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ABSTRACT

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The effects of different types foraging behaviour on the spatially explicit accumulation of contaminants are under consideration in this report. A conceptual model has been developed, which can be used to simulate the foraging behaviour of the little owl (*Athene noctua*) under different assumptions on the mode of foraging behaviour: random foraging, optimal foraging, central foraging, or a combination of optimal and central foraging. The result of the modelling exercises show that the different modes of foraging result in different accumulation rates, and associated risks. Hence, it is concluded that spatially explicit modelling of contaminant accumulation should be conducted with specific knowledge on the foraging behaviour of the organisms under study. Furthermore, it is shown in the current report that measures in habitat management may be used to alleviate risks that contaminants may pose to higher organisms.

Keywords:. Spatial explicit risk assessment, spatial planning, little owl, bioaccumulation, ecotoxicology, model development.

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Preface

The project BERISP (Breaking Ecotoxicological Constraints in Spatial Planning, see www.berisp.org) is part of the co-operative European Community Initiative INTERREGIIIB. This project brings together a transnational consortium including the following spatial planning authorities and applied knowledge institutions:

- University of Antwerp, Belgium
- RIZA, Institute for Inland Water Management and Waste Water Treatment; part of Ministry of Transport , Public Works and Water Management, Directorate-General for Public Works and Water Management, the Netherlands
- Alterra, Wageningen UR, the Netherlands
- Ministry of Transport, Public Works and Water Management, Directorate Limburg, the Netherlands
- OVAM, Public Waste Agency of Flanders, Mechelen, Belgium
- Central Science Laboratory, York, United Kingdom
- AMINAL, Flemish Department for Environmental, Nature, Land and Water Management, Belgium

The project contributes to the development of new approaches to problems in spatial planning associated with soil contamination. The main objective of BERISP is the development of a Decision Support System (DSS), which will allow an iterative procedure in spatial planning processes, in which planners can review different types of landscape use and habitat distributions against scientific knowledge on risks of pollutants for organisms.

The project is co-funded by the INTERREG IIIB initiative (www.nweurope.org) and by the Dutch Ministry of Agriculture, Nature, and Food Quality, Kennisbasis, Theme 1 'Design and utilisation of green and blue spaces' (KB-01) and Theme 9: 'Scientific Toolbox'. (KB-09).

Summary

Effects of spatial foraging behaviour on contamination risks in food webs have been modelled at Alterra. The research was part of a bigger project, called BERISP. This is a European Community initiative and stands for *Breaking Ecotoxicological Restraints in Spatial Planning*. BERISP is concerned with the redevelopment of contaminated sites. Due to population and wealth growth, the pressure on the available land has grown and hence, spatial conflicts may arise. Contaminated derelict areas need to be reused. This redevelopment can however only be successful if risks posed by contaminants are within acceptable limits. The study of ecotoxicology identifies toxic effects on populations of organisms. Within the current BERISP report, the little owl (*Athene noctua*) and the toxic effects of cadmium are considered. The project's aims are to develop:

- a new approach in soil contamination. Current methods include in situ recovery, excavating the polluted soil, or the isolation of the site. These methods may however not offer a viable solution, or may be too costly. Therefore, a new idea has originated: a spatial change in habitats in such a way that contamination risks will be reduced.
- a Decision Support System to assess the risks of soil contamination and also to involve stakeholders in the planning process.

Consequences of changes in habitat configurations, for example by changing the proportions of habitat types or by shifting habitats within a site while maintaining the habitat proportions, are investigated in order to realise these project aims. Knowledge concerning the spatial uptake of contaminants is essential to make an accurate assessment of the consequences of changes in habitat configurations or proportions.

Therefore, a basic theoretical model for spatial exploitation and contaminant uptake has been developed. This modelling approach uses grid maps as basic input. Two types of maps are required: a soil contamination map and a habitat map. It is assumed, that three different food chains are associated with different habitat types. In the first habitat type (*worm habitat*), worms take up cadmium from the soil, which is subsequently transferred to the owls which eat those worms. In the second habitat type, owls receive the contamination via vegetation and voles (*vole habitat*), and in the third habitat type via worms and shrews (*shrew habitat*). Each day, owls explore a part of the landscape, called a home range, which consists of several grid cells. The owls take up cadmium from the prey items that they consume in their daily home ranges. To calculate the daily cadmium uptake, the model multiplies for every cell in the home range the amount of food that is consumed in that cell, the cadmium concentration from that food, and an uptake constant, which stands for the fraction of the cadmium in the food that is actually taken up by the intestines of the owl. This is added for all cells in the home range. The result of this summation is attributed to the centre cell of the home range. In fact, almost all cells in a landscape are

considered to be the potential centre of a home range (except for the boundary cells). The daily cadmium uptake can therefore be calculated for all home ranges in the landscape. The output of the model consists of a grid map, with for each cell the calculated daily cadmium uptake from all cells within its home range. The average daily cadmium uptake from the output map serves as the final risk measure. The lower the mean daily uptake for the whole area, the "safer" the area.

Such output maps can be derived for each proportional and spatial distribution of habitats. By comparing the mean daily cadmium uptake, one could easily see if a change in habitat proportions or positions would lower the contamination risk.

Within the model, there is a choice of four different foraging strategies:

- *Uniform*: owls daily spend an equal amount of time in each cell within the home range, and thus each cell within the home range is exploited in equal efforts
- *Distance dependent*: consumption of food is dependent on the distance from the centre cell of the home range (e.g. location of nest), which means that the owls explore the cells close to the centre cell more intensively (cf. Central Foraging).
- *Availability dependent*: consumption is dependent on the availability of the prey items within the home range. More time is spent in cells with high prey availability. (cf. Optimal Foraging).
- *Availability and distance dependent*: consumption is both dependent on the availability of the prey items and on the distance from the centre cell (combination of both Central Foraging and Optimal Foraging).

In general, the results show that when a fraction of worm habitat is replaced by shrew habitat, so that an owl would eat more shrews instead of worms, the mean cadmium uptake will decrease. When a part of the worm habitat is replaced by vole habitat, the mean daily cadmium uptake decreases even more due to the fact that the owls eat more voles instead of worms and the internal cadmium concentration of voles is lower than that of the other prey items. Contrary, when a fraction of vole habitat is replaced by shrew habitat, the risk would increase.

Apart from these general tendencies in this specific case, the results demonstrate that an availability driven foraging pattern increases the prey uptake and at the same time, decreases the cadmium uptake or contamination risk. This is related to the fact hat when applying the optimal foraging strategy the owls will eat more voles which are heaviest and will gain the most energy per searching effort. As said earlier, voles are least contaminated, hence a strategy that focuses on the uptake of voles will decrease the accumulation of cadmium. Searching for food close to the nest (i.e. centre cell) decreases the energetic gain and increases the variability of the encountered risks. Species with a relatively small foraging area more frequently encounter localized contamination, but also less contaminated sites. Hence, the uptake of contaminants will be more variable in organisms that forage in smaller areas (close to their nest).

It can be concluded that spatial foraging behaviour may affect the contamination risk in wildlife. To assess the consequences of changes in habitat configurations properly, fieldwork should however be conducted to investigate the actual behaviour of little owls. All together, it can be concluded that a change in habitat configurations may serve as a remedy to soil contaminations. Plans for the reuse of contaminated sites should consider this new idea as a valuable measure.

1 Introduction

1.1 Ecotoxicology and the effect of spatial organisation

Industrial activities may create disturbances in ecosystems surrounding industrial facilities and infrastructures. However, these facilities have frequently been inaccessible to the public and, as a result many of these sites may actually be relatively undisturbed, and may harbour high biodiversity and large expanses of habitat that could be incorporated into ecological networks. In particular in developing countries, spatial conflicts are increasing between additional housing, commercial development, and the protection of open space. Nowadays, these countries face the challenge of planning the redevelopment of contaminated derelict areas and river basins while assuring their safe reuse for civilian, industrial, and ecological purposes.

In all cases, activities to remediate affected sites must result in the protection of biodiversity, the reduction of current and future pollution exposure levels, and the restoration of habitats in surrounding ecosystems. For conservation management purposes, desired landscape configurations to manage wildlife populations can be created by land use management practices, as is suggested by the underlying ecological principles governing patch dynamics (Linkov *et al.*, 2004a). However, the development of new nature areas can only be successful if the risks posed by the contaminants to wildlife and their prey items are within acceptable limits. Proper methods for ecological risk assessment are necessary to evaluate these risks (Kooistra *et al.*, 2001).

Ecotoxicology aims to identify toxic effects on individuals, populations and communities of organisms (Ares, 2003). Due to their industrial use and the low chemical reactivity some heavy metals can become available for uptake by species, through air, water and food and through food chain steps (Zaccaroni *et al.*, 2003) as is showed by Figure 1.1.

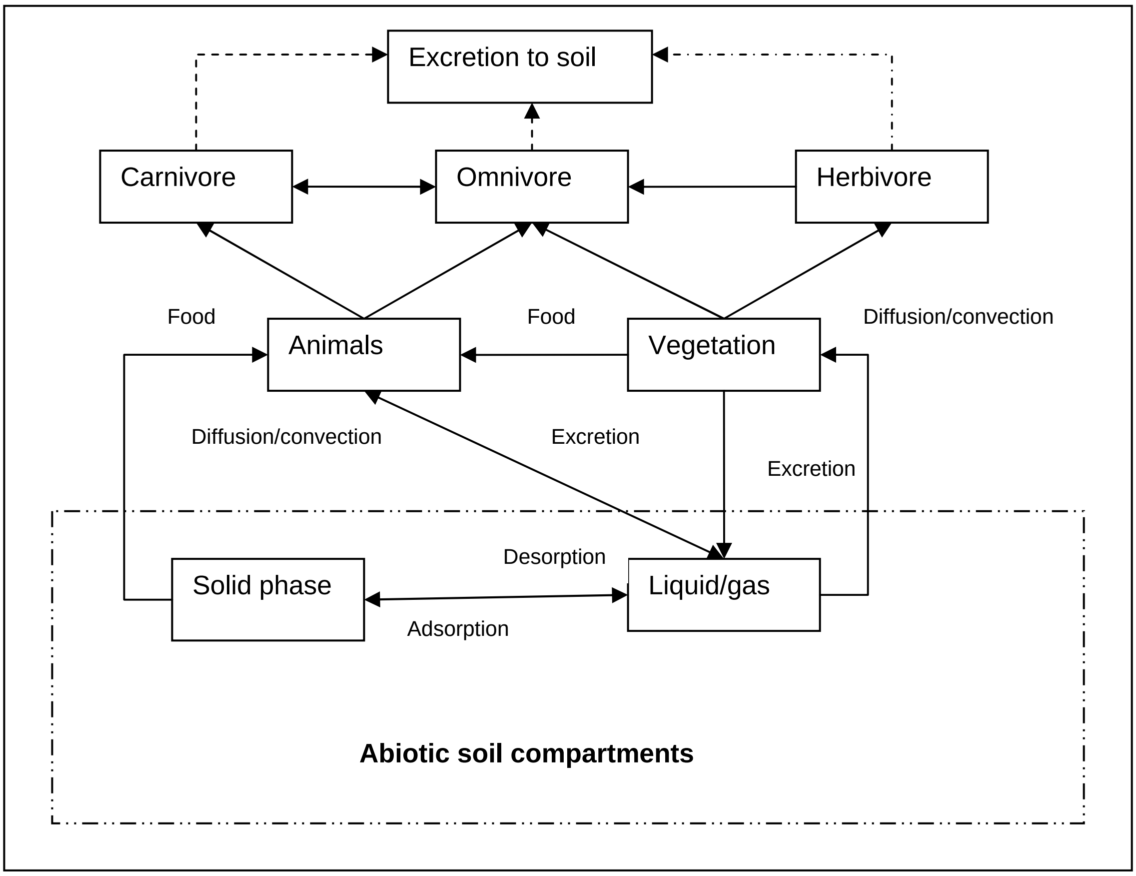


Figure 1.1: Interactions between soil pollution and terrestrial organisms (after: (Marinussen & vanderZee, 1996)

Although exposure can occur through various routes, consumption of contaminated prey items is thought to be the main route of exposure for terrestrial predators (Toal *et al.*, 2002). When contaminants are retained more efficiently than excreted, an individual animal will build up increasing levels of those contaminants (Van den Brink & Ma, 1998), and in case of cadmium mainly in its kidneys, bones, and/or liver (Esselink *et al.*, 1995). In this way, persistent toxicants can accumulate in food webs, and vertebrates can be exposed to higher concentrations than species at lower trophic levels (Traas *et al.*, 1996). This process is called biomagnification.

Because accumulation depends on the transfer of heavy metals in the food chain, the composition of the diet at different trophic levels may (partly) explain the variation in heavy metal levels found in organisms (Esselink *et al.*, 1995; Sharma & Shupe, 1977). Some predators depend heavily on a certain type of prey and others prey on a wide variety of species. Furthermore, body load increases with age if intake exceeds the metabolic rate and excretion (Esselink *et al.*, 1995; Hope, 2000; Vanstraalen *et al.*, 1988). Other sources that could be responsible for differences in heavy metal levels could include sex (Esselink *et al.*, 1995; Hope, 2000), body condition (and hence organ size) (Esselink *et al.*, 1995), the amount and duration of ingestion (Hope, 2000), contamination levels in the home range (Esselink *et al.*, 1995) and the presence of other interacting elements (Hope, 2000).

1.2 Spatial configuration and behaviour of organisms

When assessing risks posed by chemical contaminants, risk assessors must estimate a species' level of exposure to contaminants in either abiotic (soil, water, etc.) or biotic (tissues, prey items) media (Hope, 2000). However, uncertainty arises when devising a relationship between the body burden in an animal and its environmental exposure, especially when considering pollutants that are poorly absorbed across the gut. This is because most of the total body burden of the pollutant may be in the gut rather than in the body tissues (Walker *et al.*, 2002). Hence, conventional dose estimation methodologies using prey tissue concentrations alone may underestimate the total dose to a predator that ingests whole prey (Toal *et al.*, 2002).

Several studies have indicated that the relative spatial positions of organisms and contaminated media can strongly influence estimates of exposure and hence of risk (Hope, 2000; Johnson, 2002; Landis, 2002). Species with overlapping foraging areas may experience significantly different contaminant exposures from the same site due to local variability (von Stackelberg *et al.*, 2002). Mobile organisms are distributed in a complex spatial pattern resulting from vegetation patchiness, behaviour, and the distribution of other interacting populations (Ares, 2003). During their search for food, organisms integrate exposure to different contaminant concentrations over space and time (Esselink *et al.*, 1995).

Traditional approaches to ecotoxicology and ecological risk assessment have frequently ignored the complexities which arise due to the spatial heterogeneity of natural systems (Johnson, 2002). Currently applied exposure estimates assume a static and continuous exposure of an organism to a contaminant represented by some descriptive statistic, such as the mean or maximum concentration (Linkov *et al.*, 2004a). Barriers to incorporating spatial variability include: (a) a lack of simple, accessible tools for easily considering spatial relationships when estimating exposure and (b) a limited understanding of how spatial relationships may interact to influence exposure, leading to uncertainty regarding the implications and consequences of their use (Hope, 2000).In recent years, however, ecologists have become increasingly aware of the fact that assessments of risk posed by contaminant exposure need to account for spatial variability and the potential implications for recovery processes (Johnson, 2002). According to Linkov *et al.* (2002), an assessment that does not incorporate spatial or temporal aspects of exposure (i.e., assumes that species are exposed all the time) is biologically unrealistic.

Landis (2002) came to some principal conclusions, related to metapopulation theories. Firstly, low levels of toxicity in one patch in a habitat can significantly impact populations of other landscape patches that have no contact with a toxicant. Toxicants may damage local populations (called *sink* populations in a metapopulation context) within levels that could be restored by migration from neighbouring (*source*-) populations. Conversely, specimens exposed to toxicants could migrate and produce damaged offspring in non-polluted population patches, thus affecting their future dynamics. Toxic effects on local populations could be dampened by migration of the affected specimens to other patches or from healthy individuals into exposed environments (Ares, 2003). A subsequent role is played by the species' migration rate (Linkov *et al.*, 2004b). A slow moving animal covers only a fraction of the habitat and thus inter-individual variability may be high

Secondly, the arrangement of the patches or foraging areas is critical to the dynamics of the system and the overall impact of a toxicant (Landis, 2002). Freshman and Menzie (1996) found that population-level risks can vary with foraging area in a non-intuitive manner as a result of the relationship between foraging area size and the spatial distribution of contaminants. When the top level carnivores are resident species with a relatively small foraging area, they more frequently encounter localized contaminated sediments. Von Stackelberg *et al.* (2002) found for example that fish population habitat size has a strong influence on fish exposure to site contamination. If the area over which one defines the local population is large, (i.e. fish routinely migrate large distances over a short time period), spatially localized contamination is unlikely to result in significant exposure to fish. By contrast, a relatively large, with respect to habitat size, contaminated site could result in significant exposure to the entire population. Marinussen & vanderZee (1996) came to a similar conclusion by stating that both the home-range size of the organism and the spatial pattern of cadmium content affect the extent of the area where exposure to the pollution leads to exceeding of a specific cadmium concentration in the organisms. On average, larger home-range sizes lead to lower cadmium concentrations in organisms (spatial 'smoothening' of local hotspots). However, smaller home-range sizes may lead to an increase in the probability that a specific exposure level is exceeded (increase of variability in exposure levels).

In ecotoxicology, the problem of finding acceptable temporal and spatial scales needs to be dealt with. Some practical issues like the estimation of the potential for the natural attenuation of toxicity and the transport of contaminants along food chains must be addressed at the scales/levels of biological complexity of communities and ecosystems (Ares, 2003). The dispersal of organisms between contaminated and uncontaminated patches creates a situation where risk analysis must consider a spatial extent broader than the toxicant-contaminated area. Risk assessments may need to expand the area under study beyond the toxicant-contaminated area because fluxes of organisms or materials functionally link the contaminated area to the surrounding landscape. Within the contaminated area, a coarse resolution analysis may be needed to summarize the general effects, but much higher resolution in particular sub-areas or microenvironments may be needed to pick up the unique response of organisms to those special circumstances (Johnson, 2002).

1.3 InterregIIIB BERISP project

The BERISP project (see www.berisp.org)is conducted within the European Community initiative INTERREGIIIB (see www.nweurope.org), which is aimed at strengthening trans-European co-operation and promoting balanced development. BERISP recognises that contamination in field situations may have a severe impact on the occurrence and functioning of animals, or may pose a risk to humans. It is stated that contamination often obstructs the (re-)development of derelict areas, and therefore methods have been developed in order to assess the risks that contaminants pose to the environment. Current procedures used to assess these risks, are scientifically state of the art. However, these methods have not been developed in a way such that stakeholders can participate in the risk assessment. Furthermore they lack spatial information, so the information resulting from such an assessment is hardly applicable in spatial planning processes.

The project BERISP (Breaking Ecotoxicological Constraints in Spatial Planning) as a part of the INTERREGIIIB initiative, must contribute to the development of new approaches to problems in spatial planning associated with soil contamination. In the proposed project approach, spatial structure is incorporated into the risk-assessments. Contamination patterns vary at small spatial scales, often smaller than the scales spatial planners are concerned with. Larger animals however, do spread at scales that are of importance to landscape planners e.g. 100-1000 meters or even larger. Through food uptake, animals are directly coupled to contamination patterns in the soil, which indicates that small scale contamination patterns are relevant for processes and structures at larger scales, and may have effects at scales that are relevant for spatial planning processes. The currently proposed spatially explicit risk analysis of contamination includes the spatial distribution of contaminants within the area of interest, and combines this with the spatially explicit uptake of the contaminants by organisms, based upon their exploitation patterns of the landscape, within models.

This new spatially structured concept is focussed on changes in habitat configuration as a possible remedy. Therefore, application will result in new options for solving contamination problems in spatial planning processes. The concrete result of the development of the concepts and tools in the project will be a so-called 'Decision Support System' (DSS). The DSS consists on the one hand, of a section in which the risks posed by contaminants can be assessed, and on the other hand has a management tool which can be applied in order to incorporate information and arguments from other stakeholders involved in the planning process.

Within the planning cycle the DSS will assist during the planning phase to translate policy decisions into the actual implementation of measures. It will enable a planner to explore, *a priori*, several spatial planning alternatives, and to evaluate the resulting risks that contamination poses to wildlife. Current methods only allow for the evaluation of risks after implementing a particular measure, e.g. monitoring risks in the evaluation phase. An *a priori* evaluation of measures will result in a more effective implementation of planning measures and also allows for other main stakeholders to be involved in the evaluation process.

Fieldwork will be conducted to validate the models that will be developed in the BERISP project. This fieldwork will be focused on the food chains of the hedgehog (*Erinaceus europaeus*) and the little owl (*Athene noctua*) and thus will also include their prey items, like earthworms and mice (INTERREGIIIB, 2003).

1.4 Research goal

Current redevelopment methods to prevent the risks posed by contaminants mostly consider *in situ* remediation, digging off the polluted soil, or site isolation. Besides the fact that the latter offers no solution when reuse of the terrain is required, these methods can be very costly. Hence, the idea of changes in habitat configuration to reduce risks has been proposed. The consequences of both shifting habitats within a site, while maintaining the ratios of habitat types, and changing the ratios by changing types of habitats, need to be elaborated upon. For this reason, knowledge concerning spatially explicit uptake of contaminating substances by organisms is essential. Spatial patterns of exploitation possibly may influence the contamination risk in such a way that changes in habitat configuration will not be sufficient.

Models of the spatial foraging behaviour of individuals are in development. During this research, a conceptual model of such kind has been created for little owls, with which the influences of differences in spatial patterns of exploitation have been investigated. The model aids in the identification of areas with an elevated contamination risk. These can be areas with, for instance, a high concentration of pollutants in the soil, or areas that are often visited by predators to encounter their prey items.

1.5 Outline of the report

The conceptual model that has been created during this research is explained in this report, after a short review of ecotoxicological models described in the literature (Chapter 2). A contamination uptake model developed by Gorree *et al.* (1995) has been used for both prey items and the top predator species (Section 3.3). Four basic spatial exploitation strategies have been applied to simulate foraging behaviour (Section 3.4.2). Model results contain responses of daily prey digestion (Section 4.2.1) and cadmium uptake (Section 4.2.2). The influences of differences in spatial patterns of exploitation have been investigated through regression analyses (Section 4.2.2) and analyses of variance (Section 4.2.1 and 4.2.2). The model results have been plotted against the habitat composition to investigate the consequences of a change in habitat types. Spatial statistics has been used to consider the effects of the shifting of habitats (Section 4.3).

2 Conceptual outlines of contaminant flux modelling in food chains

To gain more insight into specific ecotoxicological problems, cases have been simplified and investigated by means of models. In the literature, different models can be found. In the following review, some of these models will be described, showing the basic ideas behind them and the differences between them. The models below have been divided into 2 groups: physiological-based kinetic models and models based on bioaccumulation factors. Models of the first category describe the intake of contaminants or the body burden as a time-dependent variable. Often, physiological-based kinetic or metabolic parameters that are hardly quantifiable are included into these models. Models based on bioaccumulation factors are more straightforward; however, these models cannot be applied in a spatially explicit context.

2.1 Physiological-based kinetic models

The model by Johnson (2002) is based on the assumption that an ambient toxicant concentration, $C_a(t)$, exhibits an exponential decay in a toxicant spill that instantaneously contaminates the patch, followed by a first-order environmental degradation process:

$$C_a(t) = C_0 e^{-k_d t}$$

where k_d is the degradation rate constant. The ambient toxicant concentration asymptotically approaches a maximum value when a constant rate of toxicant inputs to a patch, coupled with first-order environmental degradation:

$$C_a(t) = C_{\max}\left(1 - e^{-k_d t}\right)$$

When first-order uptake and elimination kinetics in a single compartment is assumed, the body concentration of the toxicant becomes:

$$\frac{dC_b}{dt} = k_\mu C_a - k_e C_b$$

or:

$$C_b(t+1) = \frac{k_\mu}{k_e} C_a\left(1 - e^{-k_e}\right) + C_b(t) e^{-k_e}$$

where C_b is the body concentration of the toxicant, C_a is the ambient concentration, and k_μ and k_e are uptake and elimination rate constants (Johnson, 2002).

Marinussen & vanderZee (1996) showed the same ideas in their model. The authors propose that, while a soil dwelling organism is exposed to contaminated soil, the pollutant concentration in the organism, *P*, changes as a function of time, and can be described by a one compartment toxicokinetic model:

$$\frac{dC(t)}{dt} = \frac{I(t)}{M(t)} - k(t)C(t)$$

where *dC(t)/dt* is the rate of change of the concentration per weight of the organism, *I(t)* is the assimilation rate of the contaminant, *M(t)* is the weight of the organism and *k(t)* is the excretion rate. During digestion, part of the ingested contaminants will be assimilated, depending on the assimilation efficiency of the organism:

$$I = \alpha Q_A$$

where *a* is the assimilation coefficient and Q_A is the biologically available concentration. Combining the above equations lead to:

$$C(t) = \frac{\alpha}{k} Q_A (1 - e^{-kt}) + C(0)e^{-kt}$$

where *C(t)* is the concentration in an individual that has been exposed to a contamination level Q_A during a time period *t*, and C*(0)* is the initial concentration in the organism (Marinussen & vanderZee, 1996).

The models by Linkov *et al.* (2002) and von Stackelberg *et al.* (2002) extended the differential equations for the concentration of contamination in body mass (for fish):

$$\frac{dC_f}{dt} = k_1 C_{wd} + k_d C_{diet} - (k_2 + k_e + k_m + k_g)C_f$$

where k_1, is the uptake rate; C_{wd}, the freely dissolved cadmium concentration in water; k_d, the dietary uptake rate, C_{diet}, the cadmium concentration in the diet; k_2, the elimination rate; k_e, the faecal excretion rate; k_m, the metabolic rate; k_g, the growth rate; and C_f, the cadmium concentration in fish (von Stackelberg *et al.*, 2002).

