# Egg laying on patchy resources and the importance of spatial scale

by

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Things do not, in general, run around with their measures stamped on them like the capacity of a freight car; it requires a certain amount of investigation to discover what their measures are. – *Norbert Wiener*, 1921 **Abstract** Recent ecological studies have started integrate to spatial variation of ecological patterns into the study design rather than treating it as a statistical nuisance. In particular, the influence of the spatial scale at which ecological patterns are measured has gained much attention over the last two decades. Since, for example, sensory abilities as well as the ability to disperse vary among species, different species-specific responses to heterogeneous environments may be expected.

Plant-insect interactions in heterogeneous landscapes, in particular, have gained much attention as experiments can be conducted on a more accessible scale and may yield new applications for crop and horticulture. Two hypotheses that describe insect herbivore aggregations in the landscape are: a) the resource concentration hypothesis which predicts higher numbers of specialist insect herbivores per unit biomass in dense and pure stands of their host plant, and b) the resource dilution hypothesis which predicts that insect herbivore numbers will decline with increasing plant density.

I investigated resource dilution and resource concentration patterns in egg distributions of *Pieris rapae* and *Tyria jacobaeae* in relation to host plant density, which I defined differently by applying varying spatial scales of measurement. I also tested for effects of host plant density and the scale of measurement on flight patterns of *P. rapae* females. In a natural population of *Lepidium oleraceum* I investigated effects of scale of measurement of plant density, as well as white rust and hymenopteran parasitoids on *P. rapae* egg and larvae distributions. In a separate experiment I tested for any potential effects of arthropod predators on *P. rapae* egg distributions at different spatial scales.

The number of *P. rapae* eggs per plant conformed to predictions made by the resource dilution hypothesis. However, such a pattern was only found for fine scale plant density but not for medium or coarse scale plant density. In contrast, the number of *T. jacobaeae* egg clutches per plant showed a resource concentration pattern for medium scale plant density but not for fine or coarse scale plant density. However, this result occurred only in one of two experiments with *T. jacobaeae*. A resource dilution pattern was also found for the number of visits per plant by *P. rapae* females at both coarse and fine scale measurement. Female flight paths were less directional when plants were present in the study area during fine scale observations and butterflies were attracted to areas containing host plants. Flight observations at coarse scale did not show any change in turning behaviour and butterflies moved at random across the study area. No effect of parasitism, or predation through arthropods was found on the distribution of *P. rapae* eggs. However, infection by white rust lead to a decreased number of eggs per plant in the natural *L. oleraceum* population.

The results of my thesis underline the importance of spatial scale in ecological studies. Careful thought should be given to the scale of measurement and method of abstraction when describing real world patterns.

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Chapter 1

# General Introduction

## **1.1** Spatial scales in ecological studies

In general, ecological patterns are the result of different processes that operate at varying spatial and temporal scales (Maurer, 1999), thus making scale an important factor in ecological studies (Levin, 1992; Cadotte and Fukami, 2005; Currie, 2007).

In particular, spatial scale is of great importance when measuring species distributions and dispersal processes in a heterogeneous landscape (Banks, 1998; Chust et al., 2004; Kumar et al., 2006). For example, in studies on the western harvester ant, *Pogonomyrmex occidentalis*, Chust et al. (2004) found that seed harvesting was affected differently by fine and coarse scale processes. While individual response to vegetation cover affected seed harvesting at finer spatial scales, varying degrees of predation on individual ants lead to coarse scale differences between ant colonies.

O'Neill et al. (1986) and Wiens (1989) proposed three variables to define spatial scale in ecological studies: extent, grain and lag (see also Wiens, 1990). Extent corresponds to the whole of the study area from which the samples are taken. The grain of a study corresponds to, for example, the size of the individual sampling squares or the resolution at which the environment is treated as homogeneous. The distance between those individual sampling squares is defined as the lag (Figure 1.1a, b). Defining a study's extent and grain, however, can have important implications on the outcome of the study. As shown in figure 1.1c, increasing the study extent could lead to including new resource patches into the sampling design. In addition,

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increasing the grain would cause a decrease of variance between samples while it would enlarge the variance within samples (Wiens, 1989). Increasing grain size would also add the difficulty of reduced replication for the sample design. The definition of 'isolated' or 'concentrated' would potentially change as well, as these are, in general, scale dependent phenomena (Hartley and Kunin, 2003). Choosing an appropriate scale in relation to study species and the question asked is therefore important.

In the past many studies used a similar set of scales, thus ignoring fundamental differences between study systems (Kareiva and Anderson, 1988). However, saying that only one extent or grain would be correct to use for a certain pattern would be equally wrong as data collected at different scales would add to the overall knowledge (Blackburn and Gaston, 2002). Nevertheless, study results should always be seen in relation to the set of scales they were measured at (Levin, 1992; Schneider, 2001). Using a data set collected at one scale to predict patterns at another scale can become a challenge and may introduce some degree of error into the predictions (Turner et al., 1989a,b). A better understanding of the relationships between fine and coarse scale processes, however, can help to increase the robustness of cross-scale predictions (Kunin et al., 2000; Gao et al., 2001; Morales and Ellner, 2002).

In the search for biologically meaningful scales many studies focus on the hierarchical levels of a study system. Ives et al. (1993), for example, investigated the effect of lady beetles preying on aphids among fireweed stems, whereby they followed the distribution of individual lady beetles on individual fireweed stems, the population of lady beetles on individual fireweed stems, as well as the distribution of lady beetle populations on populations of fireweed stems in response to different sized aphid colonies. A somewhat similar hierarchical structure was chosen by Rabasa et al. (2005) by measuring the number of eggs laid by the butterfly *Iolana iolas* among fragmented patches of their host plant *Colutea hispanica*. The three nested levels used in their study where the fruit-level: fruits within plants, the plant-level: plants within patches, and the patch-level. Kotliar and Wiens (1990) proposed a hierarchical framework for identifying organism-specific patch structure. The lowest spatial level where an organism responds to resource structure, named as 'grain' by Kotliar and Wiens's definition, in Rabasa et al.'s study would be the individual fruit. The 'extent' as used in the sense of Kotliar and Wiens would correspond to



(a) Study grain and lag.



(b) Increased grain and reduced lag, while extent remains the same.



(c) Change of study extent.

Figure 1.1: Changing grain and lag of a study (a, then b) can lead to crucial differences in the results as more (or less) data points are sampled; changing the extent of a study (c) can incorporate new resource patches, but could potentially also change the way a 'concentrated' resource is defined.

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the upper-most spatial scale at which an organism responds to its environment, e.g. the absolute range a female butterfly covers during its life history. Stepping away from more anthropogenic definitions of the scale of measurement, this approach requires a more careful consideration of an organism's individual behaviour and life history (O'Neill et al., 1986). Utilising such organism-specific information, Girvetz and Greco (2007) were able to describe patch structure of potential nesting habitat across different spatial scales for the western yellow-billed cuckoo, *Coccyzus americanus occidentalis*.

The implementation of hierarchical concepts of ecosystems, however, has also brought up the need for new ways to analyse such multi-level data sets. One approach utilises a method commonly used in psychology and health-related studies: Hierarchical liner models (HLM, also known as linear mixed-effect models - LME; Pinheiro and Bates, 2000; Gelman and Hill, 2007). For example a study would focus on comparing the performance of students in a class, between classes at a school, between schools in a district and so forth. In biological terms, a study could focus on measuring the amount of herbivory among individual leaves on a plant, between plants in a patch and between different patches in a region. A methodological example for using HLMs to analyse nested ecological data sets was published by McMahon and Diez (2007). However, the HLM approach requires distinct measures, such as counts of insect eggs on a leaf, and does not work for variables that are measured against a continuum, i.e. temperature gradient or mineral composition of soil along a stretch of farm land. HLMs do not contain any information of the explicit spatial context from which the samples were taken, however, HLMs are able to deal with spatial data in a spatial implicit way by ordering variables as belonging to a certain group at a certain hierarchical level

Spatial explicit methods take a more continuous view of scale and variation. An example for spatial explicit models are generalised least squares (GLS) models. GLSs have the ability to incorporate spatial information by including a spatial variance component (Venables and Ripley, 1997; Pinheiro and Bates, 2000). The spatial variance component provides information on how a variable changes with distance between samples. This method is commonly applied in geological studies where for example mineral content of rock is measured at different locations. Samples taken close together usually have more similar values than samples that are further apart. This phenomenon is called spatial auto–correlation (Legendre, 1993). Spatial auto– correlation should be considered when analysing data that was taken in some sort of spatial context, as the presence of auto-correlation may introduce a sort of pseudo– replication due to non–independence of samples (Legendre et al., 2002). Statistical measures of spatial auto–correlation are, for example, the 'Moran's I' and 'Geary's c' auto–correlation coefficients (Dutilleul and Legendre, 1993).

However, a restriction of the least squares method is that the sample residuals should be normally distributed, which may make its application to count data unsuitable (Carl and Kuehn, 2007). Nevertheless, a range of methods have been developed to deal with count data in spatial data sets (e.g. Bjørnstad and Bascompte, 2001; Christensen and Waagepetersen, 2002; Dalthorp, 2004; Legendre et al., 2004; Chiang, 2005; Dormann, 2007). A recent review by Dormann et al. (2007) also compares the ability of different linear models to deal with spatial auto–correlation in species distribution data.

Many previous studies investigated the distributions of species in heterogeneous landscapes by focusing on measuring patterns at a single spatial scale, thus many hypotheses trying to explain patterns of species distributions are based on single– scale observations. However, studies have shown that species distribution patterns may be the results of different processes, which may operate at varying spatial scales. Do hypotheses describing species distributions apply regardless of which spatial scale a pattern is observed? Is it possible to up or down scale the predictions made by such hypotheses?

# 1.2 Resource concentration and resource dilution – Two opposing hypotheses

In 1972, Tahvanainen and Root published data from a three–year project where they investigated the distribution of *Phyllotreta cruciferae*, a flea beetle, among cabbage crops (*Brassica oleracea*). The results showed that *Phyllotreta* beetles gained higher numbers in monocultures of cabbage compared to cabbage fields that were inter–planted with tomato and tobacco plants. In a second article Root (1973) compared herbivore loads (numbers of insect herbivores per unit plant biomass) among Brassi-

caceae crops of differing diversity, and found that specialist insect herbivores gained dis–proportionally high numbers on host plants that grew in dense and less diverse patches. Despite the predictions of the natural enemies hypothesis, predation and parasitism in these experiments was low in both diverse and monocultures, and therefore unlikely to be responsible for the increased number of specialist herbivores in the less diverse stands (Tahvanainen and Root, 1972; Root, 1973). Root suggests that specialist insect herbivores having once encountered a dense stand of their host plant would remain longer among plants of this resource patch and produce offspring. A reduced emigration rate and additional offspring would lead to disproportionately higher loads of the herbivore.

In experiments with *Phyllotreta cruciferae* and *P. striolata* Kareiva (1982, 1985) discovered that a decrease in host plant patch size triggered an increase in emigration and lead to low beetle densities in smaller host plant patches. The article also describes that host finding success by *Phyllotreta* beetles was significantly reduced when plants where separated by more than two metres. Higher plant diversity in the experimental fields also reduced host finding success. A study by Matter (1997) on population density of the red milkweed beetle, *Tetraopes tetraophthalmus*, found that the number of beetles increased with patch size. However, the main driver of the observed resource concentration pattern was found to be the emergence of offspring in host plant patches and longer residence time of adults, rather than increased adult dispersal towards high density host plant patches.

Habitat fragmentation and resource patchiness have previously been suggested to stabilise predator–prey dynamics (e.g. May, 1978). However, evidence provided by Kareiva (1987) suggests that such generalisations may not always hold true, and that predictions made on population dynamics of a certain species should focus more on the species–specific response to habitat fragmentation.

Although the resource concentration hypothesis was found to apply for some specialist insect herbivore species (e.g. Ralph, 1977; Turchin, 1988; Kunin, 1999), several studies discovered no consistent pattern (e.g. Bach, 1980; Boiteau, 1984; Coll and Bottrell, 1994) or even a reversed pattern to that predicted by the resource concentration hypothesis (e.g. Pimentel, 1961; Solomon, 1981; Thompson, 1995). Data published by Otway et al. (2005) on plant and insect communities in a semi–natural setting also indicated a strong negative trend of insect herbivore load per unit biomass

with increasing host plant biomass.

Observation of egg distributions of the small cabbage white butterfly, *Pieris rapae*, by Cromartie (1975) and Root and Kareiva (1984) indicated a decline in the number of eggs *per plant* with increasing plant density. Based on his studies on oviposition behaviour of *P. rapae* Yamamura (1999) proposed the resource dilution hypothesis, which states that herbivores use sparsely populated hosts more efficiently. Yamamura (1999) found that the number of individual *P. rapae* eggs declined with increasing plant density when egg number was measured relative to number of plants in a host plant patch (eggs per plant). However, the total number of eggs was higher in host plant patches of higher density (eggs per patch). This increase in the total number of eggs with increasing plant density within a patch, though, was not sufficient to accumulate a disproportional higher number of eggs among high density patches.

This egg distribution pattern, as described by Root and Kareiva (1984), is the result of an intricate flight behaviour, whereby female *P. rapae* butterflies retain their directionality during oviposition flight and pass over several suitable host plants between consecutive oviposition events. A female cabbage white butterfly therefore ends up distributing her offspring over a wider area, a behaviour which Root and Kareiva called the 'risk-spreading syndrome'. A theory on risk-spreading was previously developed by den Boer (1968). Root and Kareiva use the term in sense of an evolutionary mechanism that maximises offspring survival by assuring the survival of some offspring in case of patch extinction.

Figure 1.2 summarises three possible responses to resource density. While the resource concentration hypothesis (positive correlation between number of eggs per plant and plant density; Figure 1.2a) and the resource dilution hypothesis (negative correlation between number of eggs per plant and plant density; Figure 1.2c) predict two opposing patterns, the pattern predicted by the ideal free distribution (no correlation between number of eggs per plant and plant density; Figure 1.2b) lies in between those predicted by the resource concentration and resource dilution hypotheses.

The concept of the ideal free distribution, first described by Fretwell and Lucas (1970), is based on a set of key assumptions: resources are distributed in discrete patches and the quality of a resource patch does not change over time; foragers



Figure 1.2: Shown are examples of three possible egg distributions pattern: a) a resource concentration pattern, where the number of eggs per plant increases with increasing plant density, b) an ideal free distribution pattern showing no response to plant density, and c) a resource dilution pattern, where the number of eggs per plant declines with increasing plant density.

are equal in competition and have full knowledge of distribution and quality of resource patches; foragers are free to settle and move between resource patches at no extra cost; and a foragers individual resource consumption decreases as the number of competitor in the same patch increases. Like to the resource concentration and resource dilution hypotheses, the concept of the ideal free distribution has important implications for understanding population dynamics among different habitat or resource patches. The ideal free distribution predicts that foragers will distribute themselves according to the quality and availability of resources in such a way as to maximise profitability. A recent review on the ideal free distribution theory by Křivan et al. (2008) further summarises the development of the ideal free distribution concept. Empirical evidence supporting the ideal free distribution was found only in recent years (Haugen et al., 2006; Morris, 2006).

Different species may follow different distribution patterns, as they may rely on sensory modalities such as vision or olfaction to varying extents. In their simulation study on three different search modes Bukovinszky et al. (2005) found that contact searchers would distribute themselves among host plants independently to patch size or plant density. Their distribution would than follow a similar pattern to the ideal free distribution (Figure 1.2b). For searchers that rely mainly on olfac-

tion during host plant search and have the tendency to remain within a patch for an extended period of time, a resource concentration pattern may best describe their distribution (Figure 1.2a). Visual searchers which are also able to travel more freely and over relative long distances between host plant patches, may distribute themselves according to a resource dilution pattern (Figure 1.2c).

Similar results for the influence of vision and olfaction have been found in a simulation study by Barritt (2008), who investigated the effect of vision and olfaction in conjunction with different movement patterns on egg distributions of *P. rapae*. The results suggest that the observed response to resource density may depend on the extent to which an individual forager utilises visual or olfactory cues, which may also lead to different patterns at different scales of measurement. However, distribution patterns of species may be modified regardless of their reliance on different sensory modalities due to species–specific movement behaviours (Jones, 1977; Root and Kareiva, 1984; Bukovinszky et al., 2005).

Responses of insect herbivores to host plant density have been shown to be species-specific, and often depend on individual movement behaviour. Since different sensory modalities may apply to cues at different spatial scales, whether a resource concentration, resource dilution pattern or even a neutral response (such as optimal foraging) may be observed could therefore be dependent on the scale of observation.

While the resource concentration and resource dilution hypotheses apply a more herbivore - centric view, I would like highlight another set of hypotheses developed independently by Janzen (1970) and Connell (1971), and later on merged as the Janzen – Connell hypothesis by Clark and Clark (1984). The Janzen – Connell hypothesis postulates two mechanisms that describe how the high diversity of plant species in tropical forest communities could be maintained. The key assumption made is that seed and seedling mortality decreases with increasing distance from the adult plant. This positive change in the survival rate with increasing distance from the adult plant is thought to be driven by density - responsive, as well as distance - responsive specialist insect herbivores or plant pathogens. Density - responsive specialist herbivores are thought to focus on areas of high seed or seedling density where foraging success may be highest. Distance - responsive specialist herbivores, however, may be attracted to adult plants and take advantage of the high number of seeds or seedlings that are in close proximity to the parent plant. Evidence collected by Burkey (1994), however, did not support the predictions made by the Janzen – Connell hypothesis. However, Burkey acknowledged that responses such as those predicted by the Janzen – Connell hypothesis may be species or scale dependent. Supporting the results from Burkey's study, Schupp (1992) also found that the scale of measurement affected seed survival rates. Seed predators only affected seed survival at very local scales but not at population-level scales, therefore questioning a generalisation of the effects of distance -, and density - responsive herbivores on seed survival rates.

## **1.3** Describing animal movement patterns

The movement behaviour of individual species is a crucial factor affecting species distributions and population processes (Fahrig and Paloheimo, 1988; Fahrig, 1998, 2003). In heterogeneous landscapes resources are often distributed in an irregular manner and different species may show varying responses to habitat fragmentation and resource patchiness (Root and Kareiva, 1984; Kunin, 1999; Szabo and Meszena, 2006).

In 1977 Jones published a detailed model simulating *P. rapae* searching behaviour and egg distributions. Later on, this model was successfully applied to predict egg distributions of *P. rapae* butterflies at larger temporal and spatial scales (Jones et al., 1980). However, empirical data showed that flight behaviour differed between *P. rapae* populations in Canada and Australia (Jones, 1977). These differences in behaviour might be related to adaptation to varying climatic factors as well as differences in host plant distribution and abundance (Jones, 1987). This example shows, that knowledge about the movement of animals can be essential to better understand population processes.

Movement models have been essential to test hypotheses on movement parameters and behaviours. The simplest movement model, the random walk (RW), traces its roots back to observations by the botanist Brown (1828), who studied the irregular movement of pollen particles (later named as Brownian Motion). The direction of movement in a basic RW is unbiased and random for each step. In this case a RW is essentially Brownian motion, which is found for standard diffusion models (e.g. heat diffusion).

The day-to-day movement of *P. rapae* butterflies was described by Jones et al. (1980) to follow the pattern of a random walk. However, the flight pattern of ovipositing female cabbage white butterflies was highly directional and more similar to a correlated random walk (CRW) (Kareiva and Shigesada, 1983). As directional persistence (Patlak, 1953) is a common feature of animal movement paths it is not surprising that correlated random walks have been applied to describe animal movement patterns in a range of studies (e.g. Bovet and Benhamou, 1988; Crist and MacMahon, 1991; Austin et al., 2004; Schtickzelle et al., 2007). The main distinguishing feature of a correlated random walk is that the angle of turn of each step is dependant on the turning angle of the previous step (Turchin, 1998). As a result turning angles of a CRW tend to be concentrated around the main heading, for example 0°. The topic of random walks in biological studies has recently also been reviewed by Codling et al. (2008).

Other movement models include, for example, the biased random walk, where an external factor affects the distribution of turning angles (Marsh and Jones, 1988; Turchin, 1998), or Lévy walks (Viswanathan et al., 1996, 2000; Reynolds, 2006), where the distribution of step length is tailed, causing intermitted long–range movements. Benichou et al. (2006) and Benhamou (2007) have argued, however, that Lévy walks may be generated by random walk models that take into account environmental factors for determining turning behaviour (see also Benhamou, 2008; Reynolds, 2008).

Taking the response of a species to its environment into account may also provide a better understanding of movement patterns of animals (Lima and Zollner, 1996; Van Dyck and Baguette, 2005; Casellas et al., 2008). In particular, varying sensory abilities between species may lead to differences in responses to resource distribution. For example, by comparing search behaviour of cabbage aphids, the cabbage white butterfly and the diamondback moth Bukovinszky et al. (2005) were able to show that these three species may use senses such as vision and olfaction to varying extents. The cabbage aphid, *Brevicoryne brassicae*, is thought to rely on visual and also on olfactory cues for host plant detection (Nottingham et al., 1991; Nottingham and Hardie, 1993; Compton, 2002). *Pieris rapae* is thought to heavily rely on visual cues for host plant finding, while the exact role of olfaction during

host plant search is unclear (reviewed in Hern et al., 1996). In contrast, the diamondback moth, *Plutella xylostella*, responds strongly to host plant odours for host selection (Reddy et al., 2004). Studies have shown that cabbage aphids mainly rely on passive transport in the air column for long range dispersal (Compton, 2002), while cabbage white butterflies frequently move between host plants that are dispersed over a wider area (Root and Kareiva, 1984). The diamondback moth has been shown to mainly remain within a patch of host plants and only move between plants of that patch (Justus and Mitchell, 1996).

## **1.4** Study aim and chapter overview

The aim of my study is to describe how ecological patterns may change depending on the spatial scale that is used to measure the pattern. In particular, I will investigate the way insect herbivores distribute their offspring among different sized groups of their host plants. The observed response, e.g. number of eggs per plant, will be measured by using different spatial scales to define plant density within a certain group of host plants. I expect varying responses to different scales of measurement as the scale at which an insect herbivore responds to its environment may be set for a certain type of behaviour, but its perceptual scale might not correspond equally to all scales of measurement applied on the study system. Although the experiments undertaken as part of my thesis mainly focus on one stage in the life of the study organisms (e.g. insect eggs), and are primarily focused on single species responses to resource distributions, I aim to provide evidence that will further the understanding of the influence of spatial scales of measurement on population dynamics.

What follows is a brief description of the aims for each data chapter. As some of the chapters were written up to more closely match the style of journal publications, some repetition between chapters may occur. Each chapter also has a separate reference section that contains all references cited in the chapter. Similar to the references, each chapter contains a separate appendix section.

#### Chapter two: Patterns of egg distributions and the importance of spatial scale

In this chapter I will quantify egg distributions of the small cabbage white butterfly, *Pieris rapae*, and the cinnabar moth, *Tyria jacobaeae*, to test whether a change in the scale of measurement alters observed oviposition patterns. In particular, I will use groups of host plants of varying density to investigate whether low or high density plants will gain higher numbers of eggs per plant. I will define plant density differently by using three different spatial scales of measurement (grain) for each experiment. In addition, I will test for effects of plant size, spatial location, and for *T. jacobaeae* flowering status on the number of eggs laid. I expect to see a decline in the number of eggs per plant with increasing plant density for *P. rapae* egg distributions. As mentioned earlier, such a pattern was found by previous studies on *P. rapae* egg distributions. In contrast, I expect to observe an increase in the number of eggs per plant with increasing plant density for *T. jacobaeae* egg distributions. However, I expect both patterns to change depending at which spatial scale it is being observed.

#### Chapter three: Influence of host plant density on flight paths of *Pieris rapae* females measured at multiple scales

Here I will investigate how flight behaviour of *P. rapae* females may correspond to observed egg distributions. Therefore I will observe and map flight paths of *P. rapae* females over groups of host plants of different density, and will apply a fine and a coarse scale grid to measure path characteristics. I will analyse path segments based on whether they are above the area encompassed by the groups of host plants or outside those areas. I expect *P. rapae* females to respond to high or low plant density in a similar way. Visits to areas containing plants are expected to be of equal probability as to areas without plants. In addition, I do not expect path characteristics such as the angle of turn to change upon encountering areas containing plants.

# Chapter four: Occurrence of *Pieris rapae* on *Lepidium oleraceum* and interactions with white rust and parasitoids

The aim of this chapter is to investigate egg and larvae distributions of *P. rapae* in a natural population of cook's scurvy grass, *Lepidium oleraceum*. This endangered coastal cress is also susceptible to infection by white rust, *Albugo candida*. In addition, a hymenopteran parasitoid of *P. rapae Cotesia rubecula*, is present on the island where the population of cook's scurvy grass is found. Apart from focusing on the effect of plant size and plant density I will also analyse how white rust infection and parasitoids may affect *P. rapae* egg and larvae distributions. Part of the data analysed in this chapter, namely size and condition of *Lepidium* plants, was collected by the Department of Conservation (New Zealand).

#### Appendix I: Effect of birds and arthropods on Pieris rapae egg distributions

To further describe processes that may have an affect on egg distributions of *P. rapae* I will investigate the effect of presence or absence of arthropod predators on the number of *P. rapae* eggs in a field based experiment. The host plants for this experiment will be arranged in groups that will allow me to analyse the data based on different plant densities at two different scales of measurement. I will apply different treatments to different groups of host plants where I will: exclude all arthropods, open control without exclusion of arthropods. In addition, I will deter any birds from foraging among certain treatments to investigate any indirect effects on egg predation. However, as I was not able to show any evidence of egg predation in my field trials I have excluded these results from the main body of my thesis.

## References

- Austin, D., W. Bowen, and J. McMillan, 2004. Intraspecific variation in movement patterns: modeling individual behaviour in a large marine predator. *Oikos* **105**:15–30.
- Bach, C. E., 1980. Effects of plant density and diversity on the population dynamics of a specialist herbivore, the striped cucmber beetle, *Acalymma vittata*. *Ecology* **61**:1515–1530.
- Banks, J. E., 1998. The scale of landscape fragmentation affects herbivore response to vegetation heterogeneity. *Oecologia* **117**:239–246.
- Barritt, J., 2008. Simulation of the effects of movement patterns and resource density on the egg distribution of *Pieris rapae* (Lepidoptera) at multiple spatial scales. Master's thesis, School of Biological Sciences, Victoria University of Wellington, New Zealand.
- Benhamou, S., 2007. How many animals really do the Lévy walk? *Ecology* 88:1962–1969.
- Benhamou, S., 2008. How many animals really do the Lévy walk? reply. Ecology 89:2351-2352.
- Benichou, O., C. Loverdo, M. Moreau, and R. Voituriez, 2006. Two-dimensional intermittent search processes: An alternative to Lévy flight strategies. *Physical Review E: Statistical Nonlinear and Soft Matter Physics* 74.
- Bjørnstad, O. N. and J. Bascompte, 2001. Synchrony and second-order spatial correlation in hostparasitoid systems. *The Journal of Animal Ecology* **70**:924–933.
- Blackburn, T. M. and K. J. Gaston, 2002. Scale in macroecology. *Global Ecology and Biogeography* **11**:185–189.
- Boiteau, G., 1984. Effect of planting date, plant spacing, and weed cover on populations of insects, arachnids, and entomophthoran fungi in potato fields. *Environmental Entomology* **13**:751–756.
- Bovet, P. and S. Benhamou, 1988. Spatial analysis of animals' movements using a correlated random walk model. *Journal of Theoretical Biology* **131**:419–433.
- Brown, R., 1828. A brief account of microscopical observations made in the months of june, and august, 1827, on the particle contained in the pollen of plants; and on the general existence of active molecules in organic and inorganic bodies. *London, Edinburgh and Dublin Philosophical Magazine and Journal of Science* **4**:161.
- Bukovinszky, T., R. P. J. Potting, Y. Clough, J. C. van Lenteren, and L. E. M. Vet, 2005. The role of preand post-alighting detection mechanisms in the responses to patch size by specialist herbivores. *Oikos* 109:435–446.

- Burkey, T. V., 1994. Tropical tree species diversity: a test of the Janzen-Connell model. *Oecologia* **97**:533 540.
- Cadotte, M. W. and T. Fukami, 2005. Dispersal, spatial scale, and species diversity in a hierarchically structured experimental landscape. *Ecology Letters* **8**:548–557.
- Carl, G. and I. Kuehn, 2007. Analyzing spatial autocorrelation in species distributions using gaussian and logit models. *Ecological Modelling* **207**:159–170.
- Casellas, E., J. Gautrais, R. Fournier, S. Blanco, M. Combe, V. Fourcassie, G. Theraulaz, and C. Jost, 2008. From individual to collective displacements in heterogeneous environments. *Journal of Theoretical Biology* 250:424–434.
- Chiang, C. Y., 2005. Multidimensional scale types and invariant multivariate statistics. *British Journal of Mathematical and Statistical Psychology* **58**:83–95.
- Christensen, O. F. and R. Waagepetersen, 2002. Bayesian prediction of spatial count data using generalized linear mixed models. *Biometrics* 58:280–286.
- Chust, G., J. L. Pretus, D. Ducrot, and D. Ventura, 2004. Scale dependency of insect assemblages in response to landscape pattern. *Landscape Ecology* **19**:41–57.
- Clark, D. A. and D. B. Clark, 1984. Spacing dynamics of a tropical rain forest tree Evaluation of the Janzen Connell model. *American Naturalist* **124**:769–788.
- Codling, E. A., M. J. Plank, and S. Benhamou, 2008. Random walk models in biology. *Journal of the Royal Society Interface* **5**:813–834.
- Coll, M. and D. G. Bottrell, 1994. Effects of non-host plants on an insect herbivore in diverse habitats. *Ecology* **75**.
- Compton, S. G., 2002. Dispersal Ecology, chapter Sailing with the wind: Dispersal by small flying insects. Blackwell Publishing.
- Connell, J. H., 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In *Dynamics of populations. Proceedings of the Advanced Study Institute on Dynamics of numbers in populations, Oosterbeek, 1970, den Boer, P. J. and Gradwell, G. R.* (eds.), Centre for Agricultural Publishing and Documentation, Wageningen. pages 298 – 310.
- Crist, T. O. and J. A. MacMahon, 1991. Individual foraging components of harvester ants movement patterns and seed patch fidelity. *Insectes Sociaux* **38**:379–396.
- Cromartie, W. J., 1975. The effect of stand size and vegetational background on the colonization of cruciferous plants by herbivorous insects. *Journal of Applied Ecology* **12**:517–533.
- Currie, D. J., 2007. Disentangling the roles of environment and space in ecology. *Journal of Biogeography* **34**:2009–2011.
- Dalthorp, D., 2004. The generalized linear model for spatial data: assessing the effects of environmental covariates on population density in the field. *Entomologia Experimentalis et Applicata* **111**:117–131.
- den Boer, P. J., 1968. Spreading of risk and stabiliziation of animal numbers. *Acta Biotheoretica* **18**:165–194.
- Dormann, C. F., 2007. Effects of incorporating spatial autocorrelation into the analysis of species distribution data. *Global Ecology and Biogeography* **16**:129–138.
- Dormann, C. F., J. M. McPherson, M. B. Araujo, R. Bivand, J. Bolliger, G. Carl, R. G. Davies, A. Hirzel, W. Jetz, W. D. Kissling, I. Kuhn, R. Ohlemuller, P. R. Peres-Neto, B. Reineking, B. Schroder, F. M. Schurr, and R. Wilson, 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography* 30:609–628.
- Dutilleul, P. and P. Legendre, 1993. Spatial heterogeneity against heteroscedasticity an ecological paradigm versus a statistical concept. *Oikos* **66**:152–171.
- Fahrig, L., 1998. When does fragmentation of breeding habitat affect population survival? *Ecological Modelling* 105:273.
- Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology Evolution and Systematics* **34**:487–515.
- Fahrig, L. and J. Paloheimo, 1988. Effect of spatial arrangement of habitat patches on local-population size. *Ecology* **69**:468–475.
- Fretwell, D. S. and H. L. Lucas, 1970. On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica* **19**:16–32.
- Gao, Q., M. Yu, X. S. Yang, and J. G. Wu, 2001. Scaling simulation models for spatially heterogeneous ecosystems with diffusive transportation. *Landscape Ecology* **16**:289pp.
- Gelman, A. and J. Hill, 2007. Data analysis using regression and multilevel/hierarchical models. Cambridge Univ Press.
- Girvetz, E. H. and S. E. Greco, 2007. How to define a patch: a spatial model for hierarchically delineating organism-specific habitat patches. *Landscape Ecology* **22**:1131–1142.
- Hartley, S. and W. E. Kunin, 2003. Scale dependency of rarity, extinction risk, and conservation priority. *Conservation Biology* 17:1559–1570.

