long flights will change the estimation of μ.

Here we use on simulated Lévy walks at different values of λ to assess the influence of encounters with targets on the properties of the movement path. We are especially interested in the displacement realised by the Lévy flight and the shape of the log-log frequency distribution of the observed flight lengths. This distribution is used to estimate the value of the parameter μ that determines the shape of the movement path. We compared the distribution of chosen flights to the distribution of observed flights to estimate the error in estimating μ from this distribution and to understand the effect of λ on the macroscopic properties of the movement paths.

4.2 Methods

To investigate the effect of target encounters on Lévy flights, we simulated the Lévy flight following the description of Viswanathan *et al.* (1999):

1. If a target site lies within a direct vision distance r_v, then the forager moves on a straight line to the nearest target site.
2. If there is no target site within a distance r_v, then the forager chooses a direction at random and a distance l_j from the probability distribution $P(l) \sim l^{-\mu}$. It then incrementally moves to the new point, constantly looking for a target within a radius r_v along its way. If it does not detect a target, it stops after traversing the distance l_j and chooses a new direction and a new distance l_{j+1}; otherwise, it proceeds to the target as in rule (1).

The movement was simulated in an expanding two-dimensional environment. Initially one region containing 10 randomly distributed targets was created (the dimensions of this region were determined by λ, see Bartumeus *et al.* (2005, appendix)). Whenever the forager scanned across the boundaries of this region (with a 'direct vision' distance of 1 unit), a new region containing 10 targets was added. Both non-destructive (as an approximation of a patchy resource distribution) and destructive searches were simulated (Viswanathan *et al.*, 1999). During a destructive search, targets were replaced within the region of the old target. For both destructive and non-destructive search a delay of four time steps after consumption was used within which no targets could be found by the forager. A step increment of 0.5 units was used.

Simulations were done for both destructive and non-destructive search in environments with λ of 10, 100, 1000 and 10000. Movement paths were simulated for five values of μ, ranging from near ballistic ($\mu = 1.1$) to near Brownian ($\mu = 2.9$), with intermediate values $\mu = 1.5$, $\mu = 2.0$ (referred to as the optimal movement), and $\mu = 2.5$. Each simulation was repeated 20 times, simulations lasted 10^6 timesteps. During the simulation, the chosen movement lengths and the subsequent locations of the forager were recorded. Displacement was recorded after 10^3, 10^4, 10^5 time steps and at the end of the simulation. After the simulation the recorded locations were aggregated into flights as described in Turchin (1998), chapter 2. This resulted in the observed flight distribution. We compared the longest of the observed flights to the longest of the chosen flights and λ. This gives information about the extent to which the flight distribution is truncated; the ratio between the observed and the chosen flights shows the effect of truncation, the ratio between the observed fights and λ and between the chosen flights and λ indicate the relative importance of λ in the truncation. The downward part of the log-log plot of the frequency distribution of flights was used to estimate both μ_{in} (for the distribution of chosen flights) and μ_{obs} (for the distribution of observed flights) (Viswanathan *et al.*, 1999; Sims *et al.*, 2007). The regressions of μ_{obs} on μ_{in} were calculated for each value of λ separately. Regressions were compared using analysis of covariance, followed by a Tukey-test for multiple comparisons (Zar, 1996).

4.3 Results

Because the results of the destructive search were qualitatively similar to those of the non-destructive search, only the non-destructive search results will be shown. For the near ballistic ($\mu = 1.1$) and optimal ($\mu = 2.0$) movements, the distribution of observed flights is clearly different from the chosen flights. This difference is largest for the near ballistic motion at low λ, in this situation the largest observed flight is only 6.7% of the largest chosen flight (Table 4.1). While for near Brownian motion ($\mu = 2.9$) the maximum chosen flight is already shorter than λ and there is no truncation of these flights.

These truncations can be seen in the distribution of the flight lengths. Figure 4.1 shows the log-log frequency distribution of the observed flights for a given path for all three values of μ at the highest and lowest values of λ. In these graphs it can be seen that the truncations result in three patterns for the tail of the distribution: (1) the slope and the shape of the distribution of observed flights do not deviate from the distribution of chosen flights (Figure 4.1 b,d,f), (2) the slope of the distribution of observed flights partially follows the slope of the distribution of chosen flights, but the frequency of larger flights is much smaller for the observed than for the chosen flights (Figure 4.1 c,e), and (3) the observed flight distribution does not resemble the chosen flight distribution (Figure 4.1 a).

Figure 4.2 illustrates that the distribution of observed flights changes with decreasing λ. In this figure, the estimated μ of the observed flights (μ_{obs}) is plotted against the μ of the chosen flights μ_{in}. The regression lines for the different values of λ share a common slope ($F = 2.29$, $\nu_1 = 3$, $\nu_2 = 392$, $p = 0.08$, common slope = 0.93), but the elevations of the lines are different ($F = 175.2$, $\nu_1 = 3$, $\nu_2 = 397$, $p \ll 0.001$). Multiple

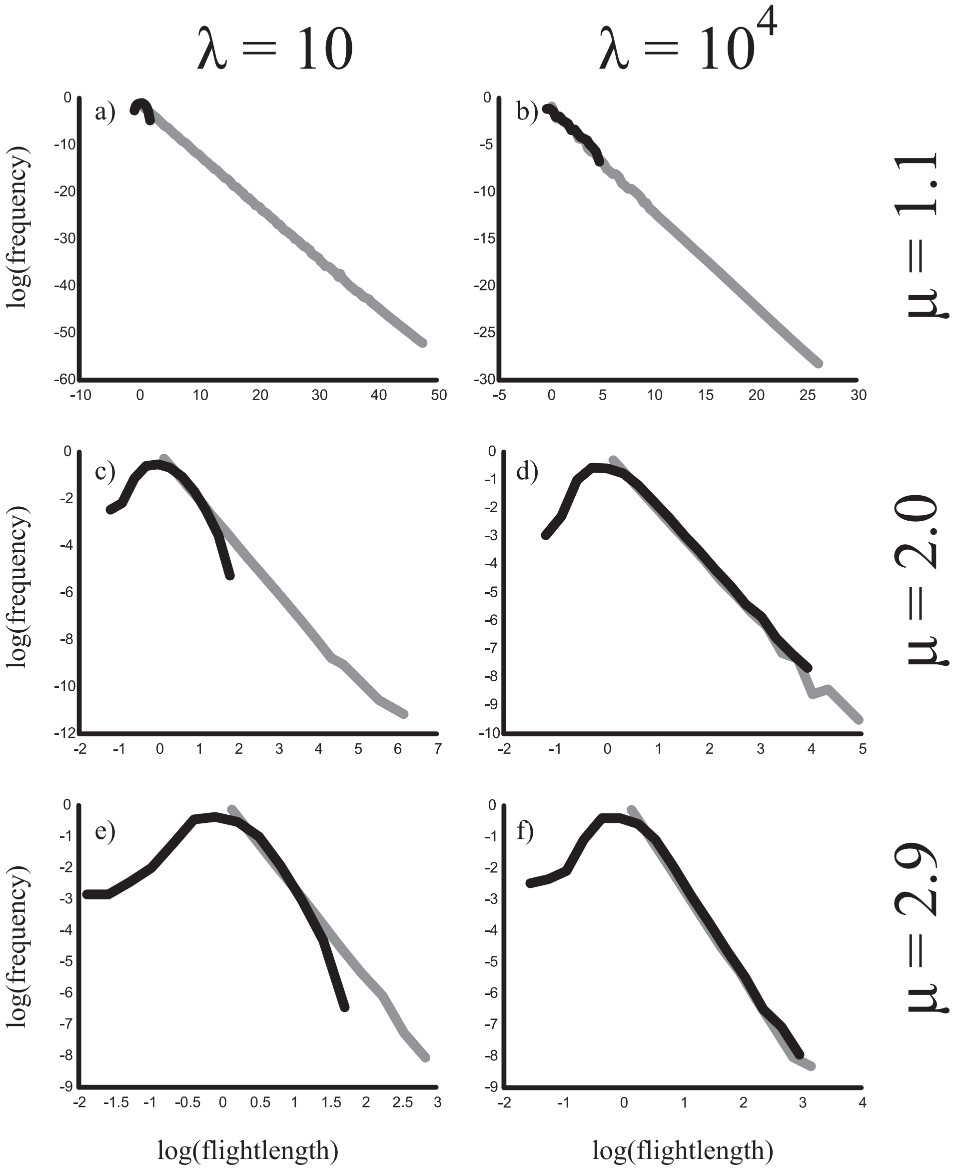

Figure 4.1: The log-log frequency distribution of chosen (gray line) and observed (black line) flights. Representative flight distributions are shown for (a) $\mu = 1.1$,$\lambda = 10$, (b) $\mu = 1.1$,$\lambda = 10^4$ (c) $\mu = 2.0$,$\lambda = 10$ (d) $\mu = 2.0$,$\lambda = 10^4$ (e) $\mu = 2.9$,$\lambda = 10$ (f) $\mu = 2.9$,$\lambda = 10^4$

Table 4.1: The maximum flights. Maxima for the chosen (M_c) and observed (M_{obs}) flights. $\frac{M_{obs}}{M_c}$ shows the relative truncation, while the relation between M_c/λ and M_{obs}/λ gives insight in the relative impact of λ on the truncation. Values for the flights and λ are all log_{10} transformed.

μ	λ	M_c	M_{obs}	$\frac{M_{obs}}{M_c}$	M_c/λ	M_{obs}/λ
1.1	1	42.716	1.999	0.067	42.716	1.999
	2	40.670	2.904	0.073	20.335	1.452
	3	31.808	3.812	0.123	10.603	1.271
	4	23.460	4.651	0.212	5.865	1.163
2	1	5.343	1.862	0.352	5.343	1.862
	2	5.087	2.724	0.541	2.544	1.362
	3	5.343	3.575	0.679	1.781	1.192
	4	4.862	4.228	0.872	1.215	1.057
2.9	1	2.935	1.734	0.598	2.935	1.734
	2	2.860	2.401	0.844	1.430	1.201
	3	2.860	2.694	0.948	0.953	0.898
	4	2.965	2.976	1.004	0.741	0.744

comparisons showed that the lines for $\lambda = 10^3$ and $\lambda = 10^4$ had no different elevation ($q = 2.14$, $\nu = 196$, $p > 0.05$). The other lines had significantly different elevations.

The MSD is shown for three values of μ (near Brownian, optimal and near ballistic) in figure 4.3. For the near Brownian movement, the MSD is scaling to time with unity. The MSD of the ballistic and optimal movements are greatly reduced by a decrease of λ. Over time the MSD of both near ballistic and optimal search converges to the MSD of Brownian motion ($\alpha = 1$).

4.4 Discussion

The assumption of scale-free extrapolation of the movement pattern across spatial scales for fractal-like movements, like the Lévy walks, is important to provide a link between small scale data-collection and landscape level spatial processes (Turchin, 1996). The simulation results presented in this study show that encounters with targets can greatly change both the macro- and microscopic properties of movement paths. These encounters limit the scales over which the macroscopic properties of the movement path are approximately scale-free. This means that the property that makes the Lévy walks an optimal movement strategy in a patchy environment, at the same time changes the macro- and microscopic properties of the movement paths. This limits the applicability of this fractal-like movement model to link local movements and landscape level processes.

At the macroscopic level, the mean square displacement of the movement paths decreases with the increase of the number of encounters with targets. This decrease

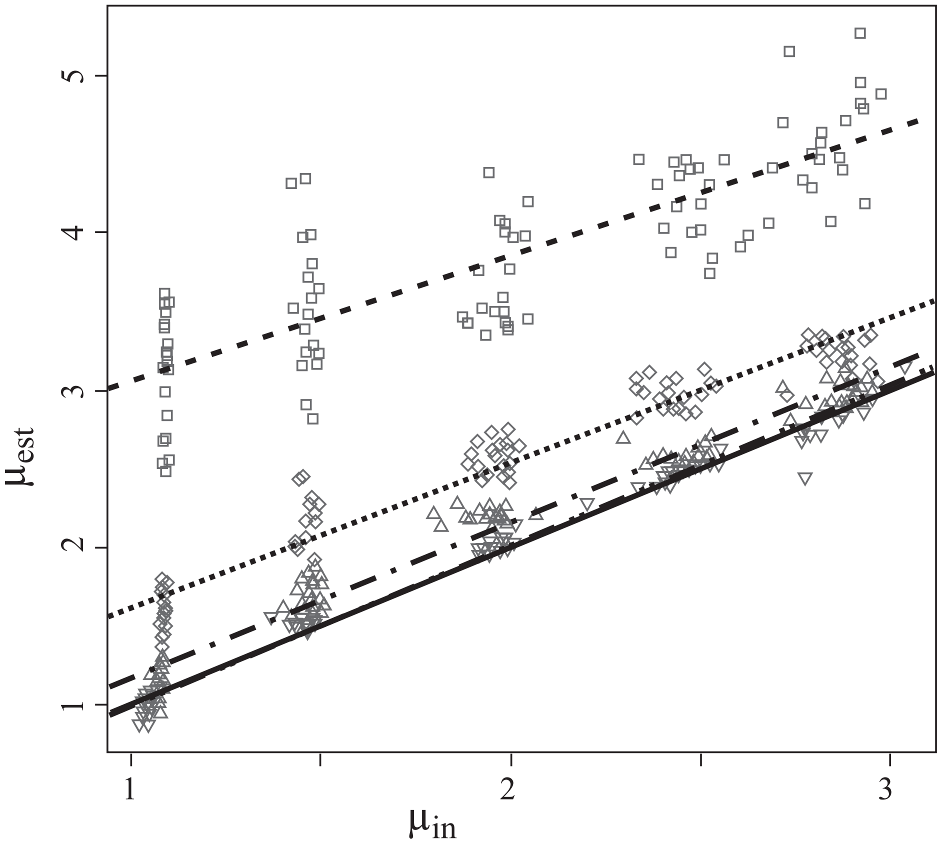

Figure 4.2: Observed vs Chosen μ. The slopes of the downward part of the log-log frequency distribution of the observed flights (μ_{obs}) are plotted against the slopes of the distribution of flight used to generate the paths μ_{in}. For four values of λ ($\lambda = 10$, (□); $\lambda = 10^2$, (◇); $\lambda = 10^3$, (△); $\lambda = 10^4$, (▽)); The solid line is the reference line $\mu_{in} = \mu_{obs}$

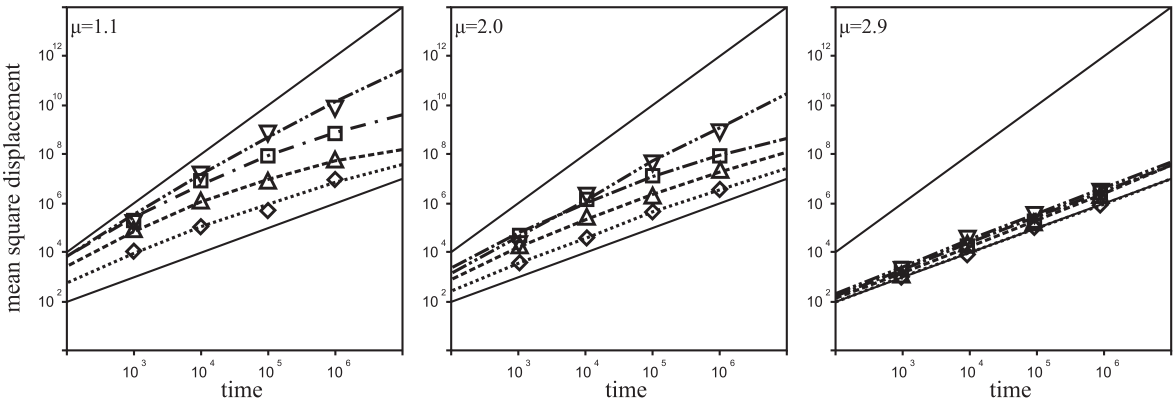

Figure 4.3: The mean square displacement (MSD) as a function of time. MSD is shown for the near ballistic ($\mu = 1.1$, left), optimal ($\mu = 2.0$, middle) and near Brownian ($\mu = 2.9$, right) motion. Each panel shows the MSD at four levels of λ ($\lambda = 10$, ◇; $\lambda = 10^2$, △; $\lambda = 10^3$, $\lambda = 10^4$, ▽). The continuous lines show the hypothetical extremes of Brownian ($\alpha = 1$) and ballistic ($\alpha = 2$) motion. Fitted lines serve only as indication of a temporal trend in MSD.

in displacement is the result of truncations of the long movement lengths at target encounter. These truncations occur at every scale of λ evaluated in this study, but have little effect on movement paths resulting from Brownian motion. This is due to the fact that the longest flight expected in a flight length distribution associated with this type of movement is about 10^3 units, which is smaller than the largest λ used. All other movement paths used in this study show a decrease in the scaling of the mean square displacement with time that will eventually make all paths converge to Brownian motion at scales much larger than the scale of the movements.

