

Olfactory cues and insects – scaling relations and immigration rates

Petter Andersson

Licentiate thesis



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Cover: Left upper corner: Sawfly larva *Tenthredo scrophulariae* feeding on a figwort leaf. Right upper corner: EAG and IDAC-box; the equipment used in Paper **I** for recording antennal responses of moths. Left lower corner: Weevils *Cionus scrophulariae* mating. Right lower corner: Adult sawfly *T. scrophulariae*. Background picture: Color-marked weevil *C. tuberculosus* from the colonization experiment in Paper **II**, feeding on a figwort plant. Photo: Petter Andersson.

OLFACTORY CUES AND INSECTS – SCALING RELATIONS AND IMMIGRATION RATES

PETTER ANDERSSON

Summary

For herbivorous insects, location of host plants and habitat patches strongly depend on the type of sensory cue that is used during the search process and the probability of detecting a patch depends on the relative attraction between patches of different size. The visual impression of a patch increases predictably with the patch diameter and consequently, immigration rates of visually searching insects are often predicted by the scaling to patch size of visual cues. However, for olfactory cues, the relative attraction between small and large patches is unknown, but has been suggested to increase faster with patch size than visual information. In this thesis, I explore the scaling relation between olfactory cues and patch size. I measured odor attraction of patches of different size and estimated scaling rules for olfactory information. The estimated scaling rules were tested with simulations and a field experiment, where immigration rates of olfactory searching insects were quantified. The estimated scaling rules for olfactory information suggested that the relative attraction did not deviate fundamentally from the scaling of visual cues to patch size. Both the simulations and the field immigration experiment supported this suggestion. Therefore, I conclude that visual and olfactory cues scale roughly to patch size in a similar way, i.e. to the patch diameter. This thesis demonstrates the importance of considering species traits for the understanding of insect responses to habitat heterogeneity.

Sammanfattning

Insektsherbivorer som söker efter värdväxter och habitatfläckar är starkt beroende av de sensoriska signaler som de använder sig av under sökprocessen. Sannolikheten att upptäcka en habitatfläck beror i sin tur på den relativa attraktionen av olika stora fläckar. Det visuella intrycket av en habitatfläck ökar proportionerligt med fläckens diameter och immigrationshastigheter hos visuellt sökande insekter kan förutsägas av hur den visuella signalen ökar med fläckstorleken. Hur doftintrycket varierar med fläckstorleken är däremot mindre känt, men har föreslagits att öka snabbare med fläckstorlek än synintrycket. I den här avhandlingen har jag undersökt hur doftsignalen varierar med fläckens storlek. Jag har mätt

upp doftattraktion från doftfläckar av olika storlek och sedan uppskattat hur doftintrycket varierar med fläckstorleken. Jag testade sedan prediktioner från mätningarna genom att kvantifiera immigration hos doftsökande insekter, både genom datorsimuleringar och immigrationsexperiment i fält. Mätningarna visade att den relativa doftattraktionen inte skiljer sig avsevärt från synattraktionen, och detta stöddes av både simuleringarna och immigrationsexperimentet. Jag drar därför slutsatsen att den relativa attraktionen hos visuella signaler och doftsignaler är likartade, och kan förutsägas av fläckens diameter. Denna avhandling påvisar vikten av att undersöka insekters egenskaper när man vill förstå insekters respons till habitatheterogenitet.

List of papers

The thesis is based on the following manuscripts, which will be referred to by their roman numerals:

- I** Andersson P, Lof ME, Löfstedt C & Hambäck PA. The spatial scaling of olfactory information. (*Manuscript*)
- II** Andersson P & Hambäck PA. Immigration of olfactory searching insects into host plant patches – testing scaling rules for olfactory information. (*Manuscript*)

Introduction

A striking feature of many insect populations is that their density and abundance show large spatial variation. One reason for this variation is the large habitat heterogeneity that occurs across landscapes. The understanding of mechanisms creating density-distributions of insects is important both for general ecological theory (Hambäck & Englund 2005), for understanding patterns of attack in agricultural systems (Root 1973; Bukovinszky et al. 2005) but also from a conservation point of view, since the understanding of responses to habitat heterogeneity may be used to predict insect responses to the ongoing habitat fragmentation (Kruess & Tschardtke 1994). Habitat heterogeneity often leads to a patchy distribution of insect populations across a landscape (Tschardtke et al. 2002). One way to understand insect responses to heterogeneity is to investigate mechanisms that affect these patchy insect populations.