- Haugen, T., I. Winfield, L. Vollestad, J. Fletcher, J. James, and N. Stenseth, 2006. The ideal free pike: 50 years of fitness-maximizing dispersal in windermere. *Proceedings of the Royal Society B: Biological Sciences* 273:2917–2924.
- Hern, A., G. EdwardsJones, and R. G. McKinlay, 1996. A review of the pre-oviposition behaviour of the small cabbage white butterfly, *Pieris rapae* (Lepidoptera: Pieridae). *Annals of Applied Biology* 128:349–371.
- Ives, A. R., P. Kareiva, and R. Perry, 1993. Response of a predator to variation in prey density at 3 hierarchical scales lady beetles feeding on aphids. *Ecology* **74**:1929–1938.
- Janzen, D. H., 1970. Herbivores and number of tree species in tropical forests. *American Naturalist* **104**:501 pp.
- Jones, R. E., 1977. Movement patterns and egg distribution in cabbage butterflies. *Journal of Animal Ecology* **46**:195–212.
- Jones, R. E., 1987. Behavioral evolution in the cabbage butterfly (Pieris rapae). Oecologia 72:69–76.
- Jones, R. E., N. Gilbert, M. Guppy, and V. Nealis, 1980. Long-distance movement of *Pieris rapae*. *Journal of Animal Ecology* 49:629–642.
- Justus, K. A. and B. K. Mitchell, 1996. Oviposition site selection by the diamondback moth, *Plutella xylostella* (L) (Lepidoptera: Plutellidae). *Journal of Insect Behavior* **9**:887–898.
- Kareiva, P., 1982. Experimental and mathematical analysis of herbivore movement quantifying the influence of plant spacing and quality on foraging discrimination. *Ecological Monographs* 52:261– 282.
- Kareiva, P., 1985. Finding and losing host plants by Phyllotreta: Patch size and surrounding habitat. *Ecology* **66**:1809–1816.
- Kareiva, P., 1987. Habitat fragmentation and the stability of predator-prey interactions. *Nature* **326**:388–390.
- Kareiva, P. and M. Anderson, 1988. Community Ecology, chapter Spatial aspects of species interactions: The wedding of models and experiments, pages 38–54. Springer-Verlag, New York.
- Kareiva, P. M. and N. Shigesada, 1983. Analyzing insect movement as a correlated random-walk. *Oecologia* **56**:234–238.
- Kotliar, N. B. and J. A. Wiens, 1990. Multiple scales of patchiness and patch structure a hierachical framework for the study of heterogeneity. *Oikos* **59**:253–260.

- Kumar, S., T. J. Stohlgren, and G. W. Chong, 2006. Spatial heterogeneity influences native and nonnative plant species richness. *Ecology* 87:3186–3199.
- Kunin, W. E., 1999. Patterns of herbivore incidence on experimental arrays and field populations of ragwort, *Senecio jacobaea*. *Oikos* 84:515–525.
- Kunin, W. E., S. Hartley, and J. J. Lennon, 2000. Scaling down: On the challenge of estimating abundance from occurrence patterns. *American Naturalist* **156**:560–566.
- Křivan, V., R. Cressman, and C. Schneider, 2008. The ideal free distribution: A review and synthesis of the game-theoretic perspective. *Theoretical Population Biology* **73**:403–425.
- Legendre, P., 1993. Spatial autocorrelation trouble or new paradigm? Ecology 74:1659–1673.
- Legendre, P., M. R. T. Dale, M. J. Fortin, P. Casgrain, and J. Gurevitch, 2004. Effects of spatial structures on the results of field experiments. *Ecology* **85**:3202–3214.
- Legendre, P., M. R. T. Dale, M.-J. Fortin, J. Gurevitch, M. Hohn, and D. Myers, 2002. The consequences of spatial structure for the design and analysis of ecological field surveys. *Ecography* **25**:601–615.
- Levin, S. A., 1992. The problem of pattern and scale in ecology. Ecology 73:1943–1967.
- Lima, S. L. and P. A. Zollner, 1996. Towards a behavioral ecology of ecological landscapes. *Trends in Ecology & Evolution* 11:131–135.
- Marsh, L. M. and R. E. Jones, 1988. The form and consequences of random walk movement models. *Journal of Theoretical Biology* **133**:113–131.
- Matter, S. F., 1997. Population density and area: The role of between- and within-patch processes. *Oecologia* **110**:533–538.
- Maurer, B., 1999. Untangling Ecological Complexity: the Macroscopic Perspective. University of Chicago Press, Chicago.
- May, R. M., 1978. Host-parasitoid systems in patchy environments: A phenomenological model. *The Journal of Animal Ecology* **47**:833–844.
- McMahon, S. M. and J. M. Diez, 2007. Scales of association: hierarchical linear models and the measurement of ecological systems. *Ecology Letters* **10**:437–452.
- Morales, J. M. and S. P. Ellner, 2002. Scaling up animal movements in heterogeneous landscapes: The importance of behavior. *Ecology* 83:2240–2247.

Morris, D. W., 2006. Ecology: Moving to the ideal free home. Nature 443:645–646.

- Nottingham, S. F. and J. Hardie, 1993. Fligth behaviour of the black bean aphid, *Aphis fabae*, and teh cabbage aphid, *Brevicoryne brassicae*, in host and non-host plant odour. *Physiological Entomology* **18**:389–394.
- Nottingham, S. F., J. Hardie, G. W. Dawson, A. J. Hick, J. A. Pickett, L. J. Wadhams, and C. M. Woodcock, 1991. Behavioural and electrophysiological responses of aphids to host and nonhost plant volatiles. *Journal of Chemical Ecology* 17:1231–1242.
- O'Neill, R. V., D. L. Angelis, J. B. Waide, and T. F. H. Allen, 1986. A Hierarchical Concept of Ecosystems. Princeton University Press, Princeton, N.J.
- Otway, S. J., A. Hector, and J. H. Lawton, 2005. Resource dilution effects on specialist insect herbivores in a grassland biodiversity experiment. *Journal of Animal Ecology* **74**:234–240.
- Patlak, C. S., 1953. Random walk with persistence and external bias. Bull Math Biophys 15:311–338.
- Pimentel, D., 1961. The influence of plant spatial patterns on insect populations. *Annals of the Entomological Society of America* 54.
- Pinheiro, J. C. and D. M. Bates, 2000. Mixed-effects models in S and S-Plus. Springer Verlag, New York.
- Rabasa, S. G., D. Gutierrez, and A. Escudero, 2005. Egg laying by a butterfly on a fragmented host plant: a multi-level approach. *Ecography* **28**:629–639.
- Ralph, C. P., 1977. Effect of host plant density on populations of a specialized, seed-sucking bug, Oncopeltus fasciatus. Ecology 58:799–809.
- Reddy, G. V. P., E. Tabone, and M. T. Smith, 2004. Mediation of host selection and oviposition behavior in the diamondback moth, *Plutella xylostella*, and its predator *Chrysoperla carnea* by chemical cues from cole crops. *Biological Control* 29:270–277.
- Reynolds, A., 2008. How many animals really do the Lévy walk? Comment. Ecology 89:2347-2351.
- Reynolds, A. M., 2006. Cooperative random Lévy flight searches and the flight patterns of honeybees. *Physics Letters A* **354**:384–388.
- Root, R. B., 1973. Organization of a plant-arthropod association in simple and diverse habitats: The fauna of collards (*Brassica oleracea*). *Ecological Monographs* **43**:95–124.
- Root, R. B. and P. M. Kareiva, 1984. The search for resources by cabbage butterflies (*Pieris rapae*): Ecological consequences and adaptive significance of markovian movements in a patchy environment. *Ecology* 65:147–165.
- Schneider, D. C., 2001. The rise of the concept of scale in ecology. *BioScience* 51:545–553.

- Schtickzelle, N., A. Joiris, H. Van Dyck, and M. Baguette, 2007. Quantitative analysis of changes in movement behaviour within and outside habitat in a specialist butterfly. *BMC Evolutionary Biology* 7:4.
- Schupp, E. W., 1992. The janzen-connell model for tropical tree diversity population implications and the importance of spatial scale. *American Naturalist* **140**:526–530.
- Solomon, B. P., 1981. Response of a host-specific herbivore to resource density, relative abundance, and phenology. *Ecology* **62**:1205–1214.
- Szabo, P. and G. Meszena, 2006. Spatial ecological hierarchies: Coexistence on heterogeneous landscapes via scale niche diversification. *Ecosystems* **9**:1009–1016.
- Tahvanainen, J. O. and R. B. Root, 1972. Influence of vegetational diversity on population ecology of a specialized herbivore, *Phyllotreta cruciferae* (Coleoptera-Chrysomelidae). *Oecologia* **10**:321–346.
- Thompson, Q. S. S., R. A., 1995. Rice plant density effect on rice water weevil (Coleoptera: Curculionidae) infestation. *Environmental Entomology* **24**:19–23.
- Turchin, P., 1988. The effect of host-plant density on the numbers of mexican bean beetles, *Epilachna varivestis*. *American Midland Naturalist* **119**:15–20.
- Turchin, P., 1998. Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants. Sinauer Associates.
- Turner, M. G., V. H. Dale, and R. H. Gardner, 1989a. Predicting across scales: Theory development and testing. *Landscape Ecology* **3**:245–252.
- Turner, M. G., R. V. O'Neill, R. H. Gardner, and B. T. Milne, 1989b. Effects of changing spatial scale on the analysis of landscape pattern. *Landscape Ecology* 3:153–162.
- Van Dyck, H. and M. Baguette, 2005. Dispersal behaviour in fragmented landscapes: Routine or special movements? *Basic and Applied Ecology* 6:535–545.
- Venables, W. and B. Ripley, 1997. Modern applied statistics with S-PLUS. Springer Verlag, second edition.
- Viswanathan, G. M., V. Afanasyev, S. V. Buldyrev, S. Havlin, M. G. E. da Luz, E. P. Raposo, and H. E. Stanley, 2000. Lévy flights in random searches. *Physica A* **282**:1–12.
- Viswanathan, G. M., V. Afanasyev, S. V. Buldyrev, E. J. Murphy, P. A. Prince, and H. E. Stanley, 1996. Lévy flight search patterns of wandering albatrosses. *Nature* **381**:413–415.

Wiens, J. A., 1989. Spatial scaling in ecology. Functional Ecology 3:385–397.

- Wiens, J. A., J. A., 1990. On the use of grain and grain size in ecology. Functional Ecology 4:720–720.
- Yamamura, K., 1999. Relation between plant density and arthropod density in cabbage. *Researches* on *Population Ecology* **41**:177–182.

Chapter Z\_\_\_\_\_

# Patterns of egg distributions and the importance of spatial scale

## 2.1 Introduction

**Scale of observation** In the natural environment patches may occur at many scales and most species, whether plants or animals, respond to the inherent heterogeneity of their environment. Therefore ecological data tends to be nested or composed of different levels. Observed natural patterns can be the outcome of different coarser or finer scale processes (Maurer, 1999; Wiens, 1991), and the relationships between pattern and process can change depending on which scale the pattern is observed (Denny et al., 2004; Cadotte and Fukami, 2005). Incorporating scale into the analysis can therefore help to better understand those relationships.

The scale of observation can be defined by three variables: extent, grain and lag (O'Neill et al., 1986). Extent is defined as the overall area of study, and grain as the size of the single units of observation (e.g. sampling squares). The lag is the distance between sampling units of a certain grain.

In a heterogeneous landscape, the extent outlines how many different patches are included in the study. Grain dictates whether smaller patches can be distinguished in the study, or whether they are averaged over with other smaller patches (Figure 2.1) (Wiens, 1989)<sup>1</sup>. Applying an appropriate study extent and sample grain

<sup>&</sup>lt;sup>1</sup>see Kotliar and Wiens (1990) for a detailed outline of how to define a patch



Figure 2.1: The extent of a study defines which patches get included into the study design (large solid square). By changing the grain (small dotted squares) and lag (distance between dotted squares) the number of sampled resource patches (solid circles) varies. If the extent of the study is kept constant (as shown) the number of sampling replicates is reduced with an increase in grain.



Figure 2.2: An increase in extent can add new resource patches to the study design, but can also change the classification of a patch from being part of a cluster (solid circles, left hand panel) to relatively isolated (compare solid and open circles in right hand panel).

when collecting data on an organism, or process is crucial. As isolation and density are scale dependent phenomena (Hartley and Kunin, 2003), changing the scale of measurement would identify different areas of high or low resource density (see Figure 2.2). Choosing an appropriate scale of measurement, though, often depends on the experimenter's prior understanding of the system at hand. And what is "appropriate" can change depending on the species involved or the question asked. As shown by Root and Kareiva (1984) the area covered by flight activities of female cabbage white butterflies, *Pieris rapae*, is reduced when going from ovipositing on host plants to foraging for nectar.

**Insect dispersal and resource distribution** The spatial and temporal distribution of resource patches is a crucial factor influencing animal movement (O'Neill et al., 1988) and population dynamics (e.g. Fahrig, 1988, 1992). This is especially true for insect species feeding on ephemeral tissues on a host (e.g. leaves, seeds), or those which have to leave the host plant at one point during their life cycle and rediscover it at a later stage (Cromartie, 1975). Depending on the host range of an insect and host abundance, dispersal onto hosts may represent the primary challenge to the herbivore's success.

In an experiment with *Brassica oleracea* and two crucifer-eating beetles, *Phyllotreta cruciferae* and *P. striolata* (Coleoptera: Chrysomelidae), host plants functioned as stepping stones for dispersal between plants (Kareiva, 1982). The movement of beetles between plants depended on the relative availability of host plant stepping stones. The collard plants in this experiment were planted in different arrays, with plant spacings ranging from three to nine meters. Diffusion of beetles between plants was highest at low plant spacings. Interestingly, observations of ovipositing female cabbage white butterflies, *Pieris rapae* (Lepidoptera: Pieridae), made in the same experiment showed no evidence that *P. rapae* females responded to collard plants as stepping stones.

Compared to *Phyllotreta* beetles, cabbage white butterflies are considered to be stronger flyers. This might explain why the distance between host plants had no obvious influence on the distribution of cabbage whites, as was the case for *Phyllotreta* species. The results from this experiment show that distance between host-plants affects the response of herbivores, when the daily displacement under or over score

inter-host distances (Kareiva, 1982). These observations are a good example for how important spatial scale is in ecology. They show that every species may perceive and operate at their own individual set of scales (Brown and West, 2000; Girvetz and Greco, 2007; Kotliar and Wiens, 1990; Levin, 1992; Szabo and Meszena, 2006).

**Responses to host plant density** The Resource Concentration Hypothesis (RCH) suggests that specialist herbivores are more likely to find and remain on host plants that are growing in dense or nearly pure stands. As a result those specialist herbivores are predicted to achieve higher loads (insect herbivore density per host plant biomass) in dense and pure patches (Tahvanainen and Root, 1972; Root, 1973).

The RCH has important implications for applied entomology (e.g. Altieri, 1995) and community ecology (e.g. Kareiva, 1983; Strong et al., 1984). Although it has a wide relevance, whether or not herbivore species will respond to concentrated resources depends on various aspects of their biology and ecology (for example host-sensing ability, dispersal, food requirements, vulnerability to competitors and natural enemies) (Kareiva, 1983; Kunin, 1999). Positive responses towards plants in high-density stands have been demonstrated for the cinnabar moth, *Tyria jacobaea* (Harrison et al., 1995; Kunin, 1999) and the chrysomelid beetle, *Trirhabda virgata* (Long et al., 2003)<sup>2</sup>.

However, there are also many examples of isolated host plants attracting a disproportionate number of individuals, i.e. the seed-head fly, *Botanophila seneciella*, utilising ragwort, *Senecio jacobaea* (Crawley and Pattrasudhi, 1988), or the cabbage white butterfly, *P. rapae*, ovipositing on cabbage, *Brassica oleracea* (Root and Kareiva, 1984). Other examples for divergence from the predictions of the resource concentration hypothesis can be found in Grez and Gonzalez (1995) and Otway et al. (2005). A reversed pattern to the one predicted by the resource concentration hypothesis can be expected when insect herbivores do not accumulate in dense clusters of their host plants, or if insect herbivores do not change the number of eggs laid in dense clusters of their host plant compared to plants that grow more isolated.

The results published in the above papers show that positive responses of insect herbivores to clusters of their host plant as predicted by the resource concentra-

<sup>&</sup>lt;sup>2</sup>other examples see Schellhorn and Sork 1997; Marques et al. 2000; Paivinen et al. 2003; Petrakis 2004

tion hypothesis, though observed for a number of species, are not a general phenomenon. And whether a corresponding pattern is found or not can even depend on how the data are collected or analysed. In a grassland biodiversity experiment, where appearance of resource concentration was tested for several specialist herbivore species, Otway et al. (2005) measured two contrasting responses of insects to host plant abundance. When presence/absence of different specialist herbivores for their host plants was analysed (as probability of occurrence of insect species per biomass of host plant), the outcome conformed to the predictions of the resource concentration hypothesis: specialist herbivores located their host plant more frequently when their host plant was more abundant. When insect load and host plant abundance (insect density/m<sup>2</sup> per host plant biomass/m<sup>2</sup>) was analysed, though, specialist herbivore loads declined with an increase in host plant abundance.

**Aim** In my experimental work I focus on how responses of insect herbivores to host plant density are influenced by spatial scales in both experimental design and observation. I expect to observe different responses to resource patch density (e.g. negative vs. positive) simply by changing the scale of measurement.

The first experiment deals with the response of ovipositing cabbage white butterfly females to different plant densities. I ask the question how does the observed pattern change if different scales of measurement are used to define plant density. In addition I investigate the effect of spatial location on the number of eggs laid per plant, to see whether large scale environmental gradients have an influence. The third question I address how size of the host plant affects the number of eggs laid.

Are the effects found in the first experiment a general phenomenon or species specific? To answer this question I focus on the relationship between the cinnabar moth and ragwort. Again I measure the number of oviposition events across different plant densities which I define differently depending on the scale of observation applied. I also look into the role host plant size and spatial location might play in forming the distribution pattern of egg batches. In addition I investigate the effects of the flowering status of the host plant.

In the last experiment I focus on how plant density and scale of measurement might affect the distribution pattern of cinnabar moth egg batches among a natural population their host plant, *Senecio jacobaea*. Here I investigate possible influences of plant size and flowering status on the egg batch distribution pattern. Lastly, I investigate the effects of plant size and surrounding plant density on the number of eggs in *Tyria jacobaeae* egg batches of the artificial and wild ragwort population.

## 2.2 Methods

To investigate the influence of different scales of measurement on observed patterns, I measured the number of eggs oviposited by cabbage whites, Pieris rapae, and cinnabar moth, Tyria jacobaeae, females among host plants. Different scales of measurement were applied to define host plant density. Those insect species were chosen because both have well established populations in New Zealand, and a large amount of information on their ecology is readily available. Pieris rapae has a broader host-range than T. jacobaeae. Cabbage whites are known to oviposit on different species in the family Brassicaceae. The cinnabar moth, however, is a more specialised herbivore, whose females usually lay their eggs on ragwort, Senecio jacobaea (Asteraceae). But T. jacobaeae has been reported to occasionally utilise other species in the genus Senecio as host plants as well (Vrieling, 2006, and references therein). Senecio jacobaea is typically known as a biennial plant, however, annual and perennial forms are known, as well (Wardle, 1987, and references therein). Both insect species also differ in the number of eggs laid in one turn. While P. rapae females lay about 1 to 2 eggs per plant before flying off to the next plant, T. jacobaeae females usually lay their eggs in batches. Clutch size in *T. jacobaeae* can vary from one egg to over 150 eggs per batch (Sjerps et al., 1993). In my first oviposition experiment I used six-week old cabbage plants, Brassica oleracea, as host plant for P. rapae. In the second experiment with T. jacobaeae I used S. jacobaea plants which were raised from seed to their second year. All S. jacobaea seeds were collected from the same site where the experiment took place.

**Field sites** The first experiment with *P. rapae* and *B. oleracea* took place in the period from the  $14^{th}$  January to the  $2^{nd}$  February 2005. We rented four fields at the AgResearch farm near Kaitoke, New Zealand (S  $41^{\circ}$  04', E  $175^{\circ}$  11'; each field about 1 hectare in size; see Figure 2.3). The experimental fields were surrounded by a post and wire fence, its height was 2m on the northern edge and 1m on the other three

sides. The fields had been grazed down by sheep before the beginning of the experiments. The farm itself was surrounded by scrub, indigenous vegetation and planted forest. A nearby field (500m north - east) held a planting of *B. oleracea var. acephala* (kale).

The experiments with the cinnabar moth were run from the  $28^{th}$  of November 2006 till the  $8^{th}$  of January 2007 at Terawhiti Station, Wellington, New Zealand (S 41° 17′, E 174° 41′). There I was able to use four paddocks, each  $64 \times 64m$  in size, for our experiments (see Figure 2.4). Three of the paddocks were used to survey the egg distribution of cinnabar moth in wild ragwort populations (paddocks numbered 1, 3 & 4; Figure 2.4). On the forth paddock (field numbered 2; Figure 2.4, and from here on called the experimental paddock or experimental field) I set up four experimental ragwort fields, each  $32 \times 32m$  in size. All four paddocks are normally used for grazing horses and cattle.



Figure 2.3: Overview of field site in Kaitoke; coloured squares indicate paddocks used for experiments.



Figure 2.4: Overview of field site in Makara; coloured squares indicate paddocks used for experiments: ① (red) = wild ragwort site 1, ② (blue) = experimental paddock with artificial plant densities and layout, ③ (orange) = wild ragwort site 2, and ④ (green) = wild ragwort site 3.

#### **Experimental design**

**Experimental blocks** - *P. rapae* Cabbage plants were set up on the fields as resource patches in different densities and spatial arrangements (see Figure 2.5). Each of the four fields was subdivided into four blocks: A, B, C, and D. To minimise the effects of local or large scale environmental gradients on the experimental set up, the blocks were replicated across the four fields in the shape of a Latin square (see Figure 2.5 a). Block A was a  $42 \times 42m$  square with 40 plants. Block B was also a  $42 \times 42m$  square, in the centre it contained 16 plants placed within a  $1 \times 1m$  square. Each of the four plants in block C were placed on the corner of a  $22 \times 22m$  square. Block D was a replicate of block A with shorter spacing between plants so that all 40 plants fitted in a  $6 \times 6m$  square (see Figure 2.5 b & c). By having single plants and clumps of four, or sixteen spatial heterogeneity was achieved throughout the treatments. I measured plant density by counting the number of plants within a square of a certain size. These (arbitrary) scales of measurement and the corresponding plant densities are shown in Table 2.1.

Block	Coarse Scale	Medium Scale	Fine Scale
	(42×42m)	(6×6m)	(1×1m)
А	40	16, 4, 1	16, 4 ,1
В	16	16	16
С	4	1	1
D	40	40	16, 4, 1

Table 2.1: Plant densities (number of plants) for the different scales of measurement used in *P. rapae* experiment in Kaitoke.

**Experimental blocks** - *T. jacobaeae* In a similar way to the previously described experiment with *P. rapae* each of the four fields was subdivided into four blocks: A, B, C, and D. These blocks were rotated in a Latin square design to account for the influence of large scale environmental gradients (see Figure 2.6). In contrast to the experiments with *P. rapae* I used a  $1 \times 1m$ ,  $4 \times 4m$  and  $16 \times 16m$  scale of measurement in this experiment (see Table 2.2). Each of the four fields is a spatial



while block C has four single plants with a spacing of 20m between plants; total number of plants n = 400; plants Figure 2.5: Spatial arrangement of cabbage plants in the four experimental fields of *P. rapae* experiment in Kaitoke; plant distribution but differ in spacing between plants, block B consists out of 16 plants within one meter square, shown are (a) the different 'Blocks' (A, B, C, D) laid out in a 'Latin Square' design, (b) a close-up of the blocks A, B, C & D, and (c) a close-up of block D showing the different sized groups of plants; Block A & D are identical in are plotted as open circles, denser colour indicates higher density of plants (1, 4, or 16). 33

replicate for the experiment. Block A was a  $16 \times 16m$  square with 40 plants. Block B had 16 plants within a  $1 \times 1m$  square. In block C the plants were placed in the  $6 \times 6m$  square. Block D was again a replicate of A but now with a square length of 4 metres. Again, an arrangement of four, sixteen and single plants provided spatial heterogeneity among the treatments. For a map of the plant layout within the different blocks refer back to Figure 2.5, but note the difference in broad scale extent.

Table 2.2: Plant densities for the different scales of measurement used in *T. jacobaeae* experiment.

D1 1	C C 1		
BIOCK	Coarse Scale	Medium Scale	Fine Scale
	(16×16m)	(4×4m)	(1×1m)
А	40	16, 4, 1	16, 4 ,1
В	16	16	16
С	4	1	1
D	40	40	16, 4, 1



Figure 2.6: Spatial arrangement of *S. jacobaea* plants of *T. jacobaeae* experiment in Makara; total number of plants, n = 400.

#### Measurement of egg distribution

**Counting cabbage white eggs** Out of a greenhouse stock of six week old cabbage plants, B. oleracea var. 'sommercross', I selected 400 plants that were of similar size. I measured plant size as the width of the largest leaf in  $cm \times the total number$ of leaves (with width > 2cm) for each plant. By standardising the size of all my plants I was able to modify the original measure used to define patterns of resource concentration. Rather than using insect load (which is defined as insect herbivore density per host plant biomass) I used the number of eggs laid per plant. Nevertheless, plant size was included as an independent variable into the analysis to account for possible small size differences between host-plants that might have affected the distribution of cabbage white eggs. The reason for not using insect load as a measure was that I was not able to accurately measure biomass after the experiment had ended because of rabbit browsing of the cabbage plants. At the beginning of the experiment I cut one small leaf off each plant in order to standardise the possible effect of defensive chemicals produced by plants because of physical damage (Chen, 2008). This precaution was taken because some plants might have been damaged during transport or as part of the planting process. While the experiment was running some cabbage plants had to be replaced because of damage caused by rabbits. Only plants on which no eggs were laid or plants with an overall damage greater than 75% were replaced. Over the experimental period four egg counts were performed. After the last count all plants were harvested and brought back to the laboratory to determine dry weight of the foliage for each plant.

**Counting cinnabar moth eggs** The *S. jacobaea* plants I used for our experiments (n = 400 plants) were treated in a similar way as described above for cabbage. Plant size, though, was measured as the height  $[cm] \times$  the (maximum) diameter [cm] of a plant  $\times$  the number of stems. I also recorded the number of flower heads that were closed and open (in bloom) on each of the ragwort plants. During the experimental period four egg and larvae counts were performed over the period December 2006 to January 2007. The number of eggs in each batch that was counted, as well as the number of cinnabar moth larvae present were recorded for every plant. Following the third egg count I re-assesed the number of flowers on each plant.

**Sampling of wild ragwort population** Each of the 64×64m wild population paddocks were subdivided into smaller squares of 16×16m, to create a four by four design. In each of the  $16 \times 16$ m squares all  $2^{nd}$  year ragwort plants were counted to provide an estimate of coarse scale plant density within a given square. The  $16 \times 16$  m square was than further divided into four  $8 \times 8m$  squares. By comparing the total number of  $2^{nd}$  year plants of each  $8 \times 8m$  square, the square was put either into the high or low plant density category. The assignment of the high or low treatment label was relative to the densities encountered within a given  $16 \times 16$  m square. Later on, the high and low density label was used to stratify the random selection of the sampled plants. In the next step a second year plant was chosen that was closest to the centre of the square. For this focal plant we measured the distance to its nearest neighbour and opposite nearest neighbour. For each of these three plants, the plant canopy diameter and canopy height as well as number of stems, and egg batches were recorded. In addition all 2<sup>nd</sup> year ragwort plants within a 1m and 4m radius around each of the three plants were counted. This process was repeated for a second set of plants. Depending on whether the first set of plants belonged to a  $8 \times 8m$  sampling square which was classed as either high or low density, the second set of plants was sampled from a randomly defined 8×8m square, which was classed as either high or low density respectively. The second focal plant was determined as the plant closest to the centre of the  $8 \times 8m$  square. The focal plant had to be at least 1m from the edge of the  $8 \times 8m$  sampling square and a minimum distance of 4m away from the first focal plant, if possible. As in the experimental field, the number of flower heads was recorded for each plant sampled. Plant height and canopy diameter as well as the number of stems were used to determine plant size. A total of 288 wild ragwort plants were sampled.

**Statistical Methods** Changing the scale applied to measure plant density shifted the number of plants in each treatment and also grouped them depending on the number of surrounding plants. As a result the data collected in my study was nested at different levels. As was shown by Rabasa et al. (2005), different scales can have changing degrees of spatial variance. Using Kotliar and Wiens (1990) definition, the heterogeneity in my study system resulted from two distinct factors: One is the difference between resource patches, and the other is the sum of varying de-

grees of contrast among lower level patches within a patch. To analyse this data I used hierarchical linear models (HLM) (Goldstein, 1995; Bryk and Raudenbush, 1992; Raudenbush and Bryk, 2002), also known as linear multi-level mixed effects models (LME), which specifically took into account the hierarchical structure of my study design. Models and graphs were created using R (v2.7.0) with package *lme4* (Bates, 2007) and *arm* (Gelman et al., 2008). For examples of how to build HLMs to analyse ecological data sets refer to McMahon and Diez (2007), or to Pinheiro and Bates (2000) as well as Gelman and Hill (2007) for a more general explanation of linear mixed effects models.

Symbol	Variable	Туре	Range (&	Description	Unit
			Q <sub>1</sub> - Q <sub>3</sub> )		
Eggs	eggs	Con	0 - (0 - 1) - 7	No. of <i>P. rapae</i> eggs per	Count
				host	
Batches	egg batches	Con	0 - (0 - 0) - 2	No. of T. jacobaeae egg	Count
				batches per host in ma-	
				nipulative experiment	
Batches	egg batches	Con	0 - (0 - 0) - 2	No. of <i>T. jacobaeae</i>	Count
				egg batches per host in	
				wild popl. survey	
Eggs/Batch	eggs per batch	Con	6 - (20 - 38) - 64	No. of <i>T. jacobaeae</i> eggs	Count
				per batch	

Table 2.3: Summary of response variables used in statistical analysis; Type: Con = Continuous.

The egg and batch count data (data taken from first count for all experiments) had a negative binomial distribution, which required HLMs with poisson errors, or quasi-poisson errors in case of over-dispersion. The method used to fit HLMs with poisson and quasi-poisson errors was log-likelihood with Laplace approximation. To assess the significance of coefficients I reported the upper and lower bounds of the 95% highest-posterior-density (HPD) interval (Lindley, 1965; Fryar et al., 1988) sampled from a simulation of the posterior distribution of the candidate model. In addition, I included the 95% confidence intervals for comparison. For more information about the implementation of the HLM (LME) and the MCMC sample methods refer to the *lme4* (Bates, 2007) and *arm* (Gelman et al., 2008) manuals.

Table 2.4: Summary	of explanatory	variables for	<i>P. rapae</i> data s	set; Type: •	Con = Con-
tinuous.					

Symbol	Variable	Туре	Range (&	Description	Unit
			Q <sub>1</sub> - Q <sub>3</sub> )		
PS	Plant size	Con	2.2 - (41.3 - 62.1) - 108.8	Width largest leaf $\times$ to-	cm
				tal no. leaves (> 2cm)	
F	Fine scale plant	Con	1 - 16	Number of host plants	Count
	density			within $1 \times 1$ m square	
M	Medium scale	Con	1 - 40	Number of host plants	Count
	plant density			within 6 $ imes$ 6m square	
C	Coarse scale	Con	4 - 40	Number of host plants	Count
	plant density			within $42 \times 42m$ square	
X	X coordinates	Con	2.75 - 195.25	Geographical x coordi-	m
				nates	
Y	Y coordinates	Con	2.75 - 195.25	Geographical y coordi-	m
				nates	

To explain the distribution of insect eggs among host-plants I included six predictor variables into the model: fine scale plant density (Fine Scale), medium scale plant density (Medium Scale) coarse scale plant density (Coarse Scale), the spatial x and y co-ordinates, and plant size. In addition the second flower count was included as a predictor for the ragwort experiments. These parameters were fitted as fixed effects into the model, while the hierarchical levels of the experiment were included as nested random effects.

Model selection was based on the Akaike Information Criterion approach (AIC; Akaike 1974). For each hypothesis I included the relevant predictor variables into the models (Table 2.7 & 2.8 & 2.9). As a matter of routine I calculated the sample size corrected AIC (AIC<sub>c</sub>) for each model, as recommended by Anderson and Burnham (2002). The different models were ranked according to their AIC<sub>c</sub> value, with one having the lowest AIC<sub>c</sub> value being the best. I calculated the relative AIC<sub>c</sub> weights (w) to determine the probability of the model being the best model of those tested (Burnham and Anderson, 2002). When models were fitted using quasi-poisson errors a quasi-likelihood adjusted AIC approach (QAIC, or QAIC<sub>c</sub> for sample size corrected QAIC) was used. The variance inflation factor (c) used to calculate the QAIC<sub>c</sub>

Table 2.5	: Summary of explanatory	y varial	oles for T. <i>jacobaeae</i> dat	ta sets; Type: Con = Continuous, Cat = Catego	rical.
Symbol	Variable	Туре	Range (&	Description	Unit
			Q <sub>1</sub> - Q <sub>3</sub> )		
Manipula	tive field experiment				
PS	Plant size	Con	136 - (540 - 1344) - 8064	Height $\times$ width $\times$ no. of stems	$cm^2$
F	Fine scale plant density	Con	1 - 16	Number of hosts within 1×1m square	Count
M	Medium scale plant density	Con	1 - 40	Number of hosts within 4×4m square	Count
C	Coarse scale plant density	Con	4 - 40	Number of hosts within 16×16m square	Count
X	X co-ordinates	Con	6.63 - 58.00	Geographical x coordinates	m
Y	Y co-ordinates	Con	7.63 - 56.88	Geographical y coordinates	m
FL	Flowers	Con	0 - (0 - 20) - 94	Number of flower heads on host plant	Count
Wild popı	lation survey				
PS	Plant size	Con	63 - (466 - 1842) - 17850	Height $\times$ width $\times$ no. of stems	$\mathrm{cm}^2$
F	Fine scale plant density	Con	0 - (1 - 6) - 20	Number of hosts within 1m radius from focal plant	Count
M	Medium scale plant density	Con	0 - (10 - 33) - 80	Number of hosts within 4m radius from focal plant	Count
C	Coarse scale plant density	Con	6 - (34 - 101) - 198	Number of hosts within 16×16m sampling square	Count
FL	Flowering status	Con	0 - (8 - 93) - 547	No. of flower heads on host plant	Count

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for all models in the egg and larvae sub-sets was based on the global model (Burnham and Anderson, 2002). The number of model parameters (k) was evaluated for each model and one was added to account for c as an extra term. The AIC<sub>c</sub> weight of model j ( $w_j$ ) takes the difference between the lowest AIC<sub>c</sub> value of all models and the AIC<sub>c</sub> value of model j ( $\Delta$  AIC<sub>cj</sub>), and sets it into relation to the  $\Delta$  AIC<sub>c</sub> values of all other models.