These truncations also change the shape of the distribution of observed flights. The shape of these distributions could be categorised into three general patterns. First (mostly observed for high values of λ and large values of μ), the slope of the distribution of observed flights coincides with the slope of the original distribution (pattern 1). With pattern 2 (found at intermediate to low values of λ and at intermediate values of μ), the slope of the original distribution only coincides with the observed distributions at intermediate flights. For patterns of type 3 (found with low values of μ and λ), the slope of the chosen distribution cannot be found in the observed distribution. For patterns 2 and 3 the estimation of the value of μ from the is no longer straight forward. As a result of this shift in patterns, the value of μ was systematically overestimated. These errors become apparent at intermediate values of λ and increase with decreasing λ. Field or experimental estimations of μ should therefore include an estimate of λ and are only valid for high values of λ.

The relation between the scale of the target distribution (λ) and the scale of the movement path, that we find in this study, will not be limited to targets which are specifically sought using a Lévy walk, but will occur with fractal movements and the scale of the distribution of other landscape features that interact with these movements. Such interactions with landscape features have been shown to influence animals' movement paths (Crist *et al.*, 1992; Crist & Wiens, 1994; Wiens *et al.*, 1995) and changes in the dominant scale of the landscape have changed the distribution of animals (*e.g.*, elephants (Murwira, 2003)). We show that interactions with landscape features reduce movements that are in principle scale free to Brownian motion that is scaled to the scale of those landscape features. Because Brownian motion can only cause limited dispersion of animals through the landscape relative to scale-free fractal movements (Bartumeus *et al.*, 2005), the simple interaction of animals with landscape features could account for changes in animal distribution if the scale at which those landscape features are expressed change.

Acknowledgments

We would like to thank G.M. Viswanathan for advise on simulating Lévy distributions and F. Bartumeus and the members of the Forest Ecology & Nature Conservation discussion group at PE&RC for stimulating discussions and comments on earlier versions of the manuscript.

5 Search Movements of Doves are not Affected by Detection Radius and Resource Density

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Animal movement is predicted to change in response to changes in the mean free path (λ) between resources. With a small λ the path is predicted to be tortuous without long stretches, while with a large λ the path will be more straight, containing many long stretches. Searching ceases at the encounter with a target, causing interruptions in the searching part of the movement path. These interruptions are predicted to alter the shape of the movement path, relative to the searching path. Using an experimental system with ring doves searching for hidden hemp seed, these predictions were tested. The experimental setup allowed for the independent manipulation of the detection radius of the doves and the density of the seeds, together determining λ. Both hypotheses were refuted by the data. This result indicates one movement strategy regardless of the density of resources.The movements of the doves could be described as a Lévy modulated correlated random walk. The distribution of intervals between large turns (l) could be described as $P(l) \sim l^{-\mu}$, with $\mu = 1.61$. This is a deviation from the predicted ballistic movement ($\mu \rightarrow 1$) in a search for random targets, and is different from the often found $\mu \approx 2.0$ that is optimal in a patchy environment.

5.1 Introduction

Whenever information about the distribution of resources is limited, animals targeting these resources are predicted to employ random movement strategies while searching (Bell, 1991; Bartumeus *et al.*, 2005). Because information limitation is expected to be common (Bell, 1991), a number of studies used random search movements within the theory of optimal foraging (Pyke, 1984; Cain, 1985; Viswanathan *et al.*, 1999; Zollner & Lima, 1999; Bartumeus *et al.*, 2005). These studies show that some movement patterns are more successful in finding resources than others. In the search for single targets that are depleted after encounter, straight line searches are most efficient (Pyke, 1984; Viswanathan *et al.*, 1999; Zollner & Lima, 1999; Bartumeus *et al.*, 2005). For multiple targets with a patchy distribution a fractal combination of frequent short with occasional very long straight searches maximises the searching efficiency (Viswanathan *et al.*, 1999;

Bartumeus *et al.*, 2005). The key environmental parameters that scale movement models are the number of resource targets (N_0) and the detection radius of the searching animal (r_v [m]) (Viswanathan *et al.*, 1999).

Many animals have been shown to follow these predictions on various scales and mostly in field situations (e.g.micro-organisms (Bartumeus *et al.*, 2003), cabbage butterfly (Root & Kareiva, 1984), painted turtles (Bowne & White, 2004), albatross (Viswanathan *et al.*, 1996),deer (Viswanathan *et al.*, 1999), reindeer (Mårell *et al.*, 2002), goats (chapter 2), grey seals (Austin *et al.*, 2004), jackals (Atkinson *et al.*, 2002), and spidermonkeys (Ramos-Fernández *et al.*, 2004)). However, most of these studies do not specifically address the effect of resource density and detection radius, on the shape of the movement path (but see Boyer *et al.* (2006)). Using ring doves (*Streptopelia roseogrisea*), we experimentally tested the effect of resource density and detection radius on the shape of the movement path.

The radius at which targets can be detected (r_v) and the density of resources (N_0/L^2, where L is the size of the area [m^2]), together determine the average distance that needs to be moved to locate a resource (the mean free path $\lambda \approx \frac{L^2}{2r_vN_0}$ (Viswanathan *et al.*, 1999; Bartumeus *et al.*, 2005)). Theoretical work has lead to the prediction that for optimal foraging at low values of λ the movement path should be more tortuous (Bell, 1991; Viswanathan *et al.*, 1999) than at higher λ. In the random walks, the tortuosity changes by changing 1) the distribution of turning angles (resulting in a correlated random walk (Kareiva & Shigesada, 1983; Turchin, 1998)), 2) the distribution of intervals between turning (for specified distributions resulting in a Lévy walk (Viswanathan *et al.*, 1999)) or 3) a combination of both (resulting in a Lévy modulated correlated random walk (Bartumeus *et al.*, 2005)). Consequently, the distribution of the turning angles and/or the intervals between turning can be used to characterise the tortuosity of the movement path. The length of the mean vector of turning angles R quantifies the average displacement per step and can be used to quantify the tortuosity of the movement path. A small R indicates a highly tortuous movement path. The exponent ($-\mu$) of the power-law describing the distribution of turning intervals ($P(l) \sim l^{-\mu}$, where l is the length of a turning interval) also captures the tortuosity of the movement path. For $1 \leq \mu \leq 3$ the movement path is referred to as a Lévy walk with $\mu \rightarrow 1$ for low tortuous, ballistic, movement and $\mu \rightarrow 3$ for high tortuosity. The predicted optimal search movement for a patchy distribution of targets is $\mu \approx 2.0$ (Viswanathan *et al.*, 1999). So to optimise the efficiency in finding targets the movement pattern needs to be adjusted (by changing either R or μ) to the environment (*i.e.,* λ).

Within the movement path of an animal searching for targets, we differentiate between 1) the 'total path' i.e. the entire travelled path and 2) the 'searching path', i.e. the traveled part of the movement path in which the animal is only searching in between encounters with targets (see Figure 5.1). Theoretical work predicts that changes in r_v or N_0 (thus changes in λ), result in a change of the shape of the movement path (as has been observed for bumblebees (Viswanathan *et al.*, 1999) and goats chapter 2). Furthermore, theoretical models predict that with decreasing λ an increasing difference between the characteristics of the total path and searching path can be expected. This latter prediction follows from the argument that at low values of λ, an animal will

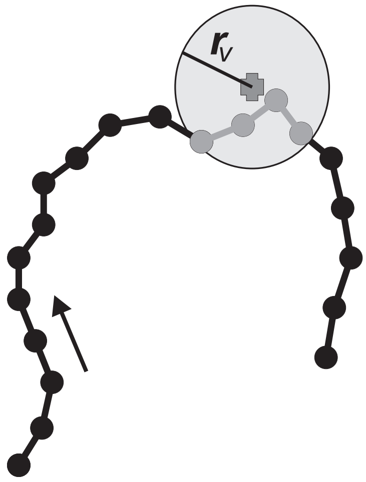

Figure 5.1: The difference between locations making up the total path (all filled circles) and the locations where the animal is searching (black circles). Those locations where the animal is within the detection radius (r_v) of a resource (+) are classified as part of a finding event, between these locations movement is not guided by searching behaviour, but directed towards the resource

encounter more targets per unit of time. Because target encounters cease searching behaviour, they influence the characteristics of the total movement path, chapter 4.

In this paper, we test the effect of changes in detection radius r_v and resource density N_0 on movement patterns in a controlled setting for the first time. Our experimental setup allows us to systematically manipulate N_0 and r_v, and to directly measure the difference between the searching path and the total path. We tested the following two hypotheses:

$H1$ The path characteristics of the searching path are different from those of the total path.

$H2$ The movement path becomes more tortuous when r_v and/or N_0 increase.

5.2 Material and Methods

Our hypotheses were tested using an experimental system with ring doves searching for hidden hemp seeds in an arena. The experimental design allowed for the independent manipulation of both r_v and N_0. The searching path could be separated from the total path, because r_v and the location of the seeds were known. Video-tracking the dove provided high temporal resolution determination of the position of the dove.

5.2.1 Animals

For the experiment, 10 domesticated ring doves of unknown sex were used. The animals' primary feathers were cropped to avoid flying during the trials. In between trials, the

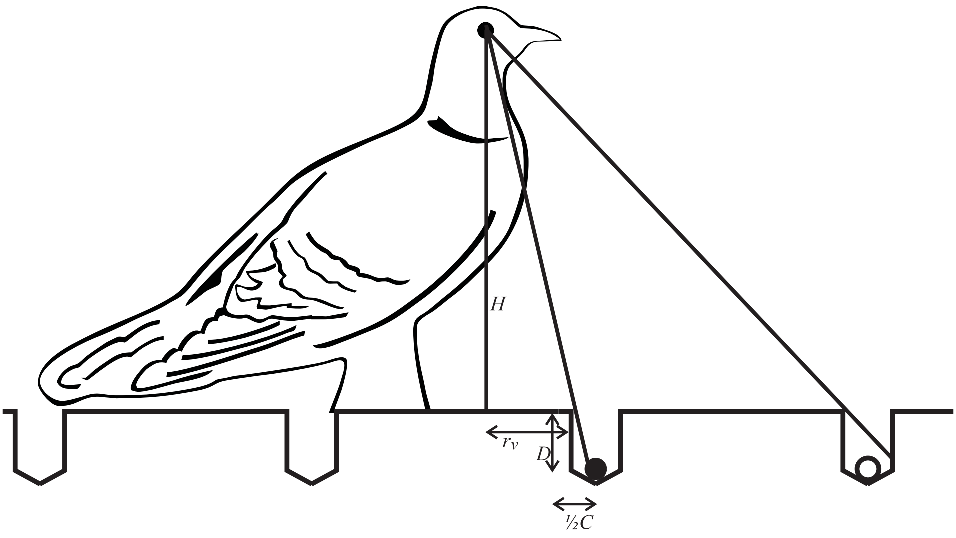

Figure 5.2: Schematic of the experimental setup. By placing the seed in a hole in the ground the minimal distance at which it can be seen by the dove can be measured. The depth (D) of the holes could be varied, the height of the dove (H) was estimated to be 18 cm. From these two parameters, the detection distance r_v could be calculated

animals were housed individually, but closely together in cages. To ensure that the animals foraged during the trials, the trails were done in the morning, and doves were deprived of food 36 hours prior to the experiment. When not in cue for the experiment, food an water were provided *ad libitum*. The animals were habituated to the arena prior to the experiment. The experiment was assessed and permission granted by the Institutional Animal Care and Use Committee of Wageningen University (entry code 2004095c).

5.2.2 Arena design

The staging arena consisted of a fenced area of 4 meter x 4 meter. The floor of this arena consisted of wood plating that contained a grid of 1917 holes (⌀ 1 cm, at an average distance of 9 cm) that formed the potential resource locations. The detection radius of the dove was altered by manipulating the depth of the holes. Adding a layer of wood plating, increased the depth of each hole from 0.4 to 0.8 cm. With an average eye height of 18 cm, this manipulation resulted in detection radii r_v of 22.5 cm and 11.25 cm, respectively (Figure 5.2). The arena was surrounded with 2.5 meter high fences that were covered with white cloth to minimise distraction for the experiment subjects. Overhead lights were used and windows were blinded during experiments to ensure that light was similar during all trials and no orientation cues (*e.g.*, the position of the sun) could affect directionality.

5.2.3 Tracking system & Image analysis

During the trials, the ring dove was video-tracked from above. The whole area was filmed at 4 Hz by four webcams (Quickcam 4000, Logitech Inc, Romanel-sur-Morges, Switzerland) resulting in a final spatial resolution of 2.3 cm pixel (Figure 5.3). The webcams were controlled using the Image Acquistion Toolbox in Matlab 7.0 (The Mathworks Inc., Natick, MA, USA). The consecutive locations of the doves were extracted from the data using a custom-written algorithm in Matlab (using the Image Processing Toolbox). For every sampling point in the time-series, a calibrated composite image of the arena was calculated by rotating, scaling and aligning the raw images of the four webcams. In essence, the position of the dove was extracted by subtracting the frame with a weighted frame of the empty arena that was acquired before the start of every trial. The resulting image was thresholded and denoised, which yielded a binary image of the arena (pixelvalue = 0) with the region of interests (ROI, pixelvalue = 1) occupied by the dove. The position of the dove was defined as the position of the centre of mass of the ROI. This algorithm proved very robust as out of 120 trails, only 2 paths could not be extracted.