Toal *et al.* (2002) used the Goldstein & Elwood-model (1971) to describe the physiological dynamics of Cd in the wood mouse. The input into the model was ingested pollutant, which entered the gut (S_G) and the tissue (S_T) compartment:

$$\frac{dS_G}{dt} = D_A - k_1 S_G - uS_G$$

$$\frac{dS_T}{dt} = uS_G - k_2 S_T$$

The rate constant u describes the rate of uptake of unabsorbed cadmium from the gut compartment to the tissue compartment. The daily dose to an individual wood mouse (D_A) was quantified by:

$$D_A = i_A \cdot WW_a \cdot C_d$$

where i_A is the normalized ingestion rate (g diet/kg wet wt/day), WW_a is the wet body weight, and C_d is the dietary Cd concentration. Two scenarios were used. In the first scenario, the predator preys on small mammals of identical age, and in the second scenario, the predator preys on a wood mouse population of normal age structure. To develop the last scenario, probability density functions for the ages of prey likely to be taken by a predator were needed (Toal *et al.*, 2002).

2.2 Models based on bioaccumulation factors

Another viewpoint on modelling contamination problems is based on the use of bioaccumulation factors. The term bioaccumulation factor (BAF) can be used for all biomagnification or bioconcentration factors, i.e., the ratio between the concentration in an organism and the concentration in its food (biomagnification factor) or its environment (bioconcentration factor) (Gorree *et al.*, 1995; Traas *et al.*, 1996). These BAF's are parameters that are assumed to be log-logistic distributed (Gorree *et al.*, 1995). Kooistra *et al.* (2001) used this perspective to model the ecological risk of contamination in the food chain of little owls. The bioconcentration of metals in vegetation and arthropods, the first level of the food web, was calculated as follows:

$$Cf_i = Cs \cdot BCF_i$$

where Cs is the metal concentration in the soil and BCF_i is the bioconcentration factor for prey item i. For metal concentrations in earthworms, the following regression equation was used (Luttik *et al.*, 1997):

$$\log(Cf_2) = X_0 + a \cdot \log(Cs) - b \cdot pH$$

where X_0, a and b are regression coefficients. For the second level of the food web, the small mammals, the bioaccumulation of cadmium can be calculated with an equation by Kooistra *et al.* (2001):

$$Cf_i = A_i \cdot \left(\frac{Fin_i}{Bw_i} \right) \cdot Uf_i \cdot \sum_{j=1}^{n} Fr_{j,i} \cdot Cf_i$$

where A_i is the age of organism i, Fin_i is the feeding rate, Bw_i is the body weight, Uf_i is the fraction of the total amount of cadmium taken up from the food by organism i, $Fr_{j,i}$ is the fraction of prey item j in the diet of organism i, and Cf_j is the concentration in prey item j.

The potential exposure concentration *PEC* for the little owl and the small mammals can be calculated using the equation (Balk *et al.*, 1992):

$$PEC_i = \left(\frac{Fin_i}{Bw_i}\right) \cdot CoF_i \cdot \sum_{j=1}^{n} Fr_{j,i} \cdot Cf_i$$

where CoF_i is the concentration factor for organism *i*.

Traas *et al.* (1996) weighted each bioaccumulation route according to its fraction in the diet. The average bioaccumulation factor for the total food web of each predator was calculated as:

$$BAF_{ft} = DFT_b \cdot BAF_b \cdot \sum_{k=0}^{n} (DFB_{ip_k} \cdot BCF_{ip_k}) + DFT_m \cdot BAF_m \cdot \sum_{k=0}^{n} (DFM_{ip_k} \cdot BCF_{ip_k})$$

$$+ \sum_{k=0}^{n} (DFT_{ip_k} \cdot BCF_{ip_k})$$

where BAF_{ft} is the *BAF* from soil to the food of a top predator species, BAF_b is the *BAF* of birds, BAF_m is the *BAF* of mammals, BCF_{ipk} is the *BCFs* of the *k*th type of invertebrates and plant parts, DFT_b is the fraction of birds in the diet of the top predator, DFT_m is the fraction of mammals in the diet of the top predator, DFT_{ipk} is the fraction of the *k*th type of invertebrates and plant parts in the diet of the top predator, DFB_{ipk} is the fraction of the *k*th type of invertebrates and plant parts in the diet of birds, DFM_{ipk} is the fraction of the *k*th type of invertebrates and plant parts in the diet of mammals, and *n* is the number of invertebrate and plant parts in the food web of the top predator (Traas *et al.*, 1996).

The model by Gorree *et al.* (1995) for the flow of pollutants through food chains, consists of an ecological section and a toxicological section. The model also starts with the bioavailable concentration of a pollutant in the soil solution. The ecological part of the model, which calculates the concentration in the food of a target animal, consists of stochastic food chain models:

$$cons = \sum per_i \cdot food_i \cdot BAF_i$$

where *cons* = concentration in the consumer; $food_i$ = concentration in food item i; per_i = percentage of food item i in the diet of the consumer; and BAF_i = BAF of food item i to the consumer. The result of the ecological part of the model is a distribution of possible concentrations of the pollutant in the food of a target animal. The toxicological part of the model uses the distribution of possible concentrations in the food as an input and calculates a distribution of possible internal concentrations of the pollutant in organs of the target species known to accumulate this pollutant, e.g. the kidney and the liver, in a relatively simple way:

$$Q(t) = \frac{dfi \cdot c_{up} \cdot food}{c_{out}} \cdot \left(1 - e^{(-c_{out} \bullet t)}\right) \cdot cf_{kidney}$$

where Q = the concentration in the target organ (in this case kidney); t = exposure time; c_{up} = the uptake constant; c_{out} = the excretion constant; *dfi* = the daily food intake per gram of dry weight; *food* = the concentration in the food of the target animal; cf_{kidney} = the concentration factor for kidney/body. The last part of the model consists of a risk assessment. By comparing the calculated organ concentrations with a threshold-level for this organ, the risk to a target species can be assessed (Gorree *et al.*, 1995).

3 Methods

3.1 Indicator components

The theoretical model that has been created during this research is focussed on the floodplains inhabited by the little owl, and includes three of its main prey items; earthworm, vole, and shrew. It could also have been based on other environments with different residing organisms. Creating such a conceptual model requires information on the contaminated landscape and on some of the species using the area for their resources. In fact, such small set of components may serve as indicators for other cases or species. Assessing changing conditions within an ecosystem by monitoring all of its components, processes, and functions, is not possible (Peakall, 1992). As a result, a small set of components has to be selected. Biological components chosen for this purpose are called biological indicators or bioindicators. Assigning bioindicators stems from general systems theory. That is, if a system is a sum of parts, described by a system of state variables, interacting subject to a set of rules or processes, the condition of the system could be assessed from a smaller set of state variables (Matsinos & Wolff, 2003).

3.1.1 Indicator species

For this research, focussed on the development of a spatially explicit ecotoxicological model, little owls have been chosen as bioindicators for the reason that a lot of (field-) data was already available at the institutions involved in the project. Top-predators are often chosen as bioindicators as their population responses can serve as signals of environmental changes occurring at lower trophic levels. The use of man-dominated landscapes by top-predators results in their exposure to a number of environmental contaminants that may cause toxic effects. Also their dependency on specific physical aspects of the habitat makes them potential indicators of changes in these physical attributes of their habitat. Furthermore, species may be of high aesthetic and recreational value to humans (*flagship-species*). However, top level carnivores may accumulate a number of persistent contaminants (Matsinos & Wolff, 2003; von Stackelberg *et al.*, 2002).

Predatory birds may be exposed to metals in the soil through several feeding routes. For the little owl earthworms and small carnivorous mammals, such as shrews (*Sorex araneus*), are sources in the food web for metal intake. The little owl is present in its territory for the entire year and thus is subjected to chronic exposure to contaminants in the soil. Therefore, the little owl is selected as an end-point species (Kooistra *et al.*, 2001).

The little owl is a small owl mainly associated with farmland and open woodland habitats, where it breeds mostly in holes in trees, but also uses cavities in stone piles and buildings, or even holes in the ground. Over the last few decades, little owl populations have declined severely throughout most of Europe, and the species is now listed as a “SPEC 3” species (i.e., a species whose global populations are not concentrated in Europe, but which have an unfavourable conservation status in Europe). This population decline may have been caused by habitat changes due to the intensification of agriculture, including the elimination of nest sites, a decrease in prey abundance, and detrimental effects of pesticides or other contaminants on the little owl’s breeding success. In western and central European farmland, where the mechanization and intensification of agriculture has led to a scarcity of nest-sites, the erection of nest-boxes has been adopted successfully to increase or maintain local populations of little owls (Tome *et al.*, 2004).

Censuses give from 2 to 4 pairs of little owls in a half-mile radius of favourable country (Soutern, 1938). The little owl is an organism that is able to transit local non-foraging areas to reach suitable areas (Kooistra *et al.*, 2005). The dimensions of the foraging range of the little owl may therefore vary depending on factors such as food availability and season (Kooistra *et al.*, 2001). Consequently, these factors may influence the owl’s diet. Esselink *et al.* (1995) studied the dietary fluctuations of the barn owl (*Tyto alba*). It was found that the barn owl goes through regular cycles of great abundance of food and great scarcity of food, depending on the density of its prey items. Vole population densities oscillate, with a period of about three or four years between very high (climax) and low (crash). The proportion of voles in the barn owl’s diet reflects the vole population density. Consequently, the diet fluctuates strongly among years, among seasons, and among regions. During climax years, the barn owl diet may consist of 70 to 100% voles. In crash years, the main source of food is the Common shrew (*Sorex araneus*), which has about half the vole’s body mass.

Esselink *et al.* (1995) found as well that this dietary fluctuation has an important impact on the transfer of heavy metals to barn owls. The cadmium and lead concentrations in kidneys and liver are orders of magnitude higher in shrews than in voles ((Ma, 1989; Ma *et al.*, 1991). The very large difference in organ metal loads between voles and shrews reflects the difference in their average daily intake of cadmium and lead. Voles, being herbivores, feed mainly on grasses that barely accumulate cadmium and lead. Shrews, being carnivores, feed mainly on earthworms, insects and their larvae, and spiders. Earthworms, the main food item of shrews, accumulate vast amounts of cadmium and lead (Denneman, 1990; Ma *et al.*, 1991). Another important fact is that barn owls need to catch at least two shrews to get the amount of food comparable to a vole. Clearly, a change in diet due to the variation in vole densities between seasons and between years must have a major impact on the intake of heavy metals in barn owls (Esselink *et al.*, 1995).

3.1.2 Habitat

The little owl is generally attracted by hollow trees, such as cropped willows and old orchards. These are characteristic floodplain trees. The main rivers in The Netherlands, the Rhine and the Meuse both have large expanses of floodplains. In general, these floodplains are considered to have a high potential value with respect to nature development and conservation; partly because of their intrinsic values, but also as corridors between nature areas along the river. However, in the 1960s and 1970s sediments were deposited in the floodplains, which were highly contaminated with organochlorines and heavy metals. Like many European rivers, the Rhine and Meuse have been used as an open sewage system for the last few centuries. Investigations during the last 15 years have revealed the presence of strongly polluted sediments throughout the Dutch river floodplains. The pollution mainly consists of heavy metals (e.g., zinc, cadmium, and lead) and organic contaminants (e.g., poly-aromatic hydrocarbons (PAHs) and polychlorinated biphenyls (PCBs) (Kooistra *et al.*, 2001). Amounts and patterns of contaminants stored in the soil are closely related to the sedimentation process (Middelkoop & Asselman, 1998). The variability of diffuse soil contamination in river floodplains is high: low pollutant concentrations can be found only a short distance from sites with relatively high contamination. In such heterogeneously contaminated areas, mobile terrestrial organisms are not chronically exposed to one level of contamination as a result of the spatial variability of soil contamination (Kooistra *et al.*, 2001; Marinussen & vanderZee, 1996). Thus, for a realistic risk characterization, spatial aspects of exposure have to be taken into account (Kooistra *et al.*, 2001; Marinussen & vanderZee, 1996)).

3.1.3 Contaminants

Cadmium (Cd) is a toxic, nonessential metal that can occur in elevated environmental concentrations as a result of anthropogenic activities such as the smelting of metals (particularly lead and zinc), mining, sewage disposal, and the application of fertilizers. Cadmium is a by-product of zinc and lead refining operations and has been used in the electroplating of metals and the manufacture of alkali storage batteries. As a result, cadmium has accumulated in the environment and the primary route of (human) exposure to cadmium is by ingestion (Lehman & Klaassen, 1986). It is readily transferred through the food chain and accumulated by small mammals (Walker *et al.*, 2002). Cadmium (and lead) exposure in raptors is due to the ingestion of prey that contained high tissue-concentrations (GarciaFernandez *et al.*, 1996)
The suppression of its immune system by cadmium could make a host prone to infectious diseases (Esselink *et al.*, 1995). The critical organs (the organs that first attain their critical concentration of the metal, above which organ toxicity occurs) for cadmium are the kidneys and liver. Metallothionein, a metal-binding protein of liver and kidney, preferentially binds cadmium and zinc, and possibly other heavy metals (Esselink *et al.*, 1995; Vallee & Ulmer, 1972). On cadmium-contaminated sites, approximately 80% of the total cadmium body burden of small mammals is located in their liver and kidneys (Walker *et al.*, 2002). A physiological effect of cadmium may be kidney failure (Nicholson *et al.* 1983).

3.2 Model framework

The model that was created during this research has been built using the programming language "Smalltalk" (CincomSystems, 1999), an object-oriented language. The model uses landscape files of 50x50 grid cells, with each grid cell representing 10x10 metres. The model requires input files for both the cadmium contamination in the soil (in mg Cd/kg DW) and habitat type, where habitat is directly linked to a food chain.

For the little owl, the following food web has been used:

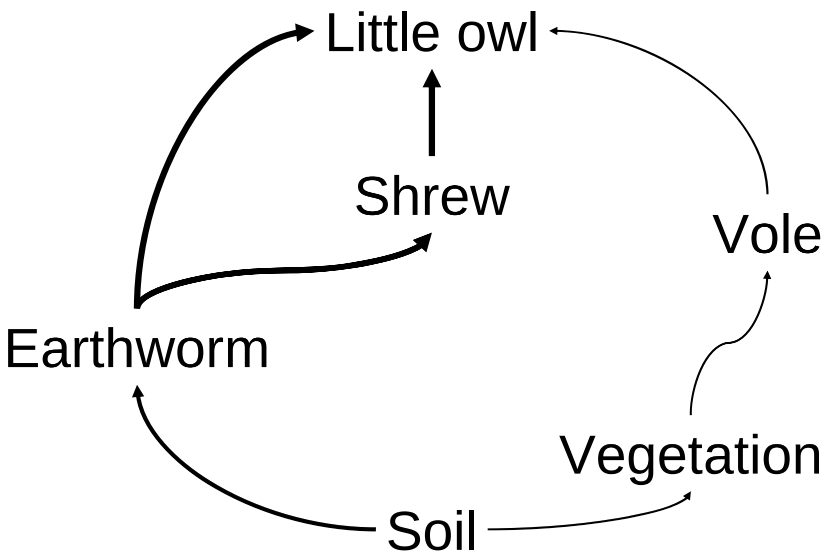


Figure 3.1: Food web used for the little owl (after: (Kooistra et al., 2001; Van den Brink et al., 2003))

Three simple food chains have been selected that go with different habitats:
worm habitat (w_habitat; grass): soil – worm – owl
vole habitat (v_habitat; grass): soil – vegetation – vole – owl
shrew habitat (s_habitat; shrubs): soil – worm – shrew – owl

Little owls are thought to take up a large proportion of their contamination via worms and shrews (red arrows in food web). For their food supply however, worms and voles are considered to be important (bold arrows in food web) (Van den Brink *et al.*, 2003). The latter species provide most energy to the owls; and the owl's diet is based on energetic choices.

The food chains form the connection between the contamination in the soil and the habitats in the landscape, as schematized in Figure 3.2.

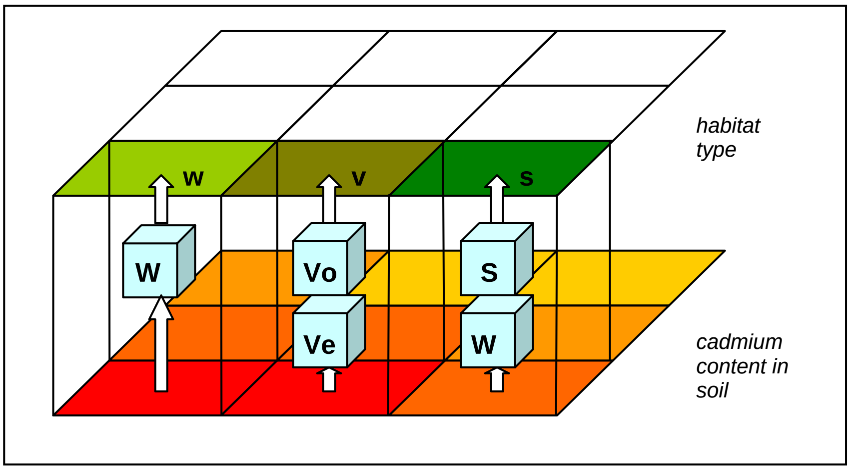


Figure 3.2: Schematized representation of the model framework (w, v, and s: habitat types, W: worm, Ve: vegetation, Vo: vole, S: shrew)

In the model, little owls forage daily on prey items within a home range of 11x11 grid cells and consume from every cell. This means, that a little owl can encounter different prey species and a variation in soil contamination, transmitted by the prey items. Furthermore, the model created in this study is a grid cell-based model, which means that all responses of daily prey digestion and cadmium uptake are attributed to grid cells.

The amount of available prey per cell follows from the prey density in the cell, which is different between prey types but constant for every prey type, through a functional response. The relationships between predators and variations in prey density have been the subject of many studies. Solomon (1949) suggested that these relationships were of two types, numerical and functional. The numerical response is the relationship between the numbers of predators and the numbers of their prey, whereas the functional response describes how the prey capture rate varies with prey abundance (Andersson & Erlinge, 1977). Under a numerical response, the predator adapts its breeding effort or its numbers to the numbers of the prey, through differential birth rates or emigration (usually without time lags). The functional response is determined by other life history traits of the predator, or its foraging or social behaviours (Andersson & Erlinge, 1977; Salamolard *et al.*, 2000). The functional response of a predator measures the prey capture rate as a function of prey abundance (Holling, 1959; Solomon, 1949), and explains variations in the proportion of prey in the predator's diet and in the number of prey items consumed by a predator at different prey densities (Korpimaki *et al.*, 1994).

Empirical and experimental studies have revealed that three types of functional response exist, according to the nature of the relationship between the predation rate and prey density (Holling, 1959): linear (Type I), convex (Type II), and concave or sigmoid (Type III). Studies of invertebrates have shown that predators that can switch to alternative prey are more likely to produce sigmoid functional responses; this has also been shown in vertebrates. Functional response curves of avian and mammalian predators are usually convex, although linear responses have sometimes been documented (Salamolard *et al.*, 2000).

Salamolard *et al.* (2000) found that raptors usually show a type II functional response to increases in their preferred prey. Vole biomass in pellets was closely related to vole abundance estimated by trapping. A type II functional response was detected, with satiation at high prey density (Salamolard *et al.*, 2000). Jedrzejewski *et al.* (1996) investigated Tawny owls (*Strix aluco*) on their dietary responses, and found that the functional response of these owls to autumn density of rodents was of Type II (logarithmic). No functional response of Tawny owls to shrew numbers was observed.

The findings of Jedrzejewski *et al.* (1996) have been used for this model. Their resulting *prey densities* (N/ha) and *prey items removed* (N/ha/season) have been converted to an expression for the functional response of little owls (FR_v) on vole density ($dens_v$) (see also Annex A for equations used in the model):

$$FR_v = \frac{280 \cdot dens_v}{0.02 + dens_v} \qquad \textit{(g FW vole/day)}$$

Because owls consume fewer shrews during their lifetime, the functional response of little owls (FR_s) on shrew density ($dens_s$) has been adapted in a way that the amount of shrew eaten per day is half-maximum at an increased prey density:

$$FR_s = \frac{280 \cdot dens_s}{0.06 + dens_s} \qquad \textit{(g FW shrew/day)}$$

A functional response of little owls (FR_w) on worm density ($dens_w$) has not been found in literature, most likely because worms as a prey items for raptors have not been studied thoroughly before. The functional response used in the model is based on expert judgement (Van den Brink, 2005):

$$FR_w = \min(600, 0.5 \cdot dens_w) \quad \textit{(g FW worm/day)}$$

Figure 3.3 combines the above functional responses:

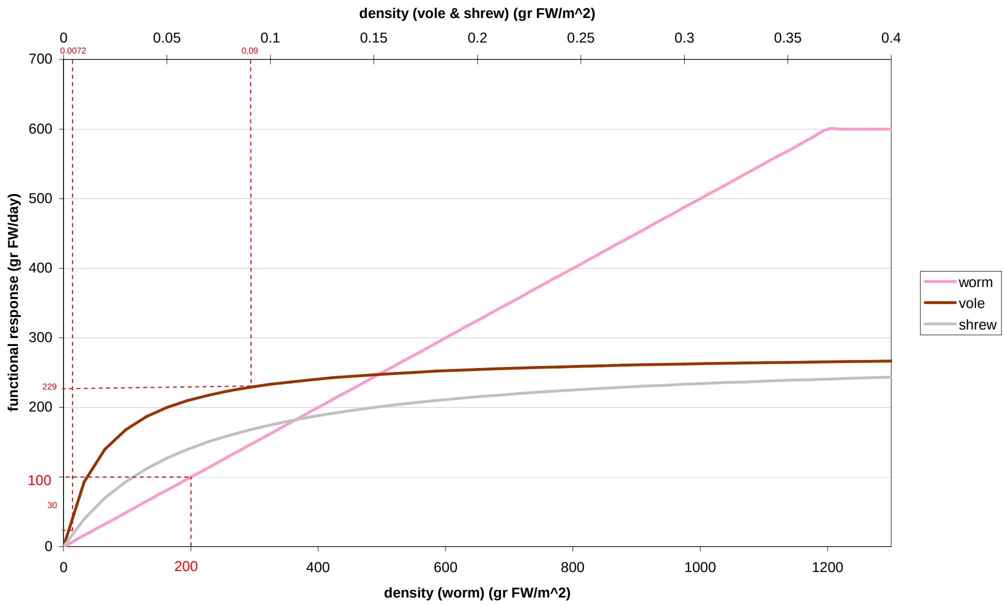


Figure 3.3: Functional responses for worms, voles, and shrews used in the model. Used densities are indicated in the graph.

3.3 Modelling contamination into prey items

The ecological risk of polluted soil to the little owl is strongly associated with the extent of the bioavailability of the contamination in its preys. Therefore, the transfer of polluting cadmium from the soil to all prey items has been included in the model.

The availability of heavy metals for uptake by earthworms depends on the concentration of free metal ions present in the dissolved soil solution phase. Typical relevant site-related variables determining the uptake would include soil pH, clay and organic matter fractions, cationic exchange capacity, and certain macro-element concentrations (Ma, 2004). A straightforward and accurate regression expression for the relationship between the soil cadmium concentration ([Cd_{soil}], dw) and the total body burden of cadmium in worms ([Cd_w]), which has been used in the model, is expressed by Corp & Morgan (1991) (see also Annex A for equations used in the model):

$$\log[Cd_w] = 1.28 - 0.56 \cdot \log[OM] - 0.23 \cdot \log[pH] + 0.324 \cdot \log[Cd_{soil}] \quad \textit{(mg/kg FW)}$$

where [OM] is the organic matter fraction of the soil.

For the mice species which both comprise intermediate steps in the food chains, an expression after Gorree *et al.* (1995) has been used. The concentrations in the food of the mice serve as inputs. Cadmium enters the body via the food and is excreted through faeces. On its way, a fraction of the cadmium in the food is taken up by the intestines of the mice. The amount of cadmium that is taken up in the body depends on the food consumption and the acidity of the intestinal canal. Over time, the mice's body burden is partly excreted, depending on the internal cadmium concentration.

Vegetation forms the main food item of voles. The expression for the vole's body burden of cadmium ($[Cd_v]$) that has been used in the model is:

$$[Cd_v] = \frac{\frac{food_v \cdot [Cd_{veg}] \cdot c\_up}{c\_out} \cdot \left(1 - e^{-c\_out \cdot age_v}\right)}{weight_v} \qquad \textit{(mg/kg FW vole)}$$

with the daily prey consumption (digestion) for voles ($food_v$) (Kooistra *et al.*, 2001; Peacock *et al.*, 2004):

$$food_v = 0.5 \cdot \left(\frac{weight_v}{1000}\right) \qquad \textit{(kg FW/day)}$$

and the cadmium concentration in vegetation ($[Cd_{veg}]$) (Römkens *et al.*, 2005; van der Pol *et al.*, 2004):

$$\log[Cd_{veg}] = (0.17 - 0.28 \cdot \log[OM] - 0.12 \cdot pH + 0.49 \cdot \log[Cd_{soil}]) / 2.5 \qquad \textit{(mg/kg FW veg)}$$

where *c_up* is the fraction of the cadmium in the food that is taken up by the intestines, *c_out* is the excretion rate, age_v is the age of voles in days (averaged), and $weight_v$ is the total body weight of voles (averaged).

For shrews, in the model the main food item is comprised of worms. Therefore, the expression above for the total body burden of cadmium in worms has been used in the shrew's body burden formula:

$$[Cd_s] = \frac{\frac{food_s \cdot [Cd_w] \cdot c\_up}{c\_out} \cdot \left(1 - e^{-c\_out \cdot age_s}\right)}{weight_s} \qquad \textit{(mg/kg FW shrew)}$$

with the daily prey consumption (digestion) for shrews ($food_s$) given by Churchfield (1990):

$$food_s = \left(\frac{weight_s}{1000}\right) \qquad \textit{(kg FW/day)}$$

where age_s is the age of shrews (averaged), and $weight_s$ is the total body weight of shrews (averaged).

3.4 Modelling contamination into predators

The above expressions are all applicable to the separate cells, because all low-level species are assumed to reside for their entire lives within the borders of a grid cell and hence face only one specific soil concentration. At these levels, population dynamics are assumed to be in equilibrium. Since the owls in the model explore several cells within their home ranges, different prey species and a variation in soil contamination, transmitted by the prey items can be encountered. This implies that the cadmium uptake by owls and the consequential contamination risk can not be represented by one simple expression, but a combination instead, depending on the foraging behaviour of owls within their home ranges.

3.4.1 Foraging behaviour and movement

The model includes a different food fraction "signature" and bioaccumulation function assigned to different habitats, reflecting changes in food and prey availability for the same organism in differing habitats. Next to this, there are two more basic issues associated with modelling the movement of an individual organism: the cell from which movement commences and whether the movement is habitat dependent (Hope, 2000).