Four different levels of nestedness were identified for the manipulative oviposition experiment with cabbage and ragwort: Field : Block : Sub-Block : Group. In Table 2.6 the number of replicates for each random variable are shown. For the wild population survey only field was used as a random effect (Table 2.6).

In addition, I investigated whether size of the host plant or surrounding plant density affected the size of *T. jacobaeae* egg batches. The number of eggs per batch from the manipulative field experiment and the wild population were combined and fitted as response variables. The previously mentioned methods were used to define plant density at fine, medium and coarse scale, which together with plant size, flowering status were fitted as fixed effects. As random variable I included field, to account for differences between the different study sites (Table 2.6).

To increase the fit of models for the manipulative experiments with cabbage and ragwort, the three scales of measurement of plant density were log-transformed. Plant size was log-transformed in all experiments. I used log+1 transformation on the number of flowers in both ragwort experiments , as well as the three scales of measurement in the wild population survey.

Table 2.6: Random variables and the number of replicates for each level used in HLMs of the different experiments.

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Random variable		No. replicates	Total
Manipulative experi	iments with cabbage and r	agwort	
Fields		4	4
Block	(coarse scale level)	4 per Field	16
Sub-Block	(medium scale level)	1, 4 or 16 per Block	88
Group	(fine scale level)	1, 4 or 16 per Sub-Block	148
Wild population sur	vey		
Fields		3	3
Analysis of combine	d number of eggs		
Fields		4	4

/bin/bash: caption[HLM: command not found

Table 2.7: Models for exploring the distribution of *P. rapae* eggs on *B. oleraceum* plants; see Table 2.4 for explanation of model parameters; all models listed also include nested random effects.

#	Model	Model description
1	$\sim 1$	unconditional model, intercept only
2	F + M + C + X + Y + PS	global model
3	F + M + C	plant densities at different scales
4	F + M + C + X + Y	plant densities at different scales, geographical x
		and y coordinates
5	F + M + C + PS	plant densities at different scales, plant size

Table 2.8: Models for exploring the distribution of *T. jacobaeae* egg batches on *S. jacobaea* plants; see Table 2.5 for explanation of model parameters; all models listed also include nested random effects.

#	Model	Model description
Mı	anipulative field experiment	
1	$\sim 1$	unconditional model, intercept only
2	F + M + C + X + Y + FL + PS	global model
3	F + M + C	plant densities at different scales
4	F + M + C + PS	plant densities at different scales, plant size
5	F + M + C + FL	plant densities at different scales flowering status
6	F + M + C + X + Y	plant densities at different scales, geographical x
		and y coordinates
Wi	ild population survey	
1	$\sim 1$	unconditional model, intercept only
2	F + M + C + PS + FL	global model
3	F + M + C	plant densities at different scales
4	F + M + C + PS	plant densities at different scales, plant size
5	F + M + C + FL	plant densities at different scales, flowering status

Table 2.9: Models for exploring the number and distribution of *T. jacobaeae* eggs in egg batches on *S. jacobaea;* see Table 2.5 for explanation of model parameters.

#	Model	Model description
M	anipulative field experiment	
1	$\sim 1$	unconditional model, intercept only
2	F + M + C + PS + FL	global model
3	F + M + C	plant densities at different scales
4	F + M + C + PS	plant densities at different scales, plant size
5	F + M + C + FL	plant densities at different scales, flowering status

## 2.3 Results

### 2.3.1 Oviposition experiment with *P. rapae* on cabbage

A total of 109 eggs were laid among plants of this experiment. When plant density was measured at fine scale (Figure 2.7 a), the number of eggs for block 'D' declined with increasing plant density. While in block 'A' the number of eggs/plant was unaffected by plant density, block 'C' received the highest number of eggs/plant. Following the predictions of the resource dilution hypothesis the number of eggs/plant was lower for block 'B' when compared to block 'C'. A similar pattern could be seen in Figure 2.7 b & c. The number of eggs is highest in block 'C', and there are no strong differences between blocks 'A', 'B' and 'D'.

The multi-level model which gained the strongest support was model 2 (w =0.682) (Table 2.10). The model included the three scales of measurement of plant density, the geographical x and y locations of all plants, as well as plant size as fixed effects. Within the model a number of predictors played an important role in explaining the observed egg distribution (Figure 2.8 a; un-transformed values for the predictor estimates and intervals can be found in Appendix 1, Table 2.14 a). Estimates of  $\beta$  were considered to be truly different from zero, if the 95% HPD intervals did not overlap with zero (we also reported the 95% confidence interval for comparison). This was the case for fine scale plant density, which had a negative effect on the number of eggs laid. In addition the geographical x co-ordinates indicated a declining trend in the number of eggs across the experimental set up from south to north. The intervals for coarse and medium scale plant density, geographical y co-ordinates and plant size all overlapped with zero, and therefore their  $\beta$  estimates are not considered to be different from zero. Although, for plant size the overlap of the lower bounds of the 95% HPD interval was marginal, and as shown by the support for model 5 (w = 0.318, Table 2.10) as second best model, a slightly positive effect of plant size on the number of eggs laid can be expected (Figure 2.8 b; un-transformed values for the predictor estimates and intervals can be found in Appendix 1, Table 2.14 b). Coarse scale, in contrast, may have a slight negative effect on the number of eggs laid, as is shown by the marginal overlap of the upper bound of the 95% HPD interval. The predicted effects of plant density at the three scales of measurement and plant size are similar between model 2 and 5.

Table 2.10: Summary of multi-model inference for explaining the distribution of *P. rapae* eggs *B. oleracea;* see Table 2.4 for explanation of model parameters.

#	Model	k	neg-logLik	$AIC_c$	$\Delta \operatorname{AIC}_c$	w
1	$\sim 1$	5	374.1507	384.3030	36.5169	0.0000
2	F + M + C + X + Y + PS	11	325.0568	347.7861	0.0000	0.682
3	F + M + C	8	363.1432	379.5115	31.7254	0.0000
4	F + M + C + X + Y	10	355.7304	376.2960	28.5099	0.0000
5	F + M + C + PS	9	330.8184	349.3129	1.5268	0.318



Figure 2.7: Number of *P. rapae* eggs/plant for the different plant density treatments at different spatial scales: a) Fine scale plant density, b) medium scale plant density, c) coarse scale plant density; mean +/- std. error.



(b) Model 5, *w* = 0.318.

Figure 2.8: Testing *P. rapae* egg distribution: Standardised parameter estimates and 95% HPD and confidence intervals for a) model 2, b) model 5; model predictors were standardised by centering and dividing by two standard deviations.

#### 2.3.2 Oviposition experiment with *T. jacobaeae*

Only a small number of egg batches (n = 11) were laid among plants of this experiment. Neither an increase nor a decline in the number of egg batches per plant was apparent from our data when plotted against the different plant densities at the three scales of measurement (Figure 2.9).

From all the models we tested, model 2, which included the three scales of measurement of plant density, plant size, number of flowers and the geographical x and y co-ordinates, gained the highest support (w = 0.416, Table 2.11). It was closely followed by model 4 (w = 0.264), and model 1, the unconditional model (w = 0.158). In model 2, plant size was predicted to have a positive affect on the number of egg batches laid (Figure 2.10 a). While bigger plants received more egg batches, the number of egg batches declines from north to south as shown by the negative effect of the geographical y co-ordinates. The 95% HPD intervals of the different scales of measurement for plant density, the number of flowers and the geographical x co-ordinates all overlapped with zero and their estimates are therefore not considered to be different from zero. A similar pattern was shown for plant size and the three scales of measurement in model 4 (Figure 2.10 b). However, the unconditional model (model 1) gained relatively high support, which indicates that our model parameters did not account for enough of the variance encountered in this experiment, and the results from model 2 and 4 must be viewed with caution.

#	Model	k	neg-logLik	$AIC_c$	$\Delta \operatorname{AIC}_c$	w
1	$\sim 1$	5	74.831	84.983	1.930	0.158
2	F + M + C + X + Y + PS + FL	12	58.247	83.053	0.000	0.416
3	F + M + C	8	70.990	87.358	4.306	0.048
4	F + M + C + PS	9	65.499	83.961	0.908	0.264
5	F + M + C + FL	9	67.883	86.345	3.292	0.080
6	F + M + C + X + Y	10	67.527	88.093	5.040	0.033

Table 2.11: Summary of multi-model inference for explaining the distribution of *T. jacobaeae* egg batches among artificial population of *S. jacobaea*; see Table 2.5 for explanation of model parameters; block treatment is included as random effect.



Figure 2.9: Number of *T. jacobaeae* egg batches per plant plotted against the different fine scale plant densities (a), medium scale plant densities (b), and coarse scale plant densities (c); data was pooled from all four fields.



<sup>(</sup>b) Model 4, *w* = 0.264.

Figure 2.10: Standardised parameter estimates and 95% HPD and confidence intervals for testing *T. jacobaeae* egg batch distribution across an experimental array of *S. jacobaea*: a) model 2, b) model 4; model predictors were standardised by centering and dividing by two standard deviations.

### 2.3.3 Survey of wild *S. jacobaea* population

The number of egg batches per plant that were laid (17 batches in total) among plants of this experiment are shown in Figure 2.11 for the different predictor variables. None of the graphs shows a strong linear relationship between number of batches per plant and the corresponding variable.

The results from the multi-model inference are summarised in Table 2.12. The strongest support was found for model 4 (w = 0.304) which included the three scales of measurement and plant size as fixed effects. The 95% HPD interval for the medium scale measurement of plant density did not overlap with zero, therefore the positive parameter estimate is considered to be truly different from zero (Figure 2.12 a; non-standardised values for the parameter estimates and intervals can be found in Table 2.19, Appendix 1)). For all other parameters the 95% HPD intervals overlapped with zero, and their estimates are therefore not considered to be truly different from zero. A similar pattern was found in model 5 (w = 0.284; Figure 2.12b), which gained was supported as being the second best model (Table 2.12). The overlap of the lower bound of the 95% HPD interval for the plant size estimate in model 4 and the number of flowers estimate in model 5 was marginal, however, the similarity in support for the models 2 to 5 makes it unlikely, that plant size or number of flowers had an important effect on the number of egg batches laid.

#	Model	k	neg-logLik	$AIC_c$	$\Delta \operatorname{AIC}_c$	w
1	$\sim 1$	2	101.501	105.543	7.455	0.007
2	F + M + C + PS + FL	7	84.727	99.127	1.039	0.181
3	F + M + C	5	88.492	98.705	0.617	0.224
4	F + M + C + PS	6	85.789	98.088	0.000	0.304
5	F + M + C + FL	6	85.928	98.227	0.140	0.284

Table 2.12: Summary of multi-model inference for explaining the distribution of *T. jacobaeae* egg batches among natural population of *S. jacobaea*; see Table 2.5 for explanation of model parameters.



Figure 2.11: Number of egg batches from natural population survey plotted against a) plant size [log-scale], b) fine scale plant density, c) medium scale plant density, d) coarse scale plant density, e) number of flowers; all y values are jittered for better transparency.


(b) Model 5, *w* = 0.284.

Figure 2.12: Standardised parameter estimates and 95% HPD and confidence intervals for testing *T. jacobaeae* egg batch distribution across an experimental array of *S. jacobaea*: a) model 4, b) model 5; model predictors were standardised by centering and dividing by two standard deviations.

### 2.3.4 Number of eggs in *T. jacobaeae* egg batches

The egg batch data from both the manipulative field experiment (n = 11 batches) and the natural population survey (n = 17 batches) were combined for this part of the analysis. The number of eggs as part of an egg batch did not differ significantly between the two experiments (Welch Two Sample t-test, t = -0.86, df = 25, p-value = 0.4). The number of eggs laid as part of an egg batch ranged from six to 64, with a total number of 817 eggs laid among all egg batches. When plotted against the different predictor variables no linear trend was apparent for the number of eggs per batch (Figure 2.13).

The model, which gained by far the strongest support, was model 1 (w = 0.986; Table 2.12). The high support for the unconditional model supports the pattern as seen in Figure 2.13, that none of the fixed effect parameters affected the number of eggs per batch laid among plants of this experiment.

Table 2.13: Summary of multi-model inference for explaining the distribution of *T. jacobaeae* egg batches among natural population of *S. jacobae*; see Table 2.5 for explanation of model parameters; c = 11.

#	Model	k	Deviance	$QAIC_c$	$\Delta \text{QAIC}_c$	w
1	$\sim 1$	3	162.584	24.136	0.000	0.986
2	F + M + C + PS + FL	8	139.393	40.343	16.207	0.000
3	F + M + C	6	154.012	33.237	9.102	0.010
4	F + M + C + PS	7	146.107	36.516	12.381	0.002
5	F + M + C + FL	7	151.080	36.957	12.821	0.002



Figure 2.13: Sizes of egg batches from manipulative (closed circles, n = 11) and wild population (open circles, n = 17) experiments plotted against a) plant size [log-scale], b) fine scale plant density, c) number of flowers, d) medium scale plant density and e) coarse scale plant density.

### 2.4 Discussion

*Pieris rapae* As shown in previous studies on *P. rapae*, the distribution pattern of cabbage white eggs contradicts the predictions made by the resource concentration hypothesis (for example Jones, 1977; Maguire, 1983; Yamamura, 1999; Bukovinszky et al., 2005). More eggs per plant are found on host plants that grow in low density stands. Spacing between host plants used in previous studies ranged from 0.5m to 2m. In each experiment the number of eggs laid per plant in a 'sparse' and a 'dense' treatment were evaluated. Although comparisons were made between different plant densities, the scale of measurement was kept constant. My study was designed to cover roughly the same plant densities, but with the intention to vary the scale of observation. Through the multi-level approach I was able to detect varying responses to resource patch structure for the three scales of measurement. While at fine scale the egg distribution followed the previously stated negative trend with increasing plant density, no such pattern was found for medium or coarse scale plant densities. The egg distribution pattern I found in this study corresponded to results of Root and Kareiva (1984), who described the distinct flight behaviour of P. rapae females during oviposition, which leads to comparatively higher egg numbers on more isolated plants. The two main features of this 'egg-spreading syndrome' are a flight path that is more linear than when foraging for food, and a flown distance of approximate 1.33 to 3m between successful egg-laying events (Root and Kareiva, 1984; Yamamura, 1999). When measuring ecological patterns the variation that results from individual behaviour of an organism is biggest at finer spatial scales (Levin, 1992). By increasing the size of the sampling squares, though, the intra-sample spatial variance will increase, but the spatial variance between samples will decline (Wiens, 1989; Bellehumeur et al., 1997). It is likely that in my experiment, using different nested spatial scales to define plant density meant that the different fine scale responses of ovipositing P. rapae females to the different sized groups of host plants were averaged out at the medium or coarse scale.

The search for host plants is affected by an organism's ability to detect cues that lead it to the desired resource. Different cues may be important at different spatial scales. Bernays and Chapman (1994) have suggested that a combination of visual and olfactory cues guide insect herbivores to a suitable host. Field and simulation experiments by Bukovinszky et al. (2005) suggest that female cabbage white butterflies use visual cues to a high extent during host plant search. However, they did not account for a combined effect of visual and volatile cues as part of their field experiments. Nonetheless, previous studies have indicated that the colour green acts as a positive cue to searching P. rapae females (Myers, 1985), even in absence of host plant volatiles (Traynier, 1979). So far, studies measuring the visual perception range of *P. rapae* butterflies are missing. But it is likely that visual cues are important at finer spatial scales during host plant searches, while plant volatiles may also be used for host plant finding at coarser spatial scales. When foraging for food as opposed to oviposition sites, Honda et al. (1998) suggested that P. rapae butterflies use a combination of visual and volatile cues for food resource selection at small spatial scales. That *P. rapae* females respond to volatiles from potential host plants was shown by Hern et al. (1996) in wind tunnel experiments. Since the volatile cues from a group of host plants may add up and are distributed over a wider area by air movement, I would have expected to see a positive response to higher plants densities at coarser scales. However, I did not account for the combined influence of visual and volatile stimuli during host plant finding in my experiment.

The wider spatial context in which my experiments took place had a strong influence on the egg distribution pattern. My study was set up to measure the colonisation pattern of cabbage white butterflies in an 'empty' cabbage patch. The majority of these 'colonisers' came from a commercial-planted kale field 500m North-East from my experimental blocks. The higher number of eggs on plants of the northern fields are reflected by the effect of the x geographical co-ordinates. The area between the commercially planted kale field and my experimental blocks was mostly paddocks used for grazing domestic stock. Female cabbage white butterflies would not had the opportunity to lay eggs prior to arriving at the northern border of my experimental set up. Therefore, the individual egg load would have been relatively high. Earlier work by Jones (1977) found that *P. rapae* females with a high egg load laid most of their daily egg complements on the first groups of plants they encountered. When egg load was low, *P. rapae* females became more selective and left host plants more readily. This behaviour may have been a factor that lead to the uneven distribution of cabbage white eggs among the four experimental fields of my study.

It has been shown that host-plant quality can have a significant effect on host

plant-choice by *P. rapae* and *P. canidia* females. Chen et al. (2004) found that fertilised plants were chosen over un-fertilised plants. Fertilised plants are usually in better physiological condition (greener and with higher water and nitrogen content) and cabbage white butterflies were found to prefer such plants (Myers, 1985; Wolfson, 1980). Differences in the quality of host plants could potentially affect fine scale patterns, but in general could also upscale if linked to processes at coarser spatial scales, such as advantageous soil types. To minimise the effects of host-plant quality on the outcome of my study, I raised the *Brassica* plants under common conditions and randomly assigned them to the different treatments.

Models, which were developed to predict coarse scale movement patterns of ovipositing *P. rapae* females showed that the day-to-day movement of *P. rapae* females resembled a random walk (step length > 450m) (Jones et al., 1980). When female butterflies are indiscriminate in their response to high or low density stands of their host plant, as found for searchers in a random walk model, isolated plants would receive a disproportionately higher number of eggs per plant, than plants that grow in high density stands. However, the results from my study, do not show the coarse scale pattern predicted by the random walk model. This might be explained by the previously mentioned upscaling effects, and the averaging of fine scale variance at coarser scales of measurement. To better understand the mechanisms of the pre-alighting phase of oviposition in *P. rapae* further empirical studies that investigate the interplay between visual and olfactory stimuli at different spatial scales are needed.

*Tyria jacobaeae* Compared to *P. rapae* the cinnabar moth is a more specialised herbivore, which lays its eggs on plants of the species *Senecio jacobaea*. The eggs are laid in batches, and more eggs are found on plants which grow in dense stands (Kunin, 1999). Therefore, the egg distribution of *T. jacobaeae* conforms to the predictions of the resource concentration hypothesis (RCH) (Tahvanainen and Root, 1972; Root, 1973).

The results from the manipulative field experiment, though, did not show any RCH responses (see Figure 2.9 and Table 2.11). However, the models indicated a trend for more egg batches being laid on larger plants. Besides this positive effect of plant size on the number of batches, the fully negative 95% HPD interval of the

geographical y co-ordinates indicate a declining trend in the number of egg batches from South to North. The density of *S. jacobaea* plants in the area surrounding the study plot did not differ greatly. But higher numbers of *T. jacobaeae* females to the south of the experimental area could have been the cause for this South-North trend to occur. The results from the multi-model inference have to be seen with caution, though, since the unconditional model gained a relatively high support. That none of the statistical models from the manipulative field experiment are strongly supported, is probably mainly due to the low number of egg batches laid during the experimental period. Spring 2006, the year in which I performed my experiments, was marked by conditions much cooler and wetter than usual for this time of year (NIWA National Climate Centre, 2006). This may have let to low population numbers of cinnabar moth at the beginning of the experimental period, which resulted in a lower number of egg batches being laid than expected. Unfortunately the low number of egg batches did not provide enough statistical power to detect any possible effects of plant density at different scales.

Nevertheless, for the survey of the wild population I detected a positive response to medium scale plant density in the number of egg batches laid. Kunin (1999) found that early instar larvae were found primarily on plants that grew in dense stands. Since early instars of *T. jacobaeae* larvae tend to feed on the same host plant on which the parent deposited her eggs (Dempster, 1982), they can be used as an indicator of the initial egg distribution. The inter-plant spacing in Kunin's experiments ranged from 0.125 - 15m, with the highest number of early instar larvae found within a one metre radius from the origin of the fan-shaped design used in Kunin's experiment. What could have lead to higher numbers of batches being laid at fine scale aggregations of host plants in experiments by Kunin (1999), are higher fine scale plant densities and lower medium to coarse scale plant densities. A study by Lancaster (2006) showed that higher numbers of *T. jacobaeae* caterpillars were found on host plants that grew in dense clusters and within a range of null to five metres from each other. As discussed for the *P. rapae* results, different factors might have influenced the distribution of egg batches at different spatial scales, and the nature of my experimental design might have introduced upscaling effects between the different scales of measurement of plant density.

Kunin (1997; 1999) suggest different mechanisms that may lead to a bias of her-

bivores on host plants of varying densities. Most notably for my results are the sensory and dispersal bias. Where searchers rely heavily on olfaction, aggregated host plant patches may receive a higher load of herbivores due to the larger volatile plume, than plants growing at low density. This bias might disappear or may even be reversed if the foragers are mainly driven by visual cues (Bukovinszky et al., 2005). While some host plants in dense stands might still receive a high level of herbivory, the overall effect might be diluted by the number of surrounding plants. The ability to disperse between host plant patches or individual plants dictates the scale at which foragers operate on (Kareiva, 1985; Matter et al., 2005). An insect herbivore with a relative high daily dispersal rate for example, may have a different perception on whether a patch of host plants is aggregated or sparse, in comparison to a herbivore that might be restricted to low daily dispersal rates (Kareiva, 1982). The positive response to plant density at medium scale might be an example of the *T. jacobaeae* aggregating in an area of relative high host plant density. While at fine scale visual cues might overweight, and single plants may stand out more and be more attractive to ovipositing T. jacobaeae females (Bernays and Chapman, 1994). Although not strongly supported by my statistical models, the number of egg batches might have been positively affected by plant size and the number of flowers in both, the manipulative experiment and natural population survey. Larger plants and plants with more flower buds may support higher numbers of caterpillars, while the food resources found in smaller and plants with less flowers might be depleted more quickly. T. jacobaeae offspring would than be forced to search for new host plants (Tinney et al., 1998), thus increasing their predation risk (Myers, 1976) and ultimately decreasing their dispersal success (Myers and Campbell, 1976).

Another factor that has been shown to influence oviposition choice of female *T. jacobaeae* is the content of organic nitrogen and sugar (Vandermeijden et al., 1989). Plants that were rich in both were more readily accepted than plants in which one or both of these nutrients were less abundant. In contrast, no evidence was found that pyrrolizidine alkaloids, a class of secondary plant metabolites found in large diversity among *Senecio* species, affect oviposition by *T. jacobaeae* females (Macel et al., 2002). In our experiments we did not measure any of these chemical qualities, but it is likely that they may have contributed to the observed egg distribution.

In general, the number of eggs a female insect is able to lay is correlated with

her body size. But a population may exceed a patch's carrying capacity for their offspring, if all individuals lay their complete set of eggs on the same host or in the same resource patch, thus reducing the fitness of their offspring (Mangel, 1987; Ives, 1989). An example for a strong positive relationship between clutch size and abundance of food was shown by Pilson and Rausher (1988) for the pipevine swallowtail butterfly, *Battus philenor*. When all edible plant material is consumed, larvae of *B*. *philenor* tend to leave their host plant in search of a new host plant. Whether their search is successful heavily relies on the size and body mass of the larvae. Female butterflies of *B. philenor* therefore have to optimise the number of eggs laid on each plant depending on the plants quality as a food plant for their offspring. Larvae of the cinnabar moth do face a similar problem during their development, which also causes a shift in the observed response to plant density (Kunin, 1999). Ives (1989) presents different models on the relationship between larval fitness and clutch size, which may help to explain why in some species an adjustment of clutch size is found and not in others. In my study, though, only one plant received more than one egg batch, which made it impossible to make any suggestions on whether T. jacobaeae do respond to previously laid con-specific egg batches. However, the number of eggs within *T. jacobaeae* egg batches was not affected by surrounding plant density or host plant size. As flowers are a major part of the diet of older *T. jacobaeae* instars, I would have expected to see an effect on clutch size depending on the number of flowers present on each plant. Although, no change in T. jacobaeae egg batch size in response to plant size was also reported by Crawley and Gillman (1989).

**Conclusion** The results from this study underline the importance of spatial scale in ecological experiments. Through the multi-scale approach I was able to show that observed patterns are scale dependent, and that the outcome of an experiment may depend on the scale of measurement used in the study. To better understand ecological patterns it is important to recognise the different mechanisms that lead their formation. These mechanisms may operate at different scales and interactions may exist between them. For example, the role of visual and olfactorial cues during the pre-alighting phase of ovipositing *P. rapae* females is still poorly understood. These two senses may be used to varying degrees during host search, and cues may be relevant at different spatial scales.

In the following chapter I will investigate how flight patterns of cabbage white butterflies may be influenced by different plant densities. In addition, I will apply a linear array of spatial scales to detect effects in egg distribution patterns.

# References

- Akaike, H., 1974. A new look at the statistical model identification. *IEEE Transactions on Automatic Control* **19**:716–723.
- Altieri, M., 1995. Biodiversity and biocontrol: lessons from insect pest management. *Advances in Plant Pathology* **11**:191–209.
- Anderson, D. R. and K. P. Burnham, 2002. Avoiding pitfalls when using information-theoretic methods. *Journal of Wildlife Management* 66:912–918.
- Bates, D. M., 2007. *lme4*: Linear mixed-effects models using s4 classes. http://cran.r-project. org/src/contrib/Descriptions/lme4.html. R package version 0.99875-9.
- Bellehumeur, C., P. Legendre, and D. Marcotte, 1997. Variance and spatial scales in a tropical rain forest: Changing the size of sampling units. *Plant Ecology* 130:89–98.
- Bernays, E. A. and R. F. Chapman, 1994. Host-plant selection by phytophagous insects. Springer.
- Brown, J. and G. West, 2000. Scaling in biology. Oxford University Press, Oxford.
- Bryk, A. and S. Raudenbush, 1992. Hierarchical linear models for social and behavioral research. Sage, Newbury Park, CA.
- Bukovinszky, T., R. P. J. Potting, Y. Clough, J. C. van Lenteren, and L. E. M. Vet, 2005. The role of preand post-alighting detection mechanisms in the responses to patch size by specialist herbivores. *Oikos* 109:435–446.
- Burnham, K. P. and D. R. Anderson, 2002. Model selection and multimodel inference: a pratical information-theoretic approach. Springer Verlag, New York, second edition.
- Cadotte, M. W. and T. Fukami, 2005. Dispersal, spatial scale, and species diversity in a hierarchically structured experimental landscape. *Ecology Letters* **8**:548–557.
- Chen, M. S., 2008. Inducible direct plant defense against insect herbivores: A review. *Insect Science* **15**:101–114.
- Chen, Y. Z., L. Lin, C. W. Wang, C. C. Yeh, and S. Y. Hwang, 2004. Response of two *Pieris* (Lepidoptera : Pieridae) species to fertilization of a host plant. *Zoological Studies* **43**:778–786.
- Crawley, M. and R. Pattrasudhi, 1988. Interspecific competition between insect herbivores: asymmetric competition between cinnabar moth and ragwort seed-head fly. *Ecological Entomology* **13**:243–249.

- Crawley, M. J. and M. P. Gillman, 1989. Population dynamics of cinnabar moth and ragwort in grassland. *The Journal of Animal Ecology* **58**:1035–1050.
- Cromartie, W. J., 1975. The effect of stand size and vegetational background on the colonization of cruciferous plants by herbivorous insects. *Journal of Applied Ecology* **12**:517–533.
- Dempster, J. P., 1982. The ecology of the cinnabar moth, *Tyria jacobaeae* L., Lepidoptera, Arctiidae. *Advances in Ecological Research* **12**:1–36.
- Denny, M. W., B. Helmuth, G. H. Leonard, C. D. G. Harley, L. J. H. Hunt, and E. K. Nelson, 2004. Quantifying scale in ecology: lessons from a wave-swept shore. *Ecological Monographs* 74:513–532.
- Fahrig, L., 1988. A general model of populations in patchy habitats. *Applied Mathematics and Computation* **27**:53.
- Fahrig, L., 1992. Relative importance of spatial and temporal scales in a patchy environment. *Theoretical Population Biology* **41**:300.
- Fryar, E. O., J. T. Arnold, and J. E. Dunn, 1988. Bayesian evaluation of a specific hypothesis. *American Journal of Agricultural Economics* 70:685–692.
- Gelman, A. and J. Hill, 2007. Data analysis using regression and multilevel/hierarchical models. Cambridge University Press.
- Gelman, A., Y.-S. Su, M. Yajima, J. Hill, M. G. Pittau, J. Kerman, and T. Zheng, 2008. arm: Data analysis using regression and multilevel/hierarchical models. r package version 1.1-15. http://cran.rproject.org/web/packages/arm/index.html.
- Girvetz, E. H. and S. E. Greco, 2007. How to define a patch: a spatial model for hierarchically delineating organism-specific habitat patches. *Landscape Ecology* **22**:1131–1142.
- Goldstein, H., 1995. Multilevel statistical models. Halstead Press, New York.
- Grez, A. A. and R. H. Gonzalez, 1995. Resource concentration hypothesis effect of host-plant patch size on density of herbivorous insects. *Oecologia* **103**:471–474.
- Harrison, S., C. D. Thomas, and T. M. Lewinsohn, 1995. Testing a metapopulation model of coexistence in the insect community on ragwort (*Senecio jacobaea*). *American Naturalist* **145**:546–562.
- Hartley, S. and W. E. Kunin, 2003. Scale dependency of rarity, extinction risk, and conservation priority. *Conservation Biology* **17**:1559–1570.
- Hern, A., R. G. McKinlay, G. Edwards-Jones, and British Crop Protection Council, 1996. Effect of host plant volatiles on the flight behaviour of *Pieris rapae*. In *Brighton crop protection conference: Pests and diseases*, volume 3, pages 431–432.

- Honda, K., H. Omura, and N. Hayashi, 1998. Identification of floral volatiles from *Ligustrum japon-icum* that stimulate flower-visiting by cabbage butterfly, *Pieris rapae*. *Journal of Chemical Ecology* 24:2167–2180.
- Ives, A. R., 1989. The optimal clutch size of insects when many females oviposit per patch. *The American Naturalist* **133**:671–687.
- Jones, R. E., 1977. Movement patterns and egg distribution in cabbage butterflies. *Journal of Animal Ecology* **46**:195–212.
- Jones, R. E., N. Gilbert, M. Guppy, and V. Nealis, 1980. Long-distance movement of *Pieris rapae*. *Journal of Animal Ecology* **49**:629–642.
- Kareiva, P., 1982. Experimental and mathematical analysis of herbivore movement quantifying the influence of plant spacing and quality on foraging discrimination. *Ecological Monographs* 52:261– 282.
- Kareiva, P., 1983. Influence of vegetation texture on herbivore populations: resource concentration and herbivore movement. Pages 295-289 in Denno, R. F. and M. S. McClure, editors. Variables plants and herbivores in natural and managed systems. Academic Press, New York.
- Kareiva, P., 1985. Finding and loosing host plants by phyllotreta patch size and surrounding habitat. *Ecology* **66**:1809–1816.
- Kotliar, N. B. and J. A. Wiens, 1990. Multiple scales of patchiness and patch structure a hierachical framework for the study of heterogeneity. *Oikos* **59**:253–260.
- Kunin, W. E., 1997. The Biology of Rarity, chapter Population biology and rarity: on the complexity of density in insect-plant interactions. Chapman and Hall, London.
- Kunin, W. E., 1999. Patterns of herbivore incidence on experimental arrays and field populations of ragwort, *Senecio jacobaea*. *Oikos* 84:515–525.
- Lancaster, J., 2006. Using neutral landscapes to identify patterns of aggregation across resource points. *Ecography* **29**:385–395.
- Levin, S. A., 1992. The problem of pattern and scale in ecology. Ecology 73:1943–1967.
- Lindley, D. V., 1965. Introduction to probability and statistics from a bayesian viewpoint: Part 2 inference. Cambridge University Press.
- Long, Z. T., C. L. Mohler, and W. P. Carson, 2003. Extending the resource concentration hypothesis to plant communities: Effects of litter and herbivores. *Ecology* **84**:652.

- Macel, M., P. G. L. Klinkhamer, K. Vrieling, and E. van der Meijden, 2002. Diversity of pyrrolizidine alkaloids in Senecio species does not affect the specialist herbivore *Tyria jacobaeae*. *Oecologia* 133:541–550.
- Maguire, L. A., 1983. Influence of collard patch size on population-density of Lepidopteran pests (Lepidoptera, Pieridae, Plutellidae). *Environmental Entomology* **12**:1415–1419.
- Mangel, M., 1987. Oviposition site selection and clutch size in insects. *Journal of mathematical biology* **25**:1–22.
- Marques, E. S. D., P. W. Price, and N. S. Cobb, 2000. Resource abundance and insect herbivore diversity on woody fabaceous desert plants. *Environmental Entomology* 29:696–703.
- Matter, S. F., T. Roslin, and J. Roland, 2005. Predicting immigration of two species in contrasting landscapes: effects of scale, patch size and isolation. *Oikos* **111**:359–367.
- Maurer, B., 1999. Untangling ecological complexity: The macroscopic perspective. University of Chicago Press, Chicago.
- McMahon, S. M. and J. M. Diez, 2007. Scales of association: hierarchical linear models and the measurement of ecological systems. *Ecology Letters* **10**:437–452.
- Myers, J. H., 1976. Distribution and dispersal in populations capable of resource depletion a simulation model. *Oecologia* 23:255–269.
- Myers, J. H., 1985. Effect of physiological condition of the host plant on the ovipositional choice of the cabbage white butterfly, *Pieris rapae. Journal of Animal Ecology* **54**:193–204.
- Myers, J. H. and B. J. Campbell, 1976. Distribution and dispersal in populations capable of resource depletion a field study on cinnabar moth. *Oecologia* **24**:7–20.
- NIWA National Climate Centre, 2006. Climate summary for spring 2006. http://www.niwa.cri. nz/ncc/cs/seasonal/ma/sclimsum\_06\_4\_spring.
- O'Neill, R. V., D. L. Angelis, J. B. Waide, and T. F. H. Allen, 1986. A hierarchical concept of ecosystems. Princeton University Press, Princeton, N.J.
- O'Neill, R. V., B. T. Milne, M. G. Turner, and R. H. Gardner, 1988. Resource utilization scales and landscape pattern. *Landscape Ecology* **2**:63–69.
- Otway, S. J., A. Hector, and J. H. Lawton, 2005. Resource dilution effects on specialist insect herbivores in a grassland biodiversity experiment. *Journal of Animal Ecology* **74**:234–240.
- Paivinen, J., P. Ahlroth, V. Kaitala, J. S. Kotiaho, J. Suhonen, and T. Virola, 2003. Species richness and regional distribution of myrmecophilous beetles. *Oecologia* 134:587–595.