5.2.4 Trial procedure

The animals foraged on three different resource densities, with 9, 19 and 95 seeds in the arena, and on two different hole depths, *i.e.*, two resource detection radii of the animal (0.4 and 0.8 cm, resulting in r_v values of 22.5 cm and 11.25 cm, respectively, based on an average dove height of 18 cm). For each density, two different distributions were presented to each dove. For these distributions, each seed was assigned a random location in the arena, with the constraint that the distance between to seeds was larger than r_v. At the densities used, the majority of holes did not contain seeds, only 0.5%, 1% and 5% of the holes were filled. Before the trial the locations of the resources were recorded with the cameras using paper markers. A ring dove was introduced in the arena, and was tracked for 15 minutes. After the trial, the remaining seeds were counted and removed.

The trials with the large detection radius were carried out from 29 June 2005 until 1 August 2005, and the trials with the small detection radius were carried out from 23 August 2005 until 22 September 2005. Doves were put in the trial in sequence, with a maximum of three doves per day. Each dove encountered the different distributions in random order.

5.2.5 Statistical analyses

The parts of each path that were not within detection distance r_v from a resource were analysed separately as searching path (Figure 5.1), next to the analysis of the total path comprising all locations. Turning angles at locations that were within the detection distance from a resource were excluded from the ‘total path’ turning angle distributions to form the ’searching path’ turning angle distributions. Intervals that

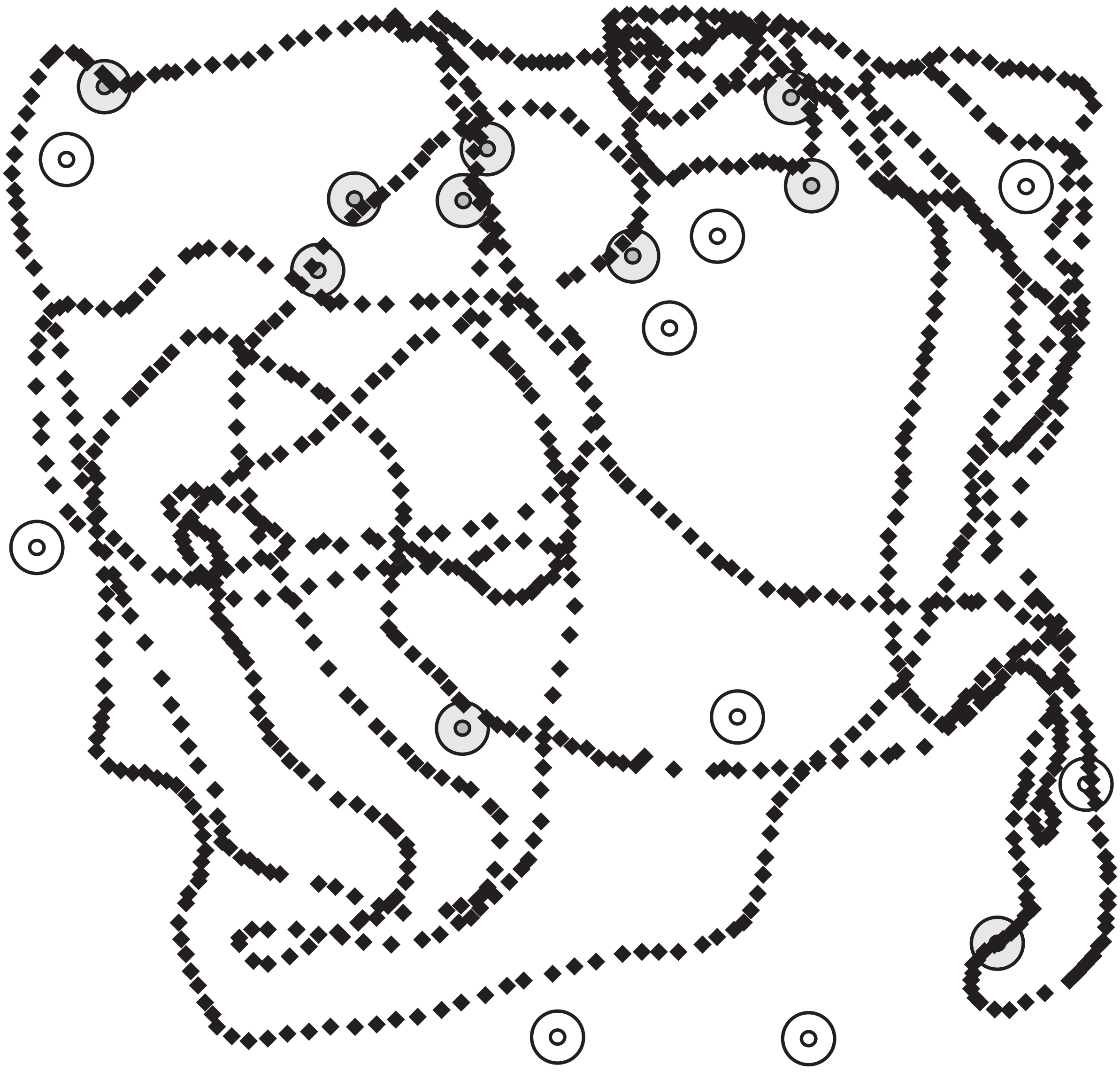

Figure 5.3: A movement path. This figure shows a typical movement path. The recorded locations of the dove are shown with a filled diamond. Seeds (small circles) and the area around it from where they can be detected (large circles, with radius r_v) are shown. Seeds that are eaten are shaded. Parts of the path that are within the radius r_v of a seed (shaded areas) are excluded from the path to derive searching path statistics

encompassed these locations were excluded from the 'total path' interval distribution, to form the 'searching path' interval distribution. The characteristics of the searching path were calculated in the same way as those of the total path. For the statistical analyses, the movement path data were lumped according to the different values of λ, *i.e.*, for each combination of N_0 and r_v. Following Bartumeus *et al.* (2003), the major discontinuity in the turning angle distribution (β) was used as an indication that there are two overlapping distributions of turning angles; a unimodal distribution of turning angles and a uniform distribution of turning angles. The turning angles were thus split into two groups, $\Psi_{<\beta}$ (small angles) and $\Psi_{>\beta}$ (large angles), that were analysed separately. The small angles were used directly, while for the large angles, the distribution of intervals between these large angles was used as an indication of the distribution of the 'flights' of a Lévy flight movement (Viswanathan *et al.*, 1999; Bartumeus *et al.*, 2003). The slope of the downward part of the log-log frequency distributions of those flights is an estimator of the parameter μ scaling such Lévy flight movements (Viswanathan *et al.*, 1999).

First, the hypothesis that there is a difference between the searching path and the total path was tested for each combination of N_0 and r_v. For the small angles ($\Psi_{<\beta}$) the probability that the turning angles of the searching paths observed were a random sample of the turning angles of the total paths with the same combination of N_0 and r_v was determined using bootstrapping. The mean vector (R) of the searching $\Psi_{<\beta}$ was compared to the R of 1000 equally sized random samples of the $\Psi_{<\beta}$ from the total path. The percentage of samples with a larger R was calculated. Percentages $> 97.5\%$ and $< 2.5\%$ were taken as indication that the searching path had a significantly lower or higher R, respectively. Subsequently the slope of the distribution of intervals between the large angles ($\Psi_{>\beta}$) for the searching and the total path were compared using the Student's t-test (Zar, 1996).

Second, the effect of N_0 and r_v on the total paths was tested. A difference in the spread of $\Psi_{<\beta}$ was tested using the two-factor Kruskall-Wallis test as proposed by Scheirer, Ray & Hare (Scheirer *et al.*, 1976; Zar, 1984). For this procedure sample sizes were reduced to the smallest sample size. The comparison between the slopes of the distribution of intervals between $\Psi_{>\beta}$ was done using analysis of covariance (Zar, 1996).

5.3 Results

Of the 120 trials performed, 102 trials were included in the analyses. The other trials were excluded because there were either difficulties with extracting the positions of the dove from the captured images (2) or there was insufficient movement during the 15 minute trial (16).

The major discontinuity in the frequency distribution of turning angles was found at $\beta = 45°$ (Figure 5.4). The turning angles were split into two groups; $\Psi_{<\beta}$ (small angles, $|angle| < \beta$) with a unimodal distribution and $\Psi_{>\beta}$ (large angles, $|angle| > \beta$) with a more uniform distribution. These groups were analysed separately. A linear regression was fitted to the log-log distribution of intervals between the large angles (Viswanathan

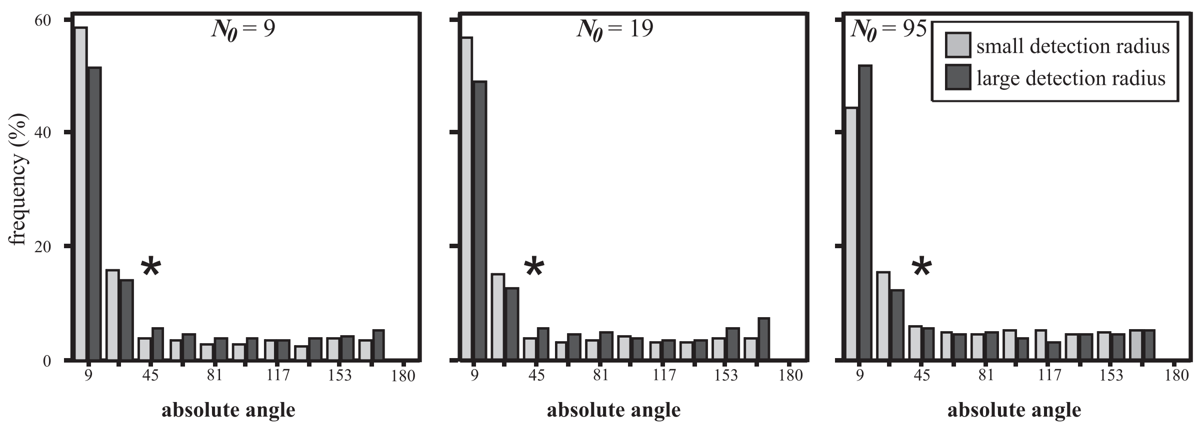

Figure 5.4: frequency distribution of the angles. The frequency distribution of the absolute turning angles are shown, summed for the different number of seeds N_0 and the different detection radii r_v. The frequency distributions of the turning angles show a discontinuity at 45°

et al., 1999; Sims *et al.*, 2007). For all separate treatments, this regression resulted in good fits: $R^2 > 0.94$ (see Figure 5.5).

First, we tested our hypothesis that the searching path was different from the total path. The small turning angles ($\Psi_{<\beta}$) in the searching paths did not differ from a random sample from $\Psi_{<\beta}$ of the total movement paths for all combinations of N_0 and r_v (Table 5.1). Furthermore, for none of these parameter combinations, a difference between the distributions flights of the searching paths and the total path was found (Table 5.2).

Second, we tested the difference in the total path between the different levels of N_0 and r_v. $\Psi_{<\beta}$ did not differ between the different values of r_v and N_0 (Schreirer-Ray-Hare-test $H = 6.8$, $\nu = 5$, $p = 0.24$). Neither did the distributions of the intervals differ between the large turning angles ($\Psi_{>\beta}$) ($F = -0.63$, $\nu_1 = 5$, $\nu_2 = 46$, $p > 0.05$, pooled slope $= -1.61$, Figure 5.5).

5.4 Discussion

The shape of the movement path determines the displacement that is reached by the animal while moving and thus the average spread of the animals in a population (Bell, 1991; Turchin, 1991; Benhamou, 2004; Bartumeus *et al.*, 2005). As such, movement behavior can have a large influence in the spatial extent over which animals interact with and have impact on their environment. Understanding the magnitude of the response of animals to the density of resources and the effect of resource encounters on the total movement path strengthens the understanding of the effect of small scale foraging movements in larger scale ecological processes, such as dispersion and consumer-resource interactions.

For the first time to out knowledge, we investigated the sensitivity of the movement patterns of ring doves to changes in the density of seeds (N_0) and the distance from which

Table 5.1: Summary of the distribution of turning angles < 45° in the total path ($_T$) and the searching path ($_S$). The table shows the number of angles, the mean vector (r) and the percentage of random samples from the angles from the total path that has a larger R than R_S.

r_v cm	N_0	##angles$_T$	R_T	##angles$_S$	R_S	% > S
22.5	9	1269	0.963	398	0.961	79.0
22.5	19	1311	0.966	294	0.963	85.5
22.5	95	647	0.955	114	0.957	34.6
11.25	9	1021	0.959	543	0.957	76.3
11.25	19	824	0.960	434	0.963	10.5
11.25	95	1263	0.960	181	0.960	57.0

Table 5.2: Comparison of the slopes of the loglog distribution of intervals between turning angles > 45° between the total path (μ_T) and the searching path (μ_S)

r_v (cm)	N_0	μ_T	μ_S	t	ν	p
22.5	9	-1.592	-1.492	0.783	12	0.45
22.5	19	-1.616	-1.620	0.030	10	0.98
22.5	95	-1.565	-1.339	0.469	5	0.66
11.25	9	-1.561	-1.569	0.081	10	0.94
11.25	19	-1.587	-1.538	0.505	12	0.62
11.25	95	-1.668	-1.715	0.370	10	0.72

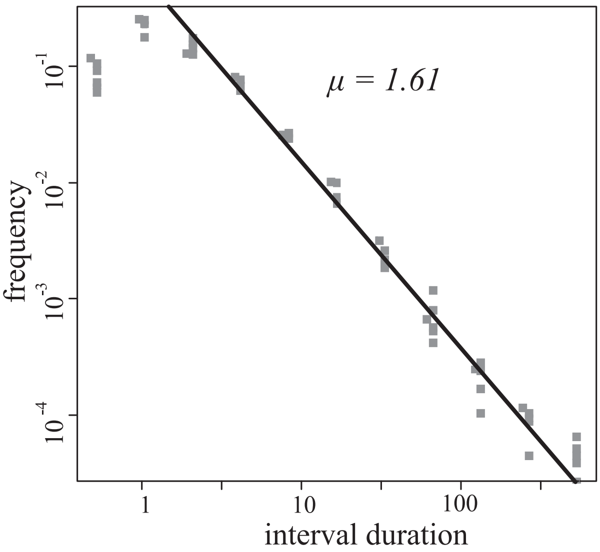

Figure 5.5: The Frequency distribution of intervals between large turning angles ($\Psi_{>\beta}$). The frequency distributions for all six combinations of N_0 and r_v are combined. The regression line fits a power-law distribution ($P(l) \sim l^{-\mu}$ with $\mu = 1.61$, $R^2 = 0.99$) . The regression excludes the first two bins.

these seeds can be detected (r_v) experimentally. Furthermore, we tested the prediction that the searching path is different from the total movement path. Within the range of densities and detection radii that we used, no change in movement pattern was found. There also was no difference between the parts of the movement path where the doves were searching for seeds and the total movement path.