The cell in which movement begins can be fixed or may vary. Movement initiated from a fixed cell and terminated in the same cell is called central place foraging. Central place foragers execute foraging trips to remote locations but consistently return to a central place (Ropert-Coudert *et al.*, 2004). Hence, the involved species determine the size of their foraging area (i.e. home range), the area within the habitat that provides the population with food (Linkov *et al.*, 2002), as this is characterized by a dispersion coefficient (Linkov *et al.*, 2002; von Stackelberg *et al.*, 2002). In the current model, little owls are assumed to be central place foragers (Kooistra *et al.*, 2001) that forage only up to a certain distance away from their home base (nest, etc.).

Furthermore, a lagging procedure is used. Lagging assumes an equal likelihood that each organism may centre its foraging range at any point in the area (Clifford *et al.*, 1995). Hence, home ranges shift like "moving windows" over a landscape map, estimating risks to organisms that potentially inhabit an area, either at present or in the future. It is assumed that an organism makes optimal use of its foraging area, i.e., the organism moves randomly around in its foraging area without avoiding high pollution levels.

The spatial use of a moving individual can moreover be modelled as habitat dependent (Hope, 2000). Spatial usage (or utilization) is defined as the proportion of time per unit area spent by an animal or group of animals in the neighbourhood of a point in space (Matthiopoulos, 2003). The average residence time per square meter or cell (Δt) can be calculated by dividing the total residence time in the living area (T) by the size of the (foraging) area (A):

$$\Delta t = \frac{T}{A} \qquad \textit{(day)}$$

Hence, as the size of the foraging area increases, the exposure time to a particular level of pollution becomes smaller (Marinussen & vanderZee, 1996).

In most cases, the distribution of usage by an individual of a population will be heterogeneous and this can be partly a reflection of the spatial distribution of the resources required by the animal(s) (Matthiopoulos, 2003). Conversely, if the spatial usage is habitat independent the residence time per square meter or cell will be similar for every part of the (foraging) area.

3.4.2 Foraging strategies

In the current model, little owls move within a home range of 11x11 grid cells (i.e. the species exhibit foraging behaviour). This is modelled by means of simulations. Within the model structure, 4 different spatial exploitation patterns or strategies have been included, each defining the prey consumption of a little owl within its home range. Factors determining these spatial exploitation patterns consider distance from the central place (cell) of the home range and the spatial distribution of the resources required by the animal. The foraging strategies have been defined as:

Uniform: The prey intake (consumption) is non-specific over time; hence owls spend an equal amount of time in each cell within the home range. The exposure time to a particular level of pollution, transmitted by the prey items, is similar for every home range cell. Thus, the equation for the residence time by Marinussen & vanderZee (1996) is applicable:

$$\Delta t_{cell} = \frac{T}{A} \qquad \textit{(day)}$$

where T is the foraging time (1 day) and A is the number of cells within the home range (121 grid cells).

Distance dependent: The prey intake is dependent on the distance between each cell within the home range and the central place (centre cell) of the home range. The owls explore the cells close to the centre cell (e.g. the nest) most intensively. The residence time per cell decreases with the distance to the centre cell, according to the function:

$$\Delta t_{cell} = \frac{\left(e^{-\lambda \cdot D}\right)_{cell}}{\sum^{foraging\_area}\left(e^{-\lambda \cdot D}\right)_{cell}} \qquad \textit{(day)}$$

where D is the distance to the centre cell and λ is the distance parameter (fixed at 0.25). Figure 3.4 shows the effect of different λ-values on the relationship between the distance to the centre cell and the residence time.

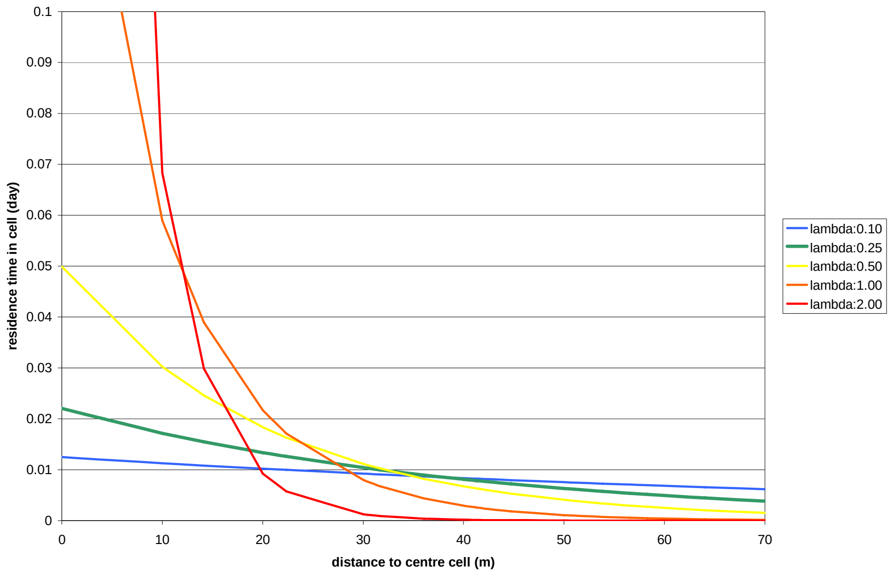


Figure 3.4: Relationship between the distance to the centre cell and the residence time, and the effects of different λ-values. In the model, a fixed λ-value of 0.25 is used.

Availability dependent: The prey intake is dependent on the availability of the resources within the cells of the home range (in grams). The residence time per cell is proportional to the fraction of the total prey availability in the home range, present in the cell. Hence, more time is spent in cells with large prey availability, and more pollution is taken up from these cells. The equation for the residence time becomes:

$$\Delta t_{cell} = \frac{\left(FR_{prey}\right)_{cell}}{\sum^{foraging\_area}\left(FR_{prey}\right)_{cell}} \qquad (day)$$

with FR_{prey} is the available food resources per cell.

Availability and distance dependent: The prey intake is dependent on the availability of the resources within the cells of the home range (in grams) and on the distance between each cell within the home range and the centre cell. The equation used for the residence time is:

$$\Delta t_{cell} = \frac{\left(FR_{prey} \cdot e^{-\lambda \cdot D}\right)_{cell}}{\sum^{foraging\_area}\left(FR_{prey} \cdot e^{-\lambda \cdot D}\right)_{cell}} \qquad (day)$$

For the daily prey intake, the following expression has been attained:

$$food_{prey} = \sum^{foraging\_area} \left(\Delta t \cdot FR_{prey} \right)_{cell} \qquad \text{(kg FW/day)}$$

Because the model created in this study is a grid cell-based model and all responses should be attributed to grid cells, the daily prey intake has been attributed to the centre cell of that home range.
By performing a lagging procedure as described above, the pollution risk of all cells within a landscape can be assessed, assuming equal likelihood that each organism may centre its foraging range at any point in the area. Therefore, the daily prey intake in each cell reflects the prey intake of an owl foraging within a certain home range during one day, with the cell being the centre cell of the home range.

3.4.3 Contaminant uptake by predators

Cadmium pollution that enters little owls via their food is partly taken up and partly excreted over time. Owls return a part of the voles and shrews ingested, i.e., the hair and the bones, in the form of pellets. About 85% of mice consumed is assumed to disappear during digestion, the rest is excreted by pellets (Van den Brink, 2005). Hence,

$$food_v = \left(\Delta t_{cell} \cdot FR_{vole} \right) \cdot 0.85$$

and:

$$food_s = \left(\Delta t_{cell} \cdot FR_{shrew} \right) \cdot 0.85$$

From the returned part, no cadmium is taken up. The fraction of the consumed preys from which the cadmium is taken up (i.e. the digested fraction, in grams) has been used for further risk calculation. Little owls use this fraction for their energy supply, which approximately diverges from 75 to 150 grams per day (Kooistra *et al.*, 2001; Van den Brink, 2005).

For the little owls in the model that encompass the top-level in the food chains, the expression for the uptake of cadmium ($[Cd_o]$) has been based on the formula by Gorree *et al.* (1995). The concentrations in the digested fraction of the consumed preys of the owls ($[Cd_{prey}]$) serve as inputs:

$$[Cd_o] = \frac{\frac{\overline{u}_o}{c\_out} \cdot \left(1 - e^{-c\_out \cdot age_o}\right)}{weight_o} \qquad \text{(mg/kg FW owl)}$$

with:

$$\bar{u}_o = average(\sum^{foraging\_area}(food_{prey} \cdot c\_up \cdot [Cd_{prey}])_{cell}) \qquad (mg/day)$$

where ($\bar{u}_o$) is the mean daily cadmium uptake, $food_{prey}$ is the daily digested resource, *c_up* is the fraction of the cadmium in the food that is taken up by the intestines, *c_out* is the excretion rate, age_o is the age of owls (averaged), and $weight_o$ is the total body weight of owls (averaged). For the cadmium uptake within one home range, the daily uptake $food_{prey} \cdot c\_up \cdot [Cd_{prey}]$ has been summed over all cells in the home range, and hence over the total time the owls spend in the home range. Subsequently, the daily uptake level has been attributed to the centre cell of the home range. When an owl spends its whole life in one home range, $food_{prey} \cdot c\_up \cdot [Cd_{prey}]$ stands as well for the mean daily uptake for the owl's lifespan and can be used as such in the owl's concentration formula. Otherwise, the daily uptake has to be either averaged over all foraging areas the owl encounters during its lifespan, or the daily uptake should be modelled numerically. In this study the daily uptake forms the ultimate risk measure.

Pascoe *et al.* (1996) found that several bird species may face no adverse effects of the cadmium in their bodies up to a value of 0.8 mg/kg-day. Recalculation of this value to little owls with an average weight of 0.175 kg and an excretion rate of 0.005 day^{-1}, results in an uptake rate of $7 \cdot 10^{-4}$ mg/day. This rate was assembled as the *lowest observed adverse effect level* (LOAEL). When all daily uptake levels in the landscape are compared to this LOAEL, the fraction of cells exceeding the LOAEL can be calculated.

3.5 Output and analysis

3.5.1 Model responses

As all responses are attributed to grid cells, the outputs of the model consist of landscape files or maps of 50x50 grid cells. The output maps include files of daily prey digestion (actually amount of prey taken) and cadmium uptake. Obtained values for daily prey digestion serve as verification and as regulation for the cadmium uptake. The fractions of prey digestion and cadmium uptake, attributed to eating either worms, voles or shrews have been derived by the model. Furthermore, from the daily cadmium uptake maps, the fraction of cells exceeding the LOAEL has been calculated by the model. Because all responses are attributed to the centre cell of the grid cells, the outer 5 rows and columns of the maps are empty, these cells not being centre cells of any home range. Therefore, the output maps contain 1600 cells, representing daily prey digestion and cadmium uptake.

3.5.2 Analyses

After building the model, several analyses were carried out to investigate the influences of differences in spatial patterns of exploitation and the consequences of a change or shift in habitat types.

First of all, the body concentrations of cadmium for the different prey items of the little owl have been plotted against the soil concentration, being an indirect resource. In this way, the transfer of soil contamination through the prey types could be compared.

The effects of changes in the ratios of habitat types, without considering the position of the habitats have been examined. For that purpose, the model has been run with randomly created habitat input files for 66 possible habitat compositions. For all compositions, the habitat fractions differed with decimal steps:

Table 3.1: 66 possible habitat compositions used for the analyses (w_hab: worm habitat (%); v_hab: vole habitat (%); s_hab: shrew habitat (%).Note: w_hab+v_hab+s_hab=100%)

w_hab *(% of occurrence)* / **v_hab** *(% of occurrence)*	0	10	20	30	40	50	60	70	80	90	100	
0	100	90	80	70	60	50	40	30	20	10	0	
10	90	80	70	60	50	40	30	20	10	0	-	
20	80	70	60	50	40	30	20	10	0	-	-	
30	70	60	50	40	30	20	10	0	-	-	-	
40	60	50	40	30	20	10	0	-	-	-	-	
50	50	40	30	20	10	0	-	-	-	-	-	
60	40	30	20	10	0	-	-	-	-	-	-	
70	30	20	10	0	-	-	-	-	-	-	-	
80	20	10	0	-	-	-	-	-	-	-	-	
90	10	0	-	-	-	-	-	-	-	-	-	**s_hab**
100	0	-	-	-	-	-	-	-	-	-	-	*(% of occurrence)*

Each composition has been constructed 30 times randomly over the landscape in order to reduce the variance, and has hence been used as an input file. This procedure was repeated for the 4 different foraging strategies, so that in total 7920 runs have been executed. For all the runs, the input file for cadmium contamination in the soil (in mg Cd/kg DW) used has been the same:

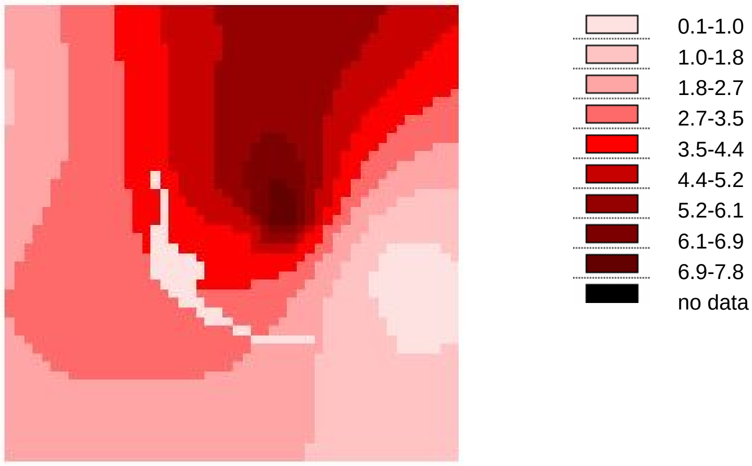


Figure 3.5: The input file for cadmium contamination in the soil (in mg Cd/kg DW; 50x50 grid cells, each grid cell representing 10x10 metres)

Responses in daily prey digestion, cadmium uptake, and the fraction exceeding the LOAEL have been evaluated for different habitat proportions, and compared by analyses of variance for the different foraging strategies:

Table 3.2: Modelling factors and responses

factor foraging strategy	factor w_hab%	factor v_hab%	factor s_hab%	response *(average& standard deviation over map)*	response *(average & standard deviation over map)*	response *(average over map)*
Uniform/				preyDigest	cdUptake	P(>LOAEL)
Availability-dep/						
Distance-dep/						
Availability&Distance-dep						

Two different habitat compositions (i.e. 0.1/0.8/0.1 and 0.4/0.2/0.4) have been highlighted to compare to Figure 3.1, considering contamination and food supply in the food web. The fractions of prey digestion and cadmium uptake, attributed to eating either worms, voles or shrews have been compared.

Consequences of shifting habitats within a site, while maintaining of the ratios of habitat types have been studied, using only the uniform foraging strategy. Therefore, the model has been run with two design landscapes with similar ratios of habitat types (i.e. 0.25/0.65/0.1), for which the habitats had been positioned parallel and perpendicular to the soil contamination pattern, respectively. The design landscapes have been turned 90° with respect to each other:

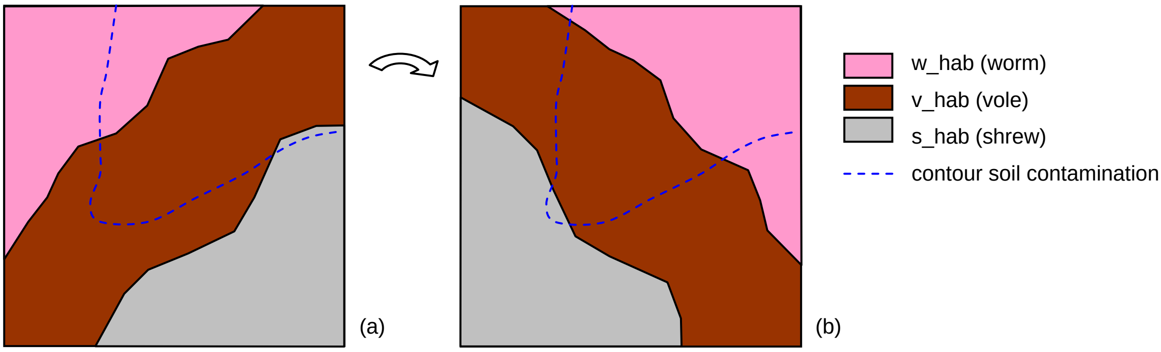


Figure 3.6: Schematized representation of landscapes parallel (a) and perpendicular (b) to soil contamination pattern

Due to the resulting difference in habitat configuration regarding the soil contamination, the output maps of the daily cadmium uptake differ spatially. This spatial variation has been analysed by variograms of the daily cadmium uptake maps. A variogram provides a measure of spatial correlation by describing how relations between sample data are related (correlated) with distance. In general, two closely neighbouring data are more likely to have similar values than two data farther apart. The variogram function, $\gamma(h)$, was originally defined by (Matheron, 1963) as half the average squared difference between points separated by a distance h. The variogram is calculated as:

$$\gamma(h) = \frac{1}{2|N(h)|} \sum_{N(h)} (z_i - z_j)^2$$

where $N(h)$ is the set of all pair wise Euclidean distances $i\text{-}j = h$, $|N(h)|$ is the number of distinct pairs in $N(h)$, and z_i and z_j are data values at spatial location i and j, respectively. Most variograms are defined through several parameters; namely, the nugget effect, sill, and range. These parameters are depicted on the generic variogram shown in Figure 3.7 and are defined as follows (Kaluzny *et al.*, 1998):

nugget effect: represents micro-scale variation or measurement error. It is estimated from the variogram as the value of $\gamma(h)$ for $h=0$
sill: the $\lim_{h\to\infty} \gamma(h)$ representing the variance of the random field
range: the distance (if any) at which data are no longer autocorrelated

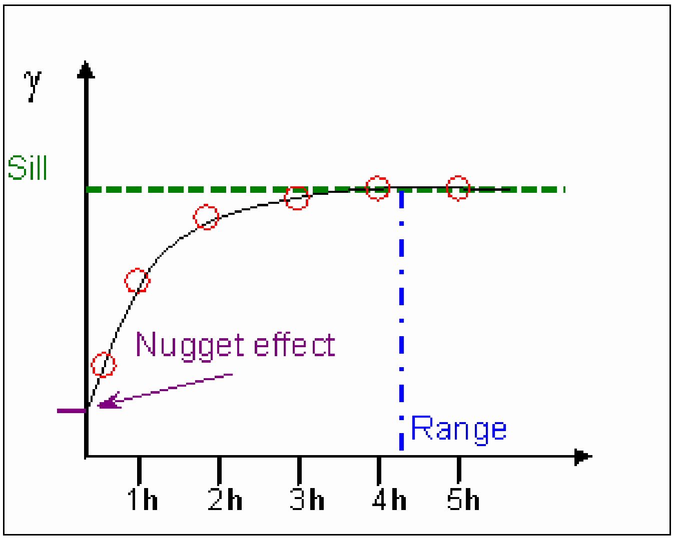


Figure 3.7: Generic variogram showing the sill, and range parameters along with a nugget effect (AI-GEOSTATS, 2005)

In reference to the variograms, it is assumed that the variance of the random field (e.g. a daily cadmium uptake map) evidently increases with the distribution of data around the mean value, as can be described by a histogram. Hence, when the variance is decreased by, for instance, a shifting of habitats within a site, the fraction exceeding the LOAEL diminishes consequently:

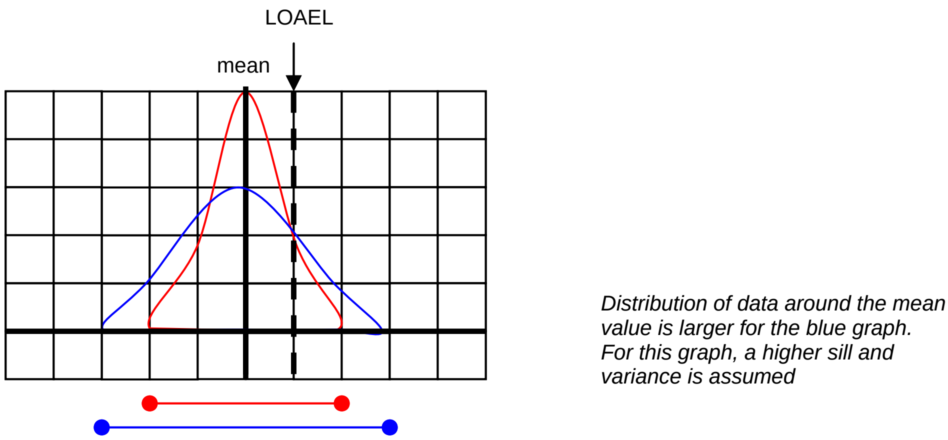


Figure 3.8: Decrease of risk, expressed by the fraction exceeding LOAEL, due to a decline of variance

Subsequently, histograms of the daily cadmium uptake and the fractions exceeding LOAEL have been compared. To examine this issue more explicitly, the spatial analysis has been performed with a designed soil contamination map as well. Hence, the habitats could be positioned exactly parallel and perpendicular to the soil contamination:

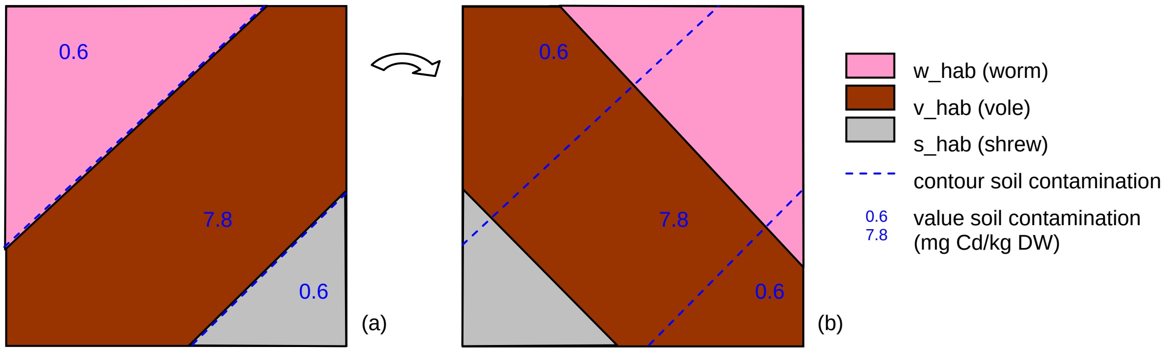


Figure 3.9: Schematized representation of landscapes parallel (a) and perpendicular (b) to designed soil contamination pattern

4 Results

4.1 Prey body concentrations and soil contamination

The body concentrations of cadmium for the different prey items of the little owl are plotted against the soil concentration in Figure 4.1. It is shown that the body concentrations of worms and shrews are about two orders of magnitude higher than the body concentrations of voles (exposed on right y-axis). However, the rate of increase in the body concentration of voles exceeds the ones for worms and shrews.

The large difference in body concentration between voles and shrews reflects the difference in their average daily intake of cadmium. Voles primarily feed on grasses that hardly accumulate cadmium. Shrews feed mainly on earthworms. Earthworms accumulate large amounts of cadmium, however their predators, shrews, hold less cadmium per kilogram of body mass.

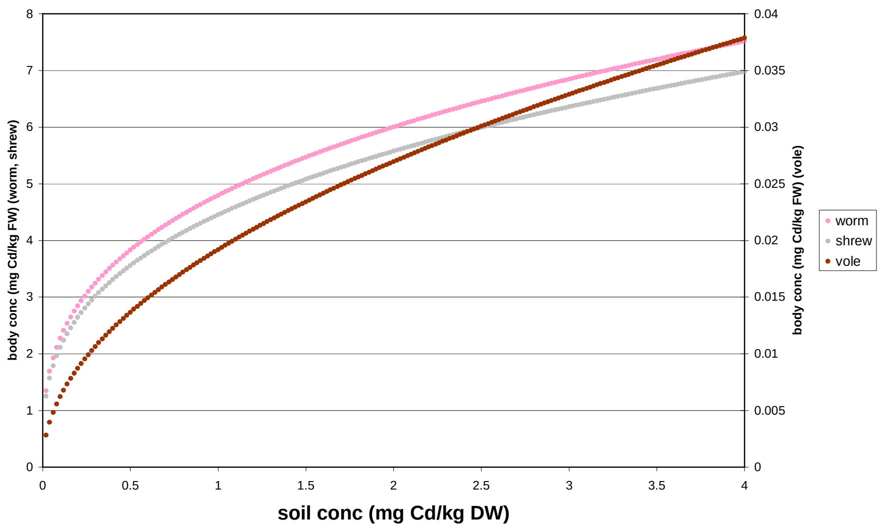


Figure 4.1: Body concentration of cadmium for the different prey items of the little owl plotted against the soil concentration

4.2 The effects of changes in the ratios of habitat types

4.2.1 Daily prey digestion

When the daily prey digestion, averaged over a map, is plotted against the fraction of s_habitat grid cells present, interesting graphs are obtained (Figures 4.2a to d). The coloured lines connect habitat configurations with the same proportions of worm habitat (w_habitat). The black dotted lines indicate some of the v_habitat-isolines, habitat configurations with the same proportions of vole habitat. The resulting shrew habitat (s_habitat) fractions are exposed on the x-axes. The digested fraction of the little owls' food, which is used for their energy supply, achieves approximately 100 grams. Much less consumption will lead to energy deficiency, while too much food is not likely to be consumed by the owls, which is represented by the increasingly grey areas in the graphs.

The figures below show the graphs for the uniform, distance dependent, availability dependent, and availability and distance dependent foraging strategies, respectively. The mean prey digestions for the 3 extreme habitat configurations (i.e. 1/0/0, 0/1/0, and 0/0/1) are naturally similar for the 4 strategies. The patterns of spatial exploitation do not have any influence on the prey digestion for these situations.

A landscape that consists solely of vole habitat, gives the highest mean prey digestion (c. 195 g/day), resulting from the high functional response (Figure 4.1). The lowest mean daily prey digestion is obtained from a landscape that consists solely of shrew habitat.

The graphs for the uniform and distance dependent foraging strategy show a large resemblance. The graph for the availability dependent foraging strategy seems different. The w_habitat-isolines decline exponentially in the direction of high s_habitat fractions. For the availability and distance dependent foraging strategy, the inclination of the isolines in the graph is less evident. Still, trends can be perceived from both the distance dependent and the availability dependent strategies.