- Petrakis, P. V., 2004. Space allocation in *Melanophila knoteki knoteki* (reitt.) var. *hellenica* (obenberger) (col., buprestidae) in the attack of greek fir *Abies cephalonica* loud. var. *graeca* (fraas) liu : a pattern to process approach. *Journal of Applied Entomology* **128**:70–80.
- Pilson, D. and M. D. Rausher, M. D., 1988. Clutch size adjustment by a swallowtail butterfly. *Nature* **333**:361–363.
- Pinheiro, J. C. and D. M. Bates, 2000. Mixed-Effects Models in S and S-Plus. Statistics and Computing. Springer Verlag, New York.
- Rabasa, S. G., D. Gutierrez, and A. Escudero, 2005. Egg laying by a butterfly on a fragmented host plant: a multi-level approach. *Ecography* **28**:629–639.
- Raudenbush, S. W. and A. S. Bryk, 2002. Hierarchical Linear Models: Applications and Data Analysis Methods. Advanced Quantitative Techniques in the Social Sciences. Sage Publications, Thousand Oaks, CA.
- Root, R. B., 1973. Organization of a plant-arthropod association in simple and diverse habitats: The fauna of collards (*Brassica oleracea*). *Ecological Monographs* **43**:95–124.
- Root, R. B. and P. M. Kareiva, 1984. The search for resources by cabbage butterflies (*Pieris rapae*): Ecological consequences and adaptive significance of markovian movements in a patchy environment. *Ecology* 65:147–165.
- Schellhorn, N. A. and V. L. Sork, 1997. The impact of weed diversity on insect population dynamics and crop yield in collards, *Brassica oleraceae* (brassicaceae). *Oecologia* **111**:233–240.
- Sjerps, M., P. Haccou, E. Meelis, and E. Vandermeijden, 1993. Egg distribution within patches: An optimality problem for insects. *Theoretical Population Biology* **43**:337–367.
- Strong, D. R., J. H. Lawton, and R. Southwood, 1984. Insects on Plants. Blackwell Scientific Publications, Oxford.
- Szabo, P. and G. Meszena, 2006. Spatial ecological hierarchies: Coexistence on heterogeneous landscapes via scale niche diversification. *Ecosystems* **9**:1009–1016.
- Tahvanainen, J. O. and R. B. Root, 1972. Influence of vegetational diversity on population ecology of a specialized herbivore, *phyllotreta cruciferae* (coleoptera-chrysomelidae). *Oecologia* **10**:321–&.
- Tinney, G. W., P. E. Hatcher, P. G. Aqres, N. D. Paul, and J. B. Whittaker, 1998. Inter- and intra- species differences in plants as hosts to *Tyria jacobaeae*. *Entomologia Experimentalis et Applicata* **88**:137–145.
- Traynier, R. M. M., 1979. Long-term changes in the oviposition behavior of the cabbage butterfly, *Pieris rapae*, induced by contact with plants. *Physiological Entomology* **4**:87–96.

- Vandermeijden, E., A. M. Vanzoelen, and L. L. Soldaat, 1989. Oviposition by the Cinnabar moth, *Tyria jacobaeae*, in Relation to Nitrogen, Sugars and Alkaloids of Ragwort, *Senecio jacobaea*. Oikos 54:337–344.
- Vrieling, K., 2006. Chemical ecology of the cinnabar moth (*Tyria jacobaeae*) on a newly recorded host Senecio adonidifolius. Acta Oecologica 30:168–172.
- Wardle, D. A., 1987. The ecology of ragwort textitSenecio jacobaea a review. *New Zealand Journal of Ecology* **10**:67 76.
- Wiens, J. A., 1989. Spatial scaling in ecology. Functional Ecology 3:385–397.
- Wiens, J. A., 1991. Ecological similarity of shrub-desert avifaunas of Australia and North America. *Ecology* **72**:479–495.
- Wolfson, J. L., 1980. Oviposition response of *Pieris rapae* to environmentally induced variation in *Brassica nigra*. *Entomologia Experimentalis et Applicata* **27**:223–232.
- Yamamura, K., 1999. Relation between plant density and arthropod density in cabbage fields. *Researches on Population Ecology* **41**:177–182.

# 2.5 Appendix

# 2.5.1 Summary tables of parameter estimates from HLMs

Oviposition experiment with *P. rapae* 

	Coeff	Estm	lowerHPD	upperHPD	lowerCI	upperCI	Std. Err.
	(Intercept)	-1.525e-01	-3.204e+00	2.832e+00	-3.231e+00	2.926e+00	1.539e+00
	log(Coarse scale)	-4.591e-01	-1.078e+00	1.388e-01	-1.079e+00	1.611e-01	3.101e-01
	log(Medium scale)	2.268e-01	-1.165e-01	5.792e-01	-1.279e-01	5.815e-01	1.774e-01
a)	log(Fine scale)	-4.590e-01	-8.130e-01	-1.106e-01	-8.181e-01	-9.998e-02	1.795e-01
	×	-9.367e-03	-1.673e-02	-1.863e-03	-1.696e-02	-1.774e-03	3.797e-03
	Υ	1.848e-04	-7.062e-03	7.431e-03	-7.217e-03	7.586e-03	3.701e-03
	log(Plant size)	2.386e-01	-2.581e-01	7.405e-01	-2.708e-01	7.479e-01	2.547e-01
	(Intercept)	-1.282e+00	-3.910e+00	1.339e+00	-3.961e+00	1.398e+00	1.340e+00
	log(Coarse scale)	-5.009e-01	-1.116e+00	1.011e-01	-1.123e+00	1.208e-01	3.109e-01
b)	log(Medium scale)	2.593e-01	-1.017e-01	6.195e-01	-1.090e-01	6.276e-01	1.841e-01
	log(Fine scale)	-4.772e-01	-8.280e-01	-1.303e-01	-8.334e-01	-1.211e-01	1.781e-01
	log(Plant size)	3.310e-01	-1.582e-01	8.187e-01	-1.674e-01	8.295e-01	2.492e-01

and b) for model 5, $w = 0.318$ ; for explanation of symbols see Table 2.4.	the number and distribution of <i>P. rapae</i> eggs on <i>B. oleracea</i> in Kaitoke experiment (2005): a) for model 2, $w = 0.682$ ,	Table 2.14: Parameter estimates and 95% HPD and confidence intervals of hierarchical linear model for testing
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Table 2.15: Summary of random effects errors of a) model 2, and b) model 5, testing the number and distribution of *P. rapae* eggs on *B. oleracea* plants in Kaitoke experiment by fitting a hierarchical linear model; shown is the variation of the intercept at a particular level, as well as the model residual variance.

	Level	Groups	Name	Variance	Std.Dev.
	1	Group:(Sub-Block:(Block:Fields))	(Intercept)	0.6690	0.818
	2	Sub-Block:(Block:Fields)	(Intercept)	0.0000	0.000
a)	3	Block:Fields	(Intercept)	0.0647	0.254
	4	Fields	(Intercept)	0.0000	0.000
	1	Group:(Sub-Block:(Block:Fields))	(Intercept)	0.5851	0.765
	2	Sub-Block:(Block:Fields)	(Intercept)	0.1512	0.389
b)	3	Block:Fields	(Intercept)	0.0456	0.214
	4	Fields	(Intercept)	0.0881	0.297

Oviposition experiments with *T. jacobaeae* 

Table 2.16: Parameter estimates and 95% HPD and confidence intervals of hierarchical linear model for testing the number and distribution of T. jacobaeae egg batches among an artificial population of S. jacobae plants: a) model 2, w = 0.416, and b) model 4, w = 0.264; for explanation of symbols see Table 2.5.

	Coeff	Estm	lowerHPD	upperHPD	lowerCI	upperCI	Std. Err.
	(Intercept)	-1.240e+01	-2.176e+01	-3.050e+00	-2.195e+01	-2.841e+00	4.777e+00
	log(Coarse scale)	3.283e-01	-1.362e+00	2.012e+00	-1.394e+00	2.051e+00	8.611e-01
	log(Medium scale)	5.714e-01	-2.402e-01	1.390e+00	-2.604e-01	1.403e+00	4.159e-01
1	log(Fine scale)	-5.879e-02	-5.697e-01	4.588e-01	-5.829e-01	4.653e-01	2.621e-01
a)	Flowers	-4.515e-02	-1.021e-01	1.172e-02	-1.032e-01	1.289e-02	2.902e-02
	×	3.624e-03	-3.924e-02	4.621e-02	-3.994e-02	4.719e-02	2.178e-02
	Y	-6.558e-02	-1.158e-01	-1.593e-02	-1.166e-01	-1.451e-02	2.553e-02
	log(Plant size)	1.121e+00	2.118e-01	2.047e+00	1.836e-01	2.058e+00	4.687e-01
	(Intercept)	-1.395e+01	-2.270e+01	-5.277e+00	-2.282e+01	-5.083e+00	4.434e+00
	log(Coarse scale)	2.490e-01	-1.251e+00	1.772e+00	-1.291e+00	1.789e+00	7.702e-01
(q	log(Medium scale)	5.441e-01	-2.822e-01	1.365e+00	-2.965e-01	1.385e+00	4.203e-01
	log(Fine scale)	-6.895e-02	-5.973e-01	4.514e-01	-6.045e-01	4.666e-01	2.678e-01
	log(Plant size)	1.011e+00	1.606e-01	1.874e+00	1.366e-01	1.885e+00	4.370e-01

Table 2.17: Summary of random effects errors of a) model 2 and b) model 4, testing the number and distribution of *T. jacobaeae* egg batches among an artificial population of *S. jacobae* plants by fitting a hierarchical linear model; shown is the variation of the intercept at a particular level, as well as the model residual variance.

	Level	Groups	Name	Variance	Std.Dev.
	1	Group:(Sub-Block:(Block:Fields))	(Intercept)	0.00e+00	0.00e+00
	2	Sub-Block:(Block:Fields)	(Intercept)	7.29e-10	2.70e-05
a)	3	Block:Fields	(Intercept)	0.00e+00	0.00e+00
	4	Fields	(Intercept)	1.14e-09	3.37e-05
	1	Group:(Sub-Block:(Block:Fields))	(Intercept)	7.61e-08	0.000276
	2	Sub-Block:(Block:Fields)	(Intercept)	1.15e-07	0.000339
b)	3	Block:Fields	(Intercept)	0.00e+00	0.000000
	4	Fields	(Intercept)	2.45e+00	1.564461

### Survey of natural population of S. jacobaea for T. jacobaeae

Table 2.18: Summary of random effects errors of a) model 4, and b) model 5 testing the number and distribution of *T. jacobaeae* eggs among a wild population of *S. jacobae* plants by fitting a hierarchical linear model; shown is the variation of the intercept at a particular level.

	Level	Groups	Name	Variance	Std.Dev.
a)	1	Field	(Intercept)	0.193	0.44
b)	1	Field	(Intercept)	0.183	0.428

	Coeff	Estm	lowerHPD	upperHPD	lowerCI	upperCI	Std. Err.
	(Intercept)	-9.103e+00	-1.416e+01	-4.022e+00	-1.429e+01	-3.919e+00	2.592e+00
	log(Coarse scale)	-1.608e-01	-1.232e+00	9.134e-01	-1.254e+00	9.321e-01	5.465e-01
a)	log(Medium scale)	1.449e+00	2.566e-01	2.637e+00	2.343e-01	2.664e+00	6.073e-01
	log(Fine scale)	-4.661e-01	-1.322e+00	3.890e-01	-1.340e+00	4.077e-01	4.369e-01
	log(Plant size)	3.932e-01	-7.580e-02	8.614e-01	-8.528e-02	8.716e-01	2.392e-01
	(Intercept)	-7.027e+00	-1.110e+01	-2.922e+00	-1.121e+01	-2.846e+00	2.090e+00
	log(Coarse scale)	-1.494e-01	-1.210e+00	9.223e-01	-1.237e+00	9.380e-01	5.437e-01
(d	log(Medium scale)	1.366e+00	1.937e-01	2.561e+00	1.602e-01	2.571e+00	6.027e-01
	log(Fine scale)	-4.484e-01	-1.305e+00	4.108e-01	-1.326e+00	4.292e-01	4.388e-01
	log(Flowers)	2.573e-01	-8.415e-02	6.011e-01	-9.301e-02	6.077e-01	1.752e-01

= 0.284; for explanation of symbols see Table 2	T. jacobaeae egg batches among a natural popu	Table 2.19: Parameter estimates, 95% HPD int
of symbols see Table 2.5.	mong a natural population of <i>S. jacobea</i> : a) for model 4, $w = 0.304$ , and b) for model 5, $w$	timates, 95% HPD intervals and 95%CIs of HLMs testing the number and distribution of

### Number of eggs within egg batches of *T. jacobaeae*

Table 2.20: Parameter estimates and 95% HPD and confidence intervals of hierarchical linear model (model 1) testing the number and distribution of *T. jacobaeae* eggs per batch among *S. jacobae* plants from manipulative experiment and wild population survey: w = 0.986; for explanation of symbols see Table 2.5.

Coeff	Estm	lowerHPD	upperHPD	lowerCI	upperCI	Std. Err.
(Intercept)	3.376e+00	1.824e+00	4.939e+00	1.787e+00	4.964e+00	7.942e-01

Table 2.21: HLM random effects errors of model 1, testing the number and distribution of *T. jacobaeae* eggs on *S. jacobae* plants; shown is the variation of the intercept at a particular level, as well as the model residual variance.

Level	Groups	Name	Variance	Std.Dev.
1	Field	(Intercept)	1.55	1.25

# Chapter 3

# Influence of host plant density on flight paths of *Pieris rapae* females measured at multiple scales

# 3.1 Introduction

One of the key goals of many ecological studies is to understand the drivers that lead to specific species distributions in the landscape. Such distributions are often patchy and correspond to the underlying structure of the environmental (Kotliar and Wiens, 1990; Levine, 2003; Lancaster, 2006). Two hypotheses that deal with different species distribution patterns that are relevant for this study are the resource concentration hypothesis (hereafter RCH; Tahvanainen and Root, 1972; Root, 1973) and the resource dilution hypothesis (hereafter RDH; Yamamura, 1999). The RCH states that numbers of specialist insect herbivores are higher in dense and pure stands of their host plants. For example, such patterns were found for the cinnabar moth, *Tyria jacobaeae*, (Harrison et al., 1995; Kunin, 1999) and the chrysomelid beetle *Trirhabda virgata* (Long et al., 2003).

However, the pattern predicted by the RCH is not a general phenomenon, and under certain circumstances species such as the small cabbage white butterfly, *Pieris rapae*, (Root and Kareiva, 1984) were observed to contradict assumptions made by the RCH. In particular, during oviposition flight female cabbage white butterflies tend to lay more eggs per plant on isolated hosts than on plants that grow in dense stands. This contrasting pattern is described by the RDH, and was also found for e.g. the ragwort seed-head fly, *Botanophila seneciella*, utilising *Senecio jacobaea* (Crawley and Pattrasudhi, 1988).

Over the last two decades ecologists have become more aware of the influence of temporal and spatial scales on observed ecological patterns (Wiens, 1989; Levin, 1992). Since space is often perceived differently by different organisms (Levin, 1992; Lima and Zollner, 1996), spatial scale in particular has been recognised to have a great importance for an animal's movement through its environment (Bovet and Benhamou, 1988; Matter, 1997; Banks and Yasenak, 2003). In turn, the ability to move through space and disperse from one resource patch to another plays a major role in forming species distributions (O'Neill et al., 1988; Ovaskainen, 2004; Doerr and Doerr, 2005) and has important implications for population processes (Lawton, 1987; Fahrig, 1988, 1992, 1998; Doak, 2000).

Many biotic and abiotic factors can affect an individual's movement, i.e. mortality risk (Cain, 1985; Hanski et al., 2000), weather conditions (Papaj et al., 2007; Srygley and Dudley, 2008), abundance of food (Dumont et al., 2007), as well as the distance between resource patches and a searcher's ability to cross the area between them (Cadotte and Fukami, 2005; Esch et al., 2005; Matter, 2006).

The understanding of population processes has recently been advanced by utilising more complex and spatially explicit models to answer population ecological questions (Patterson et al., 2008). Many movement models found in ecological studies are based on the random walk theory (Schick et al., 2008). In its simplest form a random walk (hereafter RW) describes a movement without bias of direction (e.g. Brownian motion, Brown, 1828). The random walk framework includes a range of different RW deviates such as the correlated random walk (CRW), or the biased random walk (BRW).

The key feature of a CRW is that the turning direction between consecutive steps is correlated, which also leads to some degree of directional persistence. The turning direction in a BRW, however, is affected by an external bias that increases or decreases the likelihood of turns toward this external factor. In some cases movements might be best described by a combination of both of the above, including directional persistence and influence of an external bias. Such models are named biased correlated random walks (BCRW) (reviewed in Codling et al., 2008).

Due to the directional persistence observed in many movement paths of animals CRWs have been applied in various studies to describe movement behaviour (e.g. Bovet and Benhamou, 1988; Crist and MacMahon, 1991; Austin et al., 2004; Schtickzelle et al., 2007). The model for net squared displacement  $(R_n^2)$  developed by Kareiva and Shigesada (1983) allows comparison of movement paths of different turning angle and step length distributions (see Appendix for model formula). When the distribution of turning angles corresponds for example to a zero centred von Mises distribution, the model resembles a CRW. However, if the distribution of turning angles is uniform, the model formula can be simplified to a RW. The predicted values for the net squared displacement gained from simulated paths can than be compared to empirical movement data (see also Turchin, 1998). For paths of high directional persistence the net squared displacement is expected to increase faster than for paths with low directional persistence (compare example paths shown in figure 3.1). The von Mises distribution is essentially equivalent to a normal distribution, with the exception that it accounts for the circular nature of angular data. The width of a von Mises distribution can be described by its concentration parameter  $\kappa$ . The higher  $\kappa$  is the more concentrated the distribution of angles. Illustrated in figure 3.2 are paths of varying tortuousity created by drawing turning angles from von Mises distributions of different values of  $\kappa$ .

However, predictions made for movement paths of animals face many difficulties, i.e. movement patterns may be specific to certain physiological and behavioural states of an animal (e.g. ovipositing vs nectar feeding *Pieris rapae* butterflies; Kareiva and Shigesada, 1983) or to differences in the behavioural response to landscape structure (e.g. response to habitat vs matrix in *Maniola jurtina* and *Pyronia tithonus* butterflies; Conradt and Roper, 2006). In addition, Morales and Ellner (2002) found that predicting individual behaviour is one of the key difficulties to overcome when trying to project coarse scale movement based on fine scale observations. Movement patterns may also differ between populations of the same species as found by Jones (1977) for Canadian and Australian *P. rapae* females during oviposition flight. **Aim** In this study I will examine how movement patterns of female *P. rapae* butterflies change in response to low and high density areas of their host plants. I focus on capturing the flight paths among different sized groups of host plants by using pre-arranged grids. I investigate to what extent patch size and plant density affects the number of visits to each group of host plants. As plant density can be defined differently depending on the scale of measurement used, I will compare the effect of scale (grain/resolution) at which flight paths are sampled and at which plant density is measured. In addition, I will compare the observed paths to a CRW model and test for effects of an external bias.



Figure 3.1: Hypothetical paths of equal step length (0.5m) created by a random walk (a) and correlated random walk (b); both paths were started from the centre of the graph and run for 100 steps; turning angles for the RW were drawn from a uniform distribution (min = 0, max =  $2 \times \pi$ ), and for the CRW from a von Mises distribution ( $\mu = 0, \kappa = 1$ ); c) and d) show the corresponding values for the net squared displacement at each consecutive step of the RW and CRW path.



Figure 3.2: CRW example paths of equal step lengths ( $n_{steps} = 100$ ), turning angles were drawn from a zero centred von Mises distribution; paths (a-i) show effect of varying values for  $\kappa$  on path tortuousity.

## 3.2 Methods

### 3.2.1 Study species

I used the small cabbage white butterfly, *Pieris rapae* L (Lepidoptera - Pieridae) as the study organism for my observations. *Pieris rapae* was accidentally introduced to New Zealand in 1929-30 (Muggeridge, 1942), and since then has spread all over the country. Nowadays it is well established within New Zealand, with three to five generations a year. Females lay their eggs on host plants belonging to the family Brassicaceae, which has also lead to its status as an agricultural pest species.

The flight behaviour of ovipositing *P. rapae* females has previously been described by Root and Kareiva (1984). They observed that on encountering denser host plant patches, female *P. rapae* butterflies tended to land more often, but their flight paths did not show a change in directionality (see also Jones, 1977). In addition, *P. rapae* females only laid one egg at a time and passed over several suitable hosts, often traveling about 1.3m between consecutive egg laying events (Root and Kareiva, 1984; Yamamura, 1999). As a result an individual female would potentially distribute their offspring between several host plant patches, thus increasing offspring survival in case of e.g. patch extinction. This behaviour has become known as the 'risk-spreading syndrome' (Root and Kareiva, 1984).

I recorded flight paths of *P. rapae* females over two different experimental setups. In both experiments I used six week old cabbage plants, *Brassica oleracea* (Brassicaceae), which were raised under common conditions in a green house at Victoria University, New Zealand. All plants were chosen to have an equal number of leaves of similar size (diameter of largest leaf  $\pm$  1cm).

### 3.2.2 Study design

I record flight paths of *P. rapae* females during two experiments, both of which were conducted on the Woodhaven farm in Levin, New Zealand (S 40°38′03, E 175°14′42). Pre-arranged grids were set up to record butterfly location during the observations. I used fallow fields of bare soil for both experiments.

#### Flight paths sampled at coarse scale resolution

In the first experiment flight paths of female cabbage white butterflies were recorded over an area of  $36 \times 36m$ , that was spatially replicated three times. The three  $36 \times 36m$  squares were surrounded by an area of bare soil of at least 36m on each side. Each of the three  $36 \times 36m$  squares was divided further into  $9 \times 9m$  grid cells and all nodes of the resulting grid were marked with a 30cm pole (see Figure 3.3).

Each corner of the  $36 \times 36m$  square contained a group of cabbage plants of either one, four, sixteen or forty plants. Each group of cabbage plants was set up to fit into a  $6 \times 6m$  square, with the closest corner of the  $6 \times 6m$  being one metre from the border of the  $36 \times 36m$  square (Figure 3.3). Between the three observational squares the corner location of the different groups of host plants was rotated clockwise.

When a female cabbage white butterfly flew through the observational area, I recorded which  $9 \times 9m$  grid cell it crossed, as well as any direct interaction with the host plants in the area (Figure 3.3). Paths were than analysed by using the centre of each square that a butterfly passed through as reference point. From each centre of the  $9 \times 9m$  grid cells there were eight different movement directions, either through one of the four sides or corners of the square. However, movements through corners were very rare. From all the butterflies I observed, only those that were confirmed as females were included for the analysis. I followed butterflies at a distance no less than two metres to prevent observer bias (Root and Kareiva, 1984).

Flight observations for this experiment were conducted during January 2006 over four consecutive days between 12-1pm and 3-5pm. The weather conditions for each day were sunny and a daily high between 19-21°C, with a light north-westerly breeze. In addition, the flight observations were conducted parallel to an experiment measuring egg distributions of cabbage white butterflies among different sized groups of host plants. I included the results from the egg counts to discuss the findings from the flight observation experiment in relation to overall oviposition activity (see appendix for short description of results).



Figure 3.3: Study area of coarse scale flight observation experiment with *P. rapae* : Broken lines indicate pre-arranged grid used to record butterfly movement, grid cells are  $9 \times 9$ m in size, numbers in grid cells show the number of plants contained within this grid cell, all other cells are empty; shaded areas indicate  $6 \times 6$ m squares containing plants; solid line indicates an example path. Recorded locations of butterflies passing through a grid cell are indicated by solid circles in the centre of the grid cells, filled triangle indicates start of the path.

### Flight paths sampled at fine scale resolution

The observations in this experiment were conducted over an area of  $36 \times 25.5$ m, which was divided further into squares of  $1.5 \times 1.5$ m. Each node of the resulting grid was marked by a 15cm long pole. Using grid cells and marker poles as reference points, I was able to draw flight paths of female *P. rapae* butterflies on a corresponding map.

A group of four and 40 plants were laid out as shown in Figure 3.4. Plant density

was measured at two different scales using a  $1 \times 1m$  (fine) and a  $6 \times 6m$  square. Both groups of plants were set up so that they would fit into a  $6 \times 6m$  square, resulting in plant densities of 4 and 40 per  $36m^2$ . As shown in figure 3.4, the patch of four plants was completely contained in a  $1 \times 1m$  square. The patch of forty cabbage plants, though, was composed of groups of one, four and sixteen plants contained within separate  $1 \times 1m$  squares. This fine scale heterogeneity in the patch of forty allowed for comparison of flight paths within this patch.

The study area was surrounded by a 2m high hedge on two sides and by a gravel road with a 1.5m grass strip on the other two sides. The cabbage plants were set up so that a minimum distance of 7.5m lay between the study area and the grass strip next to the gravel road, and a minimum distance of 12m between the plants and the hedges.

To compare flight paths when plants were present on the field to paths when no plants were present, I spent one hour in the afternoon of the first day and one hour in the morning of the second day observing butterfly movements on the field with no plants present. During these times plants were stored away from the observational site , also, I waited 30 minutes after the field had been cleared of cabbage plants, before recording flight paths on the empty field to allow possible plant volatiles to disperse. A total of 10.5 hours were spent recording flight paths when plants were present. In order to minimise detection bias I moved clockwise every 15 minutes from one corner of the field to the next. Only butterflies that were confirmed to be female were included in the analysis. I followed butterflies into the observational area for gender identification and to increase accuracy of mapping. However, a minimum distance of two metres was kept to the observed butterfly at all times (Root and Kareiva, 1984).

Observations were conducted over two consecutive days, between 9am - 3pm. Weather conditions on the first day were: light north-westerly breeze, light overcast and approximately 20°C over the time of the experimental period. On the second day light spells of rain fell during the morning and afternoon hours, sky was light overcast and the temperature had dropped to 18-19°C.

The paths were digitised using GIS software, and re-sampled using an arbitrary step length of 0.75m. This step length eliminated most of the auto-correlation between the turning angles, while still allowing a large enough number of paths to be
analysed. Only paths of three or more steps were retained.

The number of paths crossing the the  $6 \times 6m$  areas which contained the group of four and forty plants (see Figure 3.4) as well as the number of paths not intersecting with any of the above were compared using a binomial probability test. I also compared the relative number of paths intersecting with groups of one, four or sixteen plants in the patch of forty.



Figure 3.4: Study area of fine scale flight observation experiment with *P. rapae* : Solid circles indicate the position of the cabbage plants used in this experiment; large squares around plant patches indicate equal areas of  $6 \times 6m$  used to count the number of paths crossing the patch of four and forty plants (medium scale), smaller squares show  $1 \times 1m$  areas around each group of plants used to compare smaller scale heterogeneity in patch of 40 (fine scale); solid line shows an example path of a *Pieris rapae* female passing through the study area with re-discretized step length of 0.75m (smaller solid circles indicate steps); a circular buffer of 1m radius around each plant (not shown) was used to select path segments lying in or outside buffer area.

#### 3.2.3 Statistical analysis

Analysis of coarse scale resolution paths Data from all three observation plots were combined for this analysis. I calculated the relative number of paths per grid cell that went through grid cells which were empty or contained either of the four plant groups (Figure 3.3). I counted the number of times a grid cell was visited, which potentially also included repeat visits by returning butterflies. I also tested for effects of the different sized groups of host plants on the relative number of paths per grid cell, as well as per grid cell and per plant. The test I used was a binomial probability test assuming equal probabilities as null hypothesis.

Previous studies have shown that the movement pattern of ovipositing *P. rapae* females can be described as a correlated random walk (CRW) (Jones, 1977; Jones et al., 1980; Kareiva and Shigesada, 1983; Root and Kareiva, 1984). I tested whether the observed butterfly paths followed the predictions made by a CRW model. The path characteristic I used to compare simulated and empirical paths was the net squared displacement ( $R_n^2$ , see section on CRW model and net squared displacement below for more detail).

Analysis of fine scale resolution paths The number of paths crossing the the  $6\times 6m$  areas which contained the group of four and forty plants (see Figure 3.4) as well as the number of paths not intersecting with any of the above were compared using a binomial probability test assuming equal probability. In the next step, I tested for differences in the relative number of paths per plant crossing the patch of four and forty using a binomial probability test. I also compared the relative number of paths intersecting with groups of one, four or sixteen plants in the patch of forty. In both circumstances I tested against the null hypothesis of having an equal number of paths for each case.

To test whether butterfly paths of this experiment would have a similar net squared displacement as predicted by a correlated random walk model, I first selected path segments inside and outside a one metre buffer around each plant. From this I gained three sets of path segments: inside the patch of four ('4'), inside the patch of forty ('40') and outside the patch of four and forty ('outside'). I used a buffer of radius of 1 metre around each plant as this allowed for even coverage of

space between plants, while retaining the patches of four and forty plants.

The distribution of turning angles from the three different sets of path segments were then used to generate three corresponding sets of simulated paths based on a correlated random walk model (see section on CRW model and net squared displacement below for more detail). The net squared displacement ( $R_n^2$ ) of the observed data was than compared to the predictions made by the simulated correlated random walk model .

**Correlated random walk model** In order to interpret flight paths taken by female cabbage white butterflies I compared the net squared displacement of observed paths (Kareiva and Shigesada, 1983) to that predicted by a correlated random walk (Turchin, 1998). The CRW model is based on the assumption that the direction taken at each consecutive step n ( $\theta_{n+1}$ ) is correlated to the previous one ( $\theta_n$ ), but that there is no sequential correlation between left or right turns. The mean of the distribution of turning angles should therefore be centred around zero, and ideally be symmetrical. To test for independence in subsequent turning directions I developed contingency tables based on the turning direction of consecutive steps: first order (pairs): left-left, left-right, right-right, right-left; and second order (triplets): left-left, right-left, left-right-left, left-right, left-right, right-left, right-left, left-right, state, right-left, right-left, left-right, left-left, left-right, right-left, right-left, left-right, right-left, right-left, right-left, left-right, left-left, left-right, right-left, right-left, left-right, right-left, right-left, right-left, left-right, left-left, left-right, right-left, right-left, right-left, left-right, right-left, right-left, left-right, right-left, right-left, right-left, right-left, right-left, right-left, right-left, left-right, right-right, ri

The equivalent of a normal distribution for angular data is the von Mises distribution. In terms of angular data (radians in this case) the value around which the von Mises distribution is centred is called  $\mu$ . Instead of a dispersion parameter as used to describe the spread of a normal distribution, the von Mises distribution uses a concentration parameter labelled as  $\kappa$ . The higher the value of  $\kappa$  the more concentrated around  $\mu$  the distribution is. I used  $\mu$  and  $\kappa$  to describe the frequencies of turning angles of flight paths for this analysis. Theoretical correlated random walks usually have a  $\mu$  of zero, but can take on various values for  $\kappa$ . However, as  $\kappa$ approaches zero the resulting path will resemble a random walk (see Figure 3.2).

Diversion of the frequency distribution of turning angles from a von Mises distribution was tested using the Watson's test. I also tested for similarity of the estimated concentration parameter of the von Mises distribution ( $\kappa$ ) between the different sets

of path segments by comparing the 95% confidence intervals. The concentration parameter as well as  $\mu$  and the confidence intervals were gained from a maximum likelihood estimation. Parameter estimates were deemed to be truly different from each other if the 95% confidence intervals did not overlap. The same method was applied for the estimates of  $\mu$ .

For each set of data I simulated 1000 paths that followed the model of a CRW (see Turchin, 1998, for detailed description). The distribution of step lengths and turning angles was taken from the empirical data. For every iteration of the simulation a step length and a turning angle were drawn at random (with replacement) from the pool of observed data. To calculate the turning angle of the following step the newly drawn angle was then added to the previous heading (both in radians). The maximal number of steps of the simulated paths for a given data set was taken from the highest number of steps for any path in the corresponding empirical data set that occurred for at least two individual observations. For example, if one path would have a maximal number of steps of eight and another path would have ten the number of paths used for the simulation would have been eight.

Next I calculated  $R_n^2$  for all consecutive steps of all pseudo paths (see Appendix for model by Kareiva and Shigesada, 1983). To account for differing number of steps in the set of empirical paths, I randomly drew as many  $R_n^2$  out of the pool of simulated paths for step *n* as there were observed paths with *n* number of steps. This procedure was repeated 1000 times to calculate the  $\bar{R}_n^2$  and 95% confidence intervals for the set of simulated paths.