The distribution of the absolute turning angles of the doves showed a marked discontinuity (β) at 45°. This discontinuity was used to distinguish two different types of movement: (Bartumeus *et al.*, 2003) 1) the small angles ($\Psi_{<\beta}$) showed a unimodal distribution, indicative of a correlated random walk, and 2) the large angles ($\Psi_{>\beta}$) were uniformly distributed. The distribution of intervals between large turning angles of the doves could be described by a negative power-law distribution, this indicates scale-free Lévy flight behaviour. These two different patterns in the movement path together suggest that the doves search according to the Lévy modulated correlated random walk (LMCRW) introduced by Bartumeus *et al.* (2005). The LMCRW combines the large scale properties of the Lévy flight behaviour with small scale deviations from this behaviour.

Many studies finding Lévy flight behaviour in animals find the exponent μ to be approximately 2 (Viswanathan *et al.*, 1996, 1999; Atkinson *et al.*, 2002; Mårell *et al.*, 2002; Bartumeus *et al.*, 2003; Ramos-Fernández *et al.*, 2004) This value for μ is the theoretically predicted optimum when searching for patchy distributed targets. However, for randomly distributed targets, such as the ones the doves were confronted with in this study, theory would predict μ to approach 1, resulting in straight line movement (Viswanathan *et al.*, 1999; Zollner & Lima, 1999; Bartumeus *et al.*, 2003). Our experiment shows an exponent value of $\mu = 1.61$ to fit the distribution of the intervals between large turning angles. This exponent ($\mu = 1.61$) does, however, falls well within the range of near optimal exponents for searching for targets in patches that become temporarily unavailable after it has been visited (Raposo *et al.*, 2003). This could be an indication that doves searching for seeds employ one movement strategy that is not conditioned to the density or distribution of the seeds. Their movement pattern does allow for both patchy and non-patchy distributed seeds.

Within this experiment the animals performed a standard search strategy that was independent of the mean free path (λ). We measure no effect of target encounter on the movement path within the range of seed densities and detection radii used in this experiment. Furthermore, the doves do not seem to adjust their behaviour as a function of different densities encountered. If this finding would hold for a wider range of λ and over larger spatial extent, this allows prediction of animal movements over wide scales based on small scale movements. The Lévy modulation of the movement will ensure scale free movement properties that result in superdiffusive dispersion (Bartumeus *et al.*, 2005). The specific low value of μ found in this study would make animals interact with their environment over an even wider range than the 'optimal' $\mu \approx 2.0$ would. The doves used in this experiment will thus cover a larger range than predicted on the basis of the optimal Lévy walk.

Acknowledgments

We would like to thank Ed de Boer for taking care of the doves and helping us out whenever necessary, Martijn Hartman for his contribution to the experiments, the people at the experimental zoology group for letting us use the computers there and Thomas Groen for advise and discussions.

6 Optimal Foraging for Multiple Resources in Several Food Species

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Henrik J. de Knegt

Optimal foraging theory has rarely resulted in quantitative models for animals that need to forage for more than one resource. However, such models are needed because the concentrations of resources in food species are not perfectly balanced to the needs of an animal and forage species differ in these concentrations. Under many circumstances animals should thus forage on multiple food species to attain the maximum and most balanced intake of several resources. In this paper we present a model to extend optimal foraging theory to incorporate concurrent foraging for multiple resources from several forage species. A natural balancing of resources is achieved by representing the amount of a resource as the time during which it is used by the animal. Optimisation of decisions at two scale levels is considered simultaneously: the time spent in a patch, and the proportion of patches of each forage species that is included in the foraging path. Our results show that the balancing of resource intake is achieved at the level of the foraging path, while the maximisation of intake is realised at the nested patch level. Furthermore our results show that the choice for a forage species is dependent on the differences between the intake per forage species, and on the differences between the resource ratios in the forage species. The optimal patch residence time is a function of only local information.

6.1 Introduction

Optimal foraging theory has mainly focussed on the optimal acquisition of a single resource (generally energy as the principal forage component for animals) (Charnov, 1976; Stephens & Krebs, 1986; Newman *et al.*, 1995; Bergman *et al.*, 2001). Most extensions have involved the constraints an animal faces while trying to either maximise the intake rate of a resource or minimise the time needed to acquire a specific amount of that resource (Pulliam, 1974; Westoby, 1974; Pulliam, 1975; Belovsky, 1978; Owen-Smith & Novellie, 1983; Stephens & Krebs, 1986; Illius & Gordon, 1991; Owen-Smith, 1993; Wilmshurst *et al.*, 2000; Bergman *et al.*, 2001; Fryxell *et al.*, 2004). However, animals need to acquire more than one type of resource during foraging; many (macro-)nutrients (*e.g.*, protein or nitrogen and phosphorus) are consumed and needed (Westoby, 1974; Belovsky, 1978; Westoby, 1978; Prins & Beekman, 1989; Prins, 1996; Forbes, 1999;

Raubenheimer & Simpson, 2004; Simpson *et al.*, 2004; Anderson *et al.*, 2005; Prins & Van Langevelde, in press). The concentrations of these (macro-)nutrients differ between the different types of food. Especially for herbivores, the concentrations of (macro-)nutrients will differ both between and within forage species (Voeten & Prins, 1999; Simpson *et al.*, 2004; Prins & Van Langevelde, in press). Although linear programming studies do take minimal requirements of several nutrients into account (Westoby, 1974; Pulliam, 1975; Belovsky, 1978; Prins & Beekman, 1989; Nolet *et al.*, 1995; Voeten & Prins, 1999), the optimal acquisition of multiple resources has rarely been considered quantitatively so far (but see Simpson *et al.* (2004)).

Herbivores have been shown to make foraging decisions at different scales. These decisions involve choosing in which areas to search for food, which forage species to include in their foraging path or diet, and how long to stay in a given patch (Schoener, 1971; Owen-Smith & Novellie, 1983; Pyke, 1984; Senft *et al.*, 1987; Bailey *et al.*, 1989; Skarpe *et al.*, 2007). In this paper we extend optimal foraging theory to include foraging for multiple resources at the scale of both the patch and the foraging path.

On average, there will be a constant turnover rate of resources within a herbivore (Forbes, 1999; Prins & Van Langevelde, in press), while these resources are acquired during short and discrete bouts of foraging. During these short foraging bouts, herbivores need to acquire enough of all resources to be able to engage in non-foraging activities. In forage species the ratio between the concentrations of resources will in most cases be different from the ratio of the turnover rates for these resources in the herbivore (Prins & Beekman, 1989; Anderson *et al.*, 2004; Prins & Van Langevelde, in press). A herbivore thus faces the two-fold problem of having to choose between different forage species in order to balance the intake of several resources to its requirements, and of having to maximise the rate at which this optimal food mix is consumed.

To address this problem, we use a stoichiometric approach within the optimal foraging paradigm (Sterner & Elser, 2002; Simpson *et al.*, 2004). This is done by linking the composition of forage species to the turnover rates of the different resources in the animal.The key element of our approach is that the amount of each resource is expressed as the extent of the time during which it is used by the herbivore. This enables direct comparison between the intakes of the different resources.

Time that is spent foraging cannot be spent on non-foraging activities; therefore many optimal foraging models focus on either maximisation of the intake rate or minimisation of the foraging time (Stephens & Krebs, 1986). When a consumer is foraging for several resources, the maximum intake rate of each resource is not necessarily met by the same decisions. However, on timescales much longer than a few foraging bouts, *e.g.*, a couple of days, there is no use for the consumption of any resource if it is not matched by the consumption of other complementary resources. The time that can be spent on non-foraging activities is determined by the resource with the smallest intake rate relative to its turnover rate. When maximising the intake-rate for this most-limiting resource, the ratio between non-foraging time and foraging time is maximised. We assume that excess intake of the other resources is compensated for by post-ingestive processes (Raubenheimer & Simpson, 2004). In this paper the goal for the optimal forager is to maximise the time that can be spent on non-foraging activities, relative to the time

Table 6.1: model parameters

quantity	units	description
u_i	mass time^{-1}	turnover rate of a resource i
c_{ij}	-	mass proportion of a resource i in forage species j
t_j	time	time spend at a patch of forage species j
$I_j(t_j)$	mass	mass intake from forage species j after spending t_j time there
$\overline{t_t}$	time	average time taken to travel between two patches
D_j	-	proportion of the chosen patches that is of forage species j
$g_i(t_X, t_Y)$	mass time^{-1}	global intake rate of resource i
$\gamma_i(t_X, t_Y)$	-	proportion of time that no intake of resource i is required
$\Gamma_{\min}(t_X, t_Y)$	-	minimum of the $\gamma_i(t_X, t_Y)$ for all resources i
M_j	mass	maximum intake at a patch of forage species j
h_j	time	half-saturation constant of forage species j

spent foraging.

6.2 Model

Consider a herbivore and p potential forage species (denoted with subscript j). The forage species contain r resources (denoted with subscript i) that are used by the animal at a constant turnover rate u_i (see Table 6.1 for a full list of the parameters and their description). Let c_{ij} denote the mass proportion of resource i in forage species j. The forage species are patchily distributed within the environment. Each patch is considered to be of fixed size, homogeneous and to contain only one forage species. $\overline{t_t}$ is the average travel time between two patches. The travel time is independent of the time spent in patches, or the ratio of patches in the foraging path (Charnov, 1976). The cumulative consumption ($I_j(t_j)$) at a patch of forage species j is strictly increasing with time in the patch (t_j), and will typically be asymptotically saturating towards a maximum intake.

The herbivore can visit various patches of different forage species while foraging. A proportion D_j of all patches visited will be of forage species j (with $\sum_j^p D_j = 1$). The global intake of resource i is the weighted sum of the intake of that resource from each forage species. The total time spent foraging is the weighted sum of the time spent foraging at patches of each forage species, plus the average travel time between the patches. The global intake rate of resource i (g_i, in units mass time^{-1}) is the ratio of the global intake and the total time spent foraging.

$$g_i = \frac{\sum_j^p (D_j c_{ij} I_j(t_j))}{\overline{t_t} + \sum_j^p D_j t_j} \tag{6.1}$$

Although every g_i is expressed in the same units, these values cannot be compared in a straightforward way. Because the resources are used by the forager at different rates, a mass unit of one resource will have a totally different value to an animal than the same mass of another resource. To sidestep this problem, we convert equation 6.1 into a proportion of time by dividing c_{ij} by the turnover rate u_i. This gives us

$$\gamma_i = \frac{g_i}{u_i} = \frac{\sum_j^p (D_j \frac{c_{ij}}{u_i} I_j(t_j))}{\overline{t_t} + \sum_j^p D_j t_j} \tag{6.2}$$

In ecological terms γ_i is the proportion of the time spent foraging that the herbivore can continue without necessarily having to forage specifically for resource i. Values of γ_i below 1 can be considered as insufficient for survival, since less of the resource is consumed than is used during foraging.

An optimal forager would want to maximise the intake rate for all resources. However, as there is no direct use for excesses of a resource, increasing γ_A beyond γ_B (for two resources A and B) will not increase the time for non-foraging activities. This means that the proportion of time for non-foraging activities, Γ_{min}, is the minimum of all proportions γ_i:

$$\Gamma_{\text{min}} = \min_i^p(\gamma_i) \tag{6.3}$$

The objective for the optimal forager is to find the combination of $t_{\boldsymbol{.}}$ and $D_{\boldsymbol{.}}$ that maximises Γ_{min}, *i.e.*, to attain the maximum intake rate that is balanced to the turnover of all resources.

Γ_{min} is a function that contains two parameters that are under direct control of the herbivore:

1. t_j; the time spent in patches of forage species j

2. D_j; the proportion of visited patches that is of forage species j

The first control variable is a decision at the patch scale. The second control variable is the key determinant at the scale of the foraging path, comprising a series of patches, that determines the diet of the herbivore.

In the following we will evaluate the effect of simultaneous optimisation of foraging at these two scales using the two control variables by applying numerical methods. For simplicity, we consider only two forage species containing two resources. In the results we will first focus our attention on the optimal value of D_j. Within the suitable range, $D_j > 0$, we will analyse the values for t_j.

6.3 Numerical analyses

Let us assume two forage species (X and Y), both containing two resources (A and B). A herbivore can forage on patches of both forage species to attain the maximum and most balanced intake rate on both resources. To achieve this goal, the herbivore can decide how long to remain in a patch of any forage species (t_X and t_Y) and it can alter the proportion of patches of each forage species in the foraging path (D_X and $D_Y = (1 - D_X)$). Using numerical methods we will calculate the combination of t_X, t_Y and D_X that maximises Γ_{min}.

Because the solution cannot be found using analytical methods, an explicit form of the cumulative gain function $I_j(t_j)$ needs to be introduced. Without loss of generality we use the Michealis-Menten function because the optimal time in a patch predicted by the marginal value theorem can be derived explicitly for this function (see appendix 6.A). $I_j(t_j)$ then takes the form:

$$I_j(t_j) = \frac{M_j t_j}{h_j + t_j} \tag{6.4}$$

With M_j as the maximum intake at a patch of forage species j, and h_j as the half-saturation constant; *i.e.*, the time needed to consume half of the patch.

The numerical analyses of this model are carried out by first calculating the combination of t_X and t_Y that yields the highest Γ_{min} for all values of $D_X \in [0, 1]$. From this we find the value of D_X that yields the highest Γ_{min}.

For the analysis we compare forage species in pairs. These pairs consist of forage species X with given resource contents c_{AX} and c_{BX}, and an alternative forage species Y, from the whole range of alternative forage species, with $c_{\bullet Y} \in [0, 1]$ and $c_{AY} + c_{BY} \leq 1$. If we look at the values of D_X and $t_\bullet$ we find an interesting pattern (Figure 6.1 and Figure 6.2). The combinations of specific values of both D_X and $t_\bullet$, can be categorised into five regions in Figure 6.1. These regions all represent different sets of alternative forage species, relative to forage species X. For each set of alternative forage species we will give an ecological interpretation (for the mathematical summary see Table 6.2).

I The alternative forage species has lower proportions of both resources than forage species X. The optimal choice would be to only choose forage species X. The optimal patch residence time is equal to the marginal value theorem prediction (Charnov (1976); Appendix 6.A).

II The alternative forage species has higher proportions of both resources. The optimal choice would be to always choose the alternative forage species Y. The optimal patch residence time is equal to the marginal value theorem prediction.

III Foraging on the alternative forage species will yield more resource A, but less of resource B than foraging on forage species X. However, forage species X provides more of resource A than of resource B, making B the most limiting resource. Therefore including the alternative forage species will not increase Γ_{min}. The optimal patch residence time is equal to the marginal value theorem prediction.