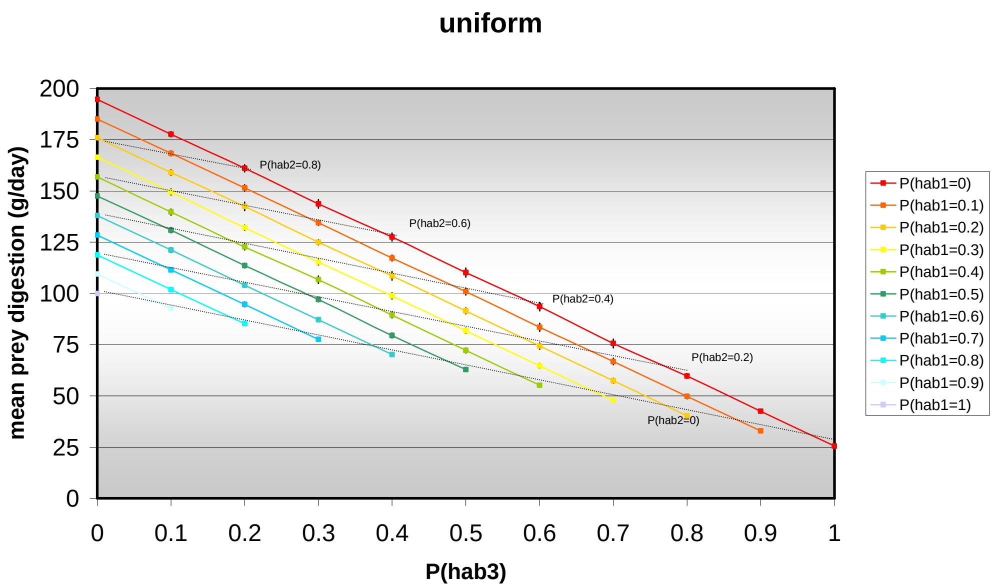


Figure 4.2a: The daily prey digestion, averaged per map, plotted against the fraction of s_habitat grid cells for the uniform foraging strategy (mean and SD). Dotted lines represent v_habitat-isolines.

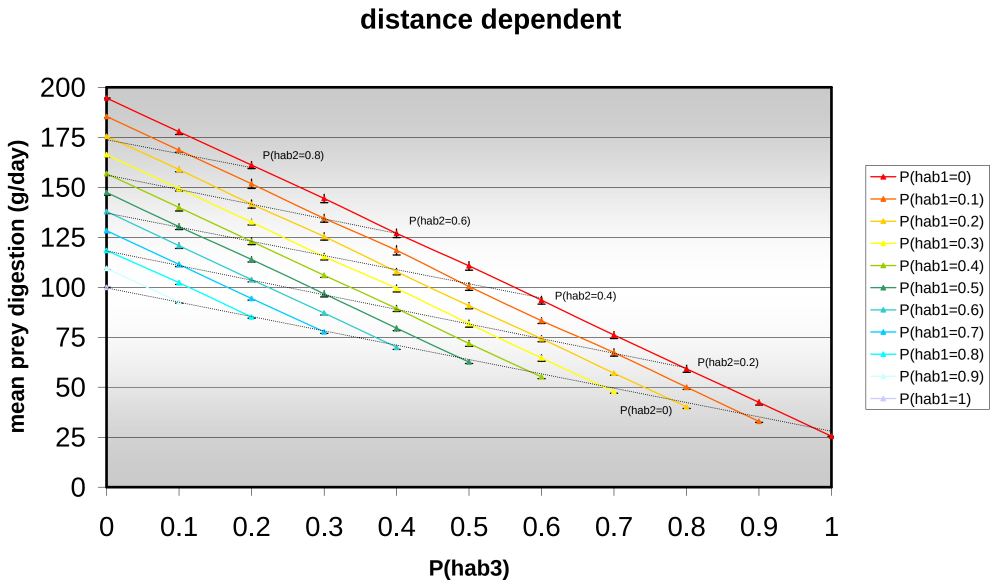


Figure 4.2b: The daily prey digestion, averaged per map, plotted against the fraction of s_habitat grid cells for the distance dependent foraging strategy (mean and SD). Dotted lines represent v_habitat-isolines.

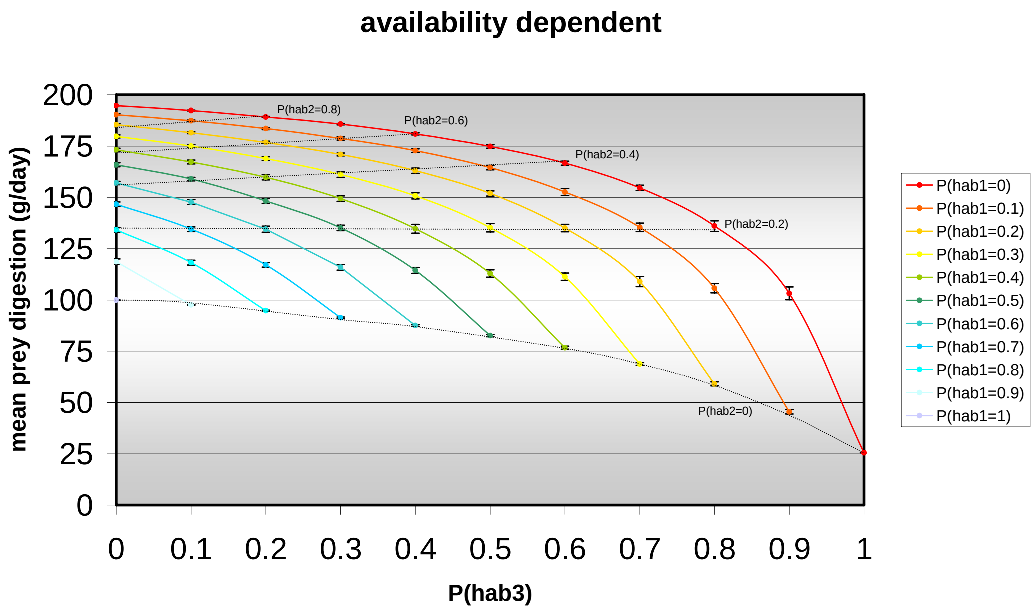


Figure 4.2c: The daily prey digestion, averaged per map, plotted against the fraction of s_habitat grid cells for the availability dependent foraging strategy (mean and SD). Dotted lines represent v_habitat-isolines.

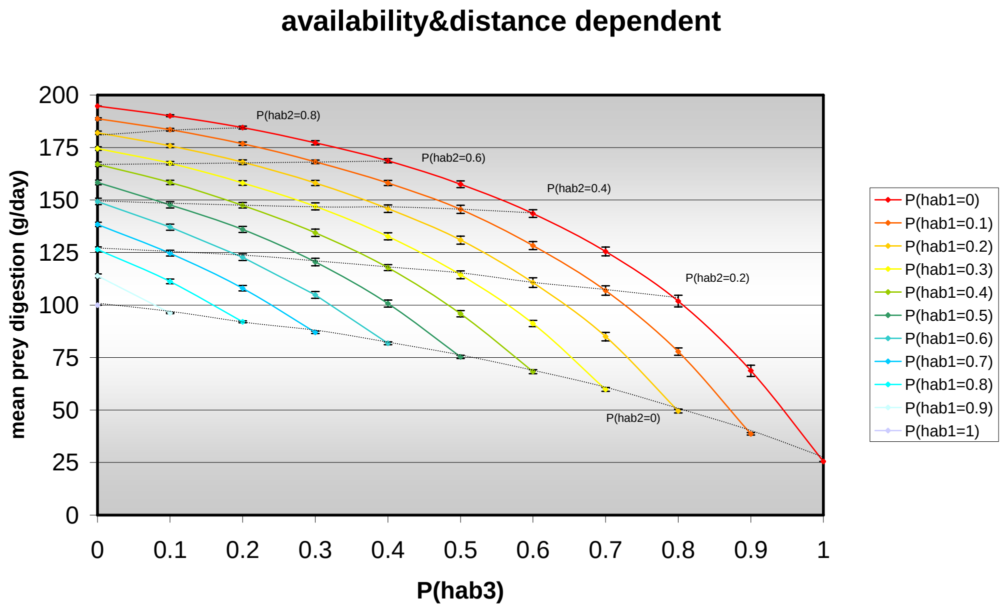
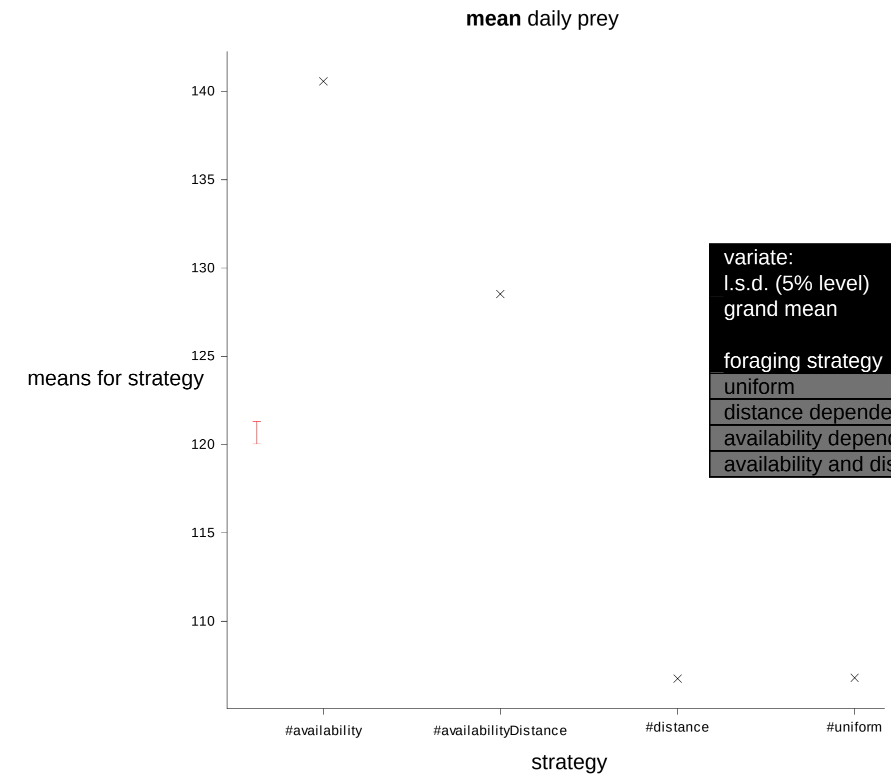


Figure 4.2d: The daily prey digestion, averaged per map, plotted against the fraction of s_habitat grid cells for the availability and distance dependent foraging strategy (mean and SD). Dotted lines represent v_habitat-isolines.

Besides the evaluation of the responses in daily prey digestion for different habitat proportions, the different foraging strategies have been compared by analyses of variance (Annex 2). The foraging strategies have been compared by the mean daily prey digestion and by the standard deviation of the mean. The different habitat proportions have not been considered explicitly, because all different compositions have been contributed evenly for all strategies (balanced within treatments).

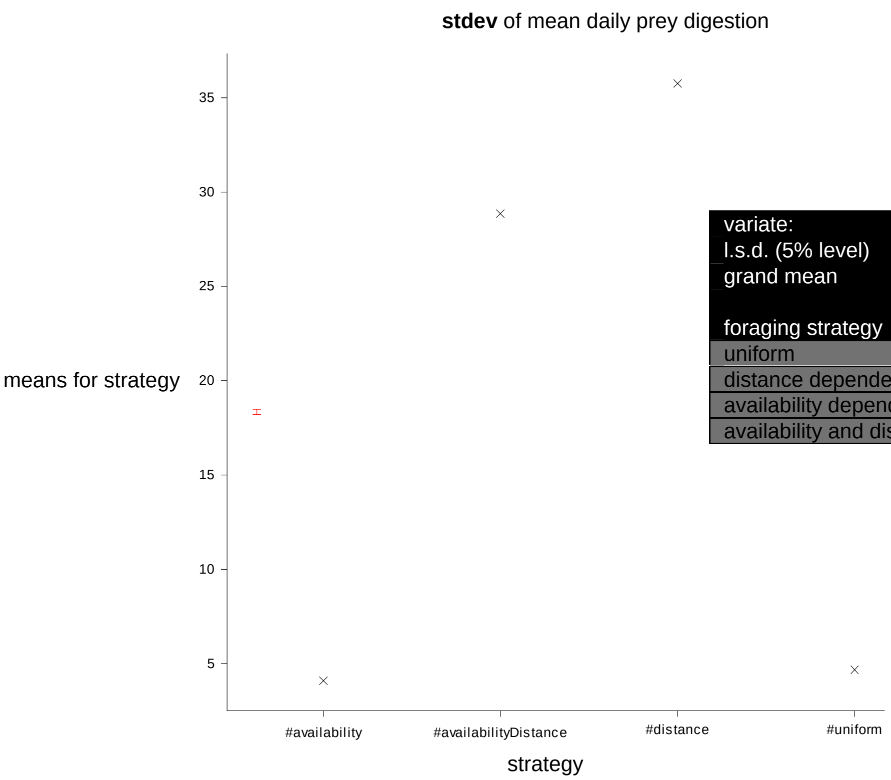
The plot of Figure 4.3 shows the position of the different foraging strategies regarding the mean daily prey digestion. The red error bar indicates the least significant difference (l.s.d.) of 2.45. According to this l.s.d., there is no significant difference between the uniform strategy and the distance dependent strategy, and these strategies can be considered as a group. Between this group and both the availability dependent strategy and the availability and distance dependent strategy there is a significant difference considering the mean daily prey digestion.

The position of the different foraging strategies regarding the standard deviation on the mean daily prey digestion is shown in Figure 4.4. The red error bar indicates the least significant difference (l.s.d.) of 0.5469. According to this l.s.d., there is a significant difference between all strategies considering the standard deviation on the mean daily prey digestion.



variate:	mean daily prey digestion
l.s.d. (5% level)	2.450
grand mean	120.67
foraging strategy	means for strategy[1]
uniform	106.81 (A)
distance dependent	106.75 (A)
availability dependent	140.57 (B)
availability and distance dependent	128.53 (B)

Figure 4.3: Analysis of variance on foraging strategies regarding the mean daily prey digestion (1: strategy with similar letter are not statistically different (ANOVA, a: 0.05)).



variate:	stdev daily prey digestion
l.s.d. (5% level)	0.5469
grand mean	18.346
foraging strategy	means for strategy[1]
uniform	4.681 (B)
distance dependent	35.757 (D)
availability dependent	4.094 (A)
availability and distance dependent	28.852 (C)

Figure 4.4: Analysis of variance on foraging strategies regarding the standard deviation on the mean daily prey digestion (1: strategy with similar letter are not statistically different (ANOVA, a: 0.05)).

4.2.2 Daily cadmium uptake

In Figure 4.5, the daily cadmium uptake, averaged over a map, is plotted for all runs and foraging strategies. The figure shows cadmium "fingerprints" of an area with a cadmium contamination in the soil similar to figure 3.5. The red line in the figure indicates the lowest observed adverse effect level (LOAEL). Variations in the shape of the fingerprints for the different foraging strategies are noticeable. The fingerprints for the uniform and distance dependent foraging strategy show a large resemblance. The fingerprint for the availability dependent foraging strategy appears to be different, while the availability and distance dependent strategy results in an intermediate fingerprint shape.

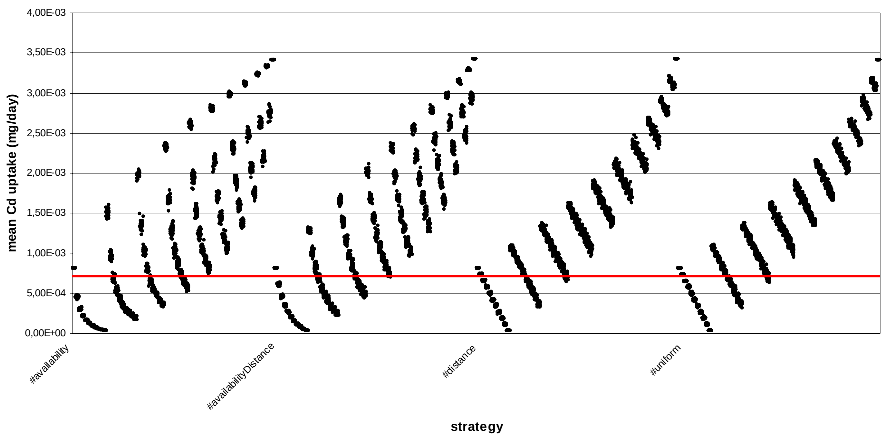


Figure 4.5: The daily cadmium uptake, averaged over a map, plotted for all runs and foraging strategies. The red line indicates the LOAEL ($7 \cdot 10^{-4}$ mg/day)

The same suggestion arises from Figures 4.6a to d, where the daily cadmium uptake, averaged over a map, is plotted against the fraction of s_habitat of the grid cells present. The figures show the graphs for the uniform, distance dependent, availability dependent, and availability and distance dependent foraging strategies, respectively. Conform figures 4.2a to d, the coloured lines connect habitat configurations with the same proportions of w_habitat. The black dotted lines indicate some of the v_habitat-isolines, habitat configurations with the same proportions of v_habitat. The resulting s_habitat fractions are exposed on the x-axes.

When the mean daily cadmium uptake is compared for the 3 extreme habitat configurations (i.e. 1/0/0, 0/1/0, and 0/0/1), a landscape that completely consists of vole habitat provides the lowest cadmium uptake. Although eating voles increases the energetic gain for the owls, the low body burdens of voles decrease the contamination risks for the owls considerably (see also Figure 4.1). However, the high body burdens of shrews do not generate extreme risks. The effects of the high body burdens of shrews are diminished by the low functional responses for shrews (see Figure 3.3). A landscape that is completely composed of worm habitat results in a relatively high cadmium uptake, due to the intermediate energetic gain and the relatively high body concentration for worms (Figure 4.1).

The graphs for the uniform and distance dependent foraging strategies show a large resemblance. The graph for the availability dependent foraging strategy seems different. The w_habitat-isolines increase exponentially in the direction of high s_habitat fractions. For the availability and distance dependent foraging strategy, the inclination of the isolines in the graph is less evident. Still, trends can be perceived from both the distance dependent and the availability dependent strategies.

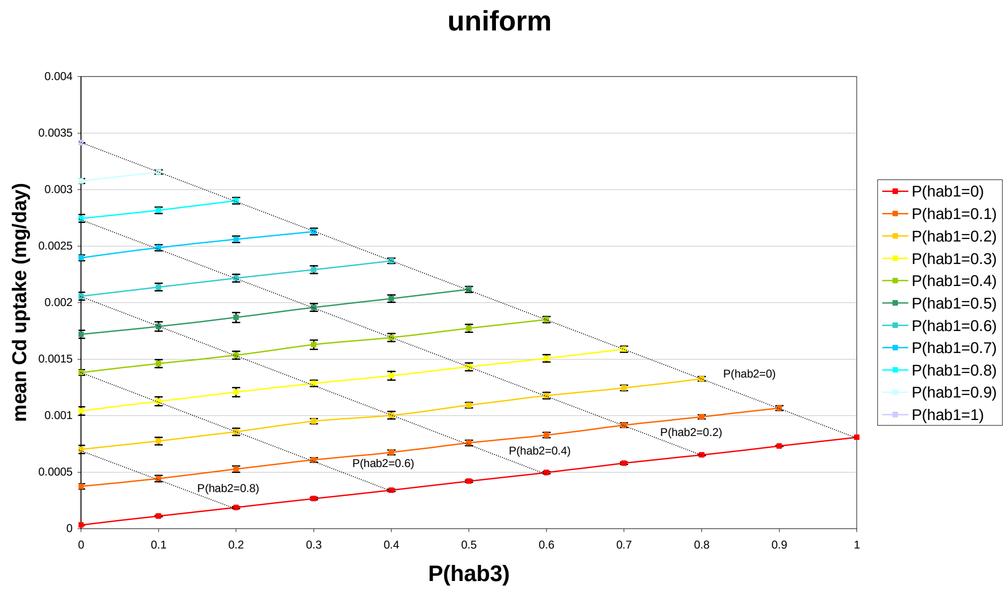


Figure 4.6a: The daily cadmium uptake, averaged per map, plotted against the fraction of s_habitat grid cells for the uniform foraging strategy (mean and SD). Dotted lines represent v_habitat-isolines.

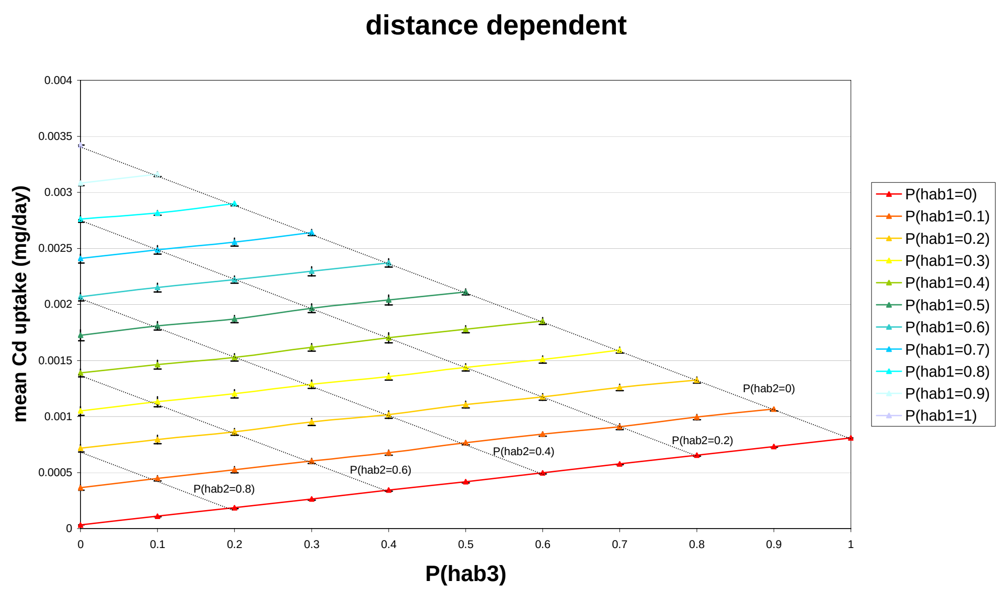


Figure 4.6b: The daily cadmium uptake, averaged per map, plotted against the fraction of s_habitat grid cells for the distance dependent foraging strategy (mean and SD). Dotted lines represent v_habitat-isolines.

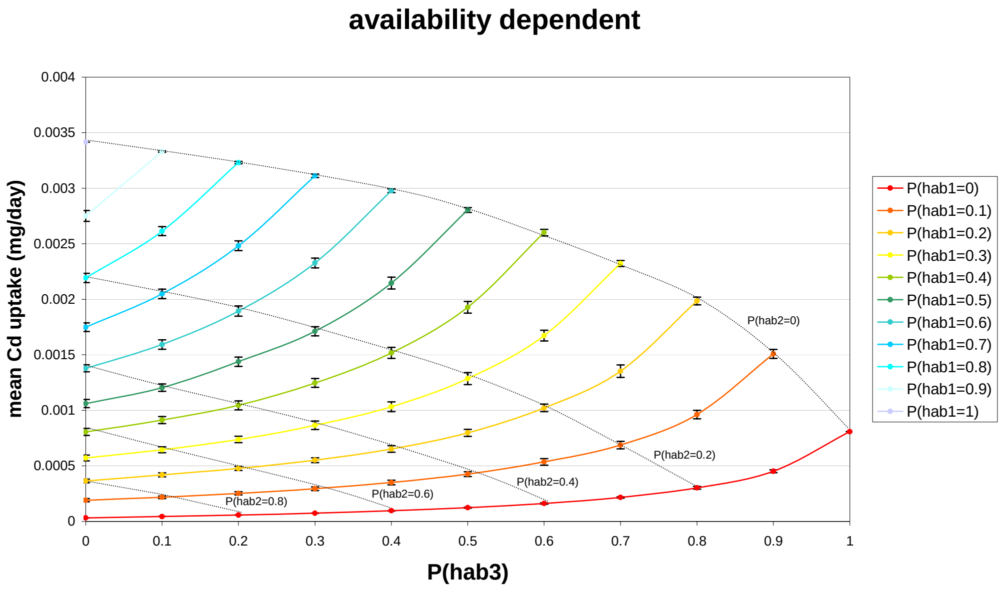


Figure 4.6c: The daily cadmium uptake, averaged per map, plotted against the fraction of s_habitat grid cells for the availability dependent foraging strategy (mean and SD). Dotted lines represent v_habitat-isolines.

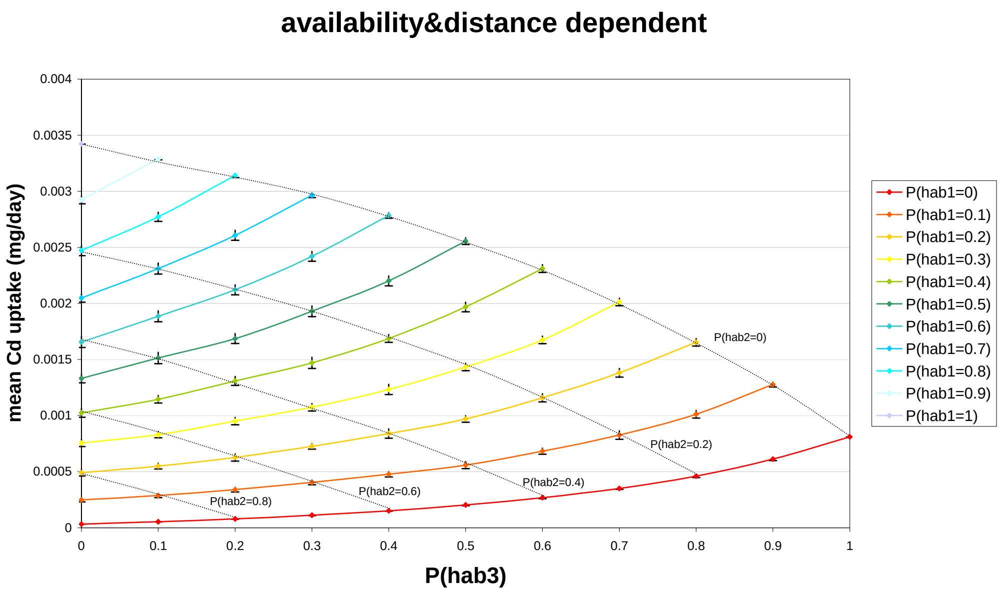


Figure 4.6d: The daily cadmium uptake, averaged per map, plotted against the fraction of s_habitat grid cells for the availability and distance dependent foraging strategy (mean and SD). Dotted lines represent v_habitat-isolines.