The main processes affecting the local insect density are local population growth and migration (Hambäck & Englund 2005). While the local growth can be affected by factors like competition (Denno et al. 1995), natural enemies (Morris 1992; Kruess & Tschardtke 1994) and edge effects (Fletcher et al. 2007), the migration process affects other populations through emigration and can be influenced by other populations through immigration (Nieminen 1996). When dispersing between habitats in the matrix, it is important for an insect to be able to localize a habitat patch. This process is highly influenced by the specific search behavior of the insect (Bowman et al. 2002; Hambäck & Englund 2005; Bukovinszky et al. 2005). This thesis deals with one process that potentially affects local densities of insects in a patchy landscape – the immigration behavior. This behavior may differ widely among insect groups and can be highly affected by search modality. I have focused on olfactory search. Before revealing the objectives and results of the specific papers in the thesis, I will first give a short review of the host plant search process of herbivorous insects. Furthermore, I will describe differences between different sensory cues and the importance of search modality in shaping density distributions of insects in a landscape.

Background

Habitat heterogeneity and the host plant search process

Most insect which rely upon specific resources are challenged by habitat heterogeneity at several spatial scales. This is highly important for herbivorous insects which may depend on specific host plants for feeding and oviposition (Schoonhoven et al. 2005). Insects that move

in a landscape can detect and locate host plants that often occur in scattered patches which may differ in size, isolation and plant density (Tschardt et al. 2002). At smaller scales, when insects have entered patches, they also must be able to distinguish host plants among non-host plants (Hambäck et al. 2003). The habitat heterogeneities have constraints on the host finding ability of insects, which has to rely upon different sensory cues in order to find patches and host plants (Schoonhoven et al. 2005).

The process of host-plant finding is a multiple-step process where different sensory cues are important at different stages (Saint-Germain et al. 2004). At larger scales, non-host cues may be just as important as host cues for the insect to find a habitat patch. For instance, an insect can visually detect the habitat *per se*, which may contain hundreds of non-host species but still indicate the presence of the host-plant (Cant et al. 2005). For an olfactory searching insect, long-range cues may be highly specific about the presence of host-species (Saint-Germain et al. 2004). At intermediate scales, when arrived at the patch, the insect may have to switch sensory cue since the long-range habitat cue no longer provide enough resolution to indicate host-specific cues (Bernays & Chapman 1994). Visual cues such as plant height or color can be important within patches (Wiklund 1984; Bernays & Chapman 1994). At small scales on the plant, insects often assess the plant by mandible chewing or drumming on plant surface with tarsi or antennae (Bernays & Chapman 1994).

Since habitat patches often differ in size, it is important to understand how the sensory cues vary with patch size, for the reason that sensory cues can predict patch detection and immigration behavior of insects (Englund & Hambäck 2007). In the following, I will describe properties and differences between visual and olfactory cues. As this thesis mainly deals with patch detection and immigration behavior, i.e. processes that mainly occur outside patches, I will not further discuss processes and sensory cues occurring at smaller scales, within patches or on single host plants.