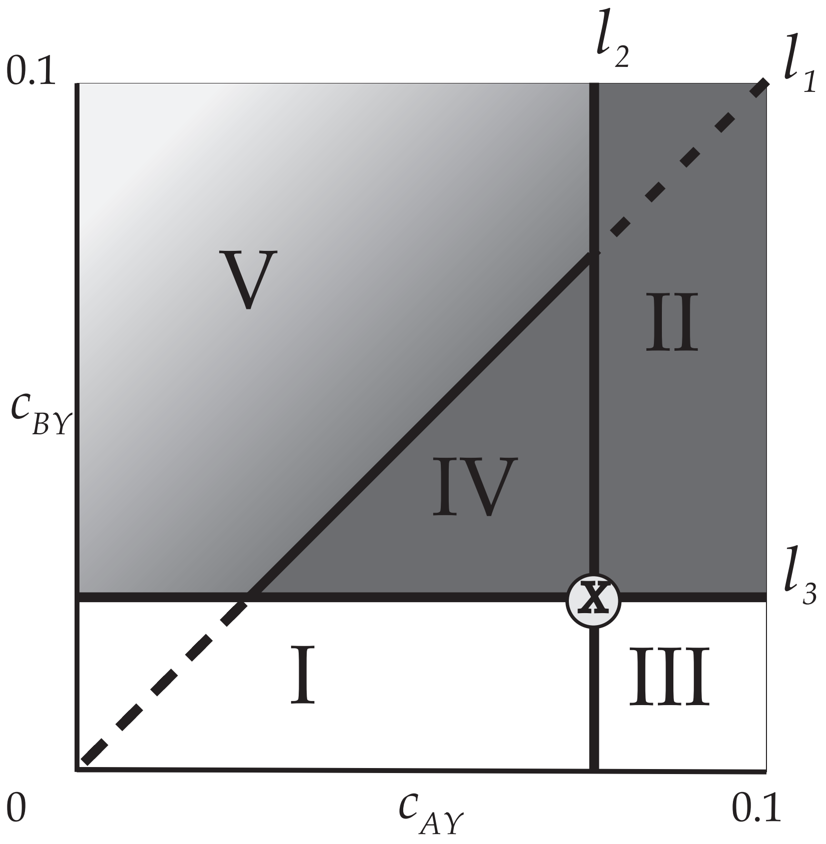

Figure 6.1: A schematic representation of the values of D_X , the optimal proportion of the diet that should consist of forage species X (on a scale from white for $D_X = 1$ to dark grey for $D_X = 0$). In the figure, one forage species X containing resources A and B in mass proportions c_{AX} and c_{BX} is compared to all alternative forage species Y for which $c_{\cdot Y} \in [0, 0.1]$. The X marks the alternative forage species Y that has the same resource composition as forage species X. The lines $l1, l2, l3$ delineate groups of alternative forage species for which the optimal behaviour in combination of forage species X is based on the same conditions (table 6.2). For two types of alternative forage species (I & III) the optimal choice is for forage species X, for two types (II & IV) the optimal choice is for forage species Y and for type V there should be a mix of both forage species, in a gradient that goes from little X near the line $l1$ to a lot of X further away from this line. This gradient is described by equation 6.8. Lines $l1$, $l2$ and $l3$ can be calculated from the model parameters using the equations 6.5, 6.6 and 6.7. If $I_X(t_X) = I_Y(t_Y)$, equations 6.6 and 6.7 reduce to the form $c_{iY} = c_{iX}$. The pattern is not limited to the range $[0, 0.1]$. *parameter values:* $c_{AX} = 0.075$, $c_{BX} = 0.025$, $u_A = u_B = 1$, $M_X = M_Y = 100$, $h_X = h_Y = 1$, $\overline{t_t} = 2$

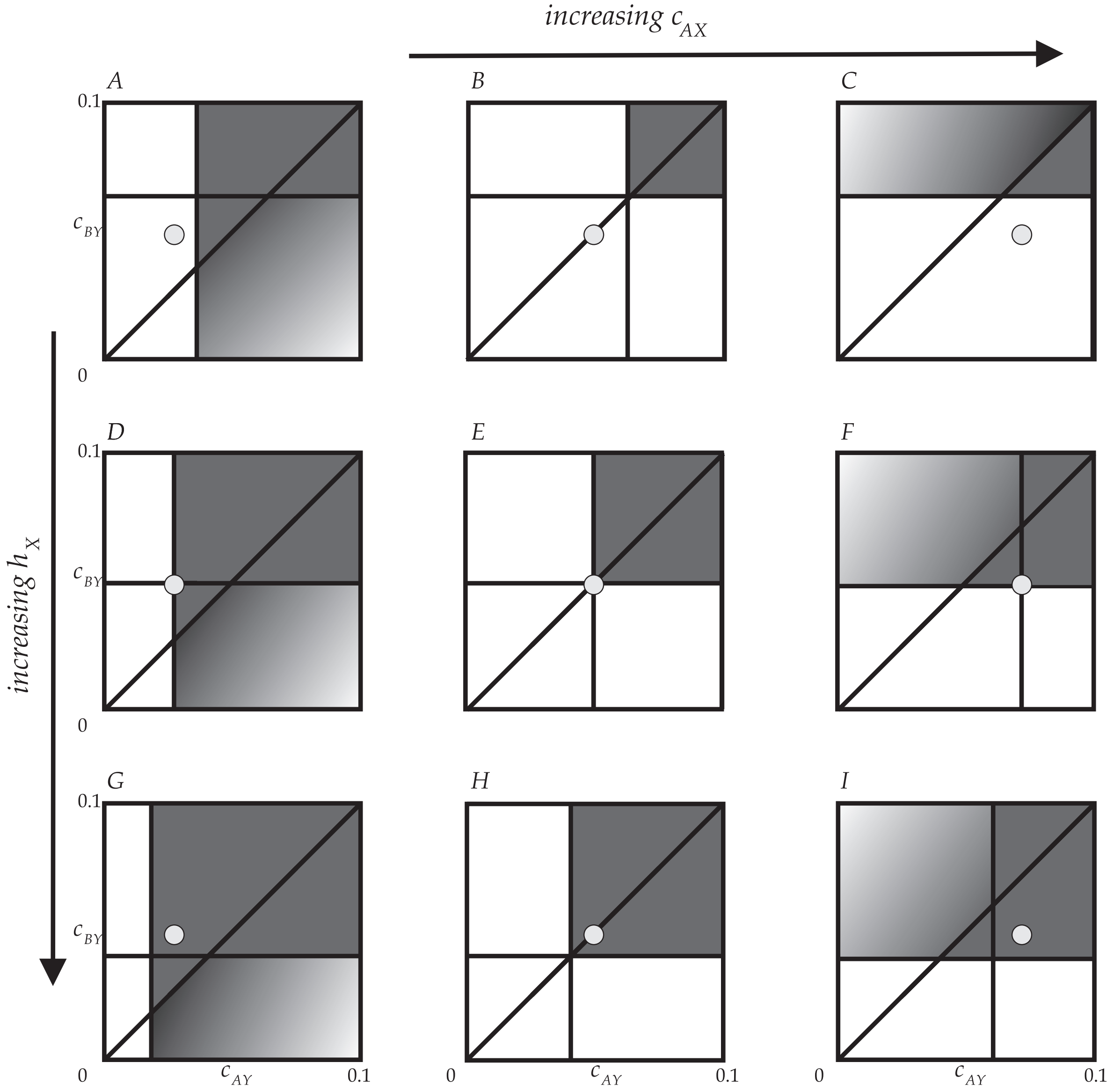

Figure 6.2: The influence of c_{AX} and h_X on D_X. Each panel represents the values of D_X, build up in the same way as Figure 6.1. If $h_X \neq h_Y$ (top panels and bottom panels) X, the locations that marks the alternative forage species Y that has the same resource composition as forage species X is no longer at the intersection of the lines $l2$ and $l3$, because $I_X \neq I_Y$. *h_X; top panels (A,B,C): $h_X = 0.5h_Y$, middle panels (D,E,F): $h_X = h_Y$, bottom panels (G,H,I): $h_X = 2h_Y$. c_{AX}; left panels (A,D,G): $c_{AX} = 0.025$, middle panels (B,E,H): $c_{AX} = 0.05$, right panels (C,F,I): $c_{AX} = 0.075$. Other parameter values: $c_{BX} = 0.05$, $u_A = u_B = 1$, $M_X = M_Y = 100$, $h_Y = 1$, $\overline{t_t} = 2$*

- IV Compared to forage species X, forage species Y has less A and more B. Since in both forage species there is more A than B, relative to the turnover rates of the herbivore, the optimal choice would be to leave forage species X for the alternative forage species Y. The optimal patch residence time is equal to the marginal value theorem prediction.
- V The shortage of resource B in forage species X can be compensated with excesses of B in forage species Y while the excesses of resource A in forage species X can compensate for the shortage in forage species Y. The optimal choice here is to feed on both forage species. The optimal patch residence time for both forage species is the product of only the local half-saturation constant (h_j) and the average travel time ($\overline{t_t}$) (see Table 6.2).

These sets of alternative forage species are separated by the lines l_1, l_2 and l_3, which are given by the equations:

$$l_1 : \frac{c_{AY}}{c_{BY}} = \frac{u_A}{u_B} \tag{6.5}$$

$$l_2 : c_{AY} = c_{AX}\frac{I_X(t_X^*)}{I_Y(t_Y^*)} \tag{6.6}$$

$$l_3 : c_{BY} = c_{BX}\frac{I_X(t_X^*)}{I_Y(t_Y^*)} \tag{6.7}$$

These lines indicate:

- l_1: those alternative forage species that contain a perfectly balanced ratio of resources (equation 6.5).
- l_2: those alternative forage species for which the potential intake of resource A is equal for both forage species (equation 6.6).
- l_3: those alternative forage species for which the potential intake of resource B is equal for both forage species (equation 6.7).

Table 6.2: types of alternative forage species

type	condition	D_X	t_X	t_Y
I	$(c_{AY} < c_{AX}) \wedge (c_{BY} < c_{BX})$	1	$\sqrt{h_X \overline{t_t}}$	-
II	$(c_{AY} > c_{AX}) \wedge (c_{BY} > c_{BX})$	0	-	$\sqrt{h_Y \overline{t_t}}$
III	$\frac{c_{AY}}{u_A} > \frac{c_{AX}}{u_A} > \frac{c_{BX}}{u_B} > \frac{c_{BY}}{u_B}$	1	$\sqrt{h_X \overline{t_t}}$	-
IV	$\frac{c_{AX}}{u_A} > \frac{c_{AY}}{u_A} > \frac{c_{BY}}{u_B} > \frac{c_{BX}}{u_B}$	0	-	$\sqrt{h_Y \overline{t_t}}$
V	$(c_{AY} < c_{AX}) \wedge (c_{BY} > c_{BX}) \wedge (\frac{c_{AY}}{u_A} < \frac{c_{BY}}{u_B}) \wedge (\frac{c_{AX}}{u_A} > \frac{c_{BX}}{u_B})$	eq. 6.8	$\sqrt{h_X \overline{t_t}}$	$\sqrt{h_Y \overline{t_t}}$

For the first four sets of alternative forage species, only patches of one forage species are visited. For the fifth set of alternative forage species the optimal diet consists of a mix of both forage species. At the optimum the condition $\gamma_A = \gamma_B$ holds. From this it follows that the optimal ratio of the proportion of patches of both forage species can be calculated using the equation:

$$\frac{D_X}{D_Y} = \frac{I_Y(t_Y^*)(\frac{c_{BY}}{u_B} - \frac{c_{AY}}{u_A})}{I_X(t_X^*)(\frac{c_{AX}}{u_A} - \frac{c_{BX}}{u_B})} \tag{6.8}$$

Where t_j^* is the optimal patch residence time in patches of forage species j. Equation 6.8 shows that patches of forage species with resource contents that are balanced more to the herbivore's needs ($i.e.,\frac{c_{BY}}{u_B} - \frac{c_{AY}}{u_A} < \frac{c_{AX}}{u_A} - \frac{c_{BX}}{u_B}$) are visited most frequently.

Whenever $D_j > 0$, the patch residence time t_j is optimised simultaneously with the optimisation of D_j. So optimisation of the foraging behaviour takes place both between patches and within the patch. For all $D_j > 0$ the optimal patch residence time t_j^* is equal to

$$t_j^* = \sqrt{h_j \overline{t_t}} \tag{6.9}$$

For $D_j = 1$, this is equal to the marginal value theorem prediction (Charnov, 1976) (see Appendix 6.A). From equation 6.9 it follows that the ratio in optimal patch residence times for two forage species is equal to the square root of the ratio of the half-saturation constants for those species.

$$\frac{t_X^*}{t_Y^*} = \sqrt{\frac{h_X}{h_Y}} \tag{6.10}$$

6.4 Discussion

In this paper we present a model that predicts the foraging behaviour that maximises and balances intake when foraging for multiple resources on several forage species. It predicts that when animals are free to choose the forage species they feed from, patch residence time is only determined by local information. Furthermore, the ratio of forage species in the foraging path is only dependent on forage species characteristics.

This model enables the prediction of the optimal combination of forage species without going through the laborious work of explicitly defining a multidimensional fitness landscape (Raubenheimer & Simpson, 2004; Simpson *et al.*, 2004) or considering independent fitness effects of surpluses or deficits in separate resources (Anderson *et al.*, 2004; Raubenheimer & Simpson, 2004; Simpson *et al.*, 2004). This makes our model robust, *i.e.*, independent to species-specific constraints, and enables testing in field experiments. Furthermore we can predict the patch residence time in patches of several forage species when more resources are taken into account.

The model presented in this paper extends the commonly used single resource approach (Charnov, 1976; Owen-Smith, 1993; Stephens & Krebs, 1986; Fryxell *et al.*, 2004). This single resource approach is applicable whenever there is one resource limiting for all combinations of forage species (Figure 6.1, sets of alternative forage species I, II, III, and IV). In these pairs of forage species, one forage species is chosen exclusively. There is, however, a large range of alternative forage species for which none of the resources is limiting in both forage species (Belovsky, 1978; Prins & Beekman, 1989; Voeten & Prins, 1999; Ludwig *et al.*, 2001; Raubenheimer & Simpson, 2004; Simpson *et al.*, 2004). These forage species are shown in Figure 6.1, region V. When such pairs of forage species are available, the ratio between the resources in the diet can be optimised by selecting patches of both forage species. We provide a model to investigate the optimal foraging behaviour for these combinations of forage species at two foraging scales simultaneously (Senft *et al.*, 1987; Bailey *et al.*, 1989).

At the landscape level, the forager optimises the balance in its intake by controlling the proportion of the patches of each forage species within the foraging path. The balance between the proportions of forage species X and forage species Y in the foraging path is determined by the ratio of the intake at patches of both forage species and the differences of the resource contents within each forage species relative to the turnover rates (equation 6.8). Predicting herbivore food selection from plant chemistry has proved to be difficult (Owen-Smith & Novellie, 1983; Skarpe *et al.*, 2007). The model presented in this paper provides testable hypotheses about forage species selection at the landscape scale.

At the patch level,the optimal patch residence time depends on the average travel time between patches and the half-saturation constant within a patch of that forage species, this information can be considered to be locally available. The predicted optimal patch residence time is the same as the marginal value theorem prediction for one forage species (see Appendix 6.A; Charnov (1976)). We show that this is the optimal patch residence time even when more than one forage species is included in the forage path, and the forager can select at both path and patch level of foraging. We predict that the ratio of patch residence times is determined by the ratio between half-saturation constants of these patches (equation 6.10). These half-saturation constants are readily assessed from field data on the cumulative intake over time (Illius *et al.*, 1999; Skarpe *et al.*, 2007).