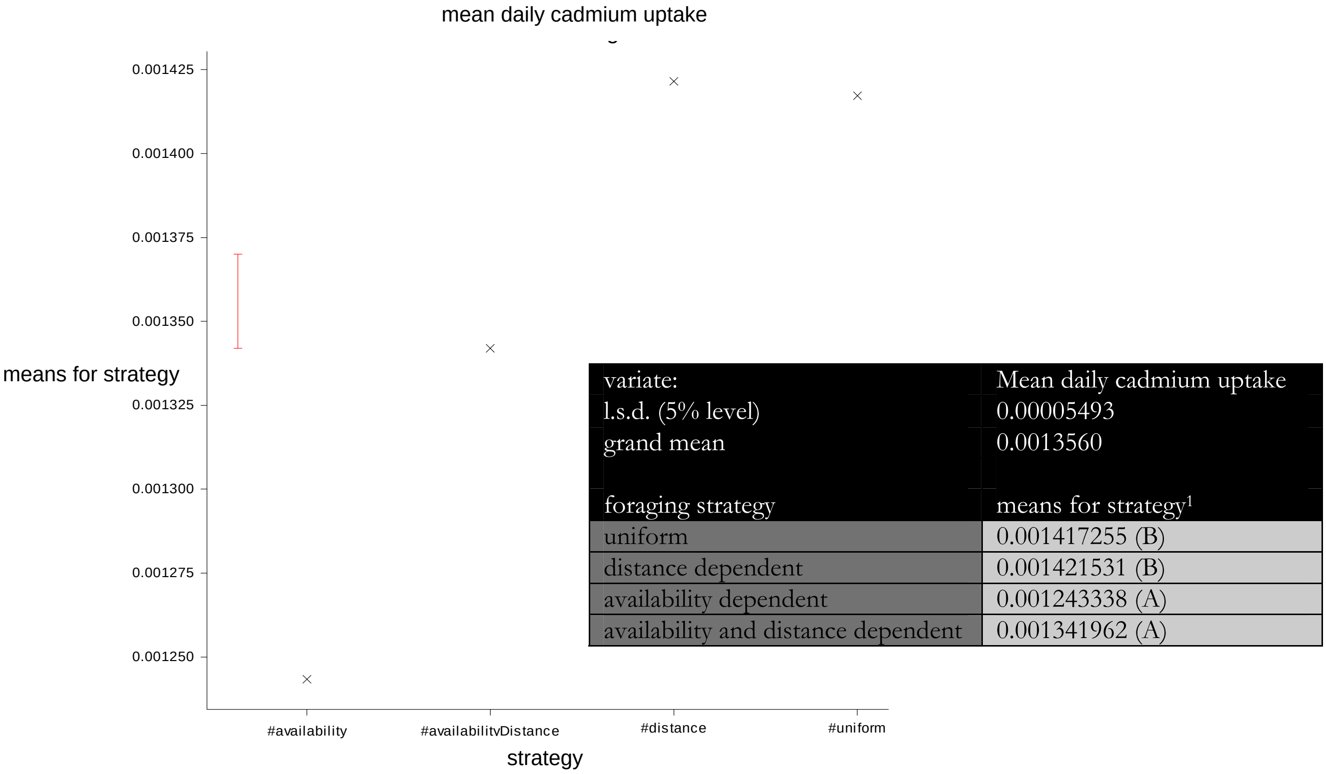
The general tendency of the effects of a change in habitat composition has been investigated by multiple linear regression analyses on the main daily cadmium uptake (see Annex C). For these analyses, one habitat type has been kept constant, while the variance accounted by the other habitat types has been estimated. Table 4.1 shows the results of the analyses, as obtained for all foraging strategies:

Table 4.1: Results of multiple linear regression analyses obtained for all foraging strategies (Annex 3):

replace … habitat	by … habitat	risk increase (+) / decrease (-)	t. probability (significance)
worm	vole	--	< 0.001
worm	shrew	-	< 0.001
vole	shrew	+	< 0.001

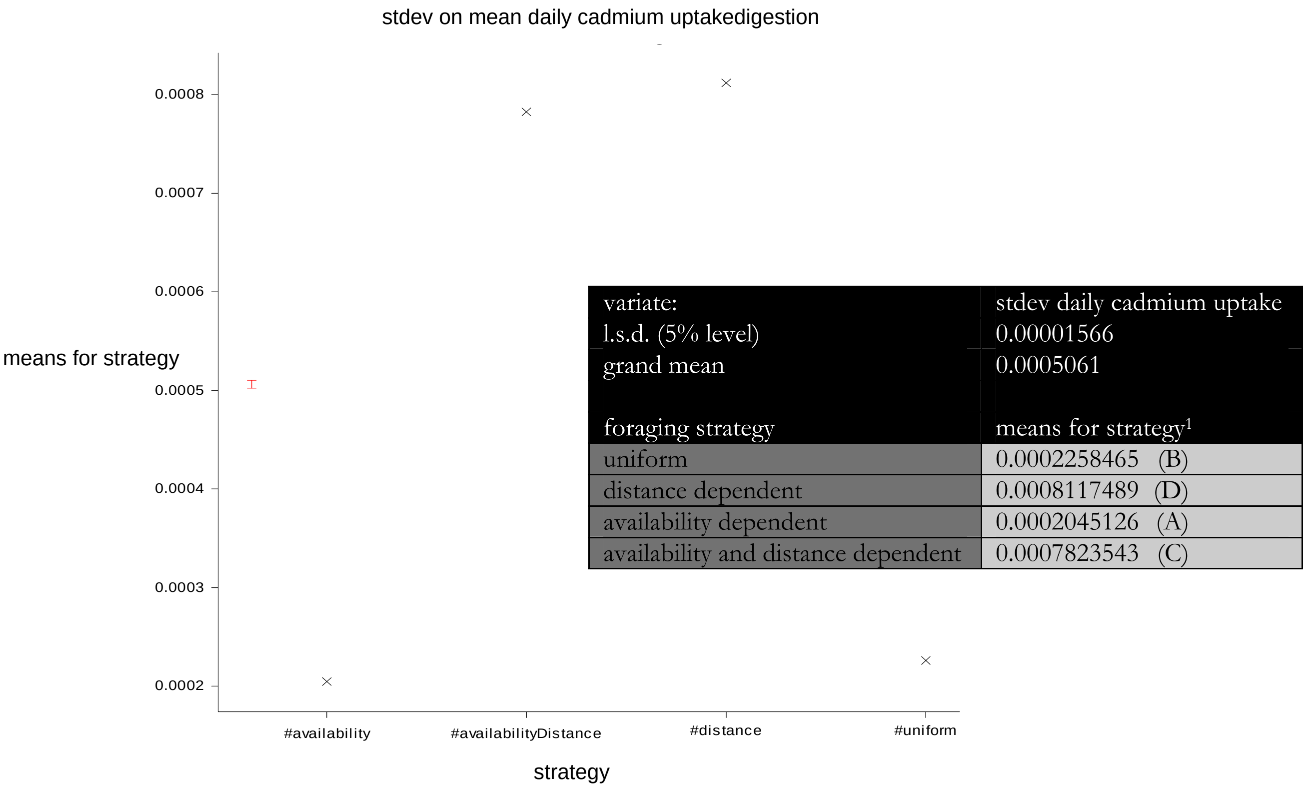
Moreover, the different foraging strategies have been compared by analyses of variance (Annex 2). The foraging strategies have been compared on the mean daily cadmium uptake and on the standard deviation of the mean. Figure 4.7 shows the position of the different foraging strategies regarding the mean daily cadmium uptake. The red error bar indicates the least significant difference (l.s.d.) of $5.493 \cdot 10^{-5}$. According to this l.s.d., there is no significant difference between the uniform strategy and the distance dependent strategy, and these strategies can be considered as a group. Between this group and both the availability dependent strategy and the availability and distance dependent strategy there is a significant difference considering the mean daily cadmium uptake.

The position of the different foraging strategies regarding the standard deviation of the mean daily cadmium uptake is shown in Figure 4.8. The red error bar indicates the least significant difference (l.s.d.) of $1.566 \cdot 10^{-5}$. According to this l.s.d., there is a significant difference between all strategies considering the standard deviation of the mean daily cadmium uptake.



variate:	Mean daily cadmium uptake
l.s.d. (5% level)	0.00005493
grand mean	0.0013560
foraging strategy	means for strategy[1]
uniform	0.001417255 (B)
distance dependent	0.001421531 (B)
availability dependent	0.001243338 (A)
availability and distance dependent	0.001341962 (A)

Figure 4.7: Analysis of variance on foraging strategies regarding the mean daily cadmium uptake (NB: LOAEL = 7·10^{-4} mg/day 1: strategy with similar letter are not statistically different (ANOVA, a: 0.05)).)



variate:	stdev daily cadmium uptake
l.s.d. (5% level)	0.00001566
grand mean	0.0005061
foraging strategy	means for strategy[1]
uniform	0.0002258465 (B)
distance dependent	0.0008117489 (D)
availability dependent	0.0002045126 (A)
availability and distance dependent	0.0007823543 (C)

Figure 4.8: Analysis of variance on foraging strategies regarding the standard deviation on the mean daily cadmium uptake (1: strategy with similar letter are not statistically different (ANOVA, a: 0.05)).

4.2.3 The fraction exceeding LOAEL

The lowest observed adverse effect level (LOAEL) has been assembled to be an uptake rate of $7 \cdot 10^{-4}$ mg/day. The fraction of cells with a daily uptake level exceeding the LOAEL, constantly averaged over 30 maps of similar habitat compositions, is plotted against the fraction of occurrence of s_habitat grid cells. The figures 4.9a to d show the graphs for the uniform, distance dependent, availability dependent, and availability and distance dependent foraging strategies, respectively. Conform figures 4.2 a-d, the coloured lines connect habitat configurations with the same proportions of w_habitat. The black dotted lines indicate some of the v_habitat-isolines. The resulting s_habitat fractions are exposed on the x-axes.

The graph for the availability dependent foraging strategy shows the same tendency as the graph for the uniform strategy. The same S-curves can be recognized for the w_habitat- and v_habitat-isolines. For maps with a high w_habitat fraction, the daily uptake level exceeds the LOAEL in all cells. The points in the graphs for distance driven foraging strategies are located relatively closely to each other. Even for maps with a high w_habitat fraction, the daily uptake level does not exceed the LOAEL in all cells, resulting in a fraction below unity. However, for maps with a low w_habitat fraction, the occurrence of cells with an uptake level exceeding the LOAEL is higher than for the uniform and availability dependent strategies (compare red lines).

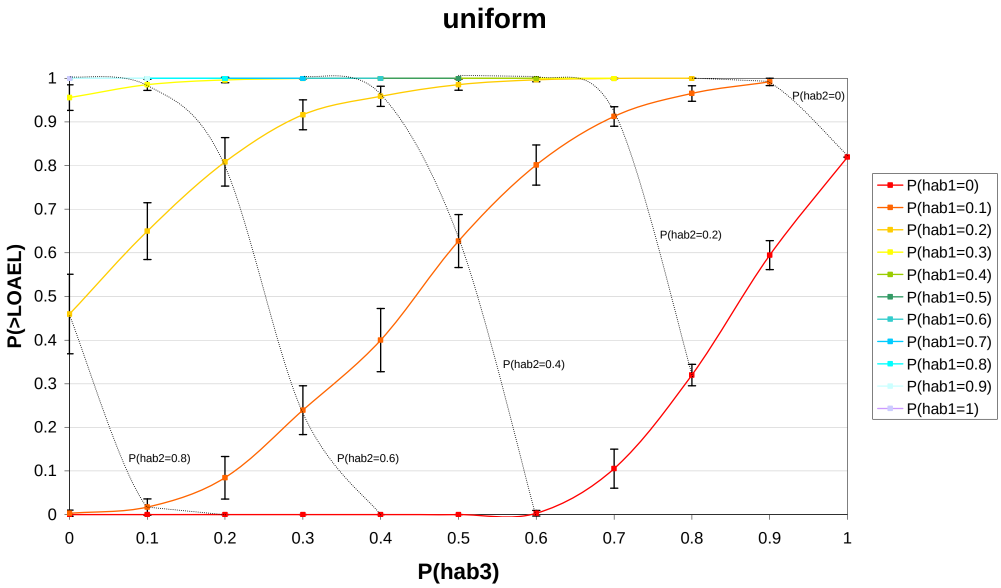


Figure 4.9a: The fraction of cells with a daily uptake level exceeding the LOAEL, averaged per map, plotted against the fraction of s_habitat grid cells for the uniform foraging strategy (mean and SD). Dotted lines represent v_habitat-isolines.

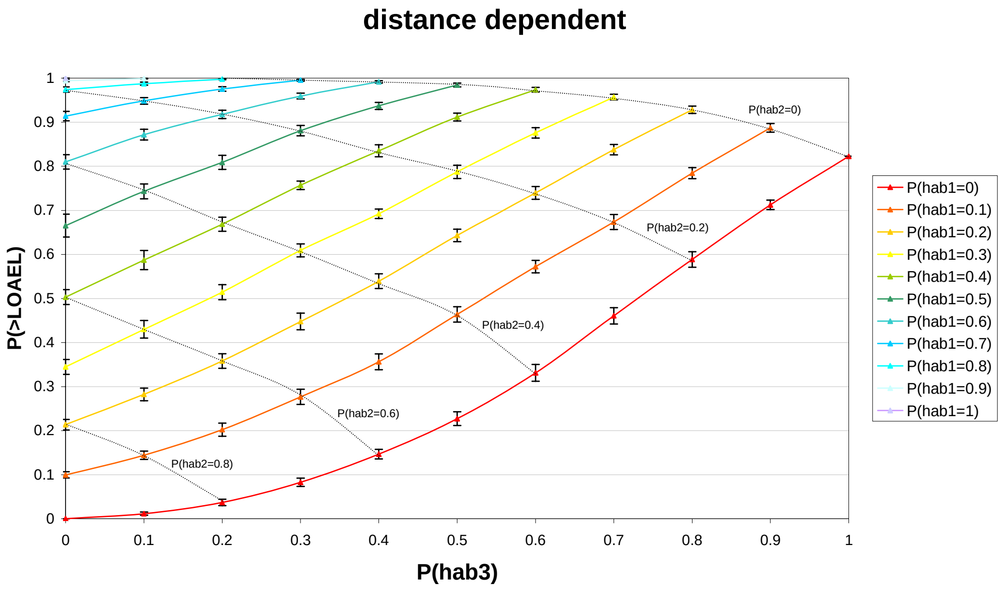


Figure 4.9b: The fraction of cells with a daily uptake level exceeding the LOAEL, averaged per map, plotted against the fraction of s_habitat grid cells for the distance dependent foraging strategy (mean and SD). Dotted lines represent v_habitat-isolines.

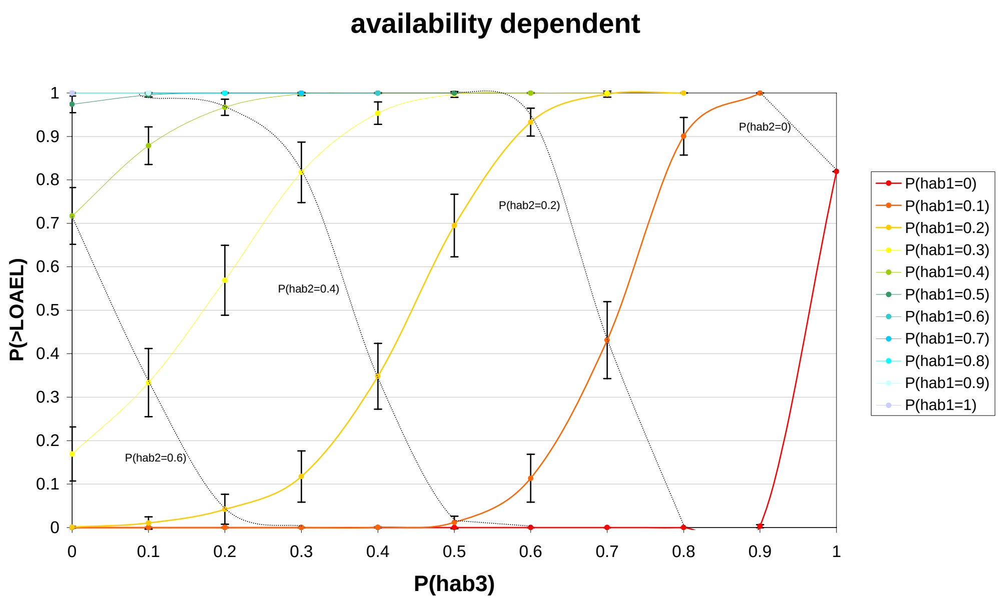


Figure 4.9c: The fraction of cells with a daily uptake level exceeding the LOAEL, averaged per map, plotted against the fraction of s_habitat grid cells for the availability dependent foraging strategy (mean and SD). Dotted lines represent v_habitat-isolines.

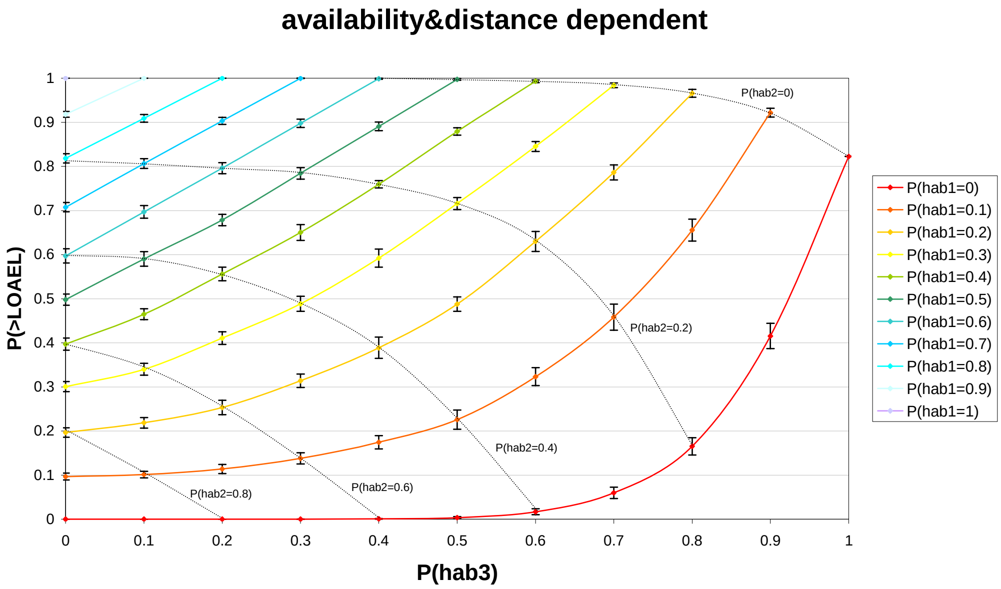


Figure 4.9d: The fraction of cells with a daily uptake level exceeding the LOAEL, averaged per map, plotted against the fraction of s_habitat grid cells for the availability and distance dependent foraging strategy (mean and SD). Dotted lines represent v_habitat-isolines.

4.2.4 Contamination and supply in the food web for two different habitat compositions

The model results for two different habitat compositions (i.e. 0.1/0.8/0.1 and 0.4/0.2/0.4) are summarized in Table 4.2, and in Figures 4.10 and 4.11:

Table 4.2a: Model results considering food supply for two different habitat compositions

variate: daily prey digestion foraging strategy	w_hab %	v_hab %	s_hab %	preyDigest (average over map)	preyDigest worms (%)	preyDigest voles (%)	preyDigest shrews (%)
uniform	0.1	0.8	0.1	168.41	0.06	0.93	0.02
distance dependent	0.1	0.8	0.1	168.41	0.08	0.89	0.03
availability dependent	0.1	0.8	0.1	187.30	0.03	0.97	0.00
availability and distance dependent	0.1	0.8	0.1	183.49	0.05	0.95	0.00
uniform	0.4	0.2	0.4	89.47	0.45	0.44	0.11
distance dependent	0.4	0.2	0.4	89.35	0.48	0.32	0.19
availability dependent	0.4	0.2	0.4	134.73	0.31	0.67	0.02
availability and distance dependent	0.4	0.2	0.4	117.83	0.44	0.49	0.06

Table 4.2b: Model results considering contamination for two different habitat compositions

variate: daily cadmium uptake foraging strategy	w_hab %	v_hab %	s_hab %	cdUptake *(average over map)*	cdUptake worms(%)	cdUptake) voles (%)	cdUptake shrews (%)
uniform	0.1	0.8	0.1	4.43E-04	0.76	0.06	0.18
distance dependent	0.1	0.8	0.1	4.49E-04	0.76	0.06	0.18
availability dependent	0.1	0.8	0.1	1.98E-04	0.88	0.15	0.06
availability and distance dependent	0.1	0.8	0.1	2.87E-04	0.82	0.10	0.08
uniform	0.4	0.2	0.4	1.70E-03	0.81	0.00	0.19
distance dependent	0.4	0.2	0.4	1.70E-03	0.81	0.00	0.19
availability dependent	0.4	0.2	0.4	1.52E-03	0.92	0.01	0.07
availability and distance dependent	0.4	0.2	0.4	1.69E-03	0.89	0.01	0.10

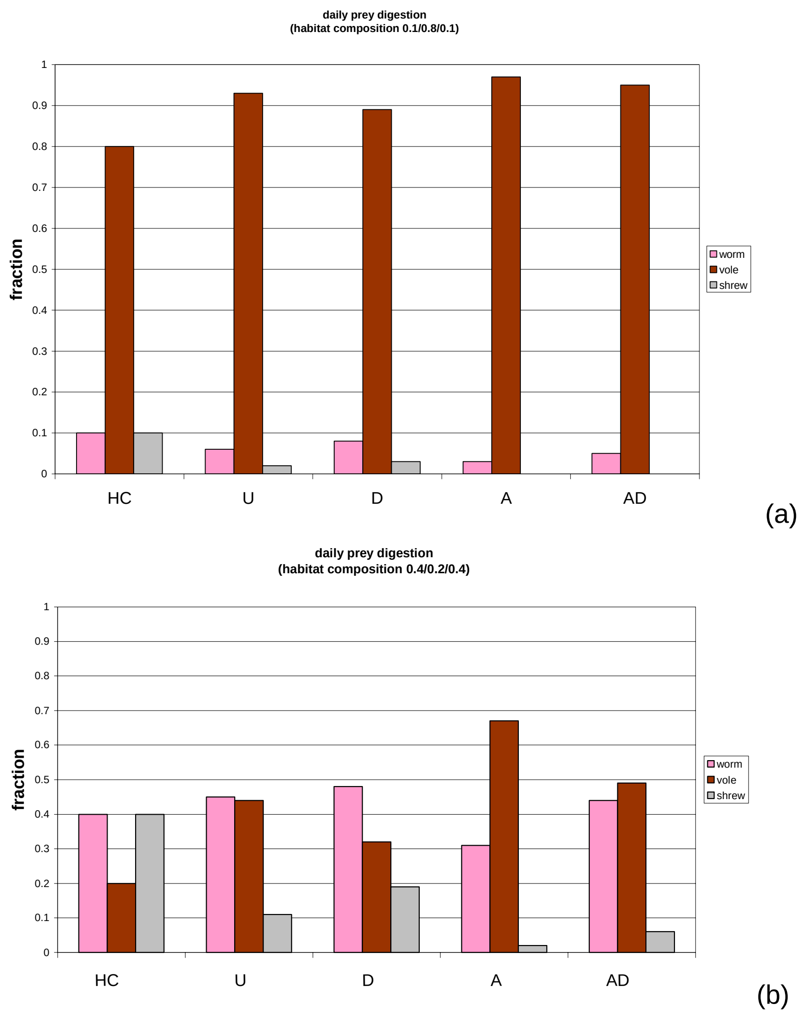
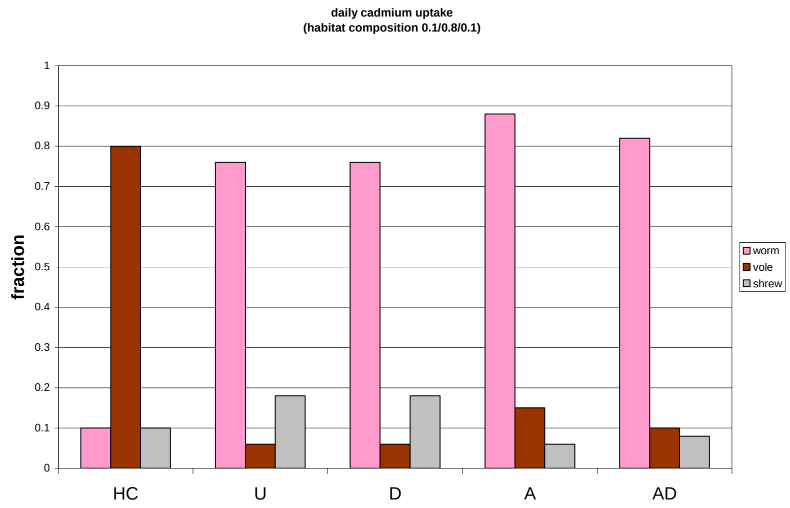
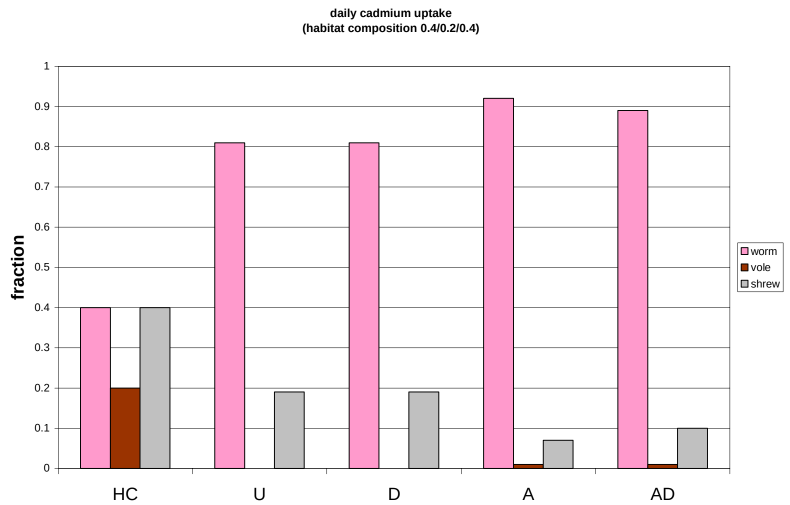


Figure 4.10: Histograms considering food supply for two different habitat compositions (HC) (a: 0.1/0.8/0.1; b: 0.4/0.2/0.4) and four foraging strategies (U: uniform; D: distance; A: availability; AD: availability&distance)



(a)



(b)

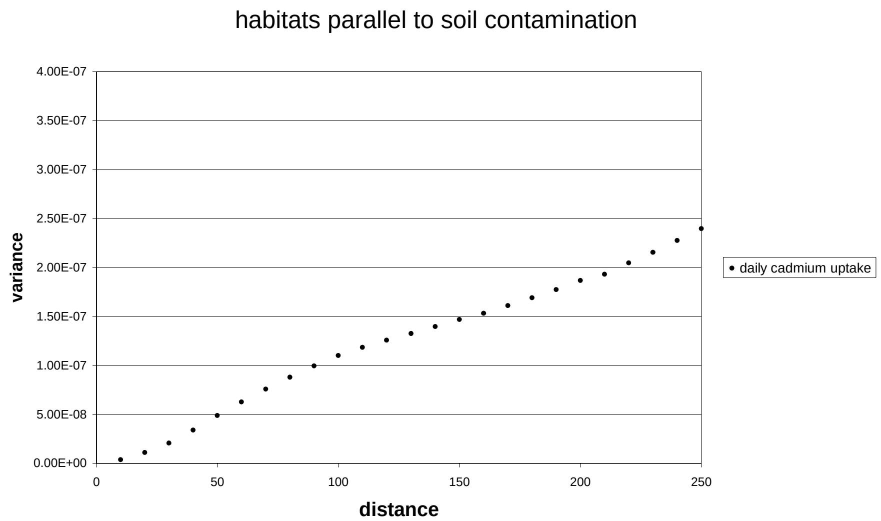
Figure 4.11: Histograms considering contamination for two different habitat compositions (HC) (a: 0.1/0.8/0.1; b: 0.4/0.2/0.4) and four foraging strategies (U: uniform; D: distance; A: availability; AD: availability&distance)

Comparing the figures considering contamination, little owls take up much contamination via worms and shrews, as is also indicated in Figure 4.1. For their food supply worms and voles are important. However, the ratios for the different prey items vary due to differences in habitat compositions and foraging strategy.

