Spatially explicit simulation of individual foraging behaviour across patchy resources.

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ABSTRACT

This Masters project intends to explore by computer simulation the effects of individual foraging behaviour and resource aggregation on foraging patterns at multiple scales. An object-oriented approach will be taken to provide a flexible framework within which different simulation methods may be applied and compared. Examples of previously published methods include observational (Jones 1977) and correlated random walk (Cain 1985) simulations. These methods will be extended to include more biologically realistic interactions with the environment such as olfactory and visual cues to examine the effects on the accuracy of predictions. The results will be in terms of visits to resources (either nectar-feeding or oviposition). Whilst some simulations will be generic, others will be parameterised for specific species such as the cabbage white butterfly, *Pieris rapae* (which already commands a wealth of previous research and observation). Taking individual level models as a starting point, the intention is to extend the scope to investigate population and community level effects by creating multi-generation and multi-species (e.g. predator / parasatoid) simulations. To complement the simulations, field observations will be made (as part of a separate project), recording flight paths and egg distributions for New Zealand populations of *Pieris rapae*. With regards to hypotheses, a key question is “Do isolated plants receive fewer visits than those which are aggregated?” Current literature tends to explore this question at various scales separately. This project aims to specifically examine the relationship between multiple scales of observation (what appears isolated at one scale may be aggregated at a larger scale) and the scale of movement of the observed species (dispersal ability). A further question is “Can different resource usage patterns be observed for the same species at different scales?” As “isolation” depends on the scale of observation, a more directed question would be “Can resources which are isolated at one scale receive a greater number of visits but at a larger scale receive fewer visits?” The flexibility of a simulation environment allows a much wider parameter space to be explored than experimentally and it is hoped that results from the simulations can help to direct and stimulate subsequent field experiments.

***Keywords and phrases*:** spatial simulation, correlated random walk, Pieris rapae, foraging, patchy resources, individual-based models, object oriented simulation, resource concentration, resource dilution, scale, isolation

1.0 INTRODUCTION

Dr Stephen Hartley et al. at Victoria University are engaged in a project that aims to explore the effect of scale on population distribution of the insect herbivores *Pieris rapae* (Cabbage white butterfly) and *Plutella xylostella* (Diamond-back moth). This Masters project will contribute towards their research.

A key factor affecting the dynamics of ecological systems is the distribution of animal populations throughout a habitat (Tilman and Kareiva 1997). Births, deaths and movements of individuals lead to these distributions. The spatial structure of the landscape and distribution of resources within it will influence the patterns of movement of the animals. The significance of resource distribution and foraging behaviour increase where resources are “patchy” (i.e. unevenly distributed) and potentially limited in connectivity between “patches” (areas where a resource is available). Further, the scale at which the populations are observed may affect the description of the process (at one scale resources may be perceived as patchy but at another scale evenly distributed).

Various models and experiments have been described which explore these interactions:

Jones (1977) Presents a specific simulation for *Pieris rapae* which is grid based and involves a behavioural model based on a set of parameters which were discovered from data observed in field experiments. The results suggested that Australian and Canadian females behaved differently; Australian butterflies moving over greater distances and thus dispersing eggs more widely and spending more time in flight than Canadians. Both populations were derived from European ancestors (Australians arriving via New Zealand). Jones (1977) suggests that the differences in behaviour imply different selective pressures in the two places. He goes on to note that widely spaced plants and plants in smaller groups receive more eggs and suggests that this should occur whenever dispersal distances are large relative to patch size, and risk of mortality whilst moving is low. Key aspects of his model include:

i) Discrete grid environment with moves possible to neighbouring grid cells.
ii) Seven parameters each representing probabilities of a certain behavioural action, e.g. “STOP” was the probability of a butterfly landing at a particular cell that may vary according to the resource found at that grid cell.
iii) Parameters were varied to discover what their values would need to be to produce observed egg patterns. This is similar to the statistical method of maximum likelihood estimation (MLE) (Aldrich 1997).

Cain (1985) created a more general simulation based on a correlated random walk (Byers 2001) in continuous space with which he was able to explore the success of herbivores with different movement patterns and the effect of distribution of resources. In particular he found that aggregation of plants (patchiness) at certain densities could reduce the number of plants discovered by the insects. Key aspects of the model include

i) A “radius of detection” surrounded each plant such that thinly distributed plants were less likely to be encountered by insects moving randomly through the space before the insects died (e.g. if only 1 plant per 100 moves of an insect and the insects can only live 50 moves, they will very rarely find a plant)
ii) Mortality was important because without it, eventually all plants would be found by the random moving insect, or at least the effects of clumping would be reduced.
iii) Upon entering the radius of detection the insect remained on that plant and no longer moved. Cain points out that for this reason, for Lepidoptera who make repeated ovipositions within a patch, the model is not suitable.

Both of these approaches are essentially abstract models in that they do not explicitly represent biological mechanisms. For example the “radius of attraction” is an abstract concept that will in reality be the result of many factors – in the paper Cain refers particularly to wind, but perception abilities of the insect and distinguishing features of resources will also play a role.

Other work can be found which explores these areas in more detail. Where perceptual abilities are concerned, two main sensory inputs are visual and olfactory perception (Finch and Collier 2000), (Olden et al. 2004). It has also been suggested that different perceptual abilities may be used at different times during a foraging behaviour sequence (Bukovinszky et al. 2005). Holmgren and Getz (2000) suggest that specialist / generalist behaviour may evolve as a result of the abilities of animals to perceive different host plants –

under certain circumstances it requiring more complex analysis to be a generalist where it is harder to distinguish more than one host species.

As Jones (1977) notes, the dispersal distance of the butterflies relative to the spatial distribution of the resources will affect the pattern of eggs laid. If insects move further then plants that are widely spaced will receive relatively greater densities of eggs – plants "in between" the length of flight will receive relatively fewer visitors.

Root (1973) developed the "resource concentration hypothesis" which states that specialist herbivores will be found in greater numbers on areas of concentrated host plants. Grez and Gonzalez (1995) carried out an experiment to test this hypothesis but their results did not support it. Otway, Hector and Lawton (2005) observed that whilst the probability of a specialist herbivore being *present* increases with the number of plants in a patch, the observed densities of herbivores were negatively correlated with plant number, therefore demonstrating a "dilution" effect. A third possibility is no relationship between plant density and herbivore numbers, this is what the "ideal free distribution" (Fretwell and Lucas 1970) would predict. These conflicting results may be explained by differences in foraging behaviour (Bukovinszky et al. 2005)

These observations introduce the importance of scale in measuring and understanding such behaviours - biological factors that are a result of the behavioural (movement patterns) and physical (perceptual constraints) characteristics of a particular species may affect the scale at which it perceives density of resources. For example, if an individual moves over large distances and is capable of distinguishing host plants at those distances, what might seem to be isolated plants may actually be perceived by the animal as relatively dense.

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