Most parameters in our model can be measured directly in experimental studies, *e.g.*, Illius *et al.* (1999); Skarpe *et al.* (2007). Most difficult will be the assessment of the turnover rates for the different resources (u_i). Turnover rates of water, energy and nitrogen are quite well known, but those of other elements such as Se, Co or even P, K and Na are much less readily available, except for some domestic herbivores.

We presented an optimal foraging approach to the challenge of achieving a balanced diet and a maximum intake for multiple resources by selecting on two scale levels. A natural balancing of resources is achieved by representing the amount of a resource as the time within which it is used by the animal. We identify the rules that make pairs of forage species exclusive or complementary. For complementary forage species the optimal balance is only achieved by taking into account the difference in intake of the resources in patches of both forage species. Both when visiting patches of multiple forage species, and when visiting one single forage species, patch residence time is dependent only on the shape of the local cumulative intake function and the average travelling time between patches.

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6.A The Marginal Value Theorem with one Forage Species

Considering one forage species (X) containing two resources (A and B), $D_X = 1$. We write equation 6.2 as

$$\gamma_i = \frac{\frac{c_{iX}}{u_i} I_X(t_X)}{t_X + \overline{t_t}} \tag{6.A.1}$$

If $\frac{c_A X}{u_A} > \frac{c_B X}{u_B}$,

$$\Gamma_{min} = \gamma_B = \frac{\frac{c_{BX}}{u_B} I_X(t_X)}{t_X + \overline{t_t}} \tag{6.A.2}$$

The marginal value theorem (Charnov, 1976) predicts that any patch should be left whenever:

$$\frac{\partial \frac{c_{BX}}{u_B} I_j(t_j)}{\partial t_j} = \Gamma^*_{min} \tag{6.A.3}$$

where Γ^*_{min} is the global intake rate when t_X is optimal. Using equation 6.4, we can write:

$$\frac{\partial \frac{c_{BX}}{u_B} I_X(t_X)}{\partial t_X} = \frac{\frac{c_{BX}}{u_B} M_X h_X}{(h_X + t_X)^2} \tag{6.A.4}$$

combining equations 6.A.2, 6.A.3, and 6.A.4, we get

$$\frac{c_{BX}}{u_B} \frac{\frac{M_X t^*_X}{h_X + t^*_X}}{(t^*_X + \overline{t_t})} = \frac{c_{BX}}{u_B} \frac{M_X h_X}{(h_X + t^*_X)^2} \tag{6.A.5}$$

which we can reduce to:

$$t^*_X = \sqrt{h_X \overline{t_t}} \tag{6.A.6}$$

7 Moving Matters; how movement can affect foraging decisions

Geerten M. Hengeveld

For many animals, the world is a heterogeneous collection of possible food. This possible food is heterogeneous with respect to the spatial distribution, but also in the constitution of (macro-) nutrients, like energy & protein or nitrogen & phosphate. To deal with this heterogeneity, animals have to make decisions on what to eat, how to find this food, and how much to feed from a patch of a chosen food type. Finding sufficient food is a major component in the daily and life-long activities of animals. Not surprisingly therefore these questions have played an important role in foraging theory (Schoener, 1971; Pyke *et al.*, 1977; Pyke, 1984; Stephens & Krebs, 1986). These questions have also been the basis of the work that is presented in this thesis.

In this thesis, I have more specifically addressed three questions: (1) Which movement pattern is used to find food; (2) What food types are chosen; (3) How much of the chosen food is eaten. The main focus has been on how to deal with the spatial heterogeneity of scarce resources (chapters 2 - 5). Spatial heterogeneity can be overcome by moving between locations of high quality or density (MacArthur & Pianka, 1966; Schoener, 1971; Jander, 1975; Bell, 1991; Turchin, 1991, 1996; Viswanathan *et al.*, 1999; Bartumeus *et al.*, 2005). With little information about where these locations are, random searching movements have to be employed (Bell, 1991; Bartumeus *et al.*, 2005). The idea of random searches has been the focus of several movement models. These random movement models differ in the aspects of movement that they address (*e.g.*, turning angles or movement length), but are similar in that they do not allow for changes in behaviour as information about the environment is gathered (Turchin, 1998). Although with homogeneous distributions of targets straight-line movement (also known as ballistic movement) has long be known to be the most efficient in finding targets (Pyke, 1984; Hogeweg, 1989; Zollner & Lima, 1999), for heterogeneous environments, Lévy walks (a class of fractal random walks) perform better than expected (Viswanathan *et al.*, 1999; Bartumeus *et al.*, 2005).

In chapters 2 – 5 I have used both experimental and theoretical approaches to increase our understanding of how these random walk models attain their super-efficiency and what the influence of changes in target density is on the scale-free properties of these movement patterns. In chapter 2, we observed that goats use different movement patterns at different resource densities. The fractal properties of these movement patterns followed the model predictions for optimal searching movements (Viswanathan *et al.*, 1999). At low density random walk models were sufficient to explain the efficiency of these searches, while at high density the goats encountered more resources than the statistically equivalent random walks. This higher search efficiency could be because at this higher density, the goats could use additional information for finding browse.

Finding Lévy walk movement made me curious about the causes of this efficiency. In chapter 3 we therefore evaluate the effect of the general assumptions of random searches on the searching efficiency. We find that interactions with targets, *i.e.*, stopping at a resource location and starting a new search from that location, are key components for efficient searching in patchy environments. These interactions ensure that scale-free movement rules produce fractal 'target area'-restricted search movements.

The consequences of these interactions at larger scales are further explored in chapter 4. We found that the interactions with targets limit the fractal properties of movement paths to the scale of the resource distribution. This is a limitation for the use of fractal movement patterns in the extrapolation from small scale to larger scale movements. This interaction between the distribution of landscape features (that would act as targets) and the displacement of animals, could be used to explain the change in population distribution of animals that has been observed as a consequence of changes in the distribution of landscape features (Murwira, 2003).

Because chapters 3 and 4 concluded that with decreasing distance between targets the shape of the total movement path would change (as a result of the increase in the number of re-orientations), while the optimal searching path should stay the same, I carried out the experiment with the doves (chapter 5). In this experiment I could manipulate the scale of the target distribution by changing the number of targets and the distance at which these targets could be detected. The ring doves (*Streptopelia roseogrisea*) used in this experiments did not show any of the predicted behaviours; (1) their movement patterns did not change with changes in the scale of the target distribution, (2) there was no difference between the movements while searching and the total movement path, and (3) the exponential distribution of movement lengths did not show the expected exponent of -2. The movements did however show a scale-free distribution of the re-orientating turning angles which was independent of the target distribution. This might indicate that the findings of chapters 3 and 4 are true in the narrow theoretical limit within which they are set, but do not hold for actual animals, for which many of the model assumptions do not hold.

Space is not the only factor that makes food heterogeneous. In chapter 6 we investigated a different type of heterogeneity; the heterogeneity of (macro-)nutrients between different types of food. All types of food consist of different macro-nutrients (*e.g.*, energy, protein or fat), or nutrients (*e.g.*, carbon, nitrogen or phosphorus) (Pulliam, 1975; Simpson *et al.*, 2004; Prins & Van Langevelde, in press). While foraging, it is these (macro-)nutrients that animals need to acquire. On average, the turnover-rates of these (macro-)nutrients level out and are more or less constant relative to each other (Prins & Van Langevelde, in press). Therefore, the goal of the animal in foraging can be expressed as a fixed ratio of the intake rates of these (macro-)nutrients. Most food types do not supply such an optimal ratio of (macro-)nutrients.

In chapter 6 we designed a new framework to address two of the main questions in foraging theory: what to eat and how long to eat from this food, with respect to the need for several (macro-)nutrients. Using time as a unifying currency across the (macro-)nutrients, we maximise the time that the animal does not need to forage relative to the time spent foraging. The initial results of this approach are interesting. In order to acquire the optimal amount of (macro-)nutrients, animals are predicted to simultaneously optimise the ratio of patch types in their diet and the time spent at any of those patches. The optimisation of the ratio of the (macro-)nutrients only affects the ratio of patch types, while the time spent foraging at a patch is independent of the quality of that patch, but only depends on the local intake rate and the time spent travelling between patches.

In the current chapter, I will further explore the effect of movement patterns on foraging. I will first extend the model presented in chapter 6, to explicitly take into account the distance between different patches (λ). To incorporate the effect of different movement patterns on the searching efficiency, I derive a relationship between λ and the distance between patches that is experienced by the animal (λ_e). Because different movement patterns result in a different searching efficiency (chapter 3), this relationship is dependent on the movement pattern used. Furthermore, when more than one type of patch is sought, it can be deduced from chapter 4 that the searching efficiency for one patch type is determined by the mean free path between all patches and not only by the mean free path between patches of that one type. These considerations are used to explicitly take the effect of different movement patterns into account while modelling the foraging decisions of an animal. The application of the relationship between the experienced distance between targets and the movement pattern used is not limited to the optimal foraging framework presented here, but can be applied in any modelling approach where mean field assumptions on movement behaviour are made.

7.1 The cost of moving

In chapter 6, we have assumed that the time spent searching for, and moving between patches of food does not change as the ratio between different types of food changes (the average travelling time between patches ($\overline{t_t}$) is constant). However, in order to change the ratio between the number of patches of different types of food visited, some patches should be passed by, which will almost inevitably lead to an increase in the distance between the patches that are visited and thus in the travelling time. In earlier chapters I have used the mean free path between patches (λ) as a scaling parameter for the movement models. Now I will use this mean free path to provide a spatial scaling of the foraging decisions. I will incorporate λ, and thus the scale of the patch distribution, explicitly into the model presented in chapter 6, in order to show that the effects of different movement patterns, and possibly the choice of movement pattern, can be dealt with in mean field approximations of foraging models.

When dealing with different types of patches (as in chapter 6), the mean free path between all patches (λ_T), is determined by the number of patches of each of the patch types in the movement path (*i.e.*, the mean free path between the patches for each of these patch types separately (λ_j)). λ_T can be calculated through the formula:

$$\frac{1}{\lambda_T} = \sum_j^p \frac{1}{\lambda_j} \tag{7.1}$$

for all p patch types j. The average time spent moving between patches ($\overline{t_t}$) is independent of the patch type visited, and thus is the ratio of the mean free path between all patches in the foraging path (λ_T) and the velocity with which the animal moves (v).

$$\overline{t_t} = \frac{\lambda_T}{v} \tag{7.2}$$

In chapter 6 the animal was given control over the relative amount of patches of each patch type in the foraging path (D_j, where $\sum_j^p D_j = 1$). Thus, for a foraging path where D_j has been adjusted by the animal, we know that λ_j in this path should satisfy:

$$D_j = \frac{\lambda_T}{\lambda_j} \tag{7.3}$$

Furthermore, the environment will provide a minimum λ for each patch type j ($\lambda_{j,\min}$, the actual distance between two patches of type j in the environment). Combining equations 7.2 and 7.3 with equation 6.2, the proportion of time gained while foraging for resource i can be expressed as a function of λ_j

$$\gamma_i = \frac{\sum_j^p\left(\frac{1}{\lambda_j}\frac{c_{ij}}{u_i}I_j(t_j)\right)}{\frac{1}{v} + \sum_j^p \frac{t_j}{\lambda_j}} \mid \lambda_j > \lambda_{j,\min} \tag{7.4}$$

where c_{ij} is the mass content of resource i in patch type j, u_i is the turn-over rate of resource i and $I_j t_j$ is the intake in visited patches of type j after having foraged there for a duration of t_j. By summing over equation 7.4 we get the equivalent of equation 6.3 and express Γ_{min} a function of λ_j.

Before I start to consider the implications of the explicit inclusion of λ for foraging decisions, I will first link the experienced distance between patches to the movement pattern used. Subsequently, I will be able to link the effect of different movement patterns to the foraging decisions.

7.2 Experienced mean free path

Different types of movement result in different encounter rates with targets and thus will result in a different searching efficiency ($\lambda\eta$) (chapter 3 and Schoener (1971); Charnov (1976); Cain (1985); Viswanathan *et al.* (1999); Zollner & Lima (1999); Bartumeus *et al.* (2005)). From chapter 3 and Viswanathan *et al.* (1999); Bartumeus *et al.* (2005) we can also see that $\lambda\eta$ changes with changing λ for some movement patterns. Determining the relationship between $\lambda\eta$ and λ The movement pattern and λ The searching efficiency that I have used in chapter 3 ($\lambda\eta$), is expressed as the number of targets found per distance moved (η) times the mean free path between all patches available (λ). As a result, $\lambda\eta$ is a scalar value that relates the mean free path (λ) to the distance that the animal has moved between patches (λ_e, the mean free path that was experienced by the animal).

$$\lambda_e = \frac{\lambda}{\lambda\eta} \tag{7.5}$$

I will not simplify this equation furhter, because the quantity $\lambda\eta$ has been commonly used in other studies as a measure of searching efficiency (Viswanathan *et al.* (1999); Raposo *et al.* (2003); Bartumeus *et al.* (2005); chapter 3) and because the two occurrences of λ in equation 7.5 will have a different interpretation further on in this chapter.

By quantifying $\lambda\eta$ for different types of movement, the distance that the animal moves between patches (λ_e) can be related directly to the density of the patches available ($\sim \lambda^{-1}$). Lévy walks (LW) provide a class of movement types that scale gradually between the two extreme cases of random movement (straight-line ballistic movement for $\mu \to 1$ and Brownian motion for $\mu \to 3$, where the distribution $P(l)$ of movement lengths (l) is given by $P(l) \sim l^{-\mu}$) (Bartumeus *et al.*, 2005). Therefore I will use the LW in this chapter to show the potential for summarising the effect of movement for the use in 'mean field' models. For convenience I will limit myself to the analysis of non-depleting searches, but I will analyse both searches in one dimension, building on the approximation of Viswanathan *et al.* (1999) for η, and searches in two dimensions, by extending the simulations as they were used in chapter 3. Non-depleting searches can be seen as a proxy for both searches for targets that are only temporarily unavailable for the searcher, or for targets that occur in a patchy distribution (Viswanathan *et al.*, 1999).

For one-dimensional searches, Viswanathan *et al.* (1999) have derived an analytical approximation of η. By scaling λ to the detection radius r_v, this approximation can be simplified this and $\lambda\eta$ can be expressed as

$$\lambda\eta_{1D} \approx \frac{\lambda}{\lambda^{\frac{3-\mu}{2}} + \frac{\mu-1}{2-\mu}(\lambda^{\frac{3-\mu}{2}} - \lambda^{\frac{\mu-1}{2}})} \tag{7.6}$$

for the one-dimensional non-depleting search.

For the two-dimensional search, I extended the simulations of chapter 3, by including more values of λ between $\lambda = 10$ and $\lambda = 10^5$. The efficiency ($\lambda\eta$) in these simulations was calculated as in chapter 3. The movement rules used were Lévy walks with $\mu = 1.1$ (ballistic search), $\mu = 2.0$ (optimal search) and $\mu = 2.9$ (Brownian search). Only non-depleting searches were simulated. For both the one-dimensional and two-dimensional searches $\lambda\eta$ is shown for λ between 10 and 10^5 in Figure 7.1. From these simulations the relationship of $\lambda\eta$ with λ can be estimated by fitting a power-law regression (Table 7.1). These estimates of $\lambda\eta$ can be used to include the effect of the different two-dimensional movement patterns in mean field models using equation 7.5.