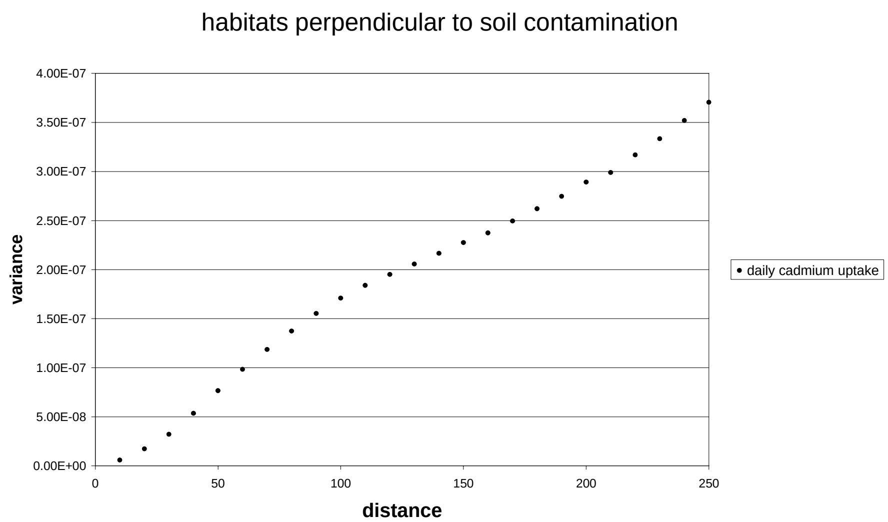
4.3 The effects of rearranging habitats

4.3.1 Spatial analyses with a realistic soil contamination map

The Figures 4.12a and b show the variograms of the daily cadmium uptake maps for two design landscapes with similar ratios of habitat types (i.e. 0.25/0.65/0.1), for which the habitats had been positioned parallel and perpendicular to the soil contamination pattern, respectively. The variogram for the landscape with habitats perpendicular to the contamination shows a larger sill, representing a higher spatial variance of the daily cadmium uptake than for the parallel landscape. However, the scale at which the sill would level off has not been reached in figures 4.12a and b. This indicates that part of the spatial variability has not been incorporated in the analyses.



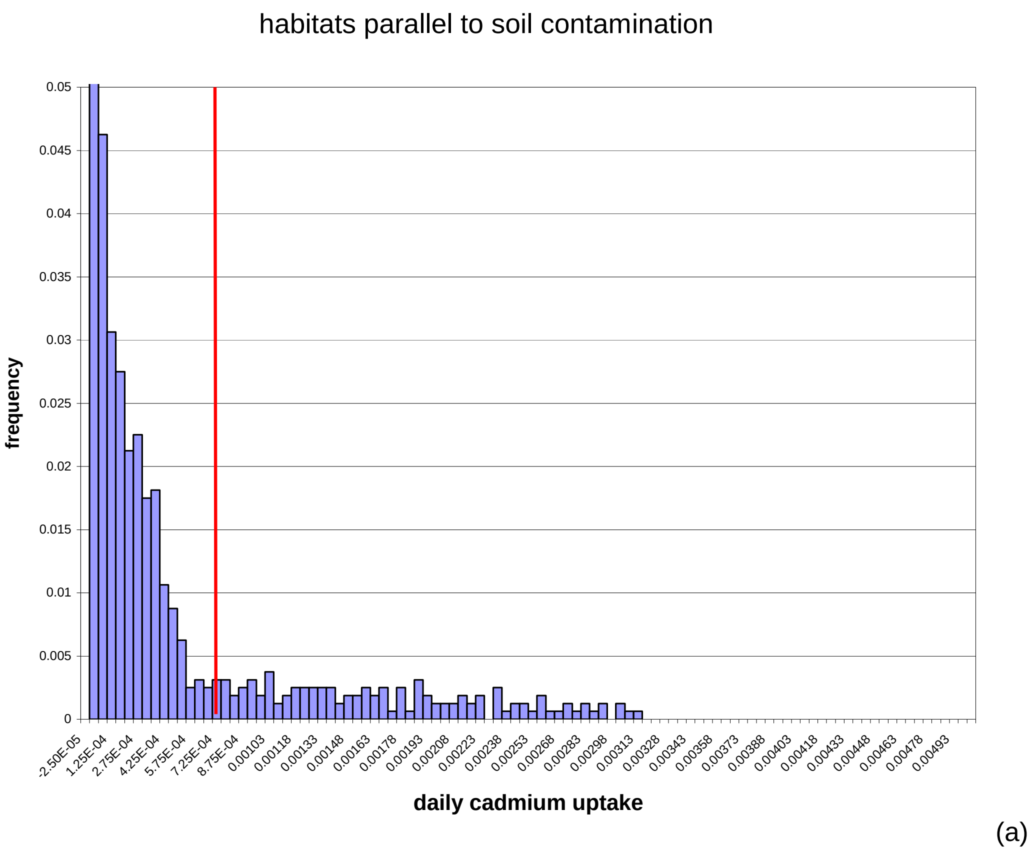
(a)



(b)

Figure 4.12: Variograms for the daily cadmium uptake map with habitats positioned parallel (a) and perpendicular (b) to realistic soil contamination

The histograms of Figures 4.13a and b show that the distribution of data around the mean value for the perpendicular landscape is also more wide-spread than for the parallel landscape.



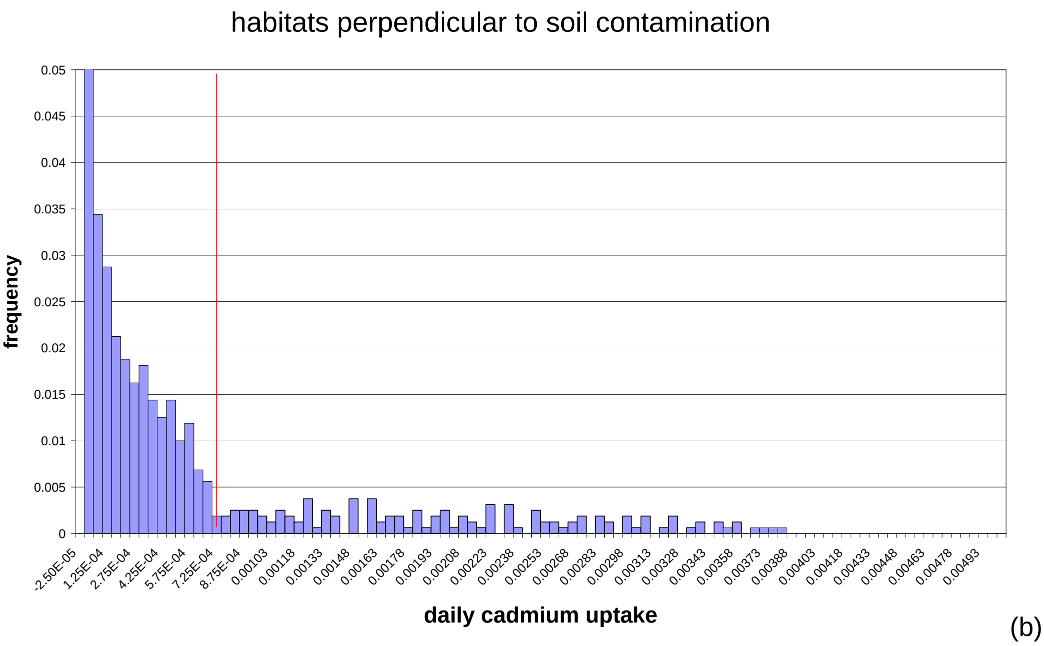


Figure 4.13: Histograms for the daily cadmium uptake map with habitats positioned parallel (a) and perpendicular (b) to realistic soil contamination. Red lines indicate LOAEL.

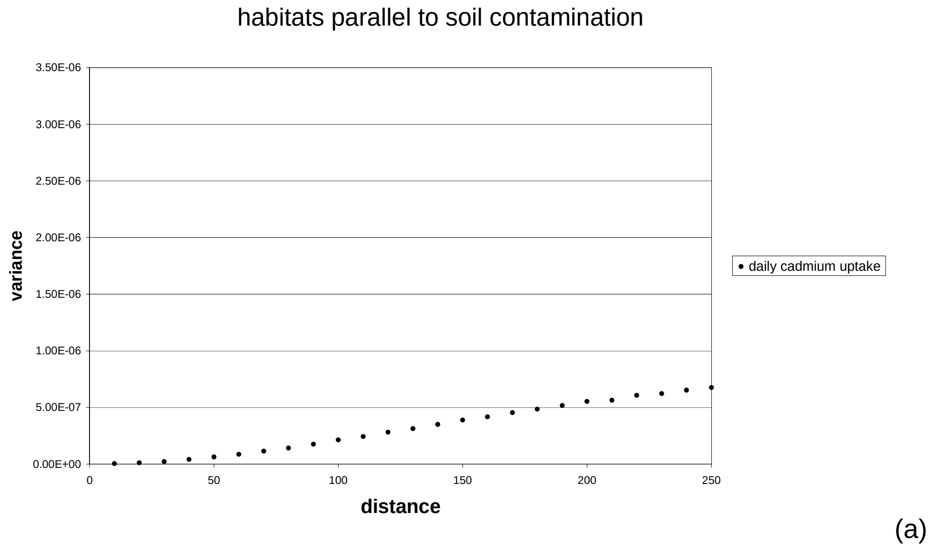
This is also indicated by the higher standard deviation (see Table 4.3). Moreover, the fraction exceeding the LOAEL is higher for the perpendicular landscape:

Table 4.3: Model results for two design landscapes, positioned differently regarding a realistic soil contamination pattern

foraging strategy: uniform habitat configuration	w_hab %	v_hab %	s_hab %	cdUptake (*average over map*)	cdUptake (*standard deviation over map*)	P(>LOAEL)
parallel	0.25	0.65	0.1	2.11E-04	4.82E-04	0.081
perpendicular	0.25	0.65	0.1	2.54E-04	5.95E-04	0.087

4.3.2 Spatial analyses with a designed soil contamination map

The variograms of Figures 4.14a and b describe a more explicit difference in the variance of the daily cadmium uptake. The landscape with habitats positioned exactly perpendicular to the designed soil contamination has a much larger spatial variation than the parallel landscape.



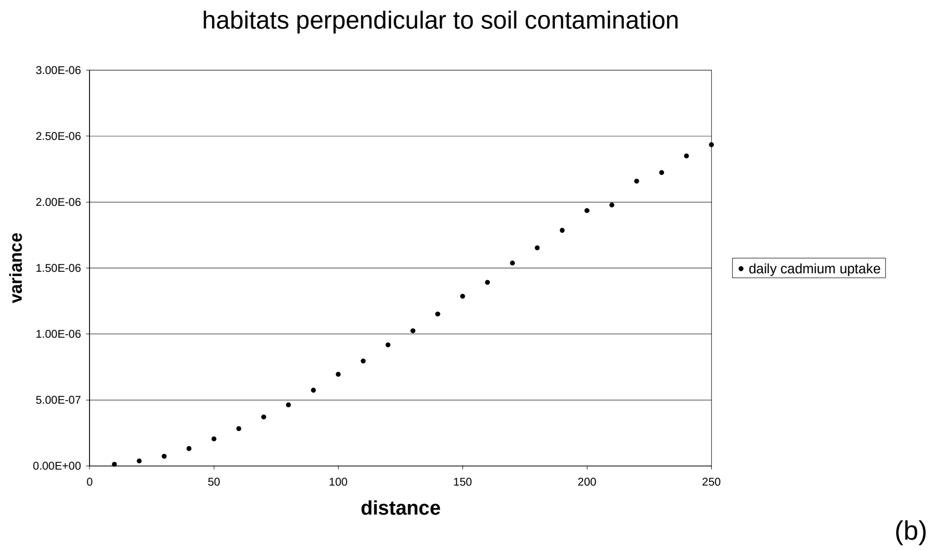
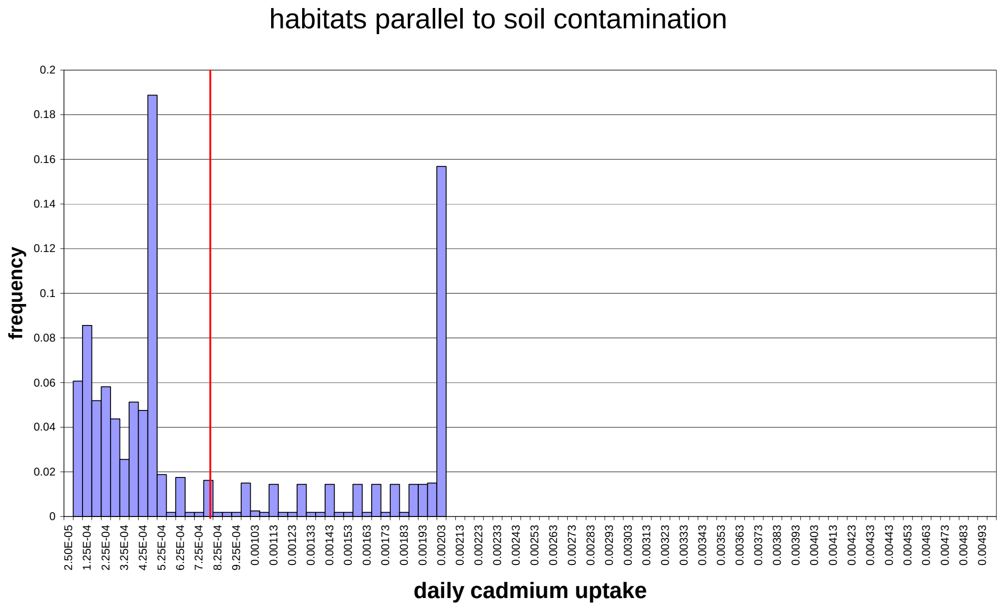
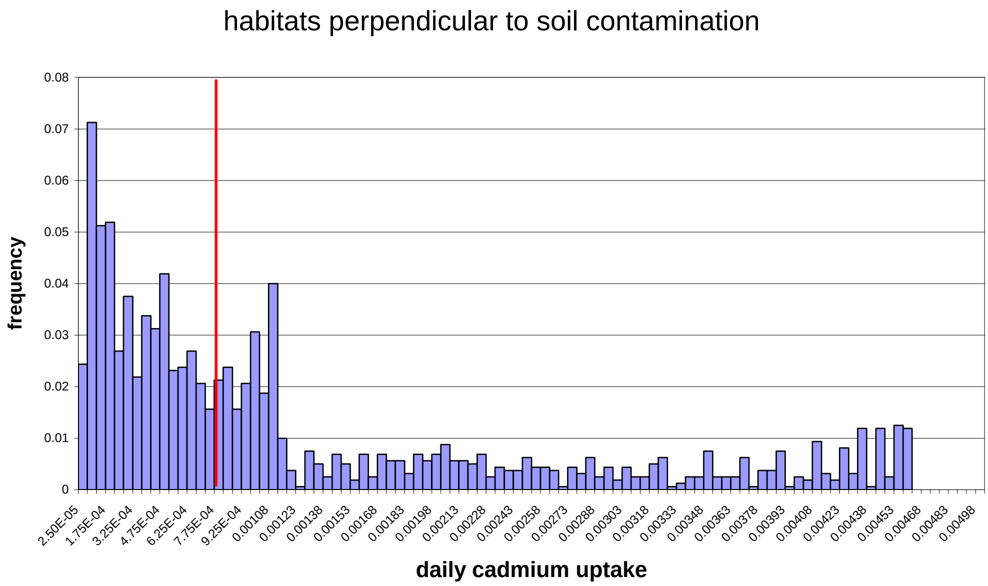


Figure 4.14: Variograms for the daily cadmium uptake map with habitats positioned parallel (a) and perpendicular (b) to designed soil contamination

The histograms of Figures 4.15a and b show that the distribution of data around the mean value for the perpendicular landscape is also much more wide-spread than for the parallel landscape.



(a)



(b)

Figure 4.15: Histograms for the daily cadmium uptake map with habitats positioned parallel (a) and perpendicular (b) to designed soil contamination. Red lines indicate LOAEL.

This is also indicated by the higher standard deviation (see Table 4.4). Moreover, the fraction exceeding the LOAEL is much higher for the perpendicular landscape:

Table 4.4: Model results for two design landscapes, positioned differently regarding a designed soil contamination pattern

foraging strategy: uniform habitat configuration	w_hab %	v_hab %	s_hab %	cdUptake (average over map)	cdUptake (standard deviation over map)	P(>LOAEL)
parallel	0.25	0.65	0.1	8.05E-04	7.16-04	0.35
perpendicular	0.25	0.65	0.1	1.26E-03	1.32-03	0.51

5 Discussion

5.1 Explanation and implication of results

5.1.1 The effects of changes in the ratios of habitat types

5.1.1.1 Responses in daily prey digestion and cadmium uptake for different habitat proportions

The graphs for the uniform and distance dependent foraging strategies indicate that for similar w_habitat fractions, the mean prey digestion increases linearly with a decrease in the fraction of s_habitat cells and a consequent increase in the fraction of v_habitat cells. Also, for similar s_habitat fractions, the mean prey digestion increases regularly when the w_habitat fraction decreases and the v_habitat fractions increases. This all implicates that if a proportion of w_habitat is replaced by v_habitat, the daily prey digestion increases. Moreover, if a part of either w_habitat or v_habitat is replaced by s_habitat, the daily prey digestion decreases in contrast (Figure 5.1).

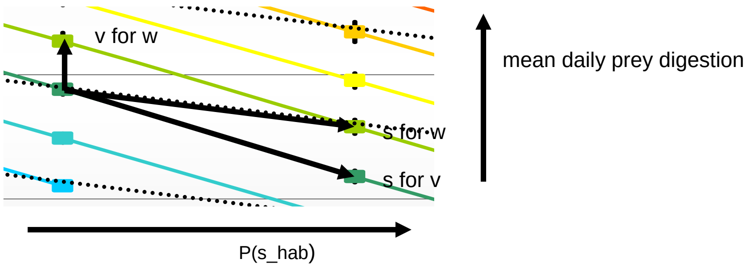


Figure 5.1: A zoomed-in view of the graphs for the uniform and distance dependent foraging strategy, showing consequences for mean daily prey digestion of the replacement of a proportion of habitat a by habitat b (b for a)

The graph for the availability dependent foraging strategy does not display the same results. For low v_habitat proportions, the prey digestion increases with increasing w_habitat fractions and decreasing s_habitat fractions. The v_habitat-isolines decline in the direction of high s_habitat fractions (x-axis). Hence, if a proportion of w_habitat is replaced by v_habitat, the daily prey digestion increases. Moreover, if a part of either w_habitat or v_habitat is replaced by s_habitat, the daily prey digestion decreases (Figure 5.2).

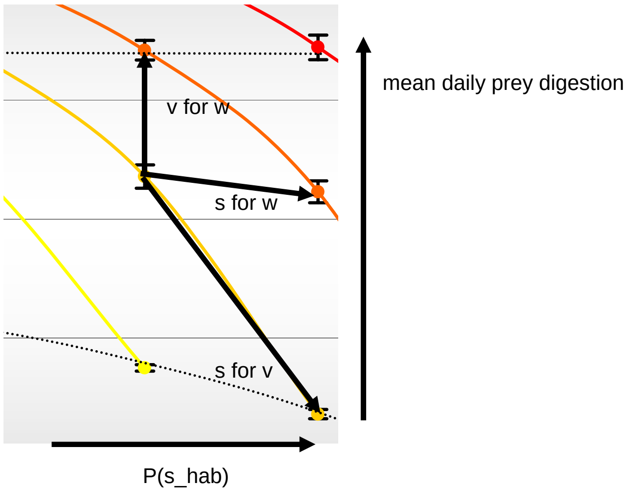


Figure 5.2: A zoomed-in view of the graph for the availability dependent foraging strategy with low v_habitat fraction, showing consequences for mean daily prey digestion of the replacement of a proportion of habitat a by habitat b (b for a)

However, for high v_habitat fractions, the isolines increase in the direction of high s_habitat fractions. Thus, if a proportion of w_habitat is either replaced by v_habitat or by s_habitat, the daily prey digestion increases. Besides, if a part of v_habitat is replaced by s_habitat, the daily prey digestion decreases. This can be explained by the fact that for this strategy, the prey intake is dependent on the availability of the resources within the cells of the home range (in grams). Hence, more time is spent in cells with large prey availability, and more food is consumed from these cells. The model created in this study is parameterized in such a way, that prey availability is largest in cells inhabiting voles (i.e. v_habitat cells). When an average home range or map consists of limited amounts of v_habitat cells, w_habitat (availability per cell: 100 gr FW/day) and s_habitat (availability per cell: 30 gr FW/day) provide for the daily prey intake and hence, digestion. Once the home range or map is composed mostly of v_habitat, a replacement of w_habitat by s_habitat means even more time spent in cells with v_habitat (Figure 5.3).

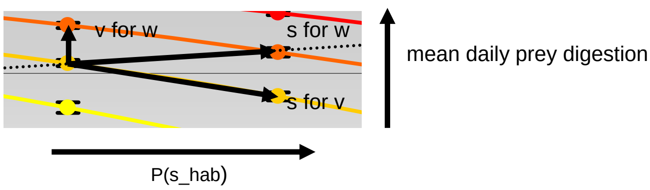


Figure 5.3: A zoomed-in view of the graph for the availability dependent foraging strategy with high v_habitat fraction, showing consequences for mean daily prey digestion of the replacement of a proportion of habitat a by habitat b (b for a)

The cadmium uptake graphs for the uniform and distance dependent foraging strategy show that for similar w_habitat fractions, the mean cadmium uptake decreases linearly with a decrease in the fraction of s_habitat cells and a consequent increase in the fraction of v_habitat cells. Also, for similar s_habitat fractions, the mean cadmium uptake increases regularly when the w_habitat fraction increases, and the v_habitat fractions decreases subsequently. This all implies that if a proportion of w_habitat is replaced by either v_habitat or s_habitat, the daily cadmium uptake decreases. Moreover, if a part of v_habitat is replaced by s_habitat, the daily cadmium uptake increases in contrast (Figure 5.4).

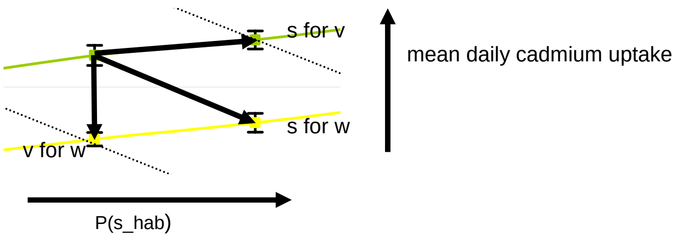


Figure 5.4: A zoomed-in view of the graphs for the uniform and distance dependent foraging strategy, showing consequences for mean daily cadmium uptake of the replacement of a proportion of habitat a by habitat b (b for a)

The graph for the availability dependent foraging strategy does not show linear responses. For low v_habitat proportions, the cadmium uptake increases rapidly with increasing w_habitat fractions and decreasing s_habitat fractions. The v_habitat-isolines decline exponentially in the direction of high s_habitat fractions (x-axis). Hence, if a proportion of w_habitat is replaced by either v_habitat or s_habitat, the daily cadmium uptake vastly decreases. Moreover, if a part of v_habitat is replaced by s_habitat, the daily prey digestion increases rapidly (Figure 5.5).

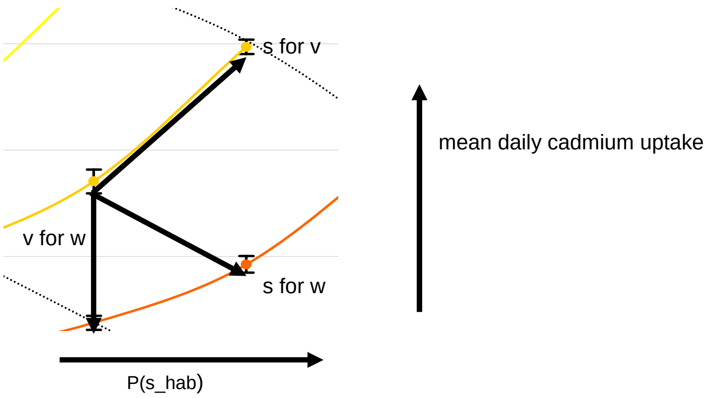


Figure 5.5: A zoomed-in view of the graph for the availability dependent foraging strategy with low v_habitat fraction, showing consequences for mean daily cadmium uptake of the replacement of a proportion of habitat a by habitat b (b for a)

However, for high v_habitat fractions, the isolines decline less rapidly in the direction of high s_habitat fractions. Still, if a proportion of w_habitat is replaced by either v_habitat or s_habitat, the daily cadmium uptake decreases. Furthermore, if a part of v_habitat is replaced by s_habitat, the daily prey digestion increases. However, this all ensues less explicitly than for low v_habitat proportions. The magnitude of the effect of a change in habitat composition can be explained by the fact that for the availability dependent strategy, the prey intake heavily depends on the availability of voles, along with the fact that voles accumulate by far less cadmium that the other prey items of little owls. When an average home range or map consists of few v_habitat cells, w_habitat and s_habitat provide for the daily prey consumption and hence, cadmium uptake. Once the home range or map is mainly composed of v_habitat, a replacement of w_habitat by s_habitat means even more time spent in less "risky" cells with v_habitat where the prey items are less contaminated (Figure 5.6).