Visual and olfactory cues – properties and constraints upon insect search

There are major differences between visual and olfactory cues. For an insect, visual cues can be highly informative about the surrounding environment. Physical objects such as host plants reflect light, which can give information about the color, shape and silhouette of the plant. Visual cues also operate at the fastest possible time-scale, i.e. the speed of light, and are multi-directional (Prokopy & Owens 1983; Miller & Strickler 1984). A visual signal is

normally not strongly affected by wind and temperature and should be fairly constant at different distances (Briscoe & Chittka 2001; Miller & Strickler 1984). The fact that light play such an important role for visual cues implies that the importance of visual cues is limited during night, although some insects have been shown to use color vision also during night conditions (Kelber et al. 2002). Further, many insects flying at night can see the ground as it passes below the flying insect, which enables orientation in other directions than just up- and downwind. However, this visual cue is mainly used for orientation and is not involved in any search for resources (Bernays & Chapman 1994). At larger scales, many insects use characteristics of horizon line for orientation. Along the horizon, shapes and silhouettes of trees and shrubs may serve as long distance cues towards where the insect can orientate (Prokopy & Owens 1983). Long-distance visual search has been studied in diurnal butterflies, which detect and orientate towards habitat at distances exceeding 100 m (Conradt et al. 2000; Cant et al. 2005).

Olfactory cues, on the other hand, are strongly affected by abiotic factors such as wind and temperature. While visual signals can be detected from multiple directions, an olfactory signal often is possible to detect only from a restricted number of directions. The reason is that there is always more or less wind making the olfactory signal travelling downwind from an odor source. The olfactory signal is often moving slowly and the odor dispersal strongly depends on wind velocity. The consequence is that insects located downwind from an odor source will have a higher probability of detecting and finding the source compared to insects located upwind from the source (Miller & Strickler 1984; Murlis et al. 1992; Bernays & Chapman 1994; Voskamp et al. 1998). When odor disperses from an odor source, the odor typically travels in the shape of a plume. Within this plume, odor molecules move in filaments interspersed with odor-less air (Fig 1). As the filaments disperse downwind, they get elongated and torn apart by eddies and wind turbulence. Consequently, the odor concentration within filaments usually decreases downwind from the odor source. As the filaments are dispersed from the odor source, also the average distance between filaments increase. This implies that the interval between filaments and the concentration within filaments provides important information for insects trying to locate odor sources. Two major physical processes affect odor dispersion; molecular diffusion and turbulent diffusion caused by wind and turbulence (Murlis et al. 1992). In molecular diffusion, random movement of molecules gradually makes them move away from each other. Under field conditions, the molecular diffusion normally acts at very short time-scale, acting only before the filaments reach the size

of the smallest eddies, after which turbulent diffusion takes over. The molecular diffusion requires ideal conditions with no wind and should consequently be very rare in the field. On the other hand, the turbulent diffusion is common and is the most frequent odor dispersal feature an insect has to deal with in order to find host plants or mating partners (Murlis et al. 1992; Bernays & Chapman 1994; Murlis et al. 2000; Farrell et al. 2002).

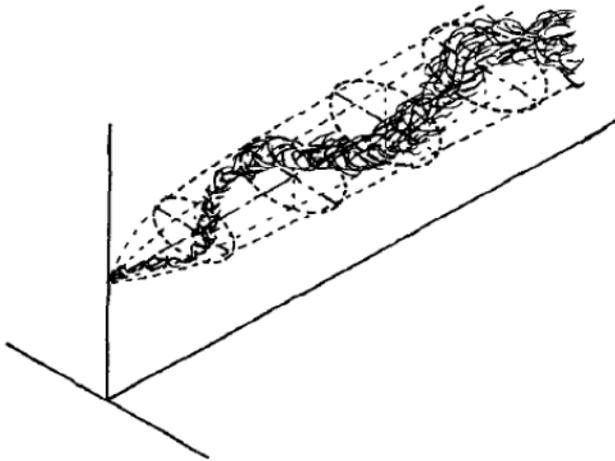


Figure 1. Schematic picture showing a meandering odor plume, with the internal structure of filamentous odor strands interspersed with odor-less air. Adapted from Murlis et al. (1992).