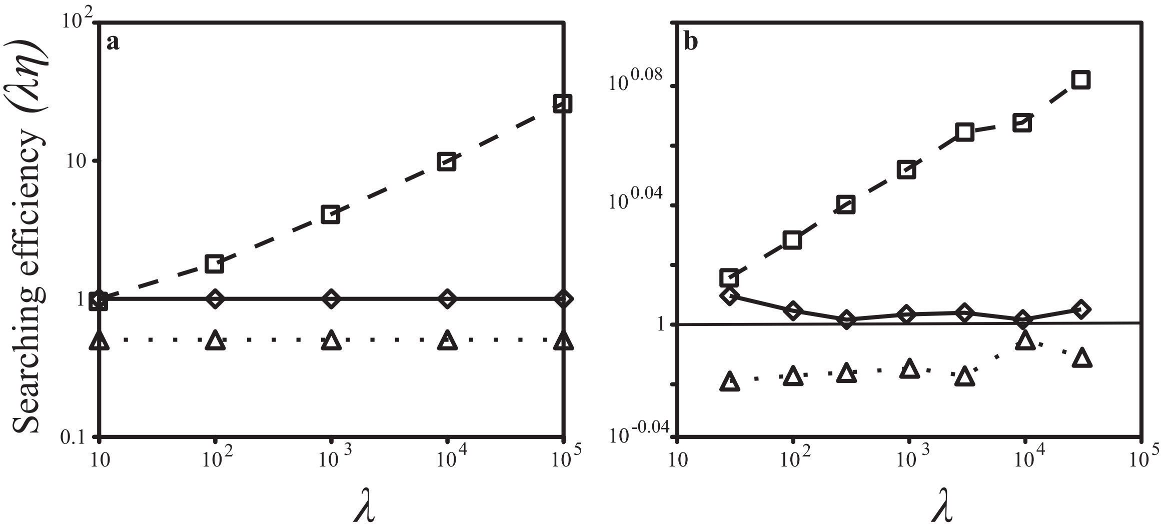

Figure 7.1: The searching efficiency $\lambda\eta$ for three selected movement patterns. (a) For the one-dimensional non-depleting search, $\lambda\eta$ is calculated using equation 7.6, for $\mu \in \{1(\Diamond), 2.01(\Box), 3(\triangle)\}$. (b) For the two-dimensional non-destructive search, simulations as described in chapter 3 were performed for $\lambda \in \{31.6, 100, 316, 1000, 3160, 10000, 31600\}$ and $\mu \in \{1.1(\Diamond), 2.0(\Box), 2.9(\triangle)\}$. Simulations lasted 10^6 time steps.

7.3 Two types of targets

In equation 7.4, there are several types of targets (the food types), each with their own λ. The experienced λ for any of these types of target will depend on the searching efficiency ($\lambda\eta$) as a result of the movement pattern and the λ for that specific target type (λ_j). In chapter 3 I have demonstrated that the interaction with targets is a major determinant of the searching efficiency of the movement pattern. In chapter 4 however, I have shown that these interactions change some properties of the movement patterns, and that this change is dependent on the density of the targets. Because animals will react similar to all patch types, it is therefore most likely that the searching efficiency ($\lambda\eta$) of a movement pattern is determined by the mean free path between all target types combined (λ_T). For each target type j, the mean free path as experienced by the animal ($\lambda_{e,j}$) can be calculated by dividing the mean free path between targets of this type (λ_j), by the searching efficiency as it is determined by the movement pattern and the mean free path between all targets of any type ($\lambda_T\eta$):

$$\lambda_{e,j} = \frac{\lambda_j}{\lambda_T\eta} \tag{7.7}$$

The movement pattern determines the dependency of $\lambda_T\eta$ on λ. Either equation 7.6, assuming one-dimensional search, or one of the relationships estimated from Figure 7.1(b) (Table 7.1) for two dimensional search can be used as an approximate for $\lambda_T\eta$ with a given μ.

Table 7.1: Estimated dependency of $\lambda\eta_\mu$ on λ. The coefficients of the power-law regression of $\lambda\eta$ to λ for non-depleting searches in two dimensions (simulation results summarised in Figure 7.1). The power-law relationship: $\lambda\eta_{2D} = \epsilon\lambda^\zeta$.

μ	ϵ	ζ	r^2
1.1	1.018	-0.0012	0.21
2	0.964	0.0218	0.99
2.9	0.944	0.0035	0.55

7.4 Movement patterns in the search for multiple nutrients

So far, I have shown how the scale of the distribution of food patches can be incorporated in the model presented in chapter 6, by making both the travelling time between patches ($\overline{t_t}$) and the relative proportion of patches of each type (D_j) a function of λ (equations 7.3 and 7.2). By substituting these equations into equation 6.2, I derived equation 7.4. Thus the proportion of the time spent foraging that an animal will have available for non-foraging activities ($\Gamma_{\min}$) can be expressed in terms of the distance between food patches (λ). Then I derived relationships between the mean free path between patches (λ) and the mean free path as experienced by the animal (λ_e) for different types of searching movements. Subsequently I expressed the experienced distance between patches of a given type ($\lambda_{e,j}$) as a function of the actual mean free patch between the patches of this type (λ_j), the mean free path between all patches (λ_T) and the movement pattern (equation 7.7). Combining equations 7.4 and 7.7, the proportion of time available for non-foraging activities can be calculated as a function of the movement pattern.

Chapter 6 concluded that in the optimal foraging path (1) the ratio between D_X and D_Y (the proportion of patches of each type in the foraging path) should balance the intake of different (macro-)nutrients, (equation 6.8: $\frac{I_Y(t_Y^*)(\frac{c_{BY}}{u_B}-\frac{c_{AY}}{u_A})}{I_X(t_X^*)(\frac{c_{AX}}{u_A}-\frac{c_{BX}}{u_B})}$) and (2) that t_j^* (the time spent at a patch) should only depend on the time spent travelling between patches and the intake rate at that patch (equation 6.9: $\sqrt{h_j\overline{t_t}}$). If we assume that the dependency of $\overline{t_t}$ on D_j, that is introduced in equations 7.2 and 7.3, does not change the results presented in chapter 6, we can substitute these equations in the conclusions of chapter 6. This gives us the optimal patch residence time (t_j^*)as a function of λ_T:

$$t_j^* = \sqrt{h_j\overline{t_t}} = \sqrt{\frac{h_j\lambda_T}{v}} \tag{7.8}$$

For the optimal ratio between λ_X and λ_Y we find (substituting equations 6.4 and 7.8):

$$\frac{\lambda_X}{\lambda_Y} = \frac{M_X(\frac{c_{AX}}{u_A} - \frac{c_{BX}}{u_B})(\sqrt{vh_Y} + \sqrt{\lambda_T})}{M_Y(\frac{c_{BY}}{u_B} - \frac{c_{AY}}{u_A})(\sqrt{vh_X} + \sqrt{\lambda_T})} \mid \lambda_j > \lambda_{j,\min} \tag{7.9}$$

which is not solved completely for λ_X or λ_Y, because t_j^* is a function of λ_T (equation 7.8). $\lambda_{j,\min}$ is the actual λ_j available, and thus the animal cannot decrease λ_j below $\lambda_{j,\min}$.

Using equation 7.7, λ_e can be substituted for λ in equation 7.4 to investigate the effect of different movement patterns on foraging decisions. For the patch residence time we see that any movement path that increases $\lambda_{e,T}$ will increase the patch residence time (Charnov, 1976). So a Brownian searcher ($\mu \rightarrow 3$) should deplete a patch further than a ballistic searcher ($\mu \rightarrow 1$), in both one and two dimensions. The optimal Lévy walker ($\mu \approx 2$) will leave a patch even sooner and thus leave most resources in the patch. Different movement patterns can thus not only influence the optimal decisions of an animal, but through those, they can also change resource dynamics.

The ratio between λ_X and λ_Y in the optimal path is dependent on the absolute value of λ_T, and thus on the absolute value of λ_X and λ_Y. Here the new dependency between $\overline{t_t}$ and D_X blurs the insight that we gained from the results obtained in chapter 6. Furthermore, a minimum value for λ_X and λ_Y ($\lambda_{j,\min}$) is imposed by the spatial context in which the animal is placed. Numerical simulations (like those presented in chapter 6) can give insight into how a forager that sets out to minimise the relative amount of time spent foraging, should balance the average distance between patches of different food types.

While foraging animals take decisions at various scales (Schoener, 1971; Pyke, 1984; Stephens & Krebs, 1986; Senft *et al.*, 1987; Bailey *et al.*, 1996; Klaassen *et al.*, 2006) and chapter 6. Therefore, optimising foraging efficiency, will be done at these various scales simultaneously. In this chapter I have opened the possibility of incorporating those various scales in foraging models. More specifically I have linked the model presented in chapter 6 to the spatial extent of the patch distribution (λ). This link enables

1. the understanding of the optimal ratio between patches of different food types in spatial space,
2. the investigation of the effect of different types of movement patterns on optimal foraging decisions by linking λ_e to λ and μ,
3. the optimisation of the type of movement pattern (μ) for one-dimensional searches simultaneous with the optimisation of foraging decisions within the patch and the choice of the absolute and relative density of patch types, by using the approximations of Viswanathan *et al.* (1999).

Therefore, this link can contribute to a more holistic approach to the foraging of animals.

7.5 Conclusion

In this thesis I have, together with my coauthors, investigated how an animal can deal with the heterogeneity in the distribution of resources, either in space or within food types, in order to find a diet that maximises the time available for non-foraging activities. We have shown that both goats (chapter 2) and doves (chapter 5) show scale-free movement patterns. But while the behaviour of the goats followed predictions and changed with changes in the target density, the doves moved with one scale-free pattern, that was different from the optimal pattern, regardless of the density of targets.

The change of the scale-free movement pattern of the goats follows predictions from Lévy walk models (Viswanathan *et al.*, 1999). To increase our understanding of the super-efficiency of these Lévy walks relative to other random walks (Bartumeus *et al.*, 2005), we performed two simulation studies. In these studies (chapters 3 and 4), we find an apparently paradoxical role of interacting with targets on the efficiency of searching on the one hand and the large scale properties of movement on the other hand. To increase the efficiency of the Lévy walk it is necessary to renew the search movement after a target has been visited (chapter 3). However, this renewal of the search movement shifts the large scale movement pattern from a scale-free Lévy walk to a Brownian motion that is bounded to the scale of the density of the targets (chapter 4). This Brownian motion does not have the benefits of the super-efficient Lévy walks (Viswanathan *et al.*, 1999; Bartumeus *et al.*, 2005). Furthermore, we have shown that the searching movements are not necessarily reflected in the total movement path. These results shows that the large probability of a small scale sequence of steps close to renewable targets is the key to the success of the searching movement. Thus the assumption of re-newed search after target encounter makes the Lévy walks a fractal approximation of the area-restricted search that has been used frequently in describing animal movements (Walsh, 1996; Fortin, 2002; Nolet & Mooij, 2002; Morales *et al.*, 2004).

Finally we extended the existing optimal foraging models to include the balance in the intake of several (macro-)nutrients. These (macro-)nutrients are distributed heterogeneous over the different types of food species available to animals (Prins & Van Langevelde, in press). In chapter 6 we open a new possibility to formalise foraging decisions based on the optimal balance of (macro-)nutrients. This formulation was extended in the current chapter to explicitly incorporate the effect of different movement rules. This extension relies heavily on the results and insights that are gained in chapters 3 and 4.

‘Movement is the glue that sticks ecological processes together’ (Turchin, 1996). The notion that different modes of movement create a different experienced density of targets is important to take into account when formulating models. It has been applied here in a mean field model of a foraging process, but is most certainly not limited to foraging situations. Many ecological processes rely on encounters of individuals with other individuals or with resources for the rate at which they take place (Schoener, 1971; Viswanathan *et al.*, 1999; Turchin, 1996). In this chapter I have shown that the efficiency differences between different movement patterns in a heterogeneous environment can be approximated through explicit simulation. This approximation can then be used to form the basis of mean field approximations of spatial processes that involve movement in a heterogeneous environment. These considerations are also important for spatial explicit modelling approaches: simplified assumptions on animal movement can greatly change the rates of encounter and can thus have an unintended influence on the processes that are the focus of the simulation. The differences in experienced target density that have been shown so often (Pyke, 1984; Hogeweg, 1989; Viswanathan *et al.*, 1999; Zollner & Lima, 1999; Bartumeus *et al.*, 2005) for different movement rules, should warn against the use of overly simple assumptions on animal movement in ecological models. In this chapter I have shown one simple approach to estimate the effect of movement on the experienced target density and incorporate this effect in a mean field foraging model. Using this approximation the effect of searching movements in a heterogeneous environment can be included in ecological models that use mean field approximations of spatial processes and spatial heterogeneity.

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Summary

Food is heterogeneous in quality and quantity with respect to the distribution in space and time. While foraging, animals have to make choices on how to deal with this heterogeneity. To maximise the time that does not have to be spent foraging, foraging animals decide on where, what, when and how much to eat. These decisions are of great importance; in many situations food intake is limiting animals in their time budget. In the first part (chapters 2 – 5) of this PhD-thesis I focus on the movements of animals that search for spatially distributed patches of food. The second part (chapters 6 & 7) focuses on animals that forage to satisfy their requirements for (macro-)nutrients (*e.g.*, energy & protein or nitrogen & phosphorous).

The movement patterns of animals are studied using both experiments and computer simulations. Chapter 2 shows results of research to the foraging behaviour of goats. While foraging, these goats use Lévy walks[1] that, theoretically, result in both super-efficient and super-diffusive search movements[2]. In the two following chapters I investigate this super-efficient and super-diffusive behaviour using computer simulations. I find that the super-efficiency is caused by the behaviour at the location of the target (*e.g.*, a patch of food) (chapter 3): when an animal that moves according to a Lévy walk stops at the location of the target, and starts a new Lévy search from this location, 'area-restricted search'-like movements emerge in the fractal search pattern. As a consequence, clustered distributions of targets can be exploited better. However, stopping and re-orienting at the location of a target hampers the super-diffusive property of the movement path at higher target densities (chapter 4). Stopping at the location of a target changes the characteristics of the searching path, because long straight path parts are interrupted and the search is restarted in a random direction. Therefore observed small scale movement paths cannot be extrapolated to predict the distribution of animals at larger scales.

From these computer simulations (chapters 3 & 4) the hypotheses are drawn that (1) the density of targets and the distance at which these targets can be detected influence the movement path of animals, and (2) the searching part of the path (where no target information is present) is different from the total movement path. These hypotheses were tested using ring doves in search for hemp seeds (chapter 5). By hiding the

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[1] The Lévy walk is a type of 'random search' movement in between ballistic (straight line) and Brownian (completely random) movements, that result in scale-free '*fractal*' movement patterns. Within a Lévy walk long straight path parts are relatively frequent.