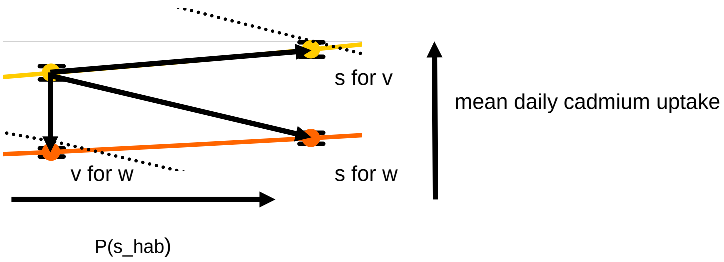


Figure 5.6: A zoomed-in view of the graph for the availability dependent foraging strategy with high v_habitat fraction, showing consequences for mean daily cadmium uptake of the replacement of a proportion of habitat a by habitat b (b for a)

The effects of changes in the ratios of habitat types as explained in this section reflect the (combined) effects of both the food supply and the body concentration of all prey items. However, it should be noted that the results for daily prey digestion and daily cadmium uptake heavily depend on the definition of the parameters in the model. Hence, the implications above are only applicable to the situation as simulated by the current model.

5.1.1.2 Analyses of variance

The analyses of variance on the mean daily prey digestion shows that all means are within or above the prey digestion range of 75 to 125 grams per day. It should however be noted that these are the means of all habitat proportions. As shown in Figures 4.2a to d, the mean daily prey digestion varies between the habitat proportions, and can be even less than 75 grams per day.

From the plot of the analyses of variance on the mean daily prey digestion and the mean daily cadmium uptake (Figures 4.3 and 4.7) it can further be derived, that a certain availability driven foraging pattern increases the prey digestion or food supply. Searching for food close to the nest (i.e. centre cell) decreases the success, as is indicated by the lower means for the strategies that are (partly) determined by distance.

At the same time, an availability driven foraging pattern decreases the cadmium uptake or contamination risk in this situation. Searching for food close to the nest (i.e. centre cell) increases the risk, as is indicated by the higher means for the strategies that are (partly) determined by distance. These results are in agreement with the findings of Freshman and Menzie (1996) and Von Stackelberg *et al.* (2002), who found that when the top level carnivores are resident species with a relatively small foraging area, they more frequently encounter localized contaminated sediments.

Evidently, the plots of the standard deviation of the mean daily prey digestion and the mean daily cadmium uptake (Figures 4.4 and 4.8), distance dependent foraging increases the distribution of values for daily prey digestion and increases the variance for daily cadmium uptake. Searching for food close to the nest narrows the foraging areas and hence decreases the overlap between neighbouring home ranges, or the autocorrelation. Consequently, the centre cell values vary more strongly in the model output maps for distance driven foraging strategies.

However, again it should be noted that the variance changes by altering the lambda value. An increase in the lambda value narrows the foraging areas even more, which results in yet more strong variations in the centre cell values for daily prey digestion and daily cadmium uptake.

5.1.1.3 The fraction exceeding the LOAEL

Both changes in the mean values and changes in the variance of the distributions of values can result in differences in the fraction exceeding the LOAEL. Figure 5.7 shows the consequences of an alteration in mean values (arrows A and C) and the effects of a change in variance (arrows B and D).

The analysis of variance of the standard deviation of the mean daily cadmium uptake shows that distance dependent foraging increases the distribution of values for daily cadmium uptake within a map due to a decrease in autocorrelation. Yet, Figure 5.7 (arrow B) shows that this widespread distribution of data around the mean value enlarges the occurrence of cells with an uptake level exceeding the LOAEL. This can be distinguished by comparing the red lines (P(w_hab=0)) in graphs for the uniform and distance dependent strategies. Moreover, the high variance increases the chance of encountering cells with an uptake level lower than the LOAEL (arrow D), even for "risky" habitat maps with a low v_habitat fraction (compare bluish lines). Hence, the points in the graph for the distance dependent foraging strategy are located closely to each other.

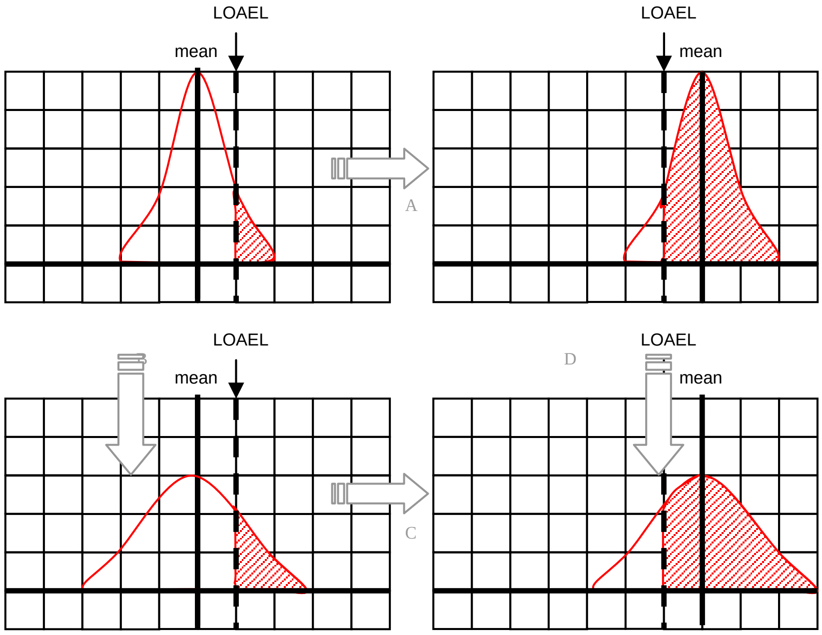


Figure 5.7: Change in risk, expressed by the fraction exceeding LOAEL, due to a change in mean value (arrows A and C) and/or a change in variance (arrows B and D)

For the availability and distance dependent foraging strategy, this tendency is less evident in the graph. Still, the data points are located more closely together than for the uniform foraging strategy due to the larger variance of the mean daily cadmium uptake within a map.

The graph for the availability dependent foraging strategy shows the same tendency as the chart for the uniform strategy. The same S-curves can be recognized for the w_habitat- and v_habitat-isolines. However, uniform foraging requires a higher v_habitat fraction to obtain a similar risk as for the availability driven foraging. For the latter strategy, v_habitat is explored in a more beneficial manner.

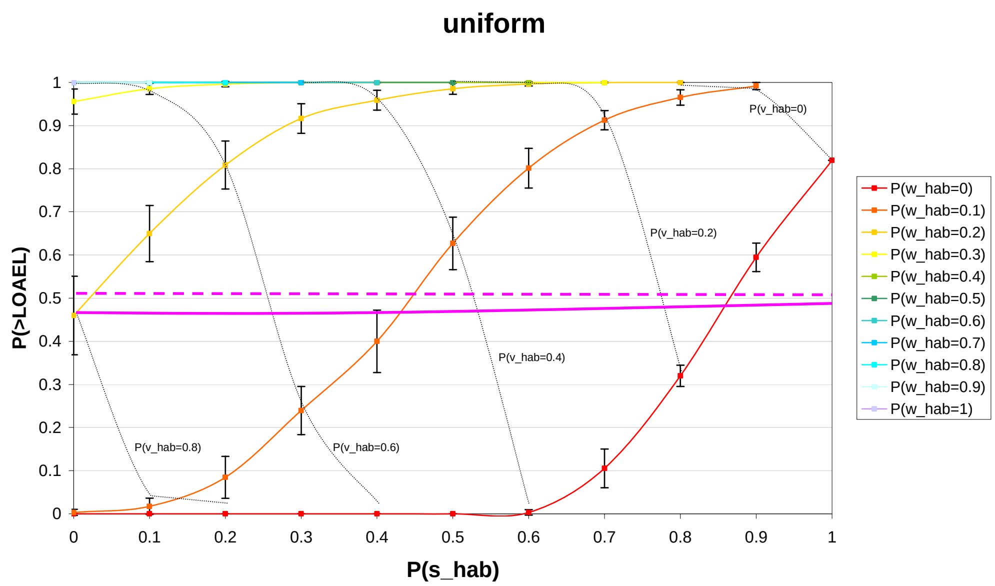
Differences in autocorrelation also follow from the error bars around the means in the graphs. Since the distribution of data around the mean value for the uniform and availability driven foraging strategies is less wide-spread than for the distance driven strategies, a small change in position regarding the LOAEL results in a large change in the fraction exceeding the LOAEL for the former strategies (see also Figure 5.7 and compare arrows A and C). Hence, the sizes of the error bars in the graphs for the uniform and availability driven foraging strategies exceed those of the error bars in the charts for the distance driven strategies.

Once the fraction of values for daily cadmium uptake exceeding the LOAEL resembles exactly 0.5, the distribution exceeds the level from its *median* value. In Figure 5.8 this is indicated by the pink dotted lines in the graphs (LOAEL=median). The continuous pink lines in the graphs represent the situations for which the LOAEL equals the values for the *mean* daily cadmium uptake (LOAEL=mean). Above these lines, the LOAEL exceeds the mean daily cadmium uptake.

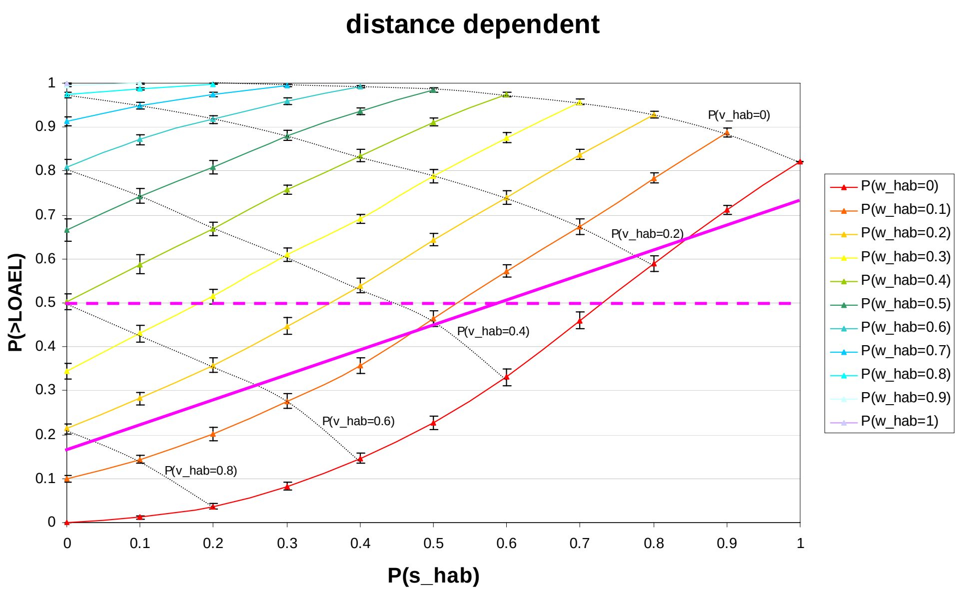
Interestingly, the locations of the pink lines, both dotted and continuous, vary in respect to each other and for the different foraging strategies. When the lines cross, the LOAEL is equal to both the median and the mean value, which implies that here the distribution of values is symmetric. If the continuous pink line is located beneath the dotted line, the mean exceeds the median value for the distributions of the situations in between the lines. The median is pulled slightly to the right tails of the distributions. However, the mean is positioned even further out the right tails than the median, which makes these distributions positively skewed. If however the continuous pink line is located above the dotted line, the median value exceeds the mean value for the distributions of the situations in between the lines. For these situations, the distributions of the values for the daily cadmium uptake are negatively skewed.

For distance driven foraging strategies, the areas between the pink lines are more profound. This implies that the resulting distributions for these strategies are more skewed. Because searching for food close to the nest decreases the overlap between neighbouring home ranges, the cell values are barely averaged over the foraging areas. As averaging leads to a more evenly balanced distribution, this is not the case for distance driven foraging strategies and asymmetrical distributions easily appear.
The occurrence of skewed distributions for the values for the daily cadmium uptake should be taken into consideration. Due to a negatively skewed distribution of data values, more than 50% of the area can be unfavourable, despite the fact that the mean daily cadmium uptake value is less than the LOAEL.

According to Kooistra *et al.* (2005), the fraction exceeding the LOAEL can be seen as a "hazard index", however it is not an absolute measure of risk. It should be interpreted within the context of the assumptions and uncertainties underlying the risk assessment procedure. A hazard index below unity is interpreted as a situation of no immediate concern, whereas a hazard index above unity requires further investigation and, possibly, risk reduction measures (Kooistra *et al.*, 2005).

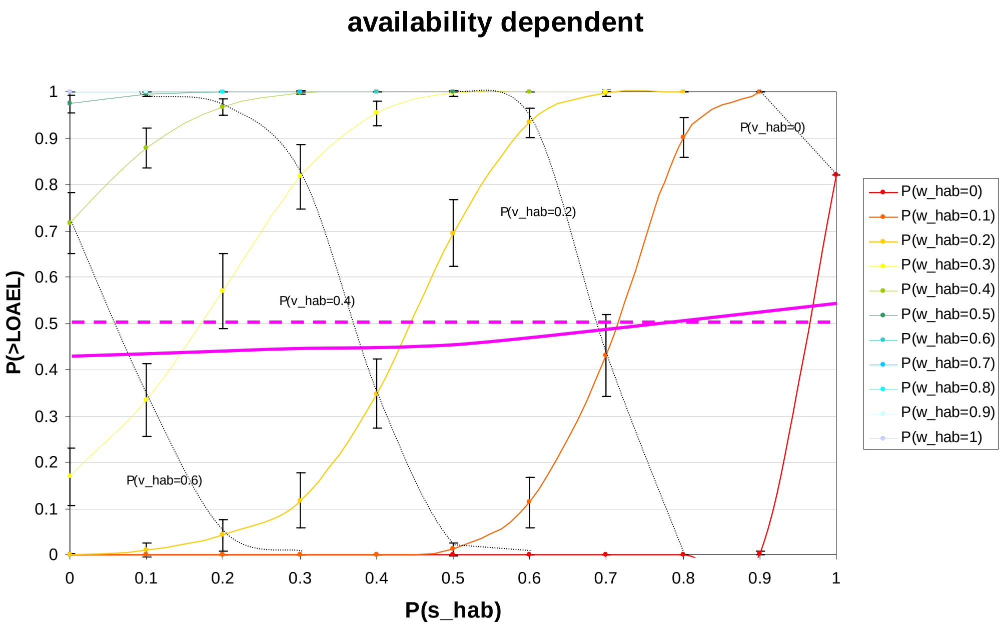


(a)

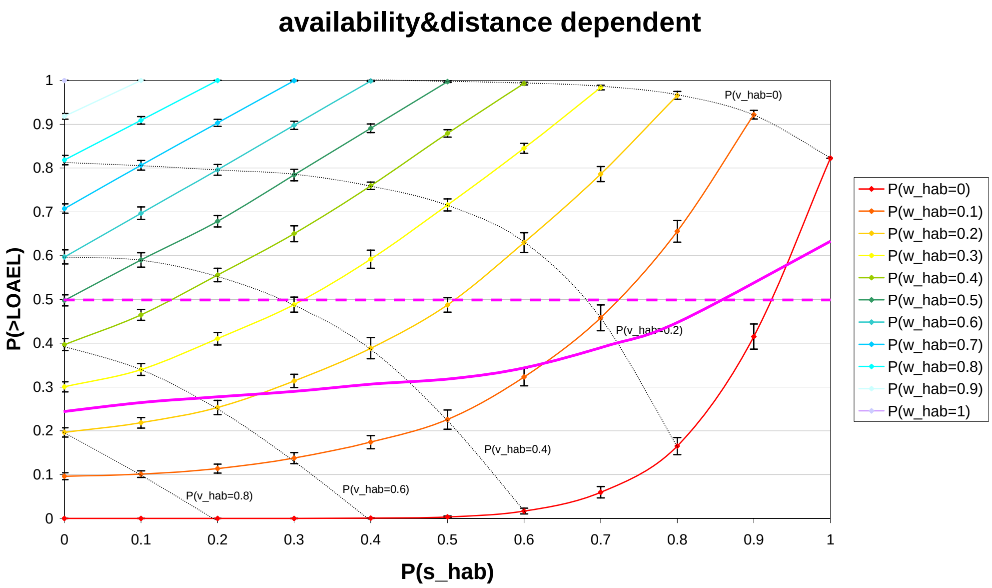


(b)

Figure 5.8: The fraction of cells with a daily uptake level exceeding the LOAEL, averaged per map, plotted against the fraction of s_habitat grid cells for the uniform foraging strategy (a), the distance dependent foraging strategy (b), the availability dependent foraging strategy (c), and the availability and distance dependent foraging strategy (d). The pink dotted lines indicate the situations for which the LOAEL equals the median values (LOAEL=median), while the continuous pink lines represent the situations for which the LOAEL equals the mean daily cadmium uptake (LOAEL=mean).



(c)



(d)

Figure 5.8

5.1.1.4 The effects of averaging over home ranges

Distance driven foraging behaviour decreases the autocorrelation in the model results, as the cell values are barely averaged over the foraging areas. The effects of averaging even decrease if the lambda value increases. Yet, when the complete home ranges are explored, the spatial scale of variations in the soil contamination can effect the averaging of the contamination risk over the home ranges.

It is expected that when the soil contamination varies within the borders of the home ranges (Figure 5.9a), the cadmium uptake per home range consequently obtains an average value, which is relatively similar for all centre cells of the map. The spatial correlation hence disappears. In contrast, if a home range falls within the spatial scale of variations in the soil contamination (Figure 5.9b), the daily cadmium uptake shows clustering. Then, the variance of daily cadmium uptake increases gradually with distance.

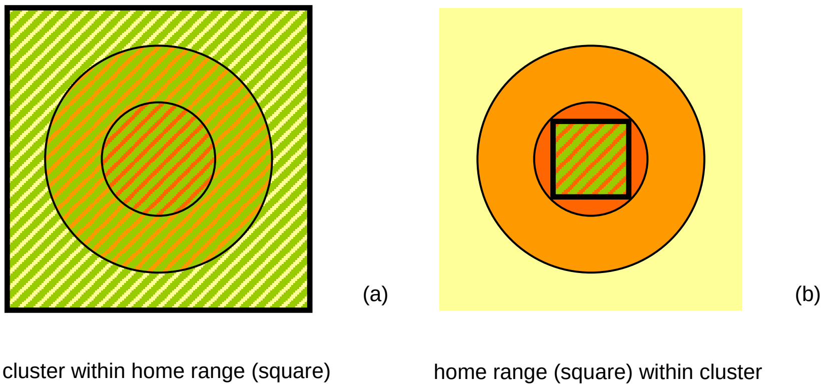


Figure 5.9: Schematized position of home range regarding the spatial pattern of soil contamination

5.1.2 The effects of shifting habitats

It is assumed that the variance of the random field as indicated by a variogram (e.g. a daily cadmium uptake map) evidently increases with the distribution of data around the mean value. Hence, when the variance is decreased, the fraction exceeding the LOAEL diminishes consequently. The variograms in the Figures 4.12a and b show that by a shifting of habitats within a site, indeed the variance and hence the fraction exceeding the LOAEL can be decreased. The distribution of data around the mean value for the perpendicular landscape is more wide-spread than for the parallel landscape, which should be attributed to the fact that more and diverse soil-habitat combinations are obtained when a perpendicular landscape is used. The spatial analyses with a designed soil contamination map, where the habitats have been positioned exactly parallel and perpendicular to the soil contamination (Figures 4.14a and b), show an even more evident decrease in the variance and fraction exceeding the LOAEL.

It should however be noted, that a shifting of habitats within a site can moreover lead to an overall decrease in values for the daily cadmium uptake. Then, the whole distribution is pulled to the left, and the fraction exceeding the LOAEL decreases.

5.2 Model attainability

In the model created in this study, the contamination risk for the little owls has been estimated by the mean daily cadmium uptake ($\bar{u}_0$). The uptake values, like all output values from the model, have been assigned to the cells of the output maps, which makes the model a grid based model. When an owl spends its whole life in one home range, the daily cadmium uptake also stands for the mean daily uptake for the owl's lifespan and can be used as such in the owl's concentration formula. Otherwise, the daily uptake has to be either averaged over all foraging areas the owl encounters during its lifespan, or the daily uptake should be modelled numerically. However, the spatially explicit approach with the mean daily cadmium uptake used as a risk estimate does not ignore the possibility that some individuals may consume mostly contaminated preys. The advantage of the approach is that it assigns a probability to the occurrence of this scenario by comparing the mean daily cadmium uptake to the LOAEL.

The model incorporates many equations and variables. The confidence of the model predictions has not yet been tested by varying (spatially explicit) variables over a wide range. Even though the presented model includes simplified assumptions about the nature of the spatial behaviour of organisms, it is useful for capturing some of the major components for a theoretical case such as this.

Fieldwork needs to specify the foraging behaviour of little owls. So far, the model denotes equal foraging strategies to all preyed items. However, individuals might show different spatial exploitation behaviour for different prey species.

In all cases, activities to redevelop affected sites must result in the protection of biodiversity. This could imply that for conservation management purposes, wildlife populations should be managed or desired landscape configurations should be maintained. Therefore, land use management practices should consider certain boundary conditions concerning the proportions and/or positions of habitat types. Possibilities to create new landscapes might not be exhaustive.

6 Conclusion

In this report, a conceptual model is formulated for little owls, with which the influences of differences in spatial patterns of exploitation have been investigated. Several conclusions can be drawn, some of which are specific for this case. A certain availability driven foraging pattern increased the little owl's prey digestion or food supply. At the same time, an availability driven foraging pattern in this case decreased the cadmium uptake or contamination risk in this situation. Searching for food close to the nest (i.e. centre cell) decreased the energetic gain and increased the hazard. Species with a relatively small foraging area may encounter more frequently localised contamination. Evidently, distance dependent foraging increased the variance for daily prey digestion and daily cadmium uptake, and decreases the autocorrelation.

Knowledge concerning the spatially explicit uptake of contaminating substances by organisms is essential in assessing the consequences of changes in habitat configuration. Both the effects of shifting habitats within a site, while maintaining the ratios of habitat types and the effects of changing the ratios by changing types of habitats have been investigated. Generally, a replacement of worm habitat by shrew habitat reduced in this case the contamination risk, as well as a substitution of shrew habitat by vole habitat. The risk reduced even more when worm habitat is replaced by vole habitat. The occurrence of skewed distributions for the values for the daily cadmium uptake should however be taken into consideration. Due to a skewed distribution of data values, the majority of an area can be unfavourable, despite the fact that the mean daily cadmium uptake value is less than the level that is hazardous to the owls.

A shifting of habitats within a site can decreased the values for the daily cadmium uptake, as well as the contamination risk. Therefore, the model developed proved that changes in habitat configuration can serve as a possible remedy to contamination problems. However, changing habitats can only be successful if the risks posed by the contaminants to wildlife and their prey items are within acceptable limits. The model facilitates the detection of areas with an elevated contamination risk for little owls.

Especially where spatial conflicts are increasing between additional housing, commercial development, and the protection of open space, the challenge of planning the redevelopment of contaminated areas may be greatest. The application of the model presented in this report in a Decision Support System facilitates assessment of risks of contaminants in such a way that the information can in spatial planning processes including information and arguments from other stakeholders involved in the planning process.

For further model development, the actual foraging behaviour of little owls needs to be specified by fieldwork. Since different spatial exploitation patterns might or might not average the contamination risk over the (foraging) areas, the foraging behaviour of little owls in the wild should be investigated carefully.

7 Recommendations

The model created in this study should be regarded as a basic theoretical model for spatial exploitation and contaminant uptake. It is however recommendable to quantify the uncertainty propagation in the model chain by sensitivity analyses.
To reflect the actual field situation more accurately, the model can be modified by:

Proper investigation and implementation of the actual foraging behaviour of little owls as specified by fieldwork. Little owls might not always be central place foragers. Hence, the effect of exploitation of an area from different spots should be examined.

Consideration of the real field situation concerning the presence of prey items in the different habitats, their densities and capture rates. In the current model, the prey species are assumed to occur in only one habitat type each. Furthermore, prey densities and the little owl's functional responses are assessed, based on expert knowledge. However, this might not properly reflect reality.

Additional modelling constraints on the consumption of foragers. Little owls may take in food within certain limits, and leave an area when the marginal (i.e. instantaneous) rate of gain from the area drops below the average rate of gain achievable in the environment. Thus, a simple learning process may be added.

Supplementary inclusion of definitions of habitat quality. "Quality" then encompasses a set of attributes that defines the suitability and attractiveness of a given habitat for the organism. Habitat quality describes the degree to which a given habitat meets the needs of a given organism. In addition, habitat quality may have a temporal dimension – changing from year to year, seasonally, or with respect to the life stage of the organism.

Making the model individually based instead of grid based. In the model created in this study, the uptake values, like all output values from the model, have been assigned to the cells of the output maps. The cadmium uptake during an owl's lifespan cannot be derived immediately from the model, because the movement the foragers undertake over their lifetime has not been modelled. An individually based model provides for lifetime foraging patterns and hence cadmium accumulation.