The importance of search mode for density-distributions of insects

When insects disperse between patches in a landscape they can either move passively, randomly or actively detect patches from a distance (Bowman et al. 2002; Bukovinszky et al. 2005; Hambäck & Englund 2005). For insects that detect patches by the use of sensory cues at longer distances, two major search modes can be distinguished – visual and olfactory search. Since habitat patches may differ considerably in size, and since the sensory impression of a patch can be related to patch size, the consequence is that the sensory impression can predict immigration rates of insects. For instance, visually searching insects, such as many butterflies, often show an immigration rate proportional to the visual impression of patches (Englund & Hambäck 2007). The underlying mechanism is that the visual impression is directly connected to the patch diameter, which corresponds to the size of the habitat patch as it appears in the visual field of the insect. Since the number of immigrating individuals also are diluted over the total patch area, the quantitative outcome is that butterflies often show a density-area relationship ($DAR, \propto A^\zeta$, where A = area, ζ = DAR-slope) that scales proportional to the diameter-area ratio (with $\zeta = -0.5$; Englund and Hambäck 2007).

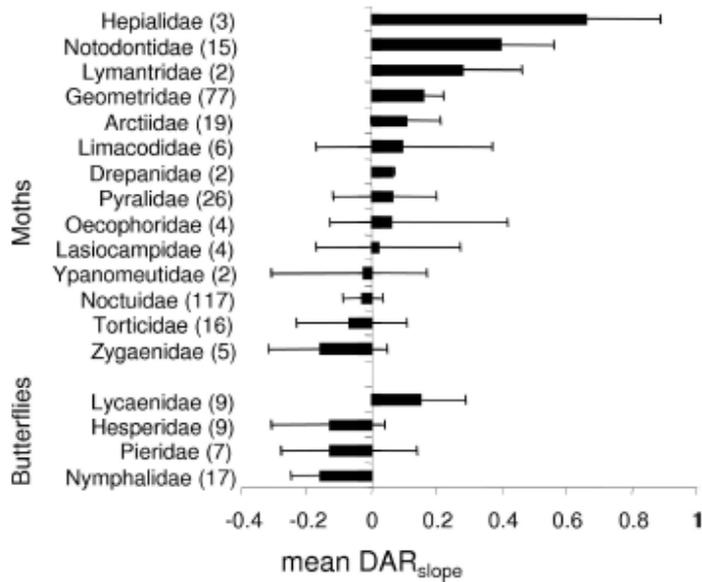


Figure 2. Comparisons of density-area relations between butterflies and moths. DAR_{slope} denotes the slope in the density-area relationship. From Hambäck et al. (2007).

While the scaling mechanism for visual cues to patch size is fairly easy to understand, the corresponding scaling of olfactory cues to patch size is less well understood. Some suggestions about the relation between odor attraction and patch size exist, but differ in predictions. The theoretical models developed by Bossert and Wilson (1963) are compatible with a scaling proportional to the diameter of the patch. On the contrary, Kunin (1999) suggested that the olfactory impression of a patch may increase faster with an increasing patch size compared to the scaling of the visual impression. Consequently, olfactory searching insects should show a different immigration rate than visually searching insects, with a more positive DAR-slope ($\zeta > -0.5$) than predicted from a purely diameter-dependent scaling. In a recent meta-analysis on several hundred lepidopteran species, Hambäck et al. (2007) found a general difference in DARs between butterflies and moths. The pattern was that butterflies on average showed a more negative DAR-slope compared to moths (Fig 2). While butterflies in general are diurnal and visually searching insects and moths in general are nocturnal and olfactory searching insects, the pattern could be a result of different scaling to patch size between visual and olfactory cues, therefore leading to different immigration rates between groups (Hambäck et al. 2007).