To test whether the observed paths diverged from a CRW, I compared the  $\bar{R}_n^2$  of the observed paths at step *n* to the average  $R_n^2$  predicted for step *n* by the CRW model. If at least half of the observed steps fell outside the 95% confidence intervals produced by the simulated data, the paths in that data set were considered to be different from a correlated random walk (Turchin, 1998; Dumont et al., 2007).

As the majority of egg laying is reported to happen during the morning hours (Root and Kareiva, 1984) I tested for differences in the net squared displacement for paths that were recorded during the morning/noon (before 1pm) and afternoon (after 1pm). As the net squared displacement did not differ significantly between morning/noon and afternoon paths (p-value > 0.05) I combined both sets of data for the analysis.

External bias vs. directional persistence I also tested how well observed paths would fit the predictions of a biased correlated random walk (BCRW). External biases may affect the frequency distribution of absolute movement direction, angle of turn, or step length (Turchin, 1998). For example, Conradt and Roper (2006) observed butterflies looping back to a resource patch after crossing the patch - matrix boundary. Marsh and Jones (1988) developed a test statistic ( $\Delta$ ) that compares predictions made by models assuming an external bias against directional persistence. A positive value of  $\Delta$  implies external bias, while a negative value indicates longrange directional persistence. To test which model would fit the observed value best, I calculated 95% confidence intervals for the predicted values of  $\Delta$  and compared the observed values to it. If an observed value would fall into either of the predicted 95% confidence intervals, no conclusion was possible. However, if an observed value would only be encompassed by one of the 95% CIs than this model would be assumed to be the better fit. The outcome of this test, however, is restricted to either bias towards an external factor or directional persistence. This test should be interpreted in conjunction with the above mentioned test for best fit to a CRW model. In addition, I tested for significant effects of coarse scale movement directions between any of the four compass directions using contingency tables. Coarse scale directional bias may be one external bias indicated by the above test.

All statistical data analysis and simulations were performed using the statistical computing software R (v2.7.2; R Development Core Team, 2008). Parameters of flight paths were calculated using functions provided by the library 'adehabitat' (v1.7.3) (Calenge, 2006). Tests for circular data were performed by utilising methods of the 'circular' (v0.3-8) and 'CircStats' (v0.2-3) libraries by U. Lund and C. Agostinelli (R port of Circular Statistics, from Jammalamadaka and SenGupta, 2001).

## 3.3 Results

## 3.3.1 Coarse scale mapping of flight paths of *P. rapae* females

A total of 80 confirmed female *P. rapae* butterflies were observed crossing the observational areas of this experiment. The experimental set up consisted of three times

as many empty grid cells as there were squares containing plants. Figure 3.5a shows the relative number of visits per empty grid cell in comparison to grid cells containing plants. No significant difference was found for the relative number of cell visits between grid cells containing plants and those that were empty (Binom. Prop. Test,  $\chi^2 = 0$ , df = 1, p-value = 1). Those *P. rapae* females that passed though grid cells containing plants did not show any significant preference for a certain sized group of plants (Figure 3.5b, Binom. Prop. Test,  $\chi^2 = 1.587$ , df = 3, p-value = 0.662). However, the number of visits per grid cell per plant showed a significant decline with increasing plant density (Figure 3.5c, Binom. Prop. Test,  $\chi^2 = 21.0843$ , df = 3, p-value < 0.001). During the observational period two eggs were oviposited on plants of the patch of forty, and a single egg on the patch of four and sixteen each. Unfortunately the number of eggs was too low to conduct any further analysis.

The distribution of turning angles for both subsets of observed data did not differ significantly from a von Mises distribution (Figure 3.6 and 3.7; Watson's Test for the von Mises distribution: 'no plants': statistic: 0.674, p-value > 0.05; 'plants encountered': statistic: 1.076, p-value > 0.05). In addition, the 95% confidence intervals for the parameter estimates of  $\mu$  (Figure 3.7a) and  $\kappa$  (Figure 3.7b) did overlap between paths that encountered grid cells containing plants and paths that only went through empty cells. The parameter estimates for  $\mu$  and  $\kappa$  respectively are therefore considered to not be truly different between the two path subsets.

In both subsets of the data, the female *P. rapae* butterflies tended to turn significantly more often to the right between two consecutive turns ('no plants': Fisher's Exact Test: p-value < 0.001; 'plants encountered': Pearson's Chi-squared test:  $\chi^2$  = 13.027, df = 1, p-value < 0.001). However, the second order analysis of turning direction showed no significant patterns of consecutive turns to the left or right ('no plants': Fisher's Exact Test: p-value = 1; 'plants encountered': Fisher's Exact Test, p-value > 0.05).



Figure 3.5: Distribution of grid cell visits by *P. rapae* females in coarse scale flight observation experiment: a) number of visits per grid cell for cells that were empty vs. those that contained plants, b) number of visits per grid cell of cells containing plants, and c) number of visits per grid cell per plant of cells containing plants; mean number of visits  $\pm$  one standard error.



Figure 3.6: Distribution of turning angles of flight paths in coarse scale flight observation experiment: distribution of turning angles (radians) of paths with a) no plants encountered, and b) that encountered plants; circumference of circle is divided into 8 groups, a sector is drawn for each group with origin in centre of circle, sector length is relative to frequency of observations within each group.



Figure 3.7: Maximum likelihood estimates of  $\mu$  and  $\kappa$  for flight paths of coarse scale flight observation experiment with *P. rapae* for paths that encountered grid cells containing plants and those that only went through empty cells; the 95% confidence estimates were gained from the maximum likelihood estimation.

#### Net squared displacement and CRW model

Comparison between the simulated and observed stepwise mean net squared displacement ( $\bar{R}_n^2$ ) showed that movement of *P. rapae* females deviated from the prediction made by the CRW model (more than 50% of steps outside 95% CIs; Figure 3.8). For both path subsets the CRW model overestimated the stepwise  $\bar{R}_n^2$ . However, the deviation of observed  $\bar{R}_n^2$  from the CRW simulation was lowest for the path subset where paths did not encounter grid cells containing plants (3.8a). For paths that crossed grid cells containing plants once or more (3.8b) the stepwise  $\bar{R}_n^2$  showed the strongest deviation from the predicted values at higher number of steps. The varying level of reduction of the observed net squared displacement is a sign of movement paths being more tortuous and less directional than expected for a pure CRW model. The stepwise mean net squared displacement for the path subset of one or more plant encounters (3.8b) lay in between the expected values for a correlated random walk and uncorrelated random walk (grey dotted line; also compare to RW - CRW illustration in figure 3.1).

The outcomes of Marsh & Jones' test statistic for external bias are summarised in table 3.1. In all four data sets the average observed value  $\Delta$  for the absolute direction of movement (in contrast to the relative angle of turn) did fall into the 95% confidence interval of the predictions made for the model assuming external bias ( $\Delta_a$ ). All average observed values of  $\Delta$  lay between 0.1 and 0.2, which suggest a weak bias in the absolute direction of movement towards an external factor.

Female cabbage white butterflies were observed to cross the study area significantly more often in an east to west or west to east direction than expected (Chi-squared test:  $\chi^2$  = 35.9941, df = 9, p-value < 0.001).



Figure 3.8: Average net squared displacement for the empirical (black solid line) and simulated CRW data (grey solid line) at each consecutive step in the coarse scale flight observation experiment with *P. rapae*; black dotted lines indicate the 95% confidence intervals gained from CRW simulation; grey dotted line indicates expected values for net squared displacement in case of an un–correlated random walk (mean cosine equal to zero and mean squared step length of 81m<sup>2</sup>); labels at bottom show the number of empirical paths of step length n.

Table 3.1: Results of test for external bias ( $\Delta_a$ ) or directional persistence ( $\Delta_b$ ) for paths of coarse scale flight observation experiment with *P. rapae* ; asterisks (\*) indicate intervals that encompass average observed  $\Delta$ .

	95% confidence intervals		
average observed $\Delta$	$\Delta_a$	$\Delta_b$	
Paths through empty squares			
0.132	(-0.403, 0.277)*	(-0.551, -0.057)	
Paths through squares containing plants			
0.116	(-0.799, 0.277)*	(-0.634, -0.064)	

### 3.3.2 Mapping flight paths of *P. rapae* females at fine resolution

#### Flight paths in relation to plant density at medium and fine scale

During the observational period when no plants were present, 15 P. rapae females were observed in the study area. Two of these butterflies crossed the  $6 \times 6m$  area in which the group of four cabbage plants were going to be placed, and two females flew across the  $6 \times 6m$  square which was going to hold the group of 40 host plants. None of the tracks entered both of the sample squares. In the observational period during which plants were present, the flight path of 54 confirmed female butterflies was followed. Here the flight paths of six butterflies were intercepted by the  $6 \times 6m$  sampling square around the group of four plants, and 23 paths crossed the  $6 \times 6m$  square which contained the group of forty plants. In addition, another three tracks passed through both sampling squares, which leaves a total of 19 flight paths that were not intercepted by either sampling square. While there was no significant difference between the number of tracks intersecting the sampling squares during times when plants were absent (2 vs. 2 paths; Binom. Prop. Test,  $\chi^2 = 0$ , df = 1, p-value = 1), the number of tracks crossing the sampling square which contained the group of four plants was significantly lower compared to the number of tracks crossing the sampling square that contained forty plants during the observational period when plants were present (6 vs. 23 paths; Binom. Prop. Test,  $\chi^2$  = 12.068, df = 1, p-value < 0.05).

Looking at the fine scale heterogeneity within the patch of forty, grid cells containing a single plant received a total of 86 visits (including repeated visits from same individual), cells containing four plants received a total of 30 visits and the group of sixteen plants was visited 14 times. Figure 3.9a shows the number of visits per grid cell for the three different plant densities. However, a binomial probability test did not reveal any significant differences between the number of visits per grid cell for the three plant densities (Binom. Prop. Test:  $\chi^2 = 3.403$ , df = 2, p-value = 0.182). However, the number of visits per grid cell and per plant showed a significant decline with increasing plant density (Figure 3.9b; Binom. Prop. Test:  $\chi^2 =$ 9.108, df = 2, p-value = 0.011).

Over the observational period cabbage white females laid a total of 16 eggs among plants of this experiment. One egg was laid on a plant of the patch of four and 15 eggs were laid among plants of the patch of forty. A generalized linear model fitted to test for effects of plant density did not indicate any significant effects of plant density measured either at fine or medium scale on the number of eggs laid (p-value > 0.05).

While in a situation where no plants were present on the field the maximum angle of turn of *P. rapae* females was no more than  $\pm$  90 degrees (Figure 3.10a), turning angles of close to  $\pm$  180 degrees were observed for butterflies when plants were present (Figure 3.10b-d).

When no plants were present the estimated concentration parameter of the distribution of turning angles ( $\kappa$ ) was higher than when plants were present, which indicates that butterflies did not engage in as sharp a turning behaviour as when plants were present (Figure 3.10 and 3.11b). The 95% confidence intervals of the concentration parameter estimates for the data subsets where plants were present during the observational period overlapped and are therefore considered not to be truly different from each other (Figure 3.11b). However, the estimated value of  $\kappa$  for the data set where plants were absent during the observational period is deemed to be truly different from all three of the above. The distribution of turning angles of paths crossing the patch of four, though, was significantly different from a von Mises distribution (Watson's test for the von Mises distribution, statistic = 0.1291, pvalue > 0.05). As the 95% confidence intervals of the  $\mu$  estimates of all three subsets of data overlapped, the parameter estimates for  $\mu$  are therefore seen as being truly similar to each other (Figure 3.11a).

I observed auto-correlation in the movement direction of consecutive steps for paths crossing the patch of '40' (Pearson's Chi-squared test:  $\chi^2 = 43.344$ , df = 1, p-value < 0.001), but not for any of the other subsets of paths (Pearson's Chi-squared test: 'no plants':  $\chi^2 = 0.984$ , df = 1, p-value = 0.321; 'outside':  $\chi^2 = 1.526$ , df = 1, p-value = 0.217; Fisher's Exact Test: '4': p-value = 1). The second-order analysis of the movement direction, however, indicated a significantly lower frequency of three consecutive left turns than expected compared to all the other combinations (Pearson's Chi-squared test:  $\chi^2 = 12.881$ , df = 3, p-value = 0.005). No such pattern was found for any of the other three data sets.



Figure 3.9: Relative number of *P. rapae* flight paths crossing fine scale heterogeneity of different sized groups of host plants (plants within 1×1m squares) within patch of forty cabbage plants: a) paths per grid cell, and b) paths per grid cell and per plant; solid circles indicate average value of at least two grid cells, open circle indicates value of single grid cell.





(a) 'no plants',  $n_{paths} = 15$ ,  $n_{angles} = 385$ ,  $\bar{\theta}$  (rad) = 0.018,  $\psi = 0.954$ 



(c) '40',  $n_{paths} = 29$ ,  $n_{angles} = 1372$ ,  $\bar{\theta}$ (rad) = -0.002,  $\psi = 0.944$ 

(b) 'outside',  $n_{paths} = 54$ ,  $n_{angles} = 1455$ ,  $\bar{\theta}$  (rad) = -0.001,  $\psi = 0.935$ 



(d) '4',  $n_{paths} = 2$ ,  $n_{angles} = 14$ ,  $\theta$ (rad) = -0.129,  $\psi = 0.774$ 

Figure 3.10: Rose diagrams showing the distribution of turning angles (radians) of the four different flight path subsets of fine scale flight observation experiment with *P. rapae* : a) no plants present, b) path segments outside 1m buffer–zone around each plant, c) path segments within 1m buffer around plants of the patch of 40, d) path segments within 1m buffer around plants of the patch of 4; circumference of the circle is divided into 18 groups, for each group a sector is drawn with origin in the circle centre, the sector length is relative to the frequency of observations within each group.



Figure 3.11: Maximum likelihood parameter estimates for  $\mu$  and  $\kappa$  for *P. rapae* flight paths that encountered grid cells containing plants and those that only went through empty cells during the fine scale flight observation experiment; the 95% confidence estimates were gained from the maximum likelihood estimation.

#### Net squared displacement and CRW model

Observed values for the stepwise mean net squared displacement deviated from those predicted by the CRW simulation. In all cases more than half of the steps of the empirical data lay outside the 95% confidence intervals of the CRW simulation. During times when plants were absent from the observational area flight paths of observed female cabbage white butterflies were highly directional which lead to an underestimating of the net squared displacement by the CRW simulation. (Figure 3.12a). However, the model overestimated the stepwise net squared displacement for times when plants were present in the study area (Figure 3.12b-d). The reduced directionality of observed flight paths is resembled more closely by the net squared displacement expected for a random walk (grey dotted line).

When no plants were present the test statistics by Marsh & Jones (1988) was inconclusive on whether the butterflies were affected by an external bias. For both model cases the 95% confidence intervals contain the observed value of  $\Delta$  (Table 3.2). A very marginal external bias was indicated for paths when plants were present. The average observed value of 0.002 is, however, very small and the confidence interval for the expected value assuming an external bias stretches from -0.403 to 0.369. Female cabbage white butterflies crossed the study area without preferring one single compass direction (no plants present: Fisher's Exact Test: p-value = 0.146; plants present: Fisher's Exact Test: p-value = 0.217).

Table 3.2: Results of test for external bias ( $\Delta_a$ ) or directional persistence ( $\Delta_b$ ) for paths of fine scale flight observation experiment with *P. rapae* ; asterisks (\*) indicate intervals that encompass average observed  $\Delta$ .

	95% confidence intervals		
average observed $\Delta$	$\Delta_a$	$\Delta_b$	
Paths when no plants were present			
-0.044	(-0.176, 0.164)*	(-0.107, -0.001)*	
Paths when plants were present			
0.002	(-0.403, 0.369)*	(-0.261, -0.001)	



Figure 3.12: Average net squared displacement for the empirical (black solid line) and simulated CRW data (grey solid line) at each consecutive step for the fine scale flight observation experiment with *P. rapae*; black dotted lines indicate the 95% confidence intervals gained from CRW simulation; grey dotted line indicates expected values for net squared displacement in case of an un–correlated random walk (with a consistent step length of 0.75m and a uniform distribution of turning angles, see Appendix); labels at bottom show the number of empirical paths of step length n, to improve readability some of these labels were omitted.

## 3.4 Discussion

In the experiment when a fine scaled grid was used to record flight paths, butterflies observed during periods when no plants were present showed the highest directionality (Figure 3.10, 3.10 and 3.11). Flight paths were observed to be significantly less directional when plants were present in the study area. The reduced directionality in a situation where plants were present is likely to be related to *P. rapae* females being attracted to patches of their host plant. Previous studies on P. rapae movement have found that cabbage white females do not alter their turning behaviour upon encountering dense host plant patches (Jones, 1977; Jones et al., 1980; Root and Kareiva, 1984). However, female cabbage white butterflies abandon their directional flight paths during periods of nectar feeding (Kareiva and Shigesada, 1983; Root and Kareiva, 1984). Changes in the movement pattern of butterflies in response to landscape features have been observed for a number of species (e.g. Conradt et al., 2000, 2001; Schultz and Crone, 2001; Schtickzelle et al., 2007). The ability to modulate between more directional long-range dispersal and short exploratory movements (foraging for food, oviposition flight etc.) can have important implications for population survival (Van Dyck and Baguette, 2005).

Being able to detect a potential resource, however, is fundamental to searching success. Together with an individual's ability to disperse, its sensory capabilities, such as range of vision or sensitivity of olfaction, determine the scale at which an individual forager interacts with its environment (Wiens, 1989; Levin, 1992; Lima and Zollner, 1996). Empirical data on the perceptual range of *P. rapae* are lacking, but studies done by Schultz and Crone (2001), Schtickzelle et al. (2007) and Crone and Schultz (2008) indicate that the visual range of butterflies lies between ~15-30m. Although I did not record flight paths outside the  $36 \times 36m$  square during the coarse scale observations, the results give no indication that *P. rapae* females discriminated between the four different sized groups of host plants. In addition, I was unable to detect any significant differences between grid cells for the number of visits by butterflies. Recordings of flight paths at fine scale showed a attraction to host plant patches, *P. rapae* females crossed the  $6 \times 6m$  area containing 40 cabbage plants more often than the  $6 \times 6m$  area containing four plants. In the fine scale experiment the patch of four and the patch of forty were only separated by a distance of six metres,

while the distance between groups of host plants in the coarse scale experiment was at least 25m. In relation to the perceptual range suggested for butterflies, cabbage white females would have been able to actively choose between the patch of four and 40, but the higher separation between patches of the coarse scale experiment would have made such a choice between patches from a distance less likely. However, the extend to which visual and volatile cues as well as the females readiness to oviposit played a role in creating this pattern is unclear from my data.

The east-west trend in the movement direction of butterflies crossing the observation area, as well as the fact that plants were set up in the corners of a square could have also added to this result. This east-west trend could have also lead to the indication of a marginal external bias on the flight paths taken by *P. rapae* females across the coarse scale set-up.

Paths recorded in the coarse scale experiment showed a closer fit of the empirical data to the CRW simulation, while the CRW model generally overestimated the net squared displacement in the fine scale experiment when plants were present. The reduced net squared displacement in the fine scale observation when plants were present (disregarding patch of '4' due to low sample number) indicates a change in the otherwise highly directional flight pattern exhibited by *P. rapae* females. Such a change in directionality could be related to the attraction of female cabbage whites towards patches of their host plant. While, as previously mentioned, female *P. rapae* butterflies are reported to not change their turning behaviour when encountering dense areas of their host plant, Root and Kareiva (1984) observed a reduction in the movement length of ovipositing female cabbage whites upon encountering plant patches of greater density. Root and Kareiva used landing sites and straight lines between consecutive landings to map flight paths of female cabbage white butterflies. The method used in this study differs from the one they used in that I focused on segmenting flight paths in relation to landscape features (Benhamou, 2004) rather than oviposition and landing sites to measure responses to different host plant densities. Nevertheless, compared with paths of greater step length, reducing the step length might lead to a more tortuous path when the turning angles between steps are drawn at random. Due to the low number of direct interactions between cabbage plants and butterflies in my experiments, I was unable to test this, but it could be that by only taking into account landing sites the true turning behaviour of ovipositing female cabbage white butterflies was obscured. However, the observations by Root and Kareiva (1984) showed that ovipositing females did respond to plant density by landing more frequently upon encountering dense stands of their host plant. The number of landings was not sufficient to accumulate disproportional high numbers of eggs amongst plants of these denser host plant patches. The number of visits per grid cell and per plant in my fine scale experiment showed a similar pattern. Although, more butterflies visited high density areas, the number of visits per grid cell and per plant was not disproportionally higher compared to low density areas. When considering number of visits per plant for the coarse scale observations, a similar decline with increasing plant density can be expected, since each group of host plants had an equal probability of being visited.

One of the drawbacks of my data set was that I recorded only a few direct interactions with plants during the coarse and fine scale experiments. The flight paths are therefore likely to contain a mix of different behaviours and are not oviposition flight alone. Nevertheless, the results of *P. rapae* egg counts that were performed parallel to the coarse scale observations of this study showed that female P. rapae butterflies did lay eggs on the different groups of host plants used in this experiment. In particular, the number of eggs per plant declined with an increase in fine scale plant density (see Appendix). However, no such pattern was found for medium or coarse scale plant density. As such, the fine scale egg distribution pattern follows the results found by previous studies (Jones, 1977; Root and Kareiva, 1984; Bukovinszky et al., 2005) and does fit the predictions made by the resource dilution hypothesis (Yamamura, 1999). That more isolated plants receive a comparatively higher number of eggs than plants in high density stands also conforms to the results found for *P. rapae* egg distributions in chapter 2 of this thesis, and is supported by the declining number of visits per grid cell and per plant observed during the fine scale experiments.

Whether previously laid eggs could have deterred ovipositing female cabbage white butterflies is unlikely, since coarse scale observations were conducted before the majority of eggs were laid. Also, plants with no conspecific eggs or larvae were used for the fine scale observations. I was not able to test whether chemical characteristics of the host plant might have played a role. Renwick and Radke (1988) suggest that chemical plant properties have a strong effect on host plant acceptance in *P*.

*rapae* females. However, Renwick (2001) showed that larvae can respond selective to potential host plants depending on previous dietary experience. Whether a feeding preference would also affect adult host plant choice is, however, unclear. The mechanism of attraction of female cabbage white butterflies to host plant patches would also require further investigation. One factor which may have played a role for long-range detection of host plants in my experiments was the colour green. Since the area in which the cabbage plants were placed was bare soil, butterflies may have got attracted to a green patch. The colour green has been shown to be an important visual stimulus for searching *P. rapae* butterflies (Traynier, 1979; Myers, 1985). Behavioural differences between *P. rapae* females may also stem from individual egg load depending on age and previous weather conditions (Gossard and Jones, 1977).

## 3.5 Conclusion

The results from this study show the importance of scale of measurement in ecological experiments. As Lima and Zollner (1996) suggested a close link between study design and sensory abilities of the study organism are necessary when investigating a species' response to its environment. In addition, when describing movement patterns the method of abstraction may have a great effect on the measured path characteristics.

# References

- Austin, D., W. Bowen, and J. McMillan, 2004. Intraspecific variation in movement patterns: modeling individual behaviour in a large marine predator. *Oikos* 105:15–30.
- Banks, J. and C. Yasenak, 2003. Effects of plot vegetation diversity and spatial scale on *Coccinella* septempunctata movement in the absence of prey. *Entomologia Experimentalis et Applicata* 108:197– 204.
- Barritt, J., 2008. Simulation of the effects of movement patterns and resource density on the egg distribution of *Pieris rapae* (Lepidoptera) at multiple spatial scales. Master's thesis, School of Biological Sciences, Victoria University of Wellington, New Zealand.
- Benhamou, S., 2004. How to reliably estimate the tortuosity of an animal's path: straightness, sinuosity, or fractal dimension? *Journal of Theoretical Biology* **229**:209–220.
- Bovet, P. and S. Benhamou, 1988. Spatial analysis of animals' movements using a correlated random walk model. *Journal of Theoretical Biology* **131**:419–433.
- Brown, R., 1828. A brief account of microscopical observations made in the months of June, and August, 1827, on the particle contained in the pollen of plants; and on the general existence of active molecules in organic and inorganic bodies. *London, Edinburgh and Dublin Philosophical Magazine and Journal of Science* **4**:161.
- Bukovinszky, T., R. P. J. Potting, Y. Clough, J. C. van Lenteren, and L. E. M. Vet, 2005. The role of preand post-alighting detection mechanisms in the responses to patch size by specialist herbivores. *Oikos* 109:435–446.
- Cadotte, M. W. and T. Fukami, 2005. Dispersal, spatial scale, and species diversity in a hierarchically structured experimental landscape. *Ecology Letters* **8**:548–557.
- Cain, M. L., 1985. Random search by herbivorous insects: A simulation model. Ecology 66:876-888.
- Cain, M. L., 1989. The analysis of angular data in ecological field studies. Ecology 70:1540–1543.
- Calenge, C., 2006. The package "adehabitat" for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling* **197**:516–519.
- Codling, E. A., M. J. Plank, and S. Benhamou, 2008. Random walk models in biology. *Journal of the Royal Society Interface* **5**:813–834.
- Conradt, L., E. J. Bodsworth, T. J. Roper, and C. D. Thomas, 2000. Non-random dispersal in the butterfly *Maniola jurtina*: implications for metapopulation models. *Proceedings of the Royal Society* of London Series B-Biological Sciences 267:1505–1510.

- Conradt, L. and T. J. Roper, 2006. Nonrandom movement behavior at habitat boundaries in two butterfly species: Implications for dispersal. *Ecology* **87**:125–132.
- Conradt, L., T. J. Roper, and C. D. Thomas, 2001. Dispersal behaviour of individuals in metapopulations of two british butterflies. *Oikos* **95**:416–424.
- Crawley, M. and R. Pattrasudhi, 1988. Interspecific competition between insect herbivores: asymmetric competition between cinnabar moth and ragwort seed-head fly. *Ecological Entomology* **13**:243–249.
- Crist, T. O. and J. A. MacMahon, 1991. Individual foraging components of harvester ants movement patterns and seed patch fidelity. *Insectes Sociaux* **38**:379–396.
- Crone, E. E. and C. B. Schultz, 2008. Old models explain new observations of butterfly movement at patch edges. *Ecology* **89**:2061–2067.
- Doak, P., 2000. Population consequences of restricted dispersal for an insect herbivore in a subdivided habitat. *Ecology* **81**:1828–1841.
- Doerr, E. D. and V. A. J. Doerr, 2005. Dispersal range analysis: quantifying individual variation in dispersal behaviour. *Oecologia* **142**:1–10.
- Dumont, C. P., J. H. Himmelman, and S. M. C. Robinson, 2007. Random movement pattern of the sea urchin *Strongylocentrotus droebachiensis*. *Journal of Experimental Marine Biology and Ecology* **340**:80– 89.
- Esch, S., P. G. L. Klinkhamer, and E. van der Meijden, 2005. Do distances among host patches and host density affect the distribution of a specialist parasitoid? *Oecologia* **146**:218–226.
- Fahrig, L., 1988. A general model of populations in patchy habitats. *Applied Mathematics and Computation* **27**:53.
- Fahrig, L., 1992. Relative importance of spatial and temporal scales in a patchy environment. *Theoretical Population Biology* **41**:300.
- Fahrig, L., 1998. When does fragmentation of breeding habitat affect population survival? *Ecological Modelling* 105:273.
- Gossard, T. W. and R. E. Jones, 1977. Effects of age and weather on egg-laying in *Pieris rapae* L. *Journal* of *Applied Ecology* **14**:65–71.
- Hanski, I., J. Alho, and A. Moilanen, 2000. Estimating the parameters of survival and migration of individuals in metapopulations. *Ecology* **81**:239–251.

- Harrison, S., C. D. Thomas, and T. M. Lewinsohn, 1995. Testing a metapopulation model of coexistence in the insect community on ragwort (*Senecio jacobaea*). *American Naturalist* **145**:546–562.
- Jammalamadaka, S. R. and A. SenGupta, 2001. Topics in circular statistics. World Scientific Press, Singapore.
- Jones, R. E., 1977. Movement patterns and egg distribution in cabbage butterflies. *Journal of Animal Ecology* **46**:195–212.
- Jones, R. E., N. Gilbert, M. Guppy, and V. Nealis, 1980. Long-distance movement of *Pieris rapae*. *Journal of Animal Ecology* 49:629–642.
- Kareiva, P. M. and N. Shigesada, 1983. Analyzing insect movement as a correlated random-walk. Oecologia 56:234–238.
- Kotliar, N. B. and J. A. Wiens, 1990. Multiple scales of patchiness and patch structure a hierachical framework for the study of heterogeneity. *Oikos* **59**:253–260.
- Kunin, W. E., 1999. Patterns of herbivore incidence on experimental arrays and field populations of ragwort, *Senecio jacobaea*. *Oikos* 84:515–525.
- Lancaster, J., 2006. Using neutral landscapes to identify patterns of aggregation across resource points. *Ecography* **29**:385–395.
- Lawton, J. H., 1987. Fluctuations in a patchy world. Nature 326:328–329.
- Levin, S. A., 1992. The problem of pattern and scale in ecology. Ecology 73:1943–1967.
- Levine, J. M., 2003. A patch modeling approach to the community-level consequences of directional dispersal. *Ecology* 84:1215–1224.
- Lima, S. L. and P. A. Zollner, 1996. Towards a behavioral ecology of ecological landscapes. *Trends in Ecology & Evolution* 11:131–135.
- Long, Z. T., C. L. Mohler, and W. P. Carson, 2003. Extending the resource concentration hypothesis to plant communities: Effects of litter and herbivores. *Ecology* **84**:652.
- Marsh, L. M. and R. E. Jones, 1988. The form and consequences of random walk movement models. *Journal of Theoretical Biology* **133**:113–131.
- Matter, S. F., 1997. Population density and area: The role of between- and within-patch processes. *Oecologia* **110**:533–538.
- Matter, S. F., 2006. Changes in landscape structure decrease mortality during migration. *Oecologia* **150**:8–16.

- Morales, J. M. and S. P. Ellner, 2002. Scaling up animal movements in heterogeneous landscapes: The importance of behavior. *Ecology* 83:2240–2247.
- Muggeridge, J., 1942. The white butterfly (*Pieris rapae* L.) I. Its establishment, spread, and control in New Zealand. *The New Zealand Journal of Science and Technology* (*A*) **24**:107–129.
- Myers, J. H., 1985. Effect of physiological condition of the host plant on the ovipositional choice of the cabbage white butterfly, *Pieris rapae*. *Journal of Animal Ecology* **54**:193–204.
- O'Neill, R. V., B. T. Milne, M. G. Turner, and R. H. Gardner, 1988. Resource utilization scales and landscape pattern. *Landscape Ecology* **2**:63–69.
- Ovaskainen, O., 2004. Habitat-specific movement parameters estimated using mark-recapture data and a diffusion model. *Ecology* **85**:242–257.
- Papaj, D. R., H. S. Mallory, and C. A. Heinz, 2007. Extreme weather change and the dynamics of oviposition behavior in the pipevine swallowtail, battus philenor. *Oecologia* 152:365–375.
- Patterson, T. A., L. Thomas, C. Wilcox, O. Ovaskainen, and J. Matthiopoulos, 2008. State-space models of individual animal movement. *Trends in Ecology & Evolution* 23:87–94.
- R Development Core Team, 2008. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Renwick, J. A. A., 2001. Variable diets and changing taste in plant-insect relationships. *Journal of Chemical Ecology* **27**:1063–1076.
- Renwick, J. A. A. and C. D. Radke, 1988. Sensory cues in host selection for oviposition by the cabbage white butterfly, *Pieris rapae. Journal of Insect Physiology* 34:251–257.
- Root, R. B., 1973. Organization of a plant-arthropod association in simple and diverse habitats: The fauna of collards (*Brassica oleracea*). *Ecological Monographs* **43**:95–124.
- Root, R. B. and P. M. Kareiva, 1984. The search for resources by cabbage butterflies *Pieris rapae*: Ecological consequences and adaptive significance of Markovian movements in a patchy environment. *Ecology* 65:147–165.
- Schick, R. S., S. R. Loarie, F. Colchero, B. D. Best, A. Boustany, D. A. Conde, P. N. Halpin, L. N. Joppa, C. M. McClellan, and J. S. Clark, 2008. Understanding movement data and movement processes: current and emerging directions. *Ecology Letters* 11.
- Schtickzelle, N., A. Joiris, H. Van Dyck, and M. Baguette, 2007. Quantitative analysis of changes in movement behaviour within and outside habitat in a specialist butterfly. *BMC Evolutionary Biology* 7:4.

- Schultz, C. B. and E. E. Crone, 2001. Edge-mediated dispersal behavior in a prairie butterfly. *Ecology* **82**:1879–1892.
- Srygley, R. B. and R. Dudley, 2008. Optimal strategies for insects migrating in the flight boundary layer: mechanisms and consequences. *Integrative and Comparative Biology* **48**:119–133.
- Tahvanainen, J. O. and R. B. Root, 1972. Influence of vegetational diversity on population ecology of a specialized herbivore, *Phyllotreta cruciferae* (Coleoptera-Chrysomelidae). *Oecologia* **10**:321–346.
- Traynier, R. M. M., 1979. Long-term changes in the oviposition behavior of the cabbage butterfly, *Pieris rapae*, induced by contact with plants. *Physiological Entomology* **4**:87–96.
- Turchin, P., 1998. Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants. Sinauer Associates.
- Van Dyck, H. and M. Baguette, 2005. Dispersal behaviour in fragmented landscapes: Routine or special movements? *Basic and Applied Ecology* 6:535–545.
- Wiens, J. A., 1989. Spatial scaling in ecology. Functional Ecology 3:385–397.
- Yamamura, K., 1999. Relation between plant density and arthropod density in cabbage. *Researches* on *Population Ecology* **41**:177–182.
- Zalucki, M. P. and R. L. Kitching, 1982. The analysis and description of movement in adult *Danaus plexippus* L (Lepidoptera, Danainae). *Behaviour* **80**:174–198.