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Appendix 1

Equations and values used in the model

description of variable	symbol	units	formula	(distribution of) parameters	source
soil concentration	$[Cd_{soil}]$	mg Cd/kg DW soil			
body concentration worm		mg Cd/kg FW worm	$\log[Cd_w] = 1.28 - 0.56 \cdot \log[OM] - 0.23 \cdot \log[pH] + 0.324 \cdot \log[Cd_{soil}]$		Corp and Morgan (1991) in Ma (2004)
pH	pH	-		8	Van den Brink (2003)
organic matter fraction	OM	%		5	Van den Brink (2003)
concentration vegetation	$[Cd_{veg}]$	mg Cd/kg FW vegetation	$\log[Cd_{veg}] = (0.17 - 0.28 \cdot \log[OM] - 0.12 \cdot pH + 0.49 \cdot \log[Cd_{soil}])/2.5$		Römkens et al. (2005) and Van der Pol et al. (2004)
body concentration vole	$[Cd_v]$	mg Cd/kg FW vole	$[Cd_v] = \dfrac{\dfrac{food_v \cdot [Cd_{veg}] \cdot c\_up}{c\_out} \cdot \left(1 - e^{-c\_out \cdot age_v}\right)}{weight_v}$		Gorree et al. (1995)
daily prey digestion vole	$food_v$	kg FW vegetation/day	$food_v = 0.5 \cdot \left(\dfrac{weight_v}{1000}\right)$		After Kooistra et al. (2001) and Peacock et al. (2004)
age vole	age_v	day		300	
body weight vole	$weight_v$	g FW		30	Van den Brink (unpubl.)
body concentration shrew	$[Cd_s]$	mg Cd/kg FW shrew	$[Cd_s] = \dfrac{\dfrac{food_s \cdot [Cd_w] \cdot c\_up}{c\_out} \cdot \left(1 - e^{-c\_out \cdot age_s}\right)}{weight_s}$		Gorree et al. (1995)

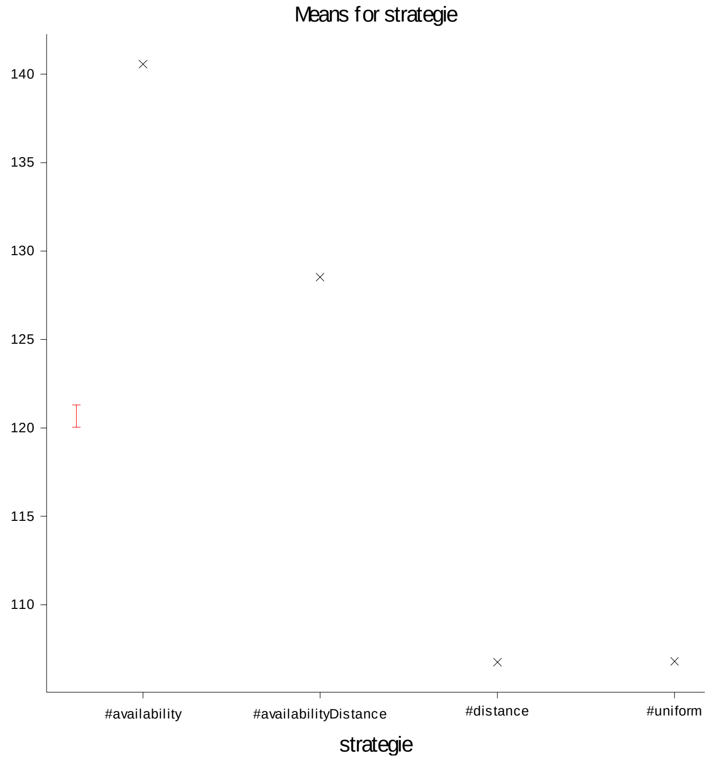
daily prey digestion shrew	$food_s$	kg FW worm/day	$food_s = \left(\frac{weight_s}{1000}\right)$		Churchfield (1990)
age shrew	age_s	day		300	
body weight shrew	$weight_s$	g FW		8	Van den Brink (unpubl.)
worm density	$dens_w$	g FW worm/m^2		200	Marinussen (PhD)
vole density	$dens_v$	g FW vole/m^2		0.09	Jedrzejewski et al. (1996)
shrew density	$dens_s$	g FW shrew/m^2		0.0072	Churchfield (1990)
functional response worm	FR_w	g FW worm/day	$FR_w = \min(600, 0.5 \cdot dens_w)$	100	
functional response vole	FR_v	g FW vole/day	$FR_v = \frac{280 \cdot dens_v}{0.02 + dens_v}$	229	Jedrzejewski et al. (1996)
functional response shrew	FR_s	g FW shrew/day	$FR_s = \frac{280 \cdot dens_s}{0.06 + dens_s}$	30	
daily Cd uptake owl	u_o	mg Cd/day	$\bar{u}_o = average(\sum^{foraging\_area}(food_{prey} \cdot c\_up \cdot [Cd_{prey}])_{cell})$		Gorree et al. (1995)
body concentration owl	$[Cd_o]$	mg Cd/kg FW owl	$[Cd_o] = \frac{\frac{\bar{u}_o}{c\_out} \cdot \left(1 - e^{-c\_out \cdot age_o}\right)}{weight_o}$		Gorree et al. (1995)
uptake fraction	c_up	%		0.005	Gorree et al. (1995)
excretion rate	c_out	1/day		0.0035	Gorree et al. (1995)

Appendix 2

Output analyses of variance

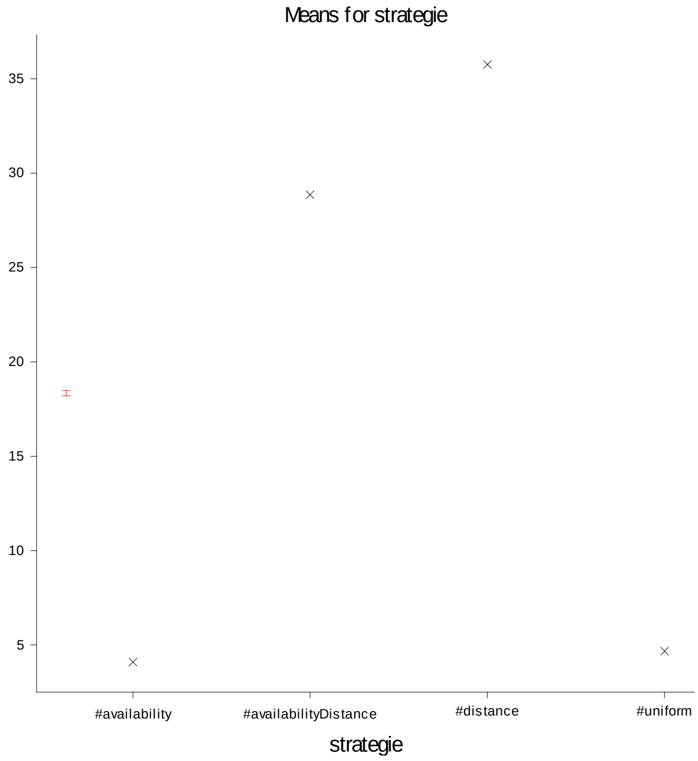
Appendix 2.1: Output analyses of variance on mean daily prey digestion

```
***** Analysis of variance *****

Variate: PreyDigestion_mean

Source of variation     d.f.       s.s.       m.s.    v.r.  F pr.
strategie                  3   1670806.    556935.  360.06  <.001
Residual                7916  12244406.      1547.
Total                   7919  13915212.


***** Tables of means *****

Variate: PreyDigestion_mean

Grand mean  120.67

 strategie         #availability #availabilityDistance
#distance
                         140.57               128.53
106.75

 strategie             #uniform
                         106.81


*** Least significant differences of means (5% level) ***

Table            strategie
rep.                  1980
d.f.                  7916
l.s.d.               2.450

12034  AGRAPH [METHOD=means] strategie
```




```
***** Analysis of variance *****

Variate: PreyDigestion_stdev

Source of variation     d.f.       s.s.       m.s.    v.r.  F pr.
strategie                  3 1590668.35  530222.78 6881.45  <.001
Residual                7916  609935.57      77.05
Total                   7919 2200603.92

 ***** Tables of means *****

Variate: PreyDigestion_stdev

Grand mean  18.346

 strategie         #availability #availabilityDistance
#distance
                           4.094                28.852
35.757

 strategie              #uniform
                           4.681


*** Least significant differences of means (5% level) ***

Table            strategie
rep.                  1980
```

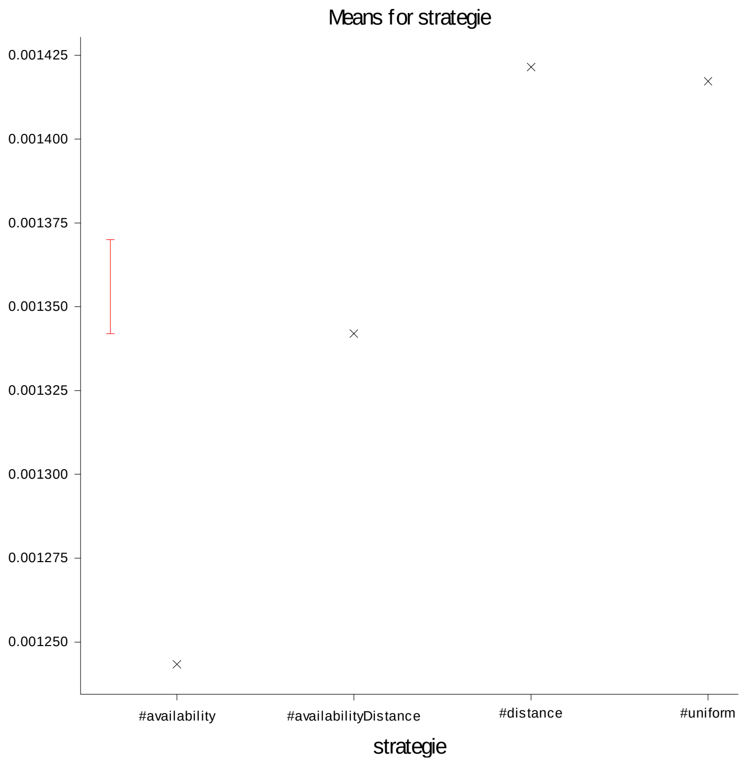
```
d.f.                  7916
l.s.d.              0.5469

12041  AGRAPH [METHOD=means] strategie
```



Appendix 2.2: Output analyses of variance on mean daily cadmium uptake

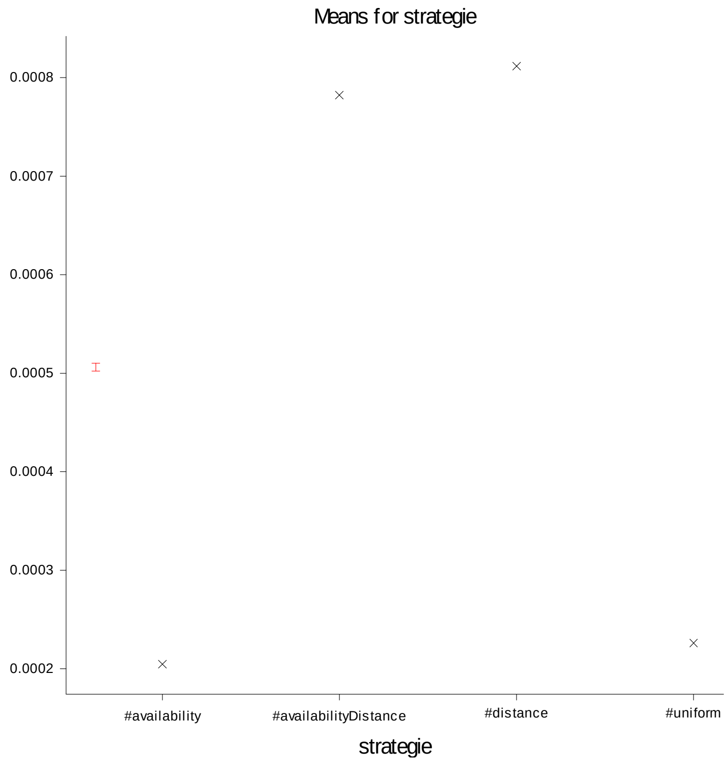
```
***** Analysis of variance *****

Variate: CdUptake_mean

Source of variation     d.f.       s.s.       m.s.    v.r.  F pr.
strategie                  3  4.145E-05  1.382E-05   17.77  <.001
Residual                7916  6.154E-03  7.774E-07
Total                   7919  6.195E-03


***** Tables of means *****

Variate: CdUptake_mean

Grand mean  0.0013560

 strategie         #availability #availabilityDistance
#distance
                    1.243338E-03         1.341962E-03
1.421531E-03
```

```
 strategie              #uniform
                    1.417255E-03


*** Least significant differences of means (5% level) ***

Table            strategie
rep.                  1980
d.f.                  7916
l.s.d.          0.00005493

5600  AGRAPH [METHOD=means] strategie
5601  "General Analysis of Variance."
5602  BLOCK "No Blocking"
5603  TREATMENTS strategie
5604  COVARIATE "No Covariate"
5605  ANOVA [PRINT=aovtable,information,means; FACT=32; FPROB=yes;
PSE=lsd; LSDLEVEL=5]\
5606   CdUptake_stdev
```




```
***** Analysis of variance *****

Variate: CdUptake_stdev

Source of variation     d.f.        s.s.        m.s.    v.r.  F pr.
strategie                  3   6.717E-04   2.239E-04 3541.94  <.001
```

```
Residual                7916  5.004E-04  6.321E-08
Total                   7919  1.172E-03


***** Tables of means *****

Variate: CdUptake_stdev

Grand mean  0.0005061

 strategie         #availability #availabilityDistance
#distance
                   2.045126E-04          7.823543E-04
8.117489E-04

 strategie              #uniform
                   2.258465E-04


*** Least significant differences of means (5% level) ***

Table            strategie
rep.                  1980
d.f.                  7916
l.s.d.          0.00001566

5607  AGRAPH [METHOD=means] strategie
5608  UNITS [NVALUES=*]
5609  DELETE [redefine=yes] _rest_
5610  READ [print=*;setnvalues=y] _rest_
5820  RESTRICT
strategie,P_w_hab,P_v_hab,P_s_hab,CdUptake_mean,CdUptake_stdev,\
5821  CdUptake_min,CdUptake_max; _rest_
5822
5823  "Multiple Linear Regression"
5824  MODEL CdUptake_mean
5825  TERMS [FACT=9] P_w_hab+P_v_hab
5826  FIT [PRINT=model,summary,estimates; CONSTANT=estimate;
FPROB=yes; TPROB=yes; FACT=9]\
5827   P_w_hab+P_v_hab
```


Means for strategie
0.0008
0.0007
0.0006
0.0005
0.0004
0.0003
0.0002
#availability
#availabilityDistance
#distance
#uniform
strategie

Appendix 3

Output regression analyses on foraging strategies

Appendix 3.1: Output regression analyses on uniform foraging strategy

```
***** Regression Analysis *****

 Response variate: CdUptake_mean
     Fitted terms: Constant + P_w_hab + P_s_hab


*** Summary of analysis ***

              d.f.          s.s.          m.s.      v.r.  F pr.
Regression       2  0.001349154    6.746E-04 878538.97  <.001
Residual      1977  0.000001518    7.678E-10
Total         1979  0.001350672    6.825E-07

Percentage variance accounted for 99.9
Standard error of observations is estimated to be 0.0000277

*** Estimates of parameters ***

                             estimate         s.e.   t(1977)  t pr.
Constant                   0.00002954   0.00000167     17.74  <.001
P_w_hab                     0.00338563   0.00000268   1265.33  <.001
P_s_hab                     0.00077750   0.00000268    290.58  <.001

7227  "Multiple Linear Regression"
7228  MODEL CdUptake_mean
7229  TERMS [FACT=9] P_w_hab+P_v_hab
7230  FIT [PRINT=model,summary,estimates; CONSTANT=estimate; FPROB=yes;
TPROB=yes; FACT=9]\
7231   P_w_hab+P_v_hab

***** Regression Analysis *****

 Response variate: CdUptake_mean
     Fitted terms: Constant + P_w_hab + P_v_hab


*** Summary of analysis ***

              d.f.          s.s.          m.s.      v.r.  F pr.
Regression       2  0.001349154    6.746E-04 878538.97  <.001
Residual      1977  0.000001518    7.678E-10
Total         1979  0.001350672    6.825E-07

Percentage variance accounted for 99.9
Standard error of observations is estimated to be 0.0000277

*** Estimates of parameters ***
```

```
                             estimate         s.e.   t(1977)  t pr.
Constant                   0.00080705   0.00000167    484.54  <.001
P_w_hab                     0.00260812   0.00000268    974.75  <.001
P_v_hab                    -0.00077750   0.00000268   -290.58  <.001

7232  "Multiple Linear Regression"
7233  MODEL CdUptake_mean
7234  TERMS [FACT=9] P_v_hab+P_s_hab
7235  FIT [PRINT=model,summary,estimates; CONSTANT=estimate; FPROB=yes;
TPROB=yes; FACT=9]\
7236   P_v_hab+P_s_hab

***** Regression Analysis *****

 Response variate: CdUptake_mean
     Fitted terms: Constant + P_v_hab + P_s_hab


*** Summary of analysis ***

              d.f.         s.s.         m.s.      v.r.  F pr.
Regression       2  0.001349154    6.746E-04 878538.97  <.001
Residual      1977  0.000001518    7.678E-10
Total         1979  0.001350672    6.825E-07

Percentage variance accounted for 99.9
Standard error of observations is estimated to be 0.0000277

*** Estimates of parameters ***

                             estimate         s.e.   t(1977)  t pr.
Constant                   0.00341517   0.00000167   2050.41  <.001
P_v_hab                    -0.00338563   0.00000268  -1265.33  <.001
P_s_hab                    -0.00260812   0.00000268   -974.75  <.001
```

Appendix 3.2: Output regression analyses on distance dependent foraging strategy

```
***** Regression Analysis *****

 Response variate: CdUptake_mean
     Fitted terms: Constant + P_w_hab + P_s_hab


*** Summary of analysis ***

              d.f.         s.s.         m.s.      v.r.  F pr.
Regression       2  0.001353296    6.766E-04 783507.62  <.001
Residual      1977  0.000001707    8.636E-10
Total         1979  0.001355004    6.847E-07

Percentage variance accounted for 99.9
Standard error of observations is estimated to be 0.0000294
```

```
*** Estimates of parameters ***

                              estimate         s.e.   t(1977)  t pr.
Constant                    0.00003338   0.00000177     18.90  <.001
P_w_hab                      0.00338964   0.00000284   1194.52  <.001
P_s_hab                      0.00077482   0.00000284    273.05  <.001

6997  "Multiple Linear Regression"
6998  MODEL CdUptake_mean
6999  TERMS [FACT=9] P_w_hab+P_v_hab
7000  FIT [PRINT=model,summary,estimates; CONSTANT=estimate; FPROB=yes;
TPROB=yes; FACT=9]\
7001   P_w_hab+P_v_hab

***** Regression Analysis *****

 Response variate: CdUptake_mean
     Fitted terms: Constant + P_w_hab + P_v_hab


*** Summary of analysis ***

              d.f.         s.s.         m.s.      v.r.  F pr.
Regression      2  0.001353296    6.766E-04 783507.62  <.001
Residual     1977  0.000001707    8.636E-10
Total        1979  0.001355004    6.847E-07

Percentage variance accounted for 99.9
Standard error of observations is estimated to be 0.0000294

*** Estimates of parameters ***

                              estimate         s.e.   t(1977)  t pr.
Constant                    0.00080820   0.00000177    457.53  <.001
P_w_hab                      0.00261481   0.00000284    921.47  <.001
P_v_hab                     -0.00077482   0.00000284   -273.05  <.001

7002  "Multiple Linear Regression"
7003  MODEL CdUptake_mean
7004  TERMS [FACT=9] P_v_hab+P_s_hab
7005  FIT [PRINT=model,summary,estimates; CONSTANT=estimate; FPROB=yes;
TPROB=yes; FACT=9]\
7006   P_v_hab+P_s_hab

***** Regression Analysis *****

 Response variate: CdUptake_mean
     Fitted terms: Constant + P_v_hab + P_s_hab


*** Summary of analysis ***

              d.f.         s.s.         m.s.      v.r.  F pr.
Regression      2  0.001353296    6.766E-04 783507.62  <.001
Residual     1977  0.000001707    8.636E-10
Total        1979  0.001355004    6.847E-07
```

```
Percentage variance accounted for 99.9
Standard error of observations is estimated to be 0.0000294

*** Estimates of parameters ***

                             estimate         s.e.   t(1977)  t pr.
Constant                   0.00342301   0.00000177   1937.81  <.001
P_v_hab                   -0.00338964   0.00000284  -1194.52  <.001
P_s_hab                   -0.00261481   0.00000284   -921.47  <.001
```

Appendix 3.3: Output regression analyses on availability dependent foraging strategy

```
***** Regression Analysis *****

 Response variate: CdUptake_mean
     Fitted terms: Constant + P_w_hab + P_s_hab


*** Summary of analysis ***

              d.f.         s.s.         m.s.      v.r.  F pr.
Regression       2    0.0058712    2.936E-03  71732.72  <.001
Residual      7917    0.0003240    4.092E-08
Total         7919    0.0061952    7.823E-07

Percentage variance accounted for 94.8
Standard error of observations is estimated to be 0.000202



*** Estimates of parameters ***

                             estimate         s.e.   t(7917)  t pr.
Constant                  -0.00022525   0.00000608    -37.05  <.001
P_w_hab                     0.00361535   0.00000977    370.16  <.001
P_s_hab                     0.00112846   0.00000977    115.54  <.001

6322  "Multiple Linear Regression"
6323  MODEL CdUptake_mean
6324  TERMS [FACT=9] P_w_hab+P_v_hab
6325  FIT [PRINT=model,summary,estimates; CONSTANT=estimate; FPROB=yes;
TPROB=yes; FACT=9]\
6326   P_w_hab+P_v_hab

***** Regression Analysis *****

 Response variate: CdUptake_mean
     Fitted terms: Constant + P_w_hab + P_v_hab


*** Summary of analysis ***

              d.f.         s.s.         m.s.      v.r.  F pr.
Regression       2    0.0058712    2.936E-03  71732.72  <.001
```

```
Residual      7917    0.0003240    4.092E-08
Total         7919    0.0061952    7.823E-07

Percentage variance accounted for 94.8
Standard error of observations is estimated to be 0.000202

*** Estimates of parameters ***

                             estimate         s.e.   t(7917)  t pr.
Constant                   0.00090321   0.00000608    148.56  <.001
P_w_hab                     0.00248689   0.00000977    254.62  <.001
P_v_hab                    -0.00112846   0.00000977   -115.54  <.001

6327  "Multiple Linear Regression"
6328  MODEL CdUptake_mean
6329  TERMS [FACT=9] P_v_hab+P_s_hab
6330  FIT [PRINT=model,summary,estimates; CONSTANT=estimate; FPROB=yes;
TPROB=yes; FACT=9]\
6331   P_v_hab+P_s_hab

***** Regression Analysis *****

 Response variate: CdUptake_mean
     Fitted terms: Constant + P_v_hab + P_s_hab


*** Summary of analysis ***

              d.f.         s.s.         m.s.      v.r.  F pr.
Regression       2    0.0058712    2.936E-03  71732.72  <.001
Residual      7917    0.0003240    4.092E-08
Total         7919    0.0061952    7.823E-07

Percentage variance accounted for 94.8
Standard error of observations is estimated to be 0.000202


*** Estimates of parameters ***

                             estimate         s.e.   t(7917)  t pr.
Constant                   0.00339010   0.00000608    557.59  <.001
P_v_hab                    -0.00361535   0.00000977   -370.16  <.001
P_s_hab                    -0.00248689   0.00000977   -254.62  <.001
```

Appendix 3.4: Output regression analyses on availability and distance dependent foraging strategy

```
 ***** Regression Analysis *****

 Response variate: CdUptake_mean
     Fitted terms: Constant + P_w_hab + P_s_hab
```

```
*** Summary of analysis ***

              d.f.         s.s.         m.s.      v.r.  F pr.
Regression       2   0.00159385    7.969E-04  28946.17  <.001
Residual      1977   0.00005443    2.753E-08
Total         1979   0.00164827    8.329E-07

Percentage variance accounted for 96.7
Standard error of observations is estimated to be 0.000166

*** Estimates of parameters ***

                             estimate         s.e.   t(1977)  t pr.
Constant                  -0.00036945   0.00000997    -37.04  <.001
P_w_hab                     0.0037994    0.0000160    237.14  <.001
P_s_hab                     0.0013348    0.0000160     83.31  <.001

6552  "Multiple Linear Regression"
6553  MODEL CdUptake_mean
6554  TERMS [FACT=9] P_w_hab+P_v_hab
6555  FIT [PRINT=model,summary,estimates; CONSTANT=estimate; FPROB=yes;
TPROB=yes; FACT=9]\
6556   P_w_hab+P_v_hab

***** Regression Analysis *****

 Response variate: CdUptake_mean
     Fitted terms: Constant + P_w_hab + P_v_hab


*** Summary of analysis ***

              d.f.         s.s.         m.s.      v.r.  F pr.
Regression       2   0.00159385    7.969E-04  28946.17  <.001
Residual      1977   0.00005443    2.753E-08
Total         1979   0.00164827    8.329E-07

Percentage variance accounted for 96.7
Standard error of observations is estimated to be 0.000166

*** Estimates of parameters ***

                             estimate         s.e.   t(1977)  t pr.
Constant                   0.00096536   0.00000997     96.79  <.001
P_w_hab                     0.0024646    0.0000160    153.83  <.001
P_v_hab                    -0.0013348    0.0000160    -83.31  <.001

6557  "Multiple Linear Regression"
6558  MODEL CdUptake_mean
6559  TERMS [FACT=9] P_v_hab+P_s_hab
6560  FIT [PRINT=model,summary,estimates; CONSTANT=estimate; FPROB=yes;
TPROB=yes; FACT=9]\
6561   P_v_hab+P_s_hab

***** Regression Analysis *****
```

```
 Response variate: CdUptake_mean
     Fitted terms: Constant + P_v_hab + P_s_hab


*** Summary of analysis ***

              d.f.         s.s.         m.s.      v.r.  F pr.
Regression       2   0.00159385    7.969E-04  28946.17  <.001
Residual      1977   0.00005443    2.753E-08
Total         1979   0.00164827    8.329E-07

Percentage variance accounted for 96.7
Standard error of observations is estimated to be 0.000166

*** Estimates of parameters ***

                              estimate         s.e.   t(1977)  t pr.
Constant                    0.00342997   0.00000997    343.91  <.001
P_v_hab                      -0.0037994    0.0000160   -237.14  <.001
P_s_hab                      -0.0024646    0.0000160   -153.83  <.001
```