Objectives

In this thesis, I explore odor dispersion and possible mechanisms involved in the scaling of olfactory information to patch size. The main objective was to estimate scaling rules for olfactory information, and test scaling rules by measuring immigration rates of olfactory searching insects. The thesis is based upon two studies (Paper I and II), which were performed by an experimental approach, partly in the lab but mainly under field conditions. In Paper I, I investigated scaling rules for olfactory information in response to patch size by measuring antennal responses of moths to odor patches of different size under field conditions. Estimated scaling rules were then compared to known scaling rules for visual information. Further, scaling rules for olfactory information was tested by modelling filamentous odor plumes originating from patches of different size and simulating immigration of olfactory searching insects. The DAR-slope derived from simulations was compared to the slope in the estimated scaling relation of olfactory information. In Paper II, I test predictions from Paper I by studying live insects in the field and allowing them to colonize experimental patches of host plants. The DAR of these insects was compared to the estimated scaling coefficient from Paper I.

Methods

The field experiment in Paper I was conducted on a short-cut lawn, where I established experimental patches of three sizes. The patches consisted of a grid of wooden sticks, where each wooden stick had a rubber dispenser mounted on the top, containing a dose of synthetic female sex pheromones from the Indian meal moth *Plodia interpunctella* Hübner (Lepidoptera: Pyralidae). The reason for choosing moth pheromones as the experimental odor is the strong specificity of male moth antennas to female sex pheromones, making responses strong and reducing bias from background odors. I measured antennal responses of male moths downwind from patches using a portable IDAC-box and electroantennogram (EAG) (Syntech, The Netherlands). The EAG-method implies mounting the moth antennas on electrodes (Fig 3a) and registers the voltage potential over the complete antenna.

In Paper I, I tested the field estimates of scaling rules for olfactory information. This was done by modeling filamentous plumes originating from patches of different sizes, and simulating immigration rates of olfactory searching moths. When the moths in the simulations encountered odor filaments, they were attracted towards the odor sources. For these

simulations, two approaches for initial moth distribution were used. In the first, moths were distributed randomly over the complete simulation area and in the second, moths were located within a defined area downwind from the patches. After immigration, I compared the DAR-slope of the moths to the predicted slope from the field experiment.

In Paper **II**, I further tested predictions from the field measurements in Paper **I** by conducting an immigration experiment in the field with live insects and their host plants. The insects were the herbivorous weevils *Cionus tuberculatus* Scop. and *C. scrophulariae* L. (Fig 3b), which are monophagous on figwort *Scrophularia nodosa* L. (see description of study system below). First, I performed a behavioral study with olfactometers (Fig 2a in Paper **II**) in order to test the attraction of weevils to odors from figwort plants. Second, I established patches of different sizes containing figwort plants on a newly cut grassland and released color-marked weevils at four release points (Fig 2b in Paper **II**). Plants within patches were subsequently searched daily for weevils, and weevils found were removed from the plants. During the experiment, I decided to also include one additional herbivore, the figwort sawfly *Tenthredo scrophulariae* L. (Fig 3c, d), which was found to be common in the field area. During the later part of the experiment, I also searched plants for figwort sawfly larvae.

The Scrophularia nodosa system

Figwort *Scrophularia nodosa* L. (Scrophulariaceae) is a perennial plant which is mainly distributed in the southern parts of Sweden and usually grows in distinct patches along road sides, forest edges, grasslands and clear-cuttings. Figwort often grows on disturbed sites and has a rather ephemeral temporal distribution, where populations may go extinct in just a few years after establishment. It has a highly characteristic odor resembling over-fried meat and is probably distasteful for many animals; for example, it is commonly rejected by grazing cattle (pers. obs.).

The weevils *Cionus tuberculatus* Scop. and *C. scrophulariae* L. (Coleoptera: Curculionidae) (Fig 3b) are herbivores feeding on figwort. Weevils appear in figwort populations by mid-May and feed and oviposit on figwort plants. Feeding from weevils may have severe negative effects on figwort capsule and seed production (Jansson 2004; P. Andersson and P. A. Hambäck unpublished). In Sweden, weevils are specialized on figwort, but are also feeding on other species in the *Scrophularia* genus in Western Europe (Morris 1991). Weevils

overwinter as adults, and colonization of new figwort patches occur in spring and late summer (pers. obs.).