# 3.6 Appendix

#### 3.6.1 Correlated random walk and net squared displacement

The equation developed by Kareiva and Shigesada (1983) for the net squared displacement for the correlated random walk is:

$$R_n^2 = nm_2 + 2m_1^2 \frac{\psi}{1-\psi} \left(n - \frac{1-\psi^n}{1-\psi}\right)$$
(3.1)

where *n* equals the number of moves,  $m_2$  is the mean of the squared move length,  $m_1$  is the mean move length and  $\psi$  is the mean cosine of the turning angle. In cases where the mean cosine of the turning angles equals 0 (uniform distribution) Eq. 3.1 simplifies to a random walk:

$$R_n^2 = nm_2 \tag{3.2}$$

# 3.6.2 Results from count of *Pieris rapae* eggs of coarse scale experiment

Female *P. rapae* butterflies laid a total of 1679 eggs among plants of the study areas used for the flight observations. The distribution of eggs followed the predictions of the resource dilution hypothesis (Yamamura, 1999). However, a decline in the number of eggs per plant with increasing plant density was only found for the fine scale measurement (Figure 3.13). Plant density was defined by counting all host plants within a  $1 \times 1$ m square. In contrast, at medium scale a  $6 \times 6$ m square was used and at coarse scale a  $36 \times 36$ m square to define plant density (refer to methods section of chapter two for a detailed description of measurements of plant density at different spatial scales).

The egg distribution data were analysed using hierarchical linear models (HLMs) in R (R Development Core Team, 2008). Table 3.3 summarises the model coefficients. The corresponding estimates for the random factors are shown in table 3.4. A more detailed description of the HLM method can be found in the statistical methods section of chapter two.



Figure 3.13: Number of *P. rapae* eggs per plant for the three different fine scale plant densities (number of plants within 1x1m square) in Levin experiment 2006.

The data on egg distributions of this experiment also served as empirical examples in a simulation study of ovipositing behaviour of *Pieris rapae* by Barritt (2008).

Table 3.3: Parameter estimates and 95% HPD and confidence intervals of hierarchical linear model for testing the number and distribution of *P. rapae* eggs on *B. oleracea* plants of Levin experiment in 2006, w = 0.817.

Coeff	Estm	lowerHPD	upperHPD	lowerCI	upperCI	Std. Err.
(Intercept)	9.100e-01	-6.076e-01	2.427e+00	-6.377e-01	2.458e+00	7.739e-01
Coarse scale	-9.050e-03	-1.304e-02	-5.069e-03	-1.312e-02	-4.974e-03	2.038e-03
Medium scale	1.306e-03	-1.206e-02	1.504e-02	-1.249e-02	1.510e-02	6.896e-03
Fine scale	-6.474e-02	-7.460e-02	-5.498e-02	-7.477e-02	-5.471e-02	5.014e-03
Plant size	4.970e-03	3.958e-03	5.990e-03	3.931e-03	6.008e-03	5.190e-04

Table 3.4: Summary of random effects errors, testing the number and distribution of *P. rapae* eggs on *B. oleracea* plants by fitting a hierarchical linear model; shown is the variation of the intercept at a particular level, as well as the model residual variance; for description of random effects see methods section of chapter two.

Level	Groups	Name	Variance	Std.Dev.
1	Group:(Sub-Block:(Block:Replicat))	(Intercept)	1.73e-02	1.32e-01
2	Sub-Block:(Block:Replicat)	(Intercept)	4.80e-01	6.93e-01
3	Block:Replicat	(Intercept)	1.39e-14	1.18e-07
4	Replicat	(Intercept)	1.07e+00	1.03e+00
	Residual		4.61e-01	6.79e-01



# Occurrence of *Pieris rapae* on *Lepidium oleraceum* and interactions with white rust and parasitoids

# 4.1 Introduction

Although found in considerable abundance during the times of Captain James Cook (Cooper and Cambie, 1991), the coastal cress *Lepidium oleraceum* Sparrm. ex G.Forst. (Capparales - Brassicaceae), also known as Cook's scurvy grass or nau, is now restricted to a few remaining coastal and offshore populations. Its threat status is classed as 'nationally endangered' by the Department of Conservation (Hitchmough et al., 2007). Several factors are implicated in the decline of coastal cress populations. These factors include a decrease in quantity and quality of suitable habitat, browsing from domestic stock or possums, extinction of local populations through natural disasters or over-collecting by humans, competition with invasive plant species, and herbivory by Brassicaceae crop pests (Esler, 1975; Norton and de Lange, 1999). In addition, *L. oleraceum* is susceptible to white rust, a disease common among brassicaceae) (Armstrong, 2007).

One of the herbivores identified to utilise *L. oleraceum* as a host plant for its offspring is the small cabbage white butterfly, *Pieris rapae* L. (Lepidoptera - Pieridae). The small cabbage white butterfly was accidentally introduced to New Zealand in 1929/30, and rapidly extended its distribution all over New Zealand in the following years (Muggeridge, 1942). Female cabbage white butterflies lay their eggs solely on plants of the family Brassicaceae, which offers them a wide range of abundant host plants.

Besides chemical measures, exotic parasitoid wasp species have been utilised to mitigate the impact of *P. rapae* on brassica crops in New Zealand (Cameron and Walker, 2002). An abundance of alternative hosts, together with a behaviour which has become known as "egg spreading syndrome" (Root and Kareiva, 1984), may have helped to protect *P. rapae* from eradication: ovipositing female cabbage white butterflies lay only one egg at a time, and their more directional flight pattern tends to result in higher egg numbers on host plants which are more isolated (Cromartie, 1975). This behaviour is in contrast to other insect species which tend to concentrate their eggs on plants which grow in dense groups (Tahvanainen and Root, 1972; Root, 1973).

Insect herbivores are guided by visual and volatile cues when searching for suitable host plants (Bernays and Chapman, 1994). Leaf colour and size of a host plant have been shown to be important factors in the detection process for *P. rapae* females (reviewed in Hern et al., 1996). In particular the colour green, a common cue among herbivorous insects (Hern et al., 1996), seems to attract ovipositing *P. rapae* females (Traynier, 1979). Greener fertilised plants were more likely to be approached by ovipositing *P. rapae* females than were unfertilised plants of a darker shade (Myers, 1985). Butterflies also responded to total leaf area by preferentially laying eggs on plants with bigger leaves (Jones, 1977; Ives, 1978). It is likely that cabbage white butterflies use leaf colour and size as a signal to determine the quality of a host plant for their offspring.

Our aim was to identify factors that may affect the distribution of *P. rapae* eggs and larvae among the examined population of Cook's scurvy grass (Figure 4.1). Therefore we asked the following questions: Do plants infected by *A. candida* receive less *P. rapae* eggs than plants with a lower proportion of white rust infection or no infection? Does the size of a host plant affect the number of cabbage white eggs laid, and how important is flowering status, and surrounding plant density? Do plants with con-specifics of later larval stages ( $3^{rd}$  to  $5^{th}$  instar) receive a lower

number of eggs than plants which are free from con-specifics? A similar set of questions was asked for the distribution of cabbage white larvae. In addition we looked at how plant characteristics may affect parasitism of *P. rapae* larvae, and how the distribution of parasitised larvae / parasitoid cocoons relates to the distribution of *P. rapae* larvae and *L. oleraceum* plants.



Figure 4.1: Graphical summary of interactions we examined in our models; broken line refers to indirect interactions, arrows point towards the organism which is affecting the organism of arrow origin; host plant: *Lepidium oleraceum*, insect herbivore: *Pieris rapae*, plant parasite: *Albugo candida*.

## 4.2 Methods

One of the remaining populations of *Lepidium oleraceum* can be found off-shore on the largest island of the Matariki Islands group in the Firth of Thames, which are privately owned by Ngāti Maru (Figure 4.2 a). The iwi kindly supports the monitoring and protection of this important population of *L. oleraceum*. The island's close proximity to the mainland allows for colonisation by winged insects like *Pieris rapae*. Our survey, which took place in March 2006, focused on the eastern part of the island where *L. oleraceum* occurred. We examined 51 plants for presence of *P. rapae* eggs and caterpillars (Figure 4.2 b).

All *P. rapae* larvae that we encountered, as well as a number of parasitoid cocoons, were collected and placed into rearing tubes containing artificial food. Larvae and parasitoid cocoons were reared in the lab at 21°C and 70% humidity. The development of both larvae and parasitoid cocoons was followed and emerged parasitoids were identified, where possible to species level. Parallel to examining plants for the presence of *P. rapae*, plant monitoring by the Department of Conservation took place (see recovery plan by Norton and de Lange, 1999). From this monitoring we incorporated data on height and width of plants, on whether plants were flowering or not, and on the proportion of the plant body infected by the oomycete *Albugo candida*. The product of plant height and width, both measured in centimetres, was used as a measure of plant size.


(a) The Matariki Islands are located in the Firth of Thames.



(b) Distribution of examined *L. oleraceum* plants (solid circles) in study area above high tide watermark (solid line; drop-off not indicated).

Figure 4.2: a) Location of the Matariki Islands and b) distribution of examined *L. oleraceum* plants

### 4.2.1 Statistical Methods

Data analyses were conducted in R v.2.7.0 (R Development Core Team, 2008). To test for effects of the presence of A. candida infection, plant size, flowering status, and number of older con-specific larvae (3rd to 5th larval instar) present, number of plants within a range of 0-1m (fine scale plant density), 1-6m (medium scale plant density), and 6-42m (coarse scale plant density) from the focal plant, and geographical x and y co-ordinates on *P. rapae* egg distribution, we fitted a log-linear model with the count of cabbage white eggs per plant as response variable (Poisson error distribution). A similar method was applied to test for effects on the number of P. rapae larvae and parasitoid cocoons, with the exception that the models did not include the number of older con-specific larvae present, or number of larvae parasitised. Models that tested for effect on the number and distribution of parasitoid cocoons included parameters of number of *P. rapae* larvae and plants present within a range of 0-1m (fine scale plant density), 1-6m (medium scale plant density), and 6-42m (coarse scale plant density) from the focal plant. Tests for spatial auto-correlation in the residuals of the base model (which had plant size as sole predictor) were executed using Moran's I and did not detect any significant levels of spatial autocorrelation. Therefore, models which did not include spatial correlation terms were deemed appropriate.

Symbol	Variable	Туре	Range (&	Description	Unit
			Q <sub>1</sub> - Q <sub>3</sub> )		
Eggs	P. rapae eggs	Con	0 - (0 - 0.5) - 8	No. of <i>P. rapae</i> eggs per host	Count
Larvae	P. rapae lar-	Con	0 - (0 - 0) - 9	No. of <i>P. rapae</i> larvae per host	Count
	vae				
Parasitism	Parasitised P.	Con	0 - (0 - 38) - 100	Proportion of non-/ and para-	%
	<i>rapae</i> larvae			sitised larvae	
Cocoons	Parasitoid	Con	0 - (0 - 0) - 4	No. of parasitoid cocoons per	Count
	cocoons			host	

Table 4.1: Summary of response variables for *P. rapae* survey on the Matariki Islands; Type: Con = Continuous, Cat = Categorical.

We tested models corresponding to different hypotheses on eggs, larvae and proportion of parasitised caterpillars (see Tables 4.3, 4.4 & 4.5). In addition we also fit-

Table 4.2: Summary of explanatory varia Cat = Categorical.	ables for <i>P. 1</i>	<i>apae</i> survey on the l	Matariki Islands; Type: Con = Continı	lous,
Symbol Variable	Type Range	(& Q <sub>1</sub> - Q <sub>3</sub> )	Description	Unit
			TT - 1 - 11	¢

Symbol	Variable	Type	Range (& Q1 - Q3)	Description	Unit
PS	Plant size	Con	0.002 - (0.073 - 0.194) - 0.849	Height $\times$ width	$m^2$
FL	Flowering status	Cat	'0' or '1'	Non-flowering vs. flowering	Binary
AS	A. candida infection	Con	0 - (0 - 2.5) - 90	Percentage of infected plant body	%
X	X co-ordinates	Con	146.75 - (177 - 196) - 216.17	Geographical x co-ordinates	ш
Y	Y co-ordinates	Con	133.79 - (187 - 231) - 287.93	Geographical y co-ordinates	ш
OC	Older con-specific <i>P. rapae</i> larvae	Con	0 - (0 - 0) - 0	Number of $3^{rd}$ to $5^{th}$ instars on host	Count
PL	Parasitised <i>P. rapae</i> larvae	Con	0 - (0 - 0) - 5	No. of parasitised larvae	Count
TL	Total <i>P. rapae</i> larvae	Con	0 - (0 - 0) - 0	Total no. of larvae on host	Count
F	Fine scale plant density	Con	0 - (0 - 2) - 8	No. of hosts within radius of 0-1m from	Count
				focal plant	
M	Medium scale plant density	Con	0 - (7 - 14) - 17	No. of hosts within radius of 1-6m from	Count
				focal plant	
C	Coarse scale plant density	Con	20 - (28 - 39) - 45	No. of hosts within radius of 6-42m	Count
				from focal plant	
LF	Fine scale larvae density	Con	0 - (0 - 0) - 0	No. of larvae within radius of 0-1m from	Count
				focal plant	
LM	Medium scale larvae density	Con	0 - (0 - 12) - 17	No. of larvae within radius of 1-6m from	Count
				focal plant	
LC	Coarse scale larvae density	Con	20 - (22 - 30) - 45	No. of larvae within radius of 6-42m	Count
				from focal plant	

No	Model	Model description
<u> </u>	≥	unconditional model, intercept only
2	PS	base model, Plant size only
ω	PS + AS + PS : AS	Plant size, A. candida infection and their interaction
4	PS + FL + PS : FL	Plant size, flowering status and their interaction
J	PS + OC + PS : OC	Plant size, presence of older con-specific larvae and their interaction
6	PS + FL + AS + PS : FL + AS : FL	Plant size, flowering status and interaction, and interaction A. candida in-
		fection and flowering status
7	PS + OC + AS + PS : OC + AS : OC	Plant size, number of older con-specifics, A. candida infection, and presence
		of older con-specifics, and their interactions
8	PS + X + Y + PS : X + PS : Y	Plant size, geographical x and y co-ordinates, and their interactions
9	PS + PL + TL + PS : PL + PS : TL + PL : TL	Plant size, number of parasitised larvae, total number of larvae present,
		and their interactions
10	PS + F + M + C + PS : F + PS : M + PS : C	Plant size and number of plants within different ranges from focal plant,
		and their interactions
11	PS + AS + FL + OC + PL + TL + X + Y + F +	global model
	M + C + PS : AS + PS : FL + PS : OC + PS :	
	PL + PS: TL + PS: F + PS: M + PS: C + AS:	
	FL + AS : OC + PL : TL	

Table 4.3: Models for exploring the distribution of *P. rapae* eggs on the Matariki Islands; for explanation of sym-

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<ul> <li>4 PS + FL + PS : FL</li> <li>5 PS + FL + AS + PS : FL + AS : Fl</li> <li>6 PS + X + Y + PS : X + PS : Y</li> <li>7 PS + F + M + C + PS : F + PS : M + PS : C</li> <li>8 PS + AS + FL + X + Y + F + M + C + PS : A + PS : C</li> <li>8 PS + AS + FL + X + Y + F + M + C + PS : A + PS : C</li> <li>9 PS + AS + FL + X + Y + F + M + C + PS : A + PS : C</li> <li>9 PS + AS + FL + X + Y + F + M + C + PS : A + PS : C</li> <li>9 PS + AS + FL + X + Y + F + M + C + PS : A + PS : C</li> <li>9 PS + AS + FL + X + Y + F + M + C + PS : A + PS : C</li> <li>9 PS + AS + FL + X + Y + F + M + C + PS : A + DS : Y + DS : C</li> </ul>		Plant size, A. candida infection, and their interaction
<ul> <li>5 PS + FL + AS + PS : FL + AS : Fl</li> <li>6 PS + X + Y + PS : X + PS : Y</li> <li>7 PS + F + M + C + PS : F + PS : M + PS : C</li> <li>8 PS + AS + FL + X + Y + F + M + C + PS : AS + AS : Bobal model</li> <li>8 PS + AS + FL + X + Y + F + M + C + PS : AS + AS : Bobal model</li> <li>8 PS + AS + FL + X + Y + F + M + C + PS : AS + AS : Bobal model</li> </ul>	$4  r0 + r\mathbf{L} + r0 : r\mathbf{L}$	Plant size, flowering status and their interaction
<ul> <li>6 PS + X + Y + PS : X + PS : Y</li> <li>7 PS + F + M + C + PS : F + PS : M + PS : C</li> <li>8 PS + AS + FL + X + Y + F + M + C + PS : AS + AS : global model</li> <li>8 PS + AS + FL + X + Y + F + M + C + PS : AS + AS : global model</li> </ul>	5  PS + FL + AS + PS : FL + AS : Fl	Plant size, flowering status, A. candida infection, and their interactions
<ol> <li>PS + F + M + C + PS : F + PS : M + PS : C</li> <li>Plant size and number of plants within different ranges from focal plant, and their interactions</li> <li>PS + AS + FL + X + Y + F + M + C + PS : AS + AS : global model</li> <li>PS + AS + FL + X + Y + F + M + C + PS : AS + AS : global model</li> </ol>	6  PS + X + Y + PS : X + PS : Y	Plant size, geographical x and y co-ordinates, and their interactions
and their interactions $\begin{array}{llllllllllllllllllllllllllllllllllll$	7 $PS + F + M + C + PS : F + PS : M + PS : C$	Plant size and number of plants within different ranges from focal plant,
8 $PS+AS+FL+X+Y+F+M+C+PS: AS+AS:$ global model $FI = PS \cdot Y = PS \cdot V = PS \cdot F = PS \cdot M = PS \cdot C$		and their interactions
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able 4.5: Models for exploring the proportion of parasitism of <i>P. rapae</i> larvae on different <i>L. oleraceum</i> plants on	able 4.5: Models for exploring the proportion of parasitism of <i>P. rapae</i> larvae on different <i>L. oleraceum</i> plant eh Matariki Islands; for explanation of symbols see Table 4.2; colon indicates interaction term.
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3h Matariki Islands; for explanation of symbols see Table 4.2; colon indicates interaction term.	

#	Model	Model description
⊢	$\sim 1$	unconditional model, intercept only
Ν	PS	base model, Plant size only
ω	PS + AS + PS : AS	Plant size, A. candida infection, and their interaction
4	PS + FL + PS : FL	Plant size, flowering status, and their interaction
ы	PS + F + M + C	Plant size, and number of plants within different ranges from focal p
6	PS + LF + LM + LC	Plant size, and number of <i>P. rapae</i> larvae within different ranges from
		plant
7	PS + FL + AS + PS : FL + AS : Fl	Plant size, flowering status, A. candida infection, and their interactior
$\infty$	PS + X + Y + PS : X + PS : Y	Plant size, geographical x and y co-ordinates, and their interactions
9	PS + AS + FL + LF + LM + LC	global model

ted an unconditional model with no fixed effects, a base model which only included plant size as predictor, and a global model which included all variables and some interaction terms. For each sub-set the different models were compared using the sample size corrected Akaike Information Criterion (AIC<sub>c</sub>; Akaike, 1974; Burnham and Anderson, 2002; Anderson and Burnham, 2002) and AIC<sub>c</sub> model weights (w). A quasi-likelihood adjusted AIC approach (QAIC, or QAIC<sub>c</sub> for sample size corrected QAIC) was used for analysing the data on *P. rapae* egg and larval distributions to account for over-dispersion. The variance inflation factor (c) used to calculate the QAIC<sub>c</sub> for all models in the egg and larvae sub-sets was based on the global model (Burnham and Anderson, 2002). The number of model parameters (k) was evaluated for each model and one was added to account for *c* as an extra term. The models testing for effects on the number of parasitoid cocoons were based on regular loglinear regression. A slightly different approach was chosen to test for effects on the proportion of parasitised P. rapae larvae on different L. oleraceum plants. Due to the low number (n = 10) of observed parasitism events (and therefore a lack of a high enough number of degrees of freedom) the global model only included main effects for plant size, proportion of A. candida infection, flowering status, and number of P. rapae larvae on neighbouring plants within a range of 0-1m (fine scale plant density), 1-6m (medium scale plant density), and 6-42m (coarse scale plant density) from the focal plant. In addition a set of candidate models was fitted using logistic regression (binomial error distribution) with teh proportion of A. candida infection, plant size, flowering status, number of *P. rapae* larvae and plants present within a range of 0-1m (fine scale plant density), 1-6m (medium scale plant density), and 6-42m (coarse scale plant density) from the focal plant, geographical x and y co-ordinates as predictor variables.

In addition we tested for effects of the size of the host plant on the proportion of *A. candida* infection (logistic regression model with binomial error distribution), as well as the flowering status of the plant (binary logistic regression model with binomial error distribution). This was done to reveal whether these parameters might be correlated with each other.

Tables containing the coefficient estimates from the most appropriate models based on the multi-model inference are included in the chapter appendix. Graphs showing the standardised parameter estimates and 95% confidence intervals were produced by centering of the predictors and division by two standard deviations (Gelman et al., 2008).

## 4.3 Results

A total of 51 *L. oleraceum* plants were examined for *P. rapae* eggs, larvae and parasitoid cocoons. For 19 plants we confirmed the presence of *P. rapae*. Among those plants a total of 28 cabbage white eggs, 36 larvae, and one *P. rapae* pupae were found. Ten of the 36 *P. rapae* larvae we collected were parasitised by the braconid wasp *Cotesia rubecula*, an introduced bio-control agent. In addition we counted 14 parasitoid cocoons present on plants (see Figure 4.3a-e) of which we collected five. All except one of the cocoons were found on plants for which *P. rapae* was recorded. Out of the five cocoons we collected, four hatched. Three of these cocoons were identified to belong to the species of *C. rubecula*. A hyper-parasitoid (Super-family Chalcidoidea) was reared from one of the unidentified cocoons.

Thirteen of the 51 *L. oleraceum* plants that were examined showed evidence of infection by the oomycete *A. candida* (Figure 4.3f). The size of the host plant was positively correlated with the proportion of *A. candida* infection on *L. oleraceum* plants (GLM;  $\beta$  = 4.123e-06; 95% CI = 3.685e-06, 4.565e-06; t = 2.720, df = 49, p = 0.009). Flowering plants were on average 0.106m<sup>2</sup> larger than non-flowering plants (GLM;  $\beta$  = 9.570e-06; 95% CI = 2.253e-06, 1.974e-05; z = 2.127, df = 49, p = 0.033), but he proportion of *A. candida* infection did not seem to affect the flowering status of a plant (GLM;  $\beta$  = -0.509; 95% CI = -2.979, 2.180; z = -0.403, df = 49, p = 0.687).



Figure 4.3: Distributions of a) *P. rapae* eggs, b) plant sizes, c) larvae, d) parasitised larvae, e) parasitoid cocoons, as well as f) the proportion of *A. candida* infection among the examined *L. oleraceum* plants; symbol size relates to value range.

The number and distribution of cabbage white eggs present on *L. oleraceum* was affected by a number of factors. Table 4.6 summarises the QAIC<sub>c</sub> and model weights (w) for the different log-linear models. The model with the highest support was model 3 (w = 0.438), which included plant size and amount of A. candida infection, and their interaction term. The two-way interaction term between plant size and proportion of A. candida infection was estimated to have a negative effect on the number of eggs (Figure 4.4 a). The slope of this two-way interaction is predicted to become more negative with higher amounts of A. candida infection, while zero percent infection means a rise in the number of eggs (Figure 4.5 a). At 30% infection and above the model predicts higher numbers of *P. rapae* eggs for small plants than were actually measured. For those values the model provides a poor fit. The second best model which had a QAIC weight of 0.347 (model 2, Table 4.6) included plant size only. Plant size affected the number of *P. rapae* eggs positively as shown by the positive estimate in Figure 4.4 b. Model 5, which included plant size and number of older con-specific larvae, was supported by a weight of 0.098 (Table 4.6). The model predicted a negative effect of the interaction term between plant size and number of older con-specific larvae (Figure 4.4 c). However, the 95% confidence interval of the interaction term overlapped with zero and is therefore not considered to be different from zero (Figure 4.5 c). In contrast, the main effect for plant size is estimated to be strongly positive, as was seen in the previous two models. Figure 4.5 b provides a graphical representation of the interaction term between plant size and older con-specific larvae. The number of eggs is predicted to decline towards zero in the presence of higher numbers of con-specific larvae.

As shown in Table 4.7 the distribution of *P. rapae* larvae was best described by model 6 (w = 0.914), which included plant size, the geographical x and y coordinates, as well as their interaction terms. The parameter estimates are summarised in Figure 4.6. Plant size and geographical x and y co-ordinates show a positive effect on the number of *P. rapae* larvae. The interaction terms between plant size and x, and plant size and y, though, predict a decline for the number of larvae found for certain parts of the island. This negative interaction resembles the reversed pattern seen for the distribution of plant sizes and number of larvae (Figure 4.3 b & c). In the western part of the study area more larvae are found on bigger plants, while in the eastern part of the study area this relationship is not as clear. The strong effect of this gradient is also reflected in model 8 (w = 0.086).

When the factors that influence the proportion of parasitism of *P. rapae* larvae among *L. oleraceum* plants were investigated, the strongest support was found for model 1, the unconditional model (w = 0.670, Table 4.8). Some support was also found for model 2, which only included plant size (w = 0.293). The effect of plant size on the proportion of parasitism of *P. rapae* larvae was predicted to be positive (GLM;  $\beta = 0.021$ , t value = 1.109, df = 8, p value = 0.267), but the 95% CI overlapped zero (95% CI = 0.069, 0.010). Therefore the positive effect of plant size on the proportion of parasitism is not strongly supported.

The number of parasitoid cocoons was affected mainly by plant size, proportion of A. candida infection, and flowering status. The greatest support was found for model 5 (w = 0.855; Table 4.9), and model 3 was the second best model with a AIC weight of 0.142. The interaction term of plant size and amount of infection by A. candida was predicted to have a negative effect on the number of parasitoid cocoons, and the lower and upper bounds of the 95%CI lay fully within the negative (Figure 4.7 a). Similar results were found for the interaction term of plant size and A. candida infection in model 3 (Figure 4.7 b). However, the 95% confidence intervals for the interaction term of flowering status and A. candida infection in model 5 overlapped with zero, so was not strongly supported. A graphical representation of the interaction term is given in Figure 4.8. The model predicts a decline in the number of parasitoid cocoons with an increase in proportion of A. candida infection. At zero infection an increase in the number of parasitoid cocoons is predicted. The model gives a bad fit for high amounts of infection for small plants, as such combinations did not occur in the data-set. The difference between flowering and non-flowering plants is relatively small and the effect on the number of parasitoid cocoons is neglect-able.

#	Model	4	Deviance	$QAIC_c$	$\Delta  \mathrm{QAIC}_c$	w
	5 1 1	5	92.850	49.273	5.587	0.027
2	PS	လ	77.624	44.151	0.465	0.347
3	PS + AS + PS : AS	Ŋ	66.719	43.685	0.000	0.438
4	PS + FL + PS : FL	Ŋ	77.208	48.771	5.086	0.034
ю	PS + OC + PS : OC	Ŋ	72.890	46.678	2.992	0.098
9	PS + FL + AS + PS : FL + AS : FL	2	77.167	54.023	10.338	0.002
2	PS + OC + AS + PS : OC + AS : OC	2	72.238	51.633	7.947	0.008
$\infty$	PS + X + Y + PS : X + PS : Y	7	71.012	51.039	7.353	0.011
6	PS + PL + TL + PS : PL + PS : TL + PL : TL	$\infty$	64.260	50.588	6.903	0.014
10	PS + F + M + C + PS : F + PS : M + PS : C	6	56.696	49.882	6.197	0.020
11	PS + AS + FL + OC + PL + TL + X + Y + F + M + C + PS:	21	23.982	85.491	41.805	0.000
	AS+PS:FL+PS:OC+PS:PL+PS:TL+PS:F+PS:					
	M + PS : C + AS : FL + AS : OC + PL : TL					



(c) Model 5, *w* = 0.098.

Figure 4.4: Standardised parameter estimates and 95% confidence intervals for testing *P. rapae* egg distribution among *L. oleraceum* plants on the Matariki Islands: a) model 3, b) model 2 and c) model 5; colon indicates interaction term; model predictors were standardised by centring and dividing by two standard deviations.



Figure 4.5: Graphical representation of interaction terms for models describing *P. rapae* egg distribution among *L. oleraceum* plants on the Matariki Islands (see Table 4.10): a) Model 3, lines represent prediction of egg numbers for different percentages of *A. candida* infection and plant sizes; b) Model 6, lines represent prediction of egg numbers for different numbers of older con-specific larvae (OC) and plant sizes; egg count is shown as open circles.

# Model	k	Deviance	$QAIC_c$	$\Delta \text{QAIC}_c$	w
1 ~ 1	2	138.522	102.672	40.086	0.000
2 PS	ω	125.300	95.538	32.952	0.000
3  PS + AS + PS : AS	сл	118.166	95.292	32.707	0.000
4  PS + FL + PS : FL	ĊJ	101.783	83.652	21.066	0.000
5  PS + FL + AS + PS : FL + AS : Fl	7	96.091	84.879	22.293	0.000
6  PS + X + Y + PS : X + PS : Y	7	64.715	62.586	0.000	0.914
7 $PS + F + M + C + PS : F + PS : M + PS : C$	9	96.822	91.184	28.598	0.000
8 $PS+AS+FL+X+Y+F+M+C+PS:AS+AS:FI$	L + PS : 18	13.992	67.317	4.731	0.086



Figure 4.6: Testing *P. rapae* larvae distribution: Standardised parameter estimates and 95% confidence intervals for model 6, w = 0.914; colon indicates interaction term; model predictors were standardised by centering and dividing by two standard deviations.

#	Model	k	NLL	$AIC_c$	$\Delta \operatorname{AIC}_c$	w
<u> </u>	$\sim 1$	1	18.786	21.286	0.000	0.670
2	PS	2	17.226	22.940	1.654	0.293
ယ	PS + AS + PS : AS	4	15.530	31.530	10.244	0.004
4	PS + FL + PS : FL	4	11.340	27.340	6.054	0.032
υ	PS + F + M + C	τU	14.262	39.262	17.976	0.000
6	PS + LF + LM + LC	τU	15.906	40.906	19.620	0.000
7	PS + FL + AS + PS : FL + AS : Fl	9	8.859	48.859	27.573	0.000
$\infty$	PS + X + Y + PS : X + PS : Y	9	8.859	48.859	27.573	0.000
9	PS + AS + FL + LF + LM + LC	7	8.859	78.859	57.573	0.000

р Table 4.8: Summary of multi-model inference for GLMs exploring the proportion of parasitism of *P. rapae* larvae

#						
	Model	4	NLL	$\mathrm{AIC}_c$	$\Delta \operatorname{AIC}_c$	m
	~ 1		78.296	80.378	21.131	0.000
2	PS	2	78.086	82.336	23.089	0.000
ŝ	PS + AS + PS : AS	4	53.962	62.832	3.585	0.142
4	PS + FL + PS : FL	4	62.375	71.245	11.998	0.002
Ŋ	PS + FL + AS + PS : FL + AS : FL	9	45.338	59.247	0.000	0.855
9	PS + X + Y + PS : X + PS : Y	9	69.523	83.432	24.185	0.000
-1	PS + F + M + C + PS : F + PS : M + PS : C	$\infty$	69.290	88.719	29.472	0.000
$\infty$	PS + LF + LM + LC + PS : LF + PS : LM + PS : LC	$\infty$	60.096	79.524	20.278	0.000
6	PS + AS + FL + X + Y + F + M + C + LF + LM + LC + PS:	23	17.145	104.034	44.787	0.000
·	AS + PS : FL + AS : FL + PS : F + PS : M + PS : C + PS :					
	LF + PS : LM + PS : LC + PS : X + PS : Y					

Table 4.9: Summary of multi-model inference for GLMs exploring the number of parasitoid cocoons among L. oleraceum plants; for explanation of symbols see Table 4.2; colon indicates interaction term.



(b) Model 3, *w* = 0.142.

Figure 4.7: Standardised parameter estimates and 95% confidence intervals of models testing the distribution of parasitoid cocoons among *L. oleraceum* plants: a) model 5 and b) model 3; colon indicates interaction term; model predictors were standard-ised by centering and dividing by two standard deviations.



Figure 4.8: Graphical representation of interaction terms for model 5 explaining distribution of parasitoid cocoons among *L. oleraceum* plants; open circles indicate number of parasitoid cocoons; dotted lines indicate number of parasitoid cocoons predicted for different amounts of *A. candida* infection (percentages given next to set of lines) for non-flowering plants; broken lines indicate number of parasitoid cocoons predicted for different amounts of *A. candida* infection (percentages given next to set of lines) for flowering plants.

## 4.4 Discussion

The size of the host plant was identified to be an important factor in oviposition choice by female *P. rapae* butterflies. Ives (1978) showed that bigger plants were more readily accepted by female butterflies for oviposition than were smaller plants. Our findings for the distribution of *P. rapae* eggs supports this. However, the models which explained the distribution of *P. rapae* eggs and larvae best included important interaction terms between plant size and either amount of white rust infection in the case of *P. rapae* eggs, or geographical x and y co-ordinates for *P. rapae* larvae.