[2] These movement patterns are super-diffusive because they cause a faster than normal diffusion of animals that move with this pattern (the animals spread out further), and they can be super-efficient because animals can find more targets using these than when they would have moved along a straight line of the same length.

seeds in little holes we could manipulate both the distance at which the seeds could be seen and the density of seeds in the experiment. The doves did however not respond to changes in either parameter. They did move using Lévy walks, but the critical parameter for the Lévy walk model deviated from the theoretically predicted optimal value.

The second part of this thesis contains a chapter on how animals satisfy their requirements for (macro-)nutrients and at the same time maximise the time within which they do not need to forage (chapters 6 & 7). In this part the emphasis is on a combination of decisions: how many patches of each food type are included in the foraging path and how long should be eaten from these patches. To optimise their diet, animals have to choose that ratio of food types that can balance their requirements for (macro-)nutrients. They have to maximise their intake rate by depleting the visited patches to the locally optimal level (chapter 6).

In chapter 7 I synthesise the results of chapters 3, 4 and 6 into a model that can address three basic foraging decisions simultaneously: (1) What to eat, (2) How long to eat at a patch of this food and (3) How to move to find this food (chapter 7). With this model I demonstrate a possibility to incorporate the effect of searching movements within a heterogeneous environment into models that use 'mean field' approximations of spatial processes.

Summarising, this thesis shows that animals can deal with the spatial heterogeneity in food distribution using Lévy walks. These walks result in a fractal 'area-restricted search'-like movement pattern, that are more efficient in exploiting clustered patch distributions. These patterns are however only scale-free at very low densities of targets, which makes fractal-like local movements less suitable for the extrapolation to larger scales. The experiments with goats and doves show that some animals do, and some animals don't use these optimal Lévy walks while searching for food. Next I present a model that can calculate how animals can maximise the time available for non-foraging activities: they have to choose the right ratio of food types in their foraging path to balance the uptake of (macro-)nutrients and then deplete the visited food patches to the locally optimal level.

Many ecological processes are, as a consequence of heterogeneity within and between ecosystems, dependent on movement. The rate of ecological processes and the connectivity of systems is to a large extent determined by the movement patterns of animals. Often it is impossible to incorporate those spatial processes and spatial heterogeneity explicitly in models. A mean-field approach is used in stead. In the final chapter (chapter 7) I use the result of my research to show how the effect of movements in a heterogeneous environment can be incorporated in models that use a mean-field approach to spatial processes and spatial heterogeneity. This opens the possibility for such models to take movement patterns into account, an important part of animals foraging behaviour and a driving factor in many ecosystem processes.

Samenvatting

Voedsel is heterogeen in kwaliteit en kwantiteit ten opzichte van haar verspreiding in ruimte en tijd. Dieren moeten tijdens het foerageren keuzes maken over hoe ze omgaan met deze heterogeniteit. Om de tijd die niet besteed hoeft te worden aan foerageren te kunnen maximaliseren, beslissen dieren over waar, wat, wanneer en hoeveel er gefoerageerd wordt. Deze beslissingen zijn van wezenlijk belang; voedselopname beperkt dieren in veel gevallen in hun overige tijdsbesteding. In het eerste deel (hoofdstukken 2–5) van dit proefschrift behandel ik de bewegingspatronen die dieren volgen bij het zoeken naar ruimtelijk verspreide foerageerplaatsen. Het tweede deel (hoofdstukken 6 & 7) gaat over dieren die foerageren om in hun behoefte aan (macro-)nutriënten (zoals energie & eiwitten of stikstof & fosfor) te voorzien.

De bewegingspatronen van dieren op zoek naar voedsel zijn zowel bestudeerd aan de hand van experimenten als van computersimulaties. Hoofdstuk 2 toont de resultaten van een onderzoek naar foerageergedrag van geiten. Tijdens het foerageren gebruiken deze geiten Lévy wandelingen[3], die theoretisch resulteren in zowel super-efficiënte als super-diffuse zoekbewegingen[4]. In de twee volgende hoofdstukken onderzoek ik dit super-efficiënte en super-diffuse gedrag met behulp van computersimulaties. De superefficiëntie blijkt te worden veroorzaakt door het gedrag van dieren op de plaats waar zich een doel (zoals een foerageerplaats) bevindt (hoofdstuk 3). Wanneer een dier dat een Lévy wandeling loopt, stopt op de plek van het doel en van daar opnieuw begint met een Lévy zoekpad, ontstaan 'omgevingsgebonden zoektocht'-achtige bewegingen in het fractale zoekpatroon. Dit heeft tot gevolg dat de geclusterde verdelingen van doelen beter benut kunnen worden. Dit stoppen en opnieuw beginnen op de plaats van een doel beperkt de super-diffuse eigenschappen van het bewegingspad bij hogere dichtheden van doelen (hoofdstuk 4). Het stoppen op de plaats van een doel verandert de eigenschappen van het zoekpad, doordat lange rechte paden ingekort worden en in een willekeurige richting opnieuw wordt gezocht. Hierdoor is het extrapoleren van op kleine schaal geobserveerde bewegingspaden naar de verspreiding van dieren op grotere schaal niet mogelijk.

Uit deze computersimulaties (hoofdstukken 3 & 4) vloeien de hypothesen dat (1) de dichtheid van doelen en de afstand waarop deze waargenomen kunnen worden het bewegingspatroon van dieren benvloedt en (2) het zoekdeel van het pad (waar geen infor-

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[3] De Lévy wandeling is een type 'willekeurig zoek' beweging in het gebied tussen ballistische (rechte lijn) en Browniaanse (compleet willekeurig) bewegingen, dat resulteert in een schaal-vrij '*fractal*' bewegingspatroon. In een Lévy wandeling komen lange rechte padstukken relatief vaak voor.

[4] Deze bewegingspatronen zijn super-diffuus in de zin dat ze een snellere dan normale diffusie van de dieren die dit bewegingspatroon volgen veroorzaken (de dieren verspreiden zich met Lévy bewegingen verder), en kunnen super-efficiënt zijn omdat dieren hiermee meer doelen kunnen vinden dan wanneer ze langs een rechte lijn van dezelfde lengte bewegen.

matie over de doelen beschikbaar is) anders zal zijn dan het totale bewegingspad. Deze hypothesen zijn getoetst in een experiment met lachduiven op zoek naar hennepzaden (hoofdstuk 5). Door de hennepzaden te verstoppen in kleine gaatjes konden zowel de afstand waarop deze zaden zichtbaar waren als de dichtheid van zaden in het experiment gemanipuleerd worden. De duiven reageerden echter niet op veranderingen in beide parameters. Ze gebruikten wel Lévy wandelingen, maar de waarde van de kritieke parameter van het Lévy wandelings-model week af van de theoretisch voorspelde optimale waarde.

Het tweede deel van dit proefschrift gaat over hoe dieren in hun behoefte aan (macro-)nutriënten kunnen voorzien en tegelijkertijd de tijd waarin ze niet hoeven te foerageren kunnen maximaliseren (hoofdstuk 6 & 7). Deze (macro-)nutriënten zijn heterogeen verdeeld over verschillende voedseltypes. De nadruk ligt in dit deel op de combinatie van de beslissingen: hoeveel foerageerplaatsen van elke voedseltype worden opgenomen in het foerageerpad, en hoelang wordt er op elk van deze foerageerplaatsen gegeten. Om hun dieet te optimaliseren moeten dieren die verhouding van voedseltypes kiezen waarmee ze hun opname van (macro-)nutriënten naar behoefte balanceren. Tegelijkertijd moet de voedselopnamesnelheid gemaximaliseerd worden door deze voedselplaatsen te gebruiken tot het lokaal optimale niveau (hoofdstuk 6).

In hoofdstuk 6 breng ik uiteindelijk de resultaten van hoofdstukken 3, 4 en 6 samen tot een model dat de mogelijkheid biedt om drie basisbeslissingen van het foerageren tegelijkertijd te behandelen: (1) wat te eten, (2) hoe lang daarvan te eten en (3) hoe te bewegen om dat eten te vinden. Dit model biedt een mogelijkheid om het effect van bewegingspatronen in een heterogene omgeving op te nemen in modellen die slechts gebruik maken van een 'veldgemiddelde' van ruimtelijke processen.

Samenvattend laat dit proefschrift zien dat dieren met behulp van Lévy wandelingen om kunnen gaan met ruimtelijke heterogeniteit in hun voedsel. Deze wandelingen resulteren in een fractaal 'omgevingsgebonden zoektocht'-achtig bewegingspatroon, waarmee voedsel met een geclusterde verdeling efficiënter gevonden kan worden. Deze patronen zijn echter alleen schaalvrij bij erg lage dichtheden van doelen, waardoor dergelijke fractale bewegingspatronen minder geschikt zijn voor de extrapolatie naar grotere schaalniveaus. De experimenten met geiten en duiven laten zien dat sommige dieren deze optimale bewegingen wel en sommige dieren deze niet gebruiken in hun zoektocht naar voedsel. Vervolgens wordt een model gepresenteerd dat berekent hoe dieren de tijd die niet besteed hoeft te worden aan foerageren kunnen maximaliseren: ze moeten de juiste verhouding van voedseltypes in hun foerageerpad kiezen om de opname van (macro-)nutriënten te balanceren en vervolgens foerageerplaatsen tot het lokaal optimale niveau gebruiken.

Veel processen in de ecologie zijn door heterogeniteit, zowel binnen als tussen ecosystemen, afhankelijk van beweging. De snelheid van ecologische processen en de verbondenheid van systemen wordt in belangrijke mate bepaald door dierlijke bewegingspatronen. Vaak is het echter niet mogelijk om dergelijke ruimtelijke processen en ruimtelijke heterogeniteit expliciet op te nemen in modellen. In plaats daarvan wordt gebruik gemaakt van een gemiddelde van het hele veld. In het laatste hoofdstuk gebruik ik de resultaten van mijn onderzoek om te laten zien hoe het effect van bewegen in een heterogene omgeving opgenomen kan worden in modellen die van ruimtelijke processen en ruimtelijke heterogeniteit slechts een 'veldgemiddelde' gebruiken. Dit maakt het mogelijk om in dergelijke modellen op een eenvoudige manier bewegingspatronen op te nemen, een belangrijk onderdeel van foerageergedrag van dieren en een bepalende factor voor veel ecosysteemprocessen.

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Working on a PhD-thesis is a search for ideas, smart plans, good analyses and strong conclusions. As described in this thesis, the best way of searching is by using a Lévy walk: with many small steps, and a few extremely long steps, until a target is reached, and the location of that target should be explored further. In this search I have had the opportunity to work with many people, find people in different fields and different parts of this world to collaborate with and to ask advise. And many people created an environment within which ideas could come to good plans. As in a Lévy walk, some of these people I ran into frequently, others only once or twice. I am thankful to those people that helped me make this search less of a random walk.

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Curriculum Vitae

Geerten Martijn Hengeveld was born on August 23, 1979 in Hilversum (NL). After living in Hilversum, Esher (UK) and Den Haag his family settled in Oegstgeest, were he attended the Rijnlands Lyceum in Oegstgeest from 1991 until 1997, when he obtained his *VWO-diploma*.

In 1997 he continued his education at the Rijks*universiteit* Groningen, where he studied Biology. During his years at the Rijks*universiteit* Groningen Geerten participated actively in the university politics. Geerten held positions in the board of the sub-department of biology and the university council, a.o.. For his *doctoraal* degree (MSc, obtained in 2003) Geerten studied the evolution of social dominance with Prof.dr. F.J. Weissing and dr. G.S. van Doorn, individual spoor recognition with Prof.dr.ir. J. Komdeur and Prof.dr. B. König (universität Zürich), community assembly rules with Prof.dr. J. van Andel and foraging movements with Prof.dr. H. Olff.

Subsequently, Geerten started as *assistent in opleiding* (AIO, 2003-2007) at the Tropical Nature Conservation and Vertabrate Ecology Group at Wageningen university (later the Resource Ecology Group (REG)). In this period he studied animal movements in heterogeneous environments with Prof.dr. H.H.T. Prins and dr.ir. F. van Langevelde, which resulted in this thesis. Next to this main topic, Geerten is and has been involved in projects on biodiversity and spoor recognition.

Currently Geerten holds a position as junior researcher at the centre for ecosystem studies at Alterra, Wageningen UR.

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Prins, H.H.T, G.M. Hengeveld, D.H.M. Cumming, H. Fritz, I.M.A. Heitkonig, H.H.F. Wijffels, and M. Loreau, in prep., *testing the insurance hypothesis for the assemblage of Africas large mammalian herbivores.*

PE&RC PhD Education Certificate

With the educational activities listed below the PhD candidate has complied with the educational 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 (5.6 credits)

- Optimisation or random walk? Modelling movement for grazing herbivores

Laboratory Training and Working Visits (3.8 credits)

- Proefdierkunde; University of Wageningen (2005)
- Lévy flight models; University of Barcelona (2006)

Post-Graduate Courses (5.9 credits)

- Population dynamics; FE, Andre de Roos (2003)
- Master-class in grazing ecology; Frontys, Herbert Prins (2003)
- Theoretical ecology; FE, Hans Metz (2003)
- Spatial and temporal aspects in resource ecology; PE&RC, Norman Owen-Smith (2005)
- Consumer-resource interactions; PE&RC and FE, Wolf Mooij (2006)

Competence Strengthening / Skills Courses (4.8 credits)

- Bayesian methods in theory & practise; Mansholt, John Geweke (2003)
- Multi agent systems for natural resources management; Mansholt, PE&RC, Francois Bousquet (2006)
- Presentation skills; CENTA (2006)

Discussion Groups / Local Seminars and other Scientific Meetings (5.9 credits)

- NVTB PhD day (2003)
- Mathematics, statistics and models; PE&RC discussion group (2003-2007)

- Forest ecology and nature conservation; PE&RC discussion group (2003-2007)

PE&RC Annual Meetings, Seminars and the PE&RC Weekend (1.2 credits)

- PE&RC day (2003-2006)

International Symposia, Workshops and Conferences (6.8 credits)

- Schoorl meeting of the Dutch society of theoretical biologist; NVTB Schoorl the Netherlands (2003)
- Schoorl meeting of the Dutch society of theoretical biologist; NVTB Schoorl the Netherlands, with presentation: ”Moving to eat” (2004)
- 12th Benelux congress of zoology; University of Wageningen (2005)
- Advances in the theory of contests and tournaments; Wissenschaftszentrum für Sozialforschung Berlin, invited discussant (2005)
- Contests in economy and biology; Wissenschaftszentrum für Sozialforschung Berlin, invited discussant (2006)

Animals moving from one place to another transport seeds, parasites, genes and grazing pressure. Insight in the spatial linkage between ecological processes can be gained from understanding the driving forces behind animal movement patterns. From this understanding predictions can be made about which patterns are most likely to be encountered.

This thesis addresses the role of foraging in animal movement. Central is the study of the searching efficiency and diffusion of Lévy random searches, both through computer simulations and experiments. Additionally, predictions are made about which foraging decisions animals should make in order to optimise their intake of several nutrients.