The figwort sawfly *Tenthredo scrophulariae* L. (Hymenoptera: Tenthredinidae) is monophagous on figwort and occurs later in summer, from mid-July to August. Adult sawflies (Fig 3c) are predators and are probably also flower-visitors (Wright 1990). Larvae (Fig 3d) feed on leaf tissue and may defoliate the complete plant. The impact on capsule and seed production of figwort is unclear, since damage mostly occur in late summer when most plants have already produced seed and capsules (pers. obs.).



Figure 3. (a) EAG-preparation of head and antennas of a male *Plodia interpunctella*. (b) Weevils *Cionus scrophulariae* (left and middle) and *C. tuberculatus* (right) sitting on a figwort *Scrophulariae nodosa* leaf. (c) Adult figwort sawfly *Tenthredo scrophulariae*. (d) Figwort sawfly larva feeding on figwort. Photo: Petter Andersson.

Results and discussion

In the field measurements in Paper I, antennal responses to pheromones decreased logarithmically with increased distance from pheromone patches (Fig 1 in Paper I). Based on these measurements, I estimated the distance at which the response was zero (i.e. where the antennal response intercepted the x-axis). The relation between the estimated distance and patch size was well described by a power relation with a slope of 0.36 ($\propto A^{0.36}$, where A=patch area; Fig 4a). This relation is somewhat more negative than the slope in the relation between visual attraction and patch size ($\propto A^{0.5}$). This finding contrasts to the previous suggestion that the olfactory impression should increase faster with increased patch size than the visual impression (Kunin 1999). As the next step, field measures were translated into predictions for immigration rates, by dividing the estimated zero response distances (Fig 4a)

with patch area. This resulted in a negative scaling relation where the slope is equivalent to a DAR-slope. If the insects should immigrate in accordance to the estimated relative attraction of olfactory information, the DAR should approximately have the scaling coefficient $\zeta = -0.64$ (Fig 4b).

The simulations resulted in DARs very close to the predicted slope. For the randomly distributed moths, the slope in the DAR was negative with $\zeta = -0.62$, and in the simulation where moths were released downwind, the DAR was negative with $\zeta = -0.63$ (Fig 4c). The strong correspondence between field measurements and simulations was promising and the next step was to test predictions in the field with live insects and host plants. The weevils in Paper II showed strong attraction to figwort odors, as suggested from the olfactometer studies (Fig 3 in Paper II). The field immigration experiment with the weevils resulted in a negative DAR with $\zeta = -0.69$ for weevils (Fig 5a). Thus, the slope was sufficiently consistent with the predicted slope from the field measurements in Paper I. Furthermore, sawfly larval densities also showed a negative DAR with $\zeta = -0.40$ (Fig 5b). However, the slope in the DAR was somewhat less negative than the slope for weevils and the predicted slope from Paper I, indicating that host search behavior of female sawflies may differ from search behavior of weevils.

The field measurements in Paper I, taken together with quantified immigration rates of simulated moths (Paper I) and live weevils colonizing host plant patches (Paper II), suggest that the estimated scaling coefficient for odor attraction can predict immigration rates of olfactory searching insects. The results, however, gave no support to the previous suggestion that olfactory attraction should increase faster with patch size than visual attraction (Kunin 1999). It is worth to note that all results points to a slope that is slightly more negative than predicted from a purely diameter-dependent scaling relationship. Although this actually could indicate other mechanisms involved in the scaling of odor information to patch size, a plausible mechanism is currently lacking. The interpretation of the results, when considering the slightly different slope in the scaling coefficient between visual and olfactory cues, may also be obstructed by the fact that visual information scales to the patch area *per se*, while olfactory information may scale more properly to the number of plants or odor sources within the patch. This should not be a problem at larger scales, since the number of odor sources within the patch are highly correlated to the patch area at larger scales (Fig 1 in Paper II).