Infection by white rust was most predominant on larger *L. oleraceum* plants. Bigger plants are also expected to be older, in which case the infection may have had more time to spread to different parts of the plant. While larger plants were also more likely to flower, no evidence was found for infection by A. candida to affect whether a plant flowered or not. The quality of the host plant is likely to be an important factor in host plant finding and oviposition choice. Langan et al. (2001) and Chen et al. (2004) showed that plants with higher physiological activity and better nutrient levels were more likely to receive eggs by female butterflies of the genus Pieris. The "appropriate/inappropriate landings theory" formulated by Finch and Collier (2000) identifies a three-link chain for finding host plants: plant volatile stimuli - visual stimuli - non-volatile plant chemicals. The acceptance of a potential host plant is based on the success in all three evaluation steps. Those host plants which are in a better physiological and morphological state could therefore fare better in all three steps than plants which are suffering from for example nutrient deficiency, or water shortage. A potential indication of decreased host plant quality is the decline in the number of eggs on *L. oleraceum* plants infected with white rust. This effect was most noticeable on larger plants, as confirmed by the two-way interaction term between plant size and amount of A. candida infection in model 3 (Figure 4.4). Such indirect three-way interactions between host plant, pathogen and herbivore are not uncommon (Hatcher, 1995). While the white pustules created by sporangia of A. candida might deter ovipositing P. rapae females, the wounds caused by feeding P. rapae larvae might be passively utilised by pathogens to gain access to a host.

The quality of a potential host plant can also be affected by the occurrence of conspecifics, in the form of previously laid eggs or larvae. Although we were not able to show strong support for this hypothesis, previous research by Sato et al. (1999) has shown that *P. rapae* females avoid potential host plants with higher loads of conspecifics, thus potentially reducing intra-specific competition for food resources and predation risk by parasitoids. This avoidance behaviour could also reduce the risk of newly laid eggs being eaten by older con-specific larvae (Gilbert, 1984).

The distribution of *P. rapae* larvae showed a strong increase towards the northwestern side of the study area. Here the island is sloping off, which potentially may create some shelter from the prevailing western winds. Female cabbage white butterflies are capable of flying upwind even in moderate wind conditions, but may choose to seek out plants in sheltered areas when possible. Plant volatiles being transported downwind may also play a role during the olfactory detection phase, causing the female cabbage white to fly upwind towards the western area of the island.

We were not able to detect patterns related to surrounding host plant density for *P. rapae* eggs or larvae. Observations on the number of *P. rapae* eggs per plant in different density settings by Root and Kareiva (1984); Jones (1977) and Yamamura (1999) showed that host plants which grew in more isolated stands received a comparatively higher number of eggs per plant than those plants which occurred in dense clusters. While these experiments mainly dealt with colonisation processes on empty host plant patches, the number of eggs and larvae in our survey could be influenced by ongoing population processes in an occupied host plant patch, which might form different patterns over time than those expected during the initial phases of a colonisation type experiment.

One of the factors that might influence *P. rapae* population dynamics are predators and parasitoid wasps (e.g. Van Driesche, 2008). We expected to see effects of plant and larval densities on the proportion of parasitised larvae, but none of our predictors strongly affected the proportion of *P. rapae* parasitised. Nevertheless, the presence of parasitoid cocoons among the examined *L. oleraceum* plants was affected in a similar way as the number of eggs and larvae. As shown in Figure 4.7 the number of cocoons found was reduced by an interaction between plant size and amount of infection by *A. candida*, which could be explained as an carry on effect from the egg and larval distributions. Fewer cocoons were also predicted for plants which flowered at the time of the survey. This is somewhat surprising since the nectar found in the flowers of *L. oleraceum* could be a potential food source for foraging parasitoid wasps (e.g. Harvey and Wagenaar, 2006) and the presence of food sources close to hosts is expected to increase parasitism rate (e.g. Lee and Heimpel, 2005). The estimated positive effect of the interaction term of flowering status and proportion of *A. candida* infection was not strongly supported, but flowering plants were larger than non-flowering plants, as were plants with signs of white rust compared to plants with a lower or no infection. Therefore a positive effect of flowering plants on parasitoid wasp cocoons may be concealed by the overruling influence of *A. candida* infection.

Hyper-parasitism of *C. rubecula* has previously been recorded by Cameron and Walker (2002) in an agricultural context in New Zealand, so presence of a hyperparasitoid on the Matariki islands (~200m offshore from mainland) is not surprising. Aerial colonisation is known for a number of invertebrate species in aquatic and terrestrial environments (Caceres and Soluk, 2002; Srygley and Dudley, 2008). Modes of wind-borne dispersal can range from active utilisation of wind speed and direction as shown for migrating *Pseudoophonus griseus* (Coleoptera : Carabidae) beetles (Feng et al., 2007), to more passive dispersal as seen for the cabbage aphid, *Brevicoryne brassicae* (Bukovinszky et al., 2005). Body size is likely to play an important role as to how wind may effect insect movement and dispersal. The small body size of the hyper-parasitoid of *C. rubecula* suggests an accidental dispersal event which brought it onto the island.

## 4.5 Conclusion

Our study shows how varied the trophic interactions involving *L. oleraceum* and *P. rapae* are on the largest of the Matariki islands. However, further research is needed to investigate the implications of these interactions for conservation of *L. oleraceum*. The extent of the impact of insect herbivores like *P. rapae* on plant fitness and survival in *L. oleraceum* needs to be investigated further. For instance, it is unclear what effects herbivory has on the recruitment of new plants, and how possible interactions with plant pathogens like *A. candida* influence host plant populations. Another aspect which is also interesting for the management of introduced pests like *P. ra* 

*pae*, is the effect which introduced parasitoid wasps and other insect predators may have on herbivore populations. Would it be effective to use bio-control agents like *C. rubecula* to mitigate the impact of insect herbivores like *P. rapae* on *L. oleraceum*? These and other questions are not confined to *L. oleraceum*, and could be extended to gain a more complete picture of the effects that introduced insect herbivores such as *P. rapae* may have on native plant populations.

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## References

- Akaike, H., 1974. A new look at the statistical model identification. *IEEE Transactions on Automatic Control* 19:716–723.
- Anderson, D. R. and K. P. Burnham, 2002. Avoiding pitfalls when using information-theoretic methods. *Journal of Wildlife Management* **66**:912–918.
- Armstrong, T., 2007. Molecular detection and pethology of the oomycete *Albugo candida* (white rust) in threatened coastal cresses. DOC Research and Development Series 274, Department of Conservation.
- Bernays, E. A. and R. F. Chapman, 1994. Host-plant selection by phytophagous insects. Springer.
- Bukovinszky, T., R. P. J. Potting, Y. Clough, J. C. van Lenteren, and L. E. M. Vet, 2005. The role of preand post-alighting detection mechanisms in the responses to patch size by specialist herbivores. *Oikos* 109:435–446.
- Burnham, K. P. and D. R. Anderson, 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York, second edition.
- Caceres, C. E. and D. A. Soluk, 2002. Blowing in the wind: a field test of overland dispersal and colonization by aquatic invertebrates. *Oecologia* **131**:402–408.
- Cameron, P. J. and G. P. Walker, 2002. Field evaluation of *Cotesia rubecula* (Hymenoptera : Braconidae), an introduced parasitoid of *Pieris rapae* (Lepidoptera : Pieridae) in New Zealand. *Environmental Entomology* **31**:367–374.
- Chen, Y. Z., L. Lin, C. W. Wang, C. C. Yeh, and S. Y. Hwang, 2004. Response of two *Pieris* (Lepidoptera : Pieridae) species to fertilization of a host plant. *Zoological Studies* **43**:778–786.
- Cooper, R. C. and R. C. Cambie, 1991. New Zealand's Economic Native Plants. Oxford University Press.
- Cromartie, W. J., 1975. The effect of stand size and vegetational background on the colonization of cruciferous plants by herbivorous insects. *Journal of Applied Ecology* **12**:517–533.
- Esler, A. E., 1975. Vegetation of the sand country bordering the Waitakere Range, Auckland: Piha Beach. *Proceedings of the New Zealand Ecological Society* **22**:52–56.
- Feng, H. Q., Y. H. Zhang, K. M. Wu, D. F. Cheng, and Y. Y. Guo, 2007. Nocturnal windborne migration of ground beetles, particularly *Pseudoophonus griseus* (Coleoptera : Carabidae), in China. *Agricultural and Forest Entomology* 9:103–113.

- Finch, S. and R. H. Collier, 2000. Host-plant selection by insects a theory based on 'appropriate/inappropriate landings' by pest insects of cruciferous plants. *Entomologia Experimentalis et Applicata* **96**:91–102.
- Gelman, A., Y.-S. Su, M. Yajima, J. Hill, M. G. Pittau, J. Kerman, and T. Zheng, 2008. arm: Data Analysis Using Regression and Multilevel/Hierarchical Models. R package version 1.1-15. http://cran.r-project.org/web/packages/arm/index.html.
- Gilbert, N., 1984. Control of fecundity in *Pieris rapae*: III. synthesis. *The Journal of Animal Ecology* **53**:599–609.
- Harvey, J. A. and R. Wagenaar, 2006. Development of the herbivore *Pieris rapae* and its endoparasitoid *Cotesia rubecula* on crucifers of field edges. *Journal of Applied Entomology* **130**:465–470.
- Hatcher, P. E., 1995. Three way interactions between plant pathogenic fungi, herbivorous insects and their host plants. *Biological Reviews of the Cambridge Philosophical Society* **70**:639–694.
- Hern, A., G. EdwardsJones, and R. G. McKinlay, 1996. A review of the pre-oviposition behaviour of the small cabbage white butterfly, *Pieris rapae* (Lepidoptera: Pieridae). *Annals of Applied Biology* 128:349–371.
- Hitchmough, R., L. Bull, and Cromarty, P. (comps), 2007. New Zealand Threat Classification System lists—2005. Technical report, Department of Conservation, Wellington.
- Ives, P. M., 1978. How discriminating are cabbage butterflies? Austral Ecology 3:261–276.
- Jones, R. E., 1977. Movement patterns and egg distribution in cabbage butterflies. *Journal of Animal Ecology* **46**:195–212.
- Langan, A. M., C. P. Wheater, and P. L. Dunleavy, 2001. Does the small white butterfly (*Pieris rapae* L.) aggregate eggs on plants with greater gas exchange activity? *Journal of Insect Behavior* **14**:459–468.
- Lee, J. C. and G. E. Heimpel, 2005. Impact of flowering buckwheat on Lepidopteran cabbage pests and their parasitoids at two spatial scales. *Biological Control* **34**:290–301.
- Muggeridge, J., 1942. The white butterfly (*Pieris rapae* L.) I. Its establishment, spread, and control in New Zealand. *The New Zealand Journal of Science and Technology* (*A*) **24**:107–129.
- Myers, J. H., 1985. Effect of physiological condition of the host plant on the ovipositional choice of the cabbage white butterfly, *Pieris rapae. Journal of Animal Ecology* **54**:193–204.
- Norton, D. A. and P. J. de Lange, 1999. Coastal cresses (nau) recovery plan. Threatened Species Recovery Plan No. 26, Department of Conservation, New Zealand.

- R Development Core Team, 2008. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org. ISBN 3-900051-07-0.
- Root, R. B., 1973. Organization of a plant-arthropod association in simple and diverse habitats: The fauna of collards (*Brassica oleracea*). *Ecological Monographs* **43**:95–124.
- Root, R. B. and P. M. Kareiva, 1984. The search for resources by cabbage butterflies (*Pieris rapae*): Ecological consequences and adaptive significance of Markovian movements in a patchy environment. *Ecology* 65:147–165.
- Sato, Y., S. Yano, J. Takabayashi, and N. Ohsaki, 1999. *Pieris rapae* (Lepidoptera : Pieridae) females avoid oviposition on *Rorippa indica* plants infested by conspecific larvae. *Applied Entomology And Zoology* 34:333–337.
- Srygley, R. B. and R. Dudley, 2008. Optimal strategies for insects migrating in the flight boundary layer: mechanisms and consequences. *Integrative and Comparative Biology* **48**:119–133.
- Tahvanainen, J. O. and R. B. Root, 1972. Influence of vegetational diversity on population ecology of a specialized herbivore, *Phyllotreta cruciferae* (Coleoptera-Chrysomelidae). *Oecologia* **10**:321 pp.
- Traynier, R. M. M., 1979. Long-term changes in the oviposition behavior of the cabbage butterfly, *Pieris rapae*, induced by contact with plants. *Physiological Entomology* **4**:87–96.
- Van Driesche, R. G., 2008. Biological control of *Pieris rapae* in New England: Host suppression and displacement of *Cotesia glomerata* by *Cotesia rubecula* (Hymenoptera : Braconidae). *Florida Entomologist* **91**:22–25.
- Yamamura, K., 1999. Relation between plant density and arthropod density in cabbage. *Researches on Population Ecology* **41**:177–182.

# 4.7 Appendix

## 4.7.1 Summary tables of parameter estimates from GLM

Table 4.10: Parameter estimates and 95% confidence intervals for of log-linear model testing the number and distribution of *P. rapae* eggs on *L. oleraceum* plants: a) model 3, w = 0.438, for explanation of symbols see Table 4.2; b) and model 2 w = 0.347; c) and model 6, w = 0.098; colon indicates interaction term; number of observations n = 51.

	95% Confidence Interval						
		Estimate	lower bound	upper bound	Std. Error	t value	p value
	(Intercept)	-1.800e+00	-2.883e+00	-9.205e-01	4.94e-01	-3.641	0.0007
	PS	5.147e-06	2.438e - 06	7.856e-06	1.32e-06	3.886	0.0003
a)	AS	5.011e+00	6.958e-01	9.276e+00	2.10e+00	2.383	0.0213
	PS:AS	-1.674e-05	-3.695e-05	-2.604e-06	8.15e-06	-2.053	0.0457
<b>b</b> )	(Intercept)	-1.318e+00	-2.278e+00	-5.219e-01	0.44266	-2.977	0.0045
0)	PS	3.175e-02	8.243e-03	5.140e-02	0.01073	2.959	0.0047
	(Intercept)	-1.515e+00	-2.593e+00	-6.148e - 01	4.99e-01	-3.035	0.0039
	PS	4.726e-06	1.376e-06	7.640e-06	1.57e-06	3.020	0.0041
0	OC	-1.624e-01	-1.599e+00	3.568e-01	4.38e-01	-0.371	0.7125
	PS:OC	-2.707e-07	-1.492e-06	1.639e-06	7.19e-07	-0.376	0.7083

Table 4.11: Parameter estimates and 95% confidence intervals of log-linear model testing the number and distribution of *P. rapae* larvae on *L. oleraceum* plants: model 6, w = 0.914, for explanation of symbols see Table 4.2; colon indicates interaction term; number of observations n = 51.

	95% Confidence Interval						
	Estimate	lower bound	upper bound	Std. Error	t value	p value	
(Intercept)	-1.055e+02	-1.779e+02	-4.294e+01	3.43e+01	-3.080	0.0035	
PS	2.242e - 04	7.657e-05	3.932e - 04	7.93e-05	2.829	0.0070	
X	3.846e-01	1.448e - 01	6.571e-01	1.30e-01	2.962	0.0049	
Y	1.332e-01	5.906e-02	2.212e-01	4.11e-02	3.239	0.0023	
PS: X	-8.933e-07	-1.560e-06	-3.019e-07	3.15e-07	-2.835	0.0069	
PS:Y	-2.226e-07	-4.220e-07	-5.135e-08	9.26e-08	-2.403	0.0204	

Table 4.12: Parameter estimates and 95% confidence intervals of models testing the proportion of parasitism of *P. rapae* larvae on *L. oleraceum* plants: a) model 1, w = 0.670, for explanation of symbols see Table 4.2; b) and model 2 w = 0.293; colon indicates interaction term; number of observations n = 10.

	95% Confidence Interval						
	Estimate lower bound upper bound Std. Error t value						p value
a)	(Intercept)	-1.2809	-2.036360	-0.619177	0.3575	-3.583	0.000339
<b>b</b> )	(Intercept)	-8.168e-01	-1.856e+00	1.697e-01	5.078e-01	-1.608	0.108
D)	PS	-2.090e-02	-6.884e - 02	1.030e-02	1.884e - 02	-1.109	0.267

Table 4.13: Parameter estimates and 95% confidence intervals of log-linear model testing the number and distribution parasitoid cocoons among *L. oleraceum* plants: a) model 5, w = 0.855, for explanation of symbols see Table 4.2; colon indicates interaction term; b) and model 3, w = 0.142; number of observations n = 51.

	95% Confidence Interval							
		Estimate	lower bound	upper bound	Std. Error	t value	p value	
	(Intercept)	-1.610e+00	-2.902e+00	-5.812e-01	5.76e-01	-2.793	0.0052	
2)	PS	6.533e-06	-9.258e - 07	1.311e-05	3.25e-06	2.009	0.0445	
a)	FL	-2.889e+00	-5.942e+00	-8.480e-01	1.21e+00	-2.382	0.0172	
	AS	8.744e+00	4.335e+00	1.514e+01	2.79e+00	3.131	0.0017	
	PS:AS	-4.051e-05	-8.530e - 05	-1.457e - 05	1.85e - 05	-2.194	0.0283	
	FL:AS	4.280e+00	-1.701e+00	1.108e+01	3.03e+00	1.413	0.1578	
	(Intercept)	-2.327e+00	-3.754e+00	-1.102e+00	6.64e-01	-3.503	0.0005	
b)	PS	2.431e-06	-5.930e-06	8.270e-06	3.44e-06	0.708	0.4792	
	AS	1.031e+01	5.476e+00	1.700e+01	3.07e+00	3.363	0.0008	
	PS:AS	-3.789e - 05	-8.143e-05	-1.122e-05	1.91e-05	-1.986	0.0471	

# Chapter 5

# Summary and general discussion

#### Summary

The main focus of my thesis was to describe how observed ecological patterns may change when measured at different spatial scales. In chapter 2 of my thesis I investigated egg distributions of the cabbage white butterfly, *Pieris rapae*, and the cinnabar moth, Tyria jacobaeae, among different densities of their host plants. I varied the scale of measurement used to define plant density in both artificial (P. rapae and T. *jacobaeae*) and wild populations (*T. jacobaeae* only). In experiments on *P. rapae* egg distributions the number of eggs per plant declined with increasing fine scale plant density. As discussed in chapter two, this pattern follows the predictions made by the resource dilution hypothesis and is in line with previous studies. However, no such pattern was found when plant density was measured at medium or coarse scale. In contrast, an increase in the number of eggs per plant with increasing plant density was found for the distribution of *T. jacobaeae* egg batches. This result conforms to the predictions made by the resource concentration hypothesis. However, the resource concentration pattern was only supported when plant density was measured at medium scale but not for fine or coarse scale plant densities. In addition, this resource concentration pattern was only found for one of the two *T*. jacobaeae experiments, as T. jacobaeae did not show any response to plant density in the second experiment. Nevertheless, this unequivocal result may have been due to low population numbers of *T. jacobaeae* in one of the study areas. As previous studies on insect herbivore distributions have shown, responses to host plant density may vary between species. The results of chapter 2, though, indicate that varying results can also occur due to incompatibilities between the scale of measurement applied onto the study system, and the actual scale at which an organism responds to its environment. In addition, species-specific responses to landscape heterogeneity may be affected by other scale dependent processes.

As discussed in chapter 3, careful consideration has also to be given to the method of abstraction used to describe real world patterns. In this chapter I recorded flight paths of *P. rapae* female butterflies at two different spatial scales of resolution among high and low density areas of their host plant. The distribution of flight paths during the coarse scale observations showed an even pattern, with neither low nor high density areas of host plants being preferred. In contrast, during fine scale observations butterflies were attracted to high density areas of their host plant. However, the number of visits was not disproportionally higher when put into relation to the number of plants within each area. The observed distribution of visits per plant in both fine and coarse scale observations declined with increasing plant density. The observed decline in the number of visits per plant with increasing plant density corresponds to the resource dilution effect found for egg distributions of P. rapae and is in line with observed flight patterns from previous studies. The results of chapter 3 give further indication on the processes that may lead to the observed egg distribution. At coarser spatial scales P. rapae butterflies were shown to move at random across the study area, leading to an almost uniform number of visits between empty areas and those containing plants. At finer spatial scales butterflies tended to be attracted towards high density areas of their host plant, but not disproportionately compared to plant density. So far it is not completely understood to what extent sensory modalities such as vision and olfaction play a role in host plant finding. However, previous studies have shown that *P. rapae* butterflies are likely to be mainly visual searchers at fine to medium scales. Therefore, at fine to medium spatial scale a directed response towards host plants may be expected, while at coarser spatial scales distances between host plant patches may exceed an individuals ability to detect those host plants and to make a comparison of their suitability, thus a random distribution of visits to host plant patches is expected.

Apart from plant density and distribution other factors that may have affected the distribution of *P. rapae* eggs include host plant quality, co-occurrence of conspecific larvae or eggs, larvae or egg parasitoids, and bird or arthropod predators. In chapter 4 I was able to show that *Lepidium oleraceum* plants showing signs of infection by white rust, Albugo candida, received a lower number of eggs than plants that did not show any sign of infection. Infection by A. candida was determined by the amount of plant material covered by white pustules. It is unclear whether A. candida could have affected survival of P. rapae eggs or larvae, however, occurrence of the white pustules might have lead to a significant colour change of the leaf material. A change in leaf colour of some plants may have deterred ovipositing female cabbage white butterflies and could have lead to higher egg numbers on plants showing less or no signs of white rust infection. As discussed in chapter 3, the colour green has been shown to function as an indicator of the host plants physiological status. Greener plants could be seen as more suitable hosts and thus would receive a higher number of eggs. The presence of con-specific larvae has also lead to a slight decline in the number of eggs per plant, a result which was also found in previous studies. However, the visual presence of later instar larvae, or plant volatiles released by larvae feeding might have deterred ovipositing *P. rapae* females is unclear. Occasional egg cannibalism has been reported for early instar larvae, but not for older larvae, thus probably having no effect on the observed egg distribution. Parasitism of larvae may affect distribution of *P. rapae* at the population level, but did not seem to influence the egg distribution pattern. As part of my thesis I also investigated the potential effect of arthropod predators on P. rapae egg distributions (see Appendix I of thesis). However, as I was not able to show any effects of arthropod predators on the distribution of *P. rapae* eggs these results are not part of the main body of my thesis. Nevertheless, these experiments suggest that *P. rapae* egg distributions as described in chapter two and four were less likely to be affected by arthropod predation. However, previous studies have shown that *P. rapae* larvae are at risk by avian and arthropod predators alike, and predation may therefore affect *P. rapae* population processes. As arthropod predators and birds may operate at different spatial scales, the effect of predation on *P. rapae* distribution patterns may therefore be scale dependent.

#### General discussion and future directions

The main conclusion of my study is that the spatial scale at which species distributions are measured has a great effect on the observed pattern. The resource concentration and resource dilution patterns I found for egg distributions of *T. jacobaeae* and *P. rapae* respectively, were specific to the spatial scale at which plant density was measured. In addition, the spatial scale at which resource concentration and resource dilution effects were detected differed between the two species.

The results of my study indicate that the knowledge gained from measuring ecological patterns at different spatial scales, may yield a better understanding of the relationships between fine and coarse scale processes. An improved understanding of how certain processes may up– or down–scale could boost the reliability of cross-scale predictions made for ecological patterns (Kunin et al., 2000). However, the range of scales for which such predictions are made may be limited by a decline of cross-scale correlations as the spatial scales diverge, due to non-overlapping processes at finer and coarser scales (Hartley et al., 2004).

Comparisons of responses to resource distribution and density between different species may encounter the problem that varying definitions of patch and habitat structure may apply for different species. Kotliar and Wiens (1990) developed a framework to define hierarchical patch structures following an organism–specific view, which was applied in a study by Rabasa et al. (2005). They investigated the number of butterfly eggs laid on individual fruits of a host plant, individual fruits being the lowest scale at which butterflies would respond to landscape heterogeneity. This approach leads away from more anthropogenic definitions of patch and habitat structure, and scale of measurement. When biologically meaningful definitions of hierarchical landscape structure and scale of measurement are used comparisons between species responses to patch size and resource density are more valid.

Species–specific responses to resource distribution and patch size, such as found for this study, have been reported many times in the recent literature. The variability of species–specific responses to resource density and patch size has lead Bowers and Matter (1997) to suggest that finding a general theory of area–density relationships across different species would be unlikely. A unifying concept of area–density relationships would have to account for differences in, for example, the life history
and dispersal behaviour of different species.

Models incorporating information on species–specific individual behaviour and wider population processes, although far from being a unifying theory, have yielded promising results for predicting species responses to resource distribution and density (Hamback and Englund, 2005). Such models, though, rely heavily on prior knowledge of the natural history and behavioural patterns of the species at hand, but their application may help to find shared patterns in population processes and distributions. Hamback and Englund (2005) view achieving a general theory of area-patch relationships as important, particularly for advancing the understanding of processes that may link different populations and communities at varying scales (see also Leibold et al., 2004).

Following on from my study I would suggest three main aspects that would advance the understanding of how ecological patterns are affected by different scale– dependant processes.

#### 1 Colonisation versus population processes – Adding a temporal scale

As most manipulative ecological experiments on plant–insect relationships usually only run over short time scales, the results rarely show patterns beyond the initial colonisation stage (Kareiva, 1983). However, observed population patterns of insect herbivores may change over time (Bach, 1986, 1988a,b). Long–term, multi– scale studies of insect herbivore distributions may help to better understand the aggregations of insect herbivores in the landscape, beyond the initial colonisation stage (Kunin, 1999).

#### 2 Spatially explicit models of species distributions and individual movement

Individual behaviour is one of the central factors driving species distributions (Doerr and Doerr, 2005). Modelling individual movement patterns in a spatially explicit way may lead to a better understanding of species responses to different structures in the landscape. Schick et al. (2008) suggest developing models which utilise a hierarchical view of habitat structure to describe an animals often complex response to heterogeneous environments. State–space models may be one way to approach modelling of spatially explicit movements of animals, as they allow a higher degree of complexity (Patterson et al., 2008). Since a reasonable amount of literature on oviposition behaviour and movement patterns of *P. rapae* butterflies is available, this species would provide a good model system for developing and

testing such spatially explicit models.

3 From single species to communities

Extending the focus to multi-species community interactions at multiple scales may lead to a better understanding of how species richness and species diversity affect processes such as predation and parasitism (Obermaier et al., 2008), and intraspecific or inter-specific interactions (Gilbert et al., 2008). Plant–insect interactions provide a good study system due to their often more accessible spatial scale. In addition, results from such studies may lead to new crop and horticultural applications. For example, Gurr et al. (2003) suggest that higher plant species diversity increases the number of natural enemies and may be beneficial to controlling agricultural pest species. A next step would be to investigate how ecological communities may be linked through processes at different spatial and temporal scales (see also review by Leibold et al., 2004). Advances in multi-scale community ecology may have important implications for topics such as the conservation of endangered ecosystems, the control of biological invasions or the development of new biological control measures against agricultural pest species.

## References

- Bach, C. E., 1986. A comparison of the responses of 2 tropical specialist herbivores to host plant patch size. *Oecologia* **68**:580–584.
- Bach, C. E., 1988a. Effects of host plant patch size on herbivore density patterns. *Ecology* **69**:1090–1102.
- Bach, C. E., 1988b. Effects of host plant patch size on herbivore density underlying mechanisms. *Ecology* 69:1103–1117.
- Bowers, M. A. and S. F. Matter, 1997. Landscape ecology of mammals: Relationships between density and patch size. *Journal of Mammalogy* **78**:999–1013.
- Doerr, E. D. and V. A. J. Doerr, 2005. Dispersal range analysis: quantifying individual variation in dispersal behaviour. *Oecologia* **142**:1–10.
- Gilbert, B., D. S. Srivastava, and K. R. Kirby, 2008. Niche partitioning at multiple scales facilitates coexistence among mosquito larvae. *Oikos* **117**:944–950.

- Gurr, G. M., S. D. Wratten, and J. M. Luna, 2003. Multi-function agricultural biodiversity: pest management and other benefits. *Basic and Applied Ecology* **4**:107–116.
- Hamback, P. A. and G. Englund, 2005. Patch area, population density and the scaling of migration rates: the resource concentration hypothesis revisited. *Ecology Letters* **8**:1057–1065.
- Hartley, S., W. E. Kunin, J. J. Lennon, and M. J. O. Pocock, 2004. Coherence and discontinuity in the scaling of species' distribution patterns. *Proceedings of the Royal Society of London Series B-Biological Sciences* 271:81–88.
- Kareiva, P., 1983. Variables plants and herbivores in natural and managed systems, chapter Influence of vegetation texture on herbivore populations: resource concentration and herbivore movement, pages 295–289. Academic Press, New York.
- Kotliar, N. B. and J. A. Wiens, 1990. Multiple scales of patchiness and patch structure a hierachical framework for the study of heterogeneity. *Oikos* **59**:253–260.
- Kunin, W. E., 1999. Patterns of herbivore incidence on experimental arrays and field populations of ragwort, *Senecio jacobaea*. *Oikos* 84:515–525.
- Kunin, W. E., S. Hartley, and J. J. Lennon, 2000. Scaling down: On the challenge of estimating abundance from occurrence patterns. *American Naturalist* **156**:560–566.
- Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, J. B. Shurin, R. Law, D. Tilman, M. Loreau, and A. Gonzalez, 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters* 7:601–613.
- Obermaier, E., A. Heisswolf, H. J. Poethke, B. Randlkofer, and T. Meiners, 2008. Plant architecture and vegetation structure: Two ways for insect herbivores to escape parasitism. *European Journal of Entomology* **105**:233–240.
- Patterson, T. A., L. Thomas, C. Wilcox, O. Ovaskainen, and J. Matthiopoulos, 2008. State-space models of individual animal movement. *Trends in Ecology & Evolution* 23:87–94.
- Rabasa, S. G., D. Gutierrez, and A. Escudero, 2005. Egg laying by a butterfly on a fragmented host plant: a multi-level approach. *Ecography* **28**:629–639.
- Schick, R. S., S. R. Loarie, F. Colchero, B. D. Best, A. Boustany, D. A. Conde, P. N. Halpin, L. N. Joppa, C. M. McClellan, and J. S. Clark, 2008. Understanding movement data and movement processes: current and emerging directions. *Ecology Letters* 11.

# Appendix I: Effect of birds and arthropods on *Pieris rapae* egg distributions

# I.1 Introduction

The egg is probably one of the more vulnerable stages in the life of a lepidopteran. Immobile, the egg has to rely on chemical defences (Eisner et al., 2000; Ware et al., 2008), oviposition behaviour of adult females (Root and Kareiva, 1984, 1986; Tallamy, 2005), and host plant exposure to predators (Tschanz et al., 2005) to deter or passively avoid predators. It is not surprising that arthropod predators can have strong influences on insect herbivore populations (Ash, 1974; Dempster, 1967; Hooks et al., 2003). The agricultural sector long had an interest to better understand the role of such arthropod predators which help controlling pest species on crop (e.g. Altieri 1995; Godin and Boivin 1998; Schmaedick and Shelton 2000). One of the more widely spread agricultural pest species on cabbage crops is the small cabbage white butterfly, Pieris rapae. Several studies have focused on egg and larvae mortality in cabbage whites (Ash, 1974; Dempster, 1967; Harcourt, 1966; Parker, 1970; Schmaedick and Shelton, 1999). The mortality of P. rapae eggs due to predation through arthropods was estimated to lie between 5.8 and 8.1% in experiments conducted by Dempster (1967). A study by Schmaedick and Shelton (1999) found a similar mortality range: between 3.2 and 12.2% of cabbage white eggs fell victim to arthropod predators. In their study Schmaedick and Shelton (1999) observed a number of potential predators of insect eggs: syrphid, coccinellid, and chrysopid

larvae, predaceous thrips, and spiders. While not a direct danger to insect eggs, the foraging of insectivorous birds affects insect numbers in general (e.g. Greenberg et al. 2000). As top predators birds might alter the number of intermediate predators such as spiders or wasp parasitoids (discussed in Hooks et al. 2003).

Females of the cabbage white butterfly are known to spread their eggs, so that host plants which grow more isolated receive a disproportional higher number of eggs, than plants which occur in dense stands (Jones, 1977; Root and Kareiva, 1984). This pattern has previously been described as resource dilution effect (Yamamura, 1999). A reversed pattern, resource concentration, has been described by Tahvanainen and Root (1972); Root (1973) for a different insect herbivore community. It shows that different species may respond differently to host plant density. But not only insect herbivores may be influenced by host plant density and isolation as was shown by Tschanz et al. (2005). In their study plant exposure affected predation and parasitism of shield beetle larvae, *Cassida rubiginosa*.

In my study I will investigate how excluding arthropod predators and, or avian predators may affect mortality of *P. rapae* eggs. In addition, though, I will use different plant densities to assess the combined effect of host plant density and predator exclusion on the mortality of cabbage white eggs. To define plant density I will also use two different scales of measurement.

# I.2 Methods

To investigate the effects of arthropods and birds on the distribution of *P. rapae* eggs among different sized groups of cabbage plants, I set up two experimental fields at the AGResearch farm in Kaitoke, New Zealand (see Figure I.1) during the period from 4-16th of April 2007.

The dimensions of one of my experimental set-ups was 18×18m with a total of 180 plants per experimental field and a spacing of 20m between the two replicates. About 10m south of the fields lay an fallow paddock whose wild *Brassica* crop sustained a large *P. rapae* source population.

**Layout of experimental fields** The two  $18 \times 18$ m patches were identical in the number of plants and the treatments used. Patch two differed from patch one in that the



Figure I.1: Experimental fields for arthropod/bird exclusion experiments at AGResearch farm, Kaitoke (New Zealand); fields are indicated by 1 & 2. set-up of the groups of plants was mirrored along the horizontal and vertical middle axes of the patch. Four different exclusion treatments were applied to certain plant groups: arthropod-exclusion (a), bird-exclusion (b), bird- and arthropod-exclusion (c), and fully accessible (d). Figure I.2 shows the set-up of the cabbage plants in the exclusion experiment. The fields were divided into three by three patches that were  $6 \times 6m$  in size. Each treatment was made up of a group of four (sub-grouping of 1 plant per  $1m^2$ ) and 40 plants (sub-groupings of 1, 4 and 16 plants per  $1m^2$ ). An exception was the fully accessible treatment which included another group of four plants within  $6 \times 6m$  in the centre of the field.

**Exclusion treatments** Cabbage plants belonging to the arthropod and arthropodbird exclusion treatments were checked for spiders and other arthropods three times a day. Were any arthropods encountered on plants belonging to those treatments they were removed by hand or brush. Netting that should prevent birds from foraging on the cabbage plants was set up after 13:00. The bird-netting was removed before 8:00 in the morning to allow visits by female cabbage white butterflies on host plants during the peak egg-laying period. During the period from 8.00 to 13.00 birds were scared off on entering the bird exclusion and arthropod-bird exclusion treatments by the loud noise created by clapping two pieces of flat wood together. Bird foraging was allowed within all other treatments. Over night all cabbage plants belonging to arthropod exclusion treatments were wrapped in a cloth, blocking access to the plants for all arthropods. This method allowed to exclude arthropods while providing a gentle climate for the plant over night (no condensation). The cloth was removed again before 8.00 to allow *P. rapae* females to visit the cabbage plants.

*P. rapae* egg count and arthropod census During the experimental period two egg counts were performed (day 5 and day 13 of the experiment) to capture the change in the number of eggs among the host plants . I also performed an arthropod census to assess the performance of my exclusion methods and to get a general idea of the number of arthropods present among a number of host plants. For the census all arthropods found on a selected number of cabbage plants were counted.



Figure I.2: Layout of arthropod/bird exclusion experiment. Four different treatments were used: arthropod-exclusion (a), bird-exclusion (b), bird- and arthropodexclusion (c), and fully accessible (d); each treatment consisted of a group of 4 plants within  $6 \times 6m$ , and a group of 40 plants within  $6 \times 6m$ ; only the fully accessible treatment included an extra group of 4 plants within  $6 \times 6m$  in the centre of the field.

**Statistical Methods** The data I collected were nested at multiple levels. To account for this nestedness in my analysis I used hierarchical linear models (HLM) (Goldstein, 1995; Bryk and Raudenbush, 1992; Raudenbush and Bryk, 2002), also known as linear mixed effects models (LME), to determine whether different scales of measurement had an influence on the number of eggs laid among the different treatments. Models and graphs were created using R (v2.7.0) <sup>1</sup> with package *lme4* (Bates, 2007). For examples of how to build HLMs to analyse ecological data sets refer to McMahon and Diez (2007), or to Pinheiro and Bates (2000) for a more general explanation of linear mixed effects models in S/S-Plus.

Since I was looking for a change in the number of eggs over the period of my experiment I included the difference in the number of eggs between the first and the second egg count as response variable into the model. The data had to be transformed by adding 1 to each value for it to be fitted as the response variable. As the change in the number of eggs was count data, I choose to fit a model using poisson errors, or quasipoisson errors in case of overdispersion. The method used to fit HLMs with poisson errors was Laplace approximation. To assess the significance of coefficients I reported the upper and lower bounds of the 95% highest-posterior density (HPD) intervals from a Markov Chain Monte Carlo simulation for the different fixed effect estimates. For more information about the implementation of the HLM (LME) and the MCMC sample methods refer to the *lme4* manual (Bates, 2007).

To explain the distribution of insect eggs among host-plants I included six predictor variables into the model: fine scale plant density (Fine Scale), medium scale plant density (Medium Scale), the spatial x and y co-ordinates, and plant size. In addition the exclusion treatment was included to test for potential effects of arthropods or birds on the distribution of cabbage white eggs. These parameters were fitted as fixed effects into the model, while the hierarchical levels of the experiment were included as nested random effects. Part of the model selection process was also the unconditional model (model 1), for which I just included the nested random effects, as well as the full factorial model (model 2), which included all fixed and random effects. My hypothesis that the different scales of measurement affected the change in the number of *P. rapae* eggs between the first and the second egg count is tested in model 3. In model 4 I included the exclusion treatments as fixed effects into the

<sup>&</sup>lt;sup>1</sup>R Development Core Team (2008), available at http://www.r-project.org

model to test for effects of arthropod and bird predators on the distribution of eggs. Possible large scale environmental gradients I tested for in model 5 by including the spatial x and y co-ordinates of all cabbage plants. The effect of host plant size on the change in the number of eggs was tested in model 6.

Model selection was based on the Akaike Information Criterion approach (AIC, first proposed in Akaike 1974). For each hypothesis I included the relevant predictor variables into the model. To account for differences in the number of model parameters between the different models I calculated the sample size corrected AIC (AIC<sub>c</sub>) for each model. The different models were ranked according to their AIC<sub>c</sub> value, with one having the lowest AIC<sub>c</sub> value being the best. I also calculated the relative AIC<sub>c</sub> weights to determine the probability of the model being the best model of those tested.

I identified three different levels of nestedness for the exclusion experiment with cabbage *P. rapae*: Block : Sub-Block : Group. In Table I.1 the number of replicates for each random variable are shown.

Table I.1: Random variables and the number of replicates for each hierarchical level in arthropod/bird exclusion experiment.

Random variable		No. replicates	Total
Block	(coarse scale level)	1 per replicate	2
Sub-Block	(medium scale level)	4, or 40 per Block	18
Group	(fine scale level)	1, 4 or 16 per Sub-Block	34

To assess whether the method used to exclude predators from the cabbage plants affected the distribution of cabbage white eggs a generalized linear model (GLM) was fitted to the egg counts with the exclusion treatment as fixed effect. To account for over-dispersion a quasi-poisson error distribution was used.

## I.3 Results

Distributed among the four different treatments a total of 133 eggs were laid. There were no significant differences in the number of eggs between treatments (p>0.05, df = 359, GLM). During the experiment I did not observe any insectivorous birds foraging on the cabbage plants. In the arthropod exclusion treatments I encountered mainly spiders. On the sixth day of the study I performed an arthropod census on all control and arthropod exclusion plants. Only one spiders was encountered on plants of the arthropod exclusion treatments. In contrast I counted 17 spiders on plants where arthropods were not excluded.

The number of eggs in the control treatment increased by 2.3% between the first and the second egg count (see Figure I.3). In all other treatments the distribution and the number of eggs remained constant. The observed change in the number of eggs for the different scales of measurement and among the different exclusion treatments was not significant as shown by the results from the multi-level model fits. The most preferred model out of those I tested was the unconditional model (see model 1 in Table I.2). None of the 95% HPD intervals of the different fixed effects I included into the models was either fully negative or positive, in respect to the mean estimate value of its parameter.

Table I.2: Model weights for models testing number of *P. rapae* eggs in exclusion experiment: ① Unconditional model with hierarchical levels as random effects; ② full factorial model; ③ model including plant density at different scales; ④ model including exclusion treatments; ⑤ model including x and y co-ordinates of plants; ⑥ model including plant size.

Model	k	neg-logLik	$AIC_c$	$\Delta \operatorname{AIC}_c$	AIC <sub>c</sub> Weight
1	4	0.770	8.889	0.000	0.603
2	12	0.738	25.692	16.803	0.000
3	6	0.768	13.020	4.131	0.076
4	7	0.760	15.097	6.208	0.027
5	6	0.768	13.020	4.131	0.076
6	5	0.753	10.932	2.043	0.217



Figure I.3: Percent change in the number of eggs among the different exclusion treatments between the first and second egg count.

# I.4 Discussion

I expected to find an egg mortality similar to the estimates by Schmaedick and Shelton (1999). Instead the number and distribution of eggs in my experiment did not change at all, apart from a trivial increase of one egg (= 2.3%) in the control treatment. It is unlikely that the time period during which the P. rapae eggs were exposed to potential predators was too short. I exposed cabbage white eggs for eight days to predation which exceeded the time period of previous experiments by Schmaedick and Shelton (1999). In their study the number of days between egg counts varied between 2-3 in which they observed the disappearance of eggs. The first egg count was done four days into the experiment enough time for potential predators to colonise all of the plants of the experimental plot, as shown by the arthropod census, during which I discovered a number of spiders having climbed onto the plants. These spiders obviously were no egg predators. No evidence of other arthropods was found on the sampled plants. I did not include a survey of the surrounding field into this study to sample the wider arthropod community. Data on the actual presence or absence of potential arthropod predators in the experimental field could have lead to a better understanding of the observed pattern. What remains as an explanation is the time of the year as well as the temperature range during the study period. I performed the experiment at the end of summer 2007. The mean daily temperature during this time was  $15^{\circ}C + - 1.2^{\circ}C$ . Only a minority of *P. rapae* eggs seemed to develop during the period of the experiment. Most of them retained their yellowishgreen colour. Muggeridge (1942) hypothesises a lower temperature bound of 8.4°C for the development of cabbage white eggs. The relatively low temperatures as well as the season probably not just slowed down the development of eggs but also the activity of arthropod predators in the area.

# References

- 1974. A study of arthropod predation of *Pieris rapae* L. using serological and exclusion techniques. *The Journal of Applied Ecology* **11**:419–425.
- Akaike, H., 1974. A new look at the statistical model identification. *IEEE Transactions on Automatic Control* **19**:716–723.
- Altieri, M., 1995. Biodiversity and biocontrol: lessons from insect pest management. *Advances in Plant Pathology* **11**:191–209.
- Bates, D. M., 2007. *lme4*: Linear mixed-effects models using s4 classes. http://cran.r-project. org/src/contrib/Descriptions/lme4.html. R package version 0.99875-9.
- Bryk, A. and S. Raudenbush, 1992. Hierarchical linear models for social and behavioral research. Sage, Newbury Park, CA.
- Dempster, J. P., 1967. The Control of *Pieris rapae* with DDT. I. The natural mortality of the young stages of Pieris. *The Journal of Applied Ecology* **4**:485–500.
- Eisner, T., M. Eisner, C. Rossini, V. K. Iyengar, B. L. Roach, E. Benedikt, and J. Meinwald, 2000. Chemical defense against predation in an insect egg. *Proceedings of the National Academy of Sciences* 97:1634–1639.
- Godin, C. and G. Boivin, 1998. Lepidopterous pests of brassica crops and their parasitoids in southwestern quebec. *Environmental Entomology* **27**:1157–1165.
- Goldstein, H., 1995. Multilevel statistical models. Halstead Press, New York.
- Greenberg, R., P. Bichier, A. C. Angon, C. MacVean, R. Perez, and E. Cano, 2000. The impact of avian insectivory on arthropods and leaf damage in some guatemalan coffee plantations. *Ecology* 81:1750–1755.
- Harcourt, D. G., 1966. Major factors in survival of immature stages of *Pieris rapae* (l). *Canadian Entomologist* **98**:653 pp.
- Hooks, C. R. R., R. R. Pandey, and M. W. Johnson, 2003. Impact of avian and arthropod predation on lepidopteran caterpillar densities and plant productivity in an ephemeral agroecosystem. *Ecological Entomology* 28:522–532.
- Jones, R. E., 1977. Movement patterns and egg distribution in cabbage butterflies. *Journal of Animal Ecology* **46**:195–212.
- McMahon, S. M. and J. M. Diez, 2007. Scales of association: hierarchical linear models and the measurement of ecological systems. *Ecology Letters* **10**:437–452.

- Muggeridge, J., 1942. The white butterfly (*Pieris rapae* L.) i. its establishment, spread, and control in New Zealand. *The New Zealand Journal of Science and Technology* (*A*) **24**:107–129.
- Parker, F. D., 1970. Seasonal mortality and survival of *Pieris rapae* (Lepidoptera Pieridae) in missouri and effect of introducing an egg parasite, *Trichogramma evanescens* (Hymenoptera - Trichogrammatidae). *Annals of the Entomological Society of America* 63:985 pp.
- Pinheiro, J. C. and D. M. Bates, 2000. Mixed-effects models in S and S-Plus. Statistics and Computing. Springer Verlag, New York.
- R Development Core Team, 2008. R: A language and environment for statistical computing. http: //www.R-project.org. R Foundation for Statistical Computing, Vienna, Austria.
- Raudenbush, S. W. and A. S. Bryk, 2002. Hierarchical linear models: Applications and data analysis methods. Advanced quantitative techniques in the social sciences. Sage Publications, Thousand Oaks, CA.
- Root, R. B., 1973. Organization of a plant-arthropod association in simple and diverse habitats: The fauna of collards (*Brassica oleracea*). *Ecological Monographs* **43**:95–124.
- Root, R. B. and P. Kareiva, 1986. Is risk-spreading so unrealistic. Oikos 47:114–116.
- Root, R. B. and P. M. Kareiva, 1984. The search for resources by cabbage butterflies (*Pieris rapae*): Ecological consequences and adaptive significance of markovian movements in a patchy environment. *Ecology* 65:147–165.
- Schmaedick, M. A. and A. M. Shelton, 2000. Arthropod predators in cabbage (Cruciferae) and their potential as naturally occurring biological control agents for *Pieris rapae* (Lepidoptera : Pieridae). *Canadian Entomologist* 132:655–675.
- Schmaedick, M. A. and H. M. Shelton, 1999. Experimental evaluation of arthropod predation on *Pieris rapae* (Lepidoptera : Pieridae) eggs and larvae in cabbage. *Environmental Entomology* 28:439– 444.
- Tahvanainen, J. O. and R. B. Root, 1972. Influence of vegetational diversity on population ecology of a specialized herbivore, *Phyllotreta cruciferae* (Coleoptera-Chrysomelidae). *Oecologia* **10**:321 pp.
- Tallamy, D. W., 2005. Egg dumping in insects. Annual Review of Entomology 50:347–370.
- Tschanz, B., E. Schmid, and S. Bacher, 2005. Host plant exposure determines larval vulnerability do prey females know? *Functional Ecology* **19**:391–395.
- Ware, R. L., F. Ramon-Portugal, A. Magro, C. Ducamp, J. L. Hemptinne, and M. E. N. Majerus, 2008. Chemical protection of *Calvia quatuordecimguttata* eggs against intraguild predation by the invasive ladybird *Harmonia axyridis*. *Biocontrol* 53:189–200.

Yamamura, K., 1999. Relation between plant density and arthropod density in cabbage fields. *Researches on Population Ecology* **41**:177–182.

# I.5 Appendix

### I.5.1 Multi-level model summaries

Bird and arthropod exclusion experiment with *P. rapae* 

```
Model1 (unconditional with random effects)
_____
Generalized linear mixed model fit using Laplace
Formula: Egg.Count.change2 ~ 1 + (1 | Level3/Level2/Level1)
  Data: cab07
Family: poisson(log link)
 AIC BIC logLik deviance
8.77 24.09 -0.3848 0.7697
Random effects:
Groups
                     Name
                             Variance Std.Dev.
Level1:(Level2:Level3) (Intercept) 5e-10 2.2361e-05
Level2:Level3 (Intercept) 5e-10 2.2361e-05
                     (Intercept) 5e-10 2.2361e-05
Level3
number of obs: 340, groups: Level1:(Level2:Level3), 34; Level2:Level3, 18; Level3, 2
Estimated scale (compare to 1 ) 0.05407318
Fixed effects:
          Estimate Std. Error z value Pr(>|z|)
(Intercept) 0.002943 0.054153 0.05434 0.957
95% Confidence Intervals from MCMC sampling
_____
step size truncated due to divergence
Iterations = 1:30000
Thinning interval = 1
Number of chains = 1
Sample size per chain = 30000
1. Empirical mean and standard deviation for each variable,
  plus standard error of the mean:
                   Mean
                        SD Naive SE Time-series SE
```

#### APPENDIX: PREDATOR EFFECTS ON PIERIS RAPAE EGGS 1.5 179

```
(Intercept)
                 0.001203 0.0644 0.0003718
                                                0.000424
   log(L1:(.(In)) -48.753410 31.2523 0.1804355
                                                 NA
   log(L2:L.(In)) -45.655585 27.3623 0.1579762
                                               3.478697
   log(Lvl3.(In)) -81.217057 45.8833 0.2649076
                                               5.907797
   2. Quantiles for each variable:
                    2.5%
                           25%
                                      50%
                                                75% 97.5%
                 -0.109 -0.03557 0.001367 0.03826 0.1095
   (Intercept)
   log(L1:(.(In)) -108.112 -74.36838 -36.719738 -22.03609 -7.2432
   log(L2:L.(In)) -100.663 -72.00035 -37.443633 -23.23418 -8.2265
   log(Lvl3.(In)) -158.667 -118.69282 -86.487465 -38.65111 -7.1045
   Warning message:
   In glm.fit(x = X, y = Y, weights = weights, start = start, etastart = etastart, :
    algorithm did not converge
     _____
  Model2 (full factorial)
   _____
  Generalized linear mixed model fit using Laplace
   Formula: Egg.Count.change2 ~ Exclusion.Treatment + Medium + Fine + Plant.Size +
                                                                               Global.X
+ Global.Y + (1 | Level3/Level2/Level1)
     Data: cab07
   Family: poisson(log link)
     AIC BIC logLik deviance
   24.74 70.69 -0.3692 0.7383
   Random effects:
                       Name Variance Std.Dev.
   Groups
   Level1:(Level2:Level3) (Intercept) 5e-10 2.2361e-05
   Level2:Level3
                        (Intercept) 5e-10 2.2361e-05
                        (Intercept) 5e-10 2.2361e-05
   Level3
   number of obs: 340, groups: Level1:(Level2:Level3), 34; Level2:Level3, 18; Level3, 2
   Estimated scale (compare to 1 ) 0.0523897
   Fixed effects:
                       Estimate Std. Error z value Pr(|z|)
   (Intercept)
                      1.709e-02 3.041e-01 0.05622 0.955
   Exclusion.Treatmentc 9.392e-03 1.605e-01 0.05850 0.953
   Exclusion.Treatments -5.872e-03 1.582e-01 -0.03711 0.970
   Exclusion.Treatmentsb -3.931e-03 1.536e-01 -0.02559 0.980
                       2.032e-04 5.071e-03 0.04007 0.968
  Medium
                      -4.871e-04 8.636e-03 -0.05640 0.955
  Fine
   Plant.Size
                    -3.700e-04 2.890e-03 -0.12803
                                                     0.898
```

#### I.5 APPENDIX: PREDATOR EFFECTS ON PIERIS RAPAE EGGS 180

Global.X		3.630e-05	2.797e-03	0.01297	0.990
Global.Y		-3.976e-06	1.165e-02	-0.00034	1.000
Correlation of H	Fixed E	ffects:			
	(Intr)	Exclsn.Tr	tmntc Exclu	sn.Trtmnts	s Exclsn.Trtmntsb
Exclsn.Trtmntc	-0.445				
Exclusn.Trtmnts	-0.418	0.510			
Exclsn.Trtmntsb	-0.360	0.501	0.52	4	
Medium	-0.570	0.125	0.01	4	0.008
Fine	-0.071	-0.008	0.03	5	0.025
Plant.Size	-0.604	0.211	0.29	5	0.192
Global.X	-0.390	0.105	0.07	4	0.046
Global.Y	-0.215	-0.024	-0.05	3	-0.037
	Medium	Fine Pl	nt.S Glbl.X		
Exclsn.Trtmntc					
Exclusn.Trtmnts					
Exclsn.Trtmntsb					
Medium					
Fine	-0.329				
Plant.Size	0.036	0.132			
Global.X	0.026	0.012 0	.230		
Global.Y	-0.007	-0.032 -0	.190 -0.046		
95% Confidence .	Interva	ls from MC	MC sampling		
The section 1.1	20000				
Thinning interve					
Number of sheir	al – I				
Sample size per	s – I	- 30000			
Sampie Size per	Chain	- 30000			
1 Empirical m	aan and	atandard	domintion f	or orch w	riable
I. Empirical me	an anu	stanuaru	deviation i	OI EACH Va	ariabie,
pius standaid	i error	or the me	all <b>.</b>		
		Mean	D2	Naivo SF	Time-series SF
(Intercent)		-7 930o-03	0 31/521	1 8160-03	2 623o=03
(Incercept) Exclusion Treatr	mento	8 080e-03	0.162567	9 3860-04	2.025e 05
Exclusion Treat	ments ·	-8.627e-03	0 161540	9 327e-04	1.2090-03
Exclusion Treat	mentsh	-3 393e-03	0 155757	8 993e-04	1 192e-03
Medium		5 669e-04	0 005138	2 966e-05	3 608e-05
Fine		-3.944e-04	0.008726	5.038e-05	6.734e-05
Plant Size		-3.743e-04	0.002879	1.662e-05	2.245e-05
Global.X		2.128e-05	0.002951	1.704e-05	2.187e-05
Global.Y		-8.412e-05	0.011829	6.830e-05	7.916e-05
log(L1:(.(In))		-4.457e+01	15.417420	8.901e-02	1.959e+00
log(L2:L.(In))		-2.255e+01	13.695136	7.907e-02	1.858e+00
log(Lvl3.(In))		-8.651e+01	43.105958	2.489e-01	5.907e+00

#### 2. Quantiles for each variable:

	0 E 9	25%	E O %	7 5 9	
(Intercent)	-6 370-01	-2 1350-01	-4 5260-03	7.5% 0.200594	
Fyclusion Treatments	-3 065e-01	-1 0210-01	8 7340-03	0.117406	
Exclusion Treatments	-3 214e-01	-1 166e-01	-1 074e-02	0 099734	
Exclusion Treatmentsh	-3 082e-01	-1 086e-01	-2 520e-03	0 101137	
Medium	-9.262e-03	-2.988e-03	4.700e-04	0.003993	
Fine	-1.742e-02	-6.270e-03	-3.656e-04	0.005521	
Plant.Size	-6.012e-03	-2.297e-03	-3.900e-04	0.001557	
Global.X	-5.615e-03	-1.895e-03	1.715e-05	0.001919	
Global.Y	-2.328e-02	-8.056e-03	-1.171e-04	0.007834	
log(L1:(.(In))	-7.704e+01	-5.386e+01	-4.372e+01	-33.528330	
log(L2:L.(In))	-4.962e+01	-3.360e+01	-1.847e+01	-10.901970	
log(Lvl3.(In))	-1.692e+02	-1.176e+02	-8.371e+01	-55.474641	
	97.5%				
(Intercept)	0.589362				
Exclusion.Treatmentc	0.327748				
Exclusion.Treatments	0.310625				
Exclusion.Treatmentsb	0.301360				
Medium	0.010884				
Fine	0.016910				
Plant.Size	0.005358				
Global.X	0.005693				
Global.Y	0.023076				
log(L1:(.(In))	-16.498553				
log(L2:L.(In))	-4.798616				
log(Lvl3.(In))	-9.002087				
Warning message:					
In glm.fit(x = X, y = $(x - x)^{2}$	Y, weights	= weights,	start = sta	art, etastart =	= etastart, :
algorithm did not co	onverge				
Model3 (scales of meas	surement)				
Generalized linear mix	xed model f	it using Lap	place		
Formula: Egg.Count.cl	hange2 ~ Meo	dium + Fine	+ (1   Leve	13/Level2/Leve	11)
Data: cab07					
Family: poisson(log	link)				
AIC BIC logLik de	eviance				
12.77 35.74 -0.384	0.768				
Random effects:					
Groups	Name	Variance	e Std.Dev.		
Level1: (Level2:Level2	3) (Interce	ot) 5e-10	2.2361e-05	ō	

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Level2:Level3 (Intercept) 5e-10 2.2361e-05 Level3 (Intercept) 5e-10 2.2361e-05 number of obs: 340, groups: Level1:(Level2:Level3), 34; Level2:Level3, 18; Level3, 2 Estimated scale (compare to 1) 0.05398694 Fixed effects: Estimate Std. Error z value Pr(>|z|)(Intercept) -0.0003056 0.1780446 -0.00172 0 999 0.0001507 0.0050154 0.03004 0.976 Medium -0.0002980 0.0085514 -0.03485 Fine 0.972 Correlation of Fixed Effects: (Intr) Medium Medium -0.894 Fine -0.010 -0.335 95% Confidence Intervals from MCMC sampling \_\_\_\_\_ step size truncated due to divergence Iterations = 1:30000Thinning interval = 1 Number of chains = 1Sample size per chain = 30000 1. Empirical mean and standard deviation for each variable, plus standard error of the mean: Mean SD Naive SE Time-series SE -1.316e-02 0.224847 1.298e-03 1.669e-03 (Intercept) 3.917e-04 0.005042 2.911e-05 Medium 3.241e-05 Fine -3.421e-04 0.008630 4.983e-05 5.099e-05 log(L1:(.(In)) -3.637e+01 16.840310 9.723e-02 2.076e+00 log(L2:L.(In)) -3.007e+01 18.846671 1.088e-01 NA log(Lvl3.(In)) -1.035e+02 55.558772 3.208e-01 7.239e+00 2. Quantiles for each variable:

2.5%25%50%75%97.5%(Intercept)-3.808e-01-1.289e-01-9.079e-030.1106560.32706Medium-9.288e-03-3.044e-033.387e-040.0037370.01050Fine-1.739e-02-6.114e-03-3.100e-040.0055650.01637log(L1:(.(In))-6.440e+01-5.034e+01-3.767e+01-23.115297-6.44650log(L2:L.(In))-6.684e+01-4.567e+01-2.528e+01-12.988709-6.60406log(Lv13.(In))-2.089e+02-1.425e+02-1.048e+02-66.498180-7.68912

```
Model4 (exclusion treatments)
_____
Generalized linear mixed model fit using Laplace
Formula: Egg.Count.change2 ~ Exclusion.Treatment + (1 | Level3/Level2/Level1)
  Data: cab07
 Family: poisson(log link)
  AIC BIC logLik deviance
 14.76 41.56 -0.3799 0.7597
Random effects:
Groups
                     Name Variance Std.Dev.
Level1:(Level2:Level3) (Intercept) 5e-10 2.2361e-05
                     (Intercept) 5e-10 2.2361e-05
Level2:Level3
                     (Intercept) 5e-10 2.2361e-05
Level3
number of obs: 340, groups: Level1:(Level2:Level3), 34; Level2:Level3, 18; Level3, 2
Estimated scale (compare to 1 ) 0.05354244
Fixed effects:
                     Estimate Std. Error z value Pr(|z|)
(Intercept)
                    0.0004911 0.1065742 0.00461 0.996
Exclusion.Treatmentc 0.0120527 0.1555094 0.07750 0.938
Exclusion.Treatments -0.0008286 0.1511826 -0.00548 0.996
Exclusion.Treatmentsb -0.0008364 0.1507502 -0.00555 0.996
Correlation of Fixed Effects:
              (Intr) Exclsn.Trtmntc Exclusn.Trtmnts
Exclsn.Trtmntc -0.685
Exclusn.Trtmnts -0.705 0.483
Exclsn.Trtmntsb -0.707 0.484
                                  0.498
95% Confidence Intervals from MCMC sampling
_____
Iterations = 1:30000
Thinning interval = 1
Number of chains = 1
Sample size per chain = 30000
1. Empirical mean and standard deviation for each variable,
  plus standard error of the mean:
                                 SD Naive SE Time-series SE
                          Mean
```

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(Intercept) -5.147e-03 0.1071 0.0006183 0.0008102 0.0010134 Exclusion.Treatments -1.023e-03 0.1523 0.0008795 0.0012008 Exclusion.Treatmentsb 3.670e-05 0.1513 0.0008733 0.0011795 Log(L2:L.(In)) -4.103e+01 28.2419 0.1630547 log(Lvl3.(In)) -8.319e+01 25 0015 1.6630453 3.6421757 -8.319e+01 35.9217 0.2073938 4.8852224

2. Quantiles for each variable:

	2.5%	25%	50%	75%		
(Intercept)	-0.2200	-0.07747	-3.463e-03	0.06829		
Exclusion.Treatmentc	-0.2892	-0.09216	1.205e-02	0.11653		
Exclusion.Treatments	-0.3030	-0.10225	-5.824e-04	0.10143		
Exclusion.Treatmentsb	-0.2963	-0.10259	-8.394e-04	0.10280		
log(L1:(.(In))	-55.1914	-41.30987	-2.906e+01	-20.91060		
log(L2:L.(In))	-128.0247	-54.10350	-3.351e+01	-22.19447		
log(Lvl3.(In))	-158.9078	-104.41240	-8.482e+01	-59.79303		
	97.5%					
(Intercept)	0.1990					
Exclusion.Treatmentc	0.3147					
Exclusion.Treatments	0.2973					
Exclusion.Treatmentsb	0.2959					
log(L1:(.(In))	-9.6302					
log(L2:L.(In))	-7.4810					
log(Lvl3.(In))	-13.6118					
Model5 (spatial locat:	lon)					
Generalized linear mix	(ed model I	it using La	apiace	1   T 1 2 /T	10 (T11)	
Data: cab07	langez Gi	.odal.X + G.	LODAL.I + (.	I   Level3/L	evelz/levell)	
Family: poisson(log	link)					
AIC BIC logLik o	leviance					
12.77 35.74 -0.3839	0.7678					
Random effects:						
Groups	Name	Variano	ce Std.Dev.			
Level1: (Level2:Level2	3) (Interce	ept) 5e-10	2.2361e-0	05		
Level2:Level3	(Interce	ept) 5e-10	2.2361e-0	05		
Level3	(Interce	ept) 5e-10	2.2361e-0	05		
number of obs: 340, o	jroups: Le	evell:(Leve	l2:Level3),	34; Level2:	Level3, 18; Level3,	2

Estimated scale (compare to 1 ) 0.05396932

```
Fixed effects:
            Estimate Std. Error z value Pr(>|z|)
(Intercept) 0.0029603 0.1368585 0.02163 0.983
          0.0001015 0.0027146 0.03740 0.970
Global.X
Global.Y -0.0003229 0.0114240 -0.02827 0.977
Correlation of Fixed Effects:
        (Intr) Glbl.X
Global.X -0.536
Global.Y -0.743 -0.004
95% Confidence Intervals from MCMC sampling
_____
Iterations = 1:30000
Thinning interval = 1
Number of chains = 1
Sample size per chain = 30000
1. Empirical mean and standard deviation for each variable,
  plus standard error of the mean:
                             SD Naive SE Time-series SE
                   Mean
             -4.321e-04 0.179782 1.038e-03
(Intercept)
                                              1.397e-03
              8.546e-05 0.002824 1.631e-05
Global.X
                                               2.182e-05
             -2.734e-04 0.011422 6.595e-05
Global.Y
                                                6.666e-05
log(L1:(.(In)) -3.476e+01 14.316201 8.265e-02
                                                1.817e+00
log(L2:L.(In)) -5.338e+01 20.964072 1.210e-01
                                                2.647e+00
log(Lvl3.(In)) -1.750e+02 75.892960 4.382e-01
                                               9.658e+00
2. Quantiles for each variable:
                   2.5%
                             25%
                                         50%
                                                   7.5%
                                                            97.5%
             -2.710e-01 -9.481e-02 -2.226e-03 9.208e-02 0.269435
(Intercept)
             -5.406e-03 -1.748e-03 8.581e-05 1.920e-03
                                                        0.005532
Global.X
Global.Y
              -2.278e-02 -7.976e-03 -2.358e-04 7.546e-03
                                                        0.021864
log(L1:(.(In)) -6.143e+01 -4.527e+01 -3.406e+01 -2.355e+01 -9.883849
log(L2:L.(In)) -8.742e+01 -7.081e+01 -5.659e+01 -3.430e+01 -15.869458
log(Lvl3.(In)) -2.949e+02 -2.280e+02 -1.863e+02 -1.214e+02 -24.455875
Warning messages:
1: In glm.fit(x = X, y = Y, weights = weights, start = start, etastart = etastart, :
 algorithm did not converge
2: In glm.fit(x = X, y = Y, weights = weights, start = start, etastart = etastart, :
 algorithm did not converge
3: In glm.fit(x = X, y = Y, weights = weights, start = start, etastart = etastart, :
 algorithm did not converge
```

```
_____
Model6 (plant size)
_____
Generalized linear mixed model fit using Laplace
Formula: Egg.Count.change2 ~ Plant.Size + (1 | Level3/Level2/Level1)
  Data: cab07
Family: poisson(log link)
  AIC BIC logLik deviance
10.75 29.9 -0.3763 0.7526
Random effects:
                           Variance Std.Dev.
Groups
                    Name
Level1:(Level2:Level3) (Intercept) 5e-10 2.2361e-05
                    (Intercept) 5e-10 2.2361e-05
Level2:Level3
                    (Intercept) 5e-10 2.2361e-05
Level3
number of obs: 340, groups: Level1:(Level2:Level3), 34; Level2:Level3, 18; Level3, 2
Estimated scale (compare to 1 ) 0.0531509
Fixed effects:
           Estimate Std. Error z value Pr(>|z|)
(Intercept) 0.0200108 0.1412336 0.1417 0.887
Plant.Size -0.0003409 0.0026224 -0.1300 0.897
Correlation of Fixed Effects:
         (Intr)
Plant.Size -0.924
95% Confidence Intervals from MCMC sampling
_____
step size truncated due to divergence
Iterations = 1:30000
Thinning interval = 1
Number of chains = 1
Sample size per chain = 30000
1. Empirical mean and standard deviation for each variable,
  plus standard error of the mean:
                           SD Naive SE Time-series SE
                  Mean
            1.927e-02 1.417e-01 8.183e-04 7.548e-04
(Intercept)
Plant.Size
            -3.868e-04 2.634e-03 1.521e-05
                                            1.317e-05
```

log(L1:(.(In)) -2.988e+01 1.475e+01 8.515e-02 1.879e+00 log(L2:L.(In)) -5.838e+01 4.694e+01 2.710e-01 NA log(Lv13.(In)) -2.581e+02 1.045e+02 6.035e-01 1.311e+01

2. Quantiles for each variable:

2.5%25%50%75%97.5%(Intercept)-2.606e-01-7.589e-022.038e-021.142e-010.295424Plant.Size-5.552e-03-2.145e-03-3.711e-041.389e-030.004794log(L1:(.(In))-5.961e+01-4.108e+01-2.843e+01-1.797e+01-6.851442log(L2:L.(In))-1.593e+02-8.943e+01-5.054e+01-1.450e+01-6.417555log(Lv13.(In))-4.559e+02-3.299e+02-2.556e+02-1.890e+02-47.588199

Warning message:

In glm.fit(x = X, y = Y, weights = weights, start = start, etastart = etastart, :
 algorithm did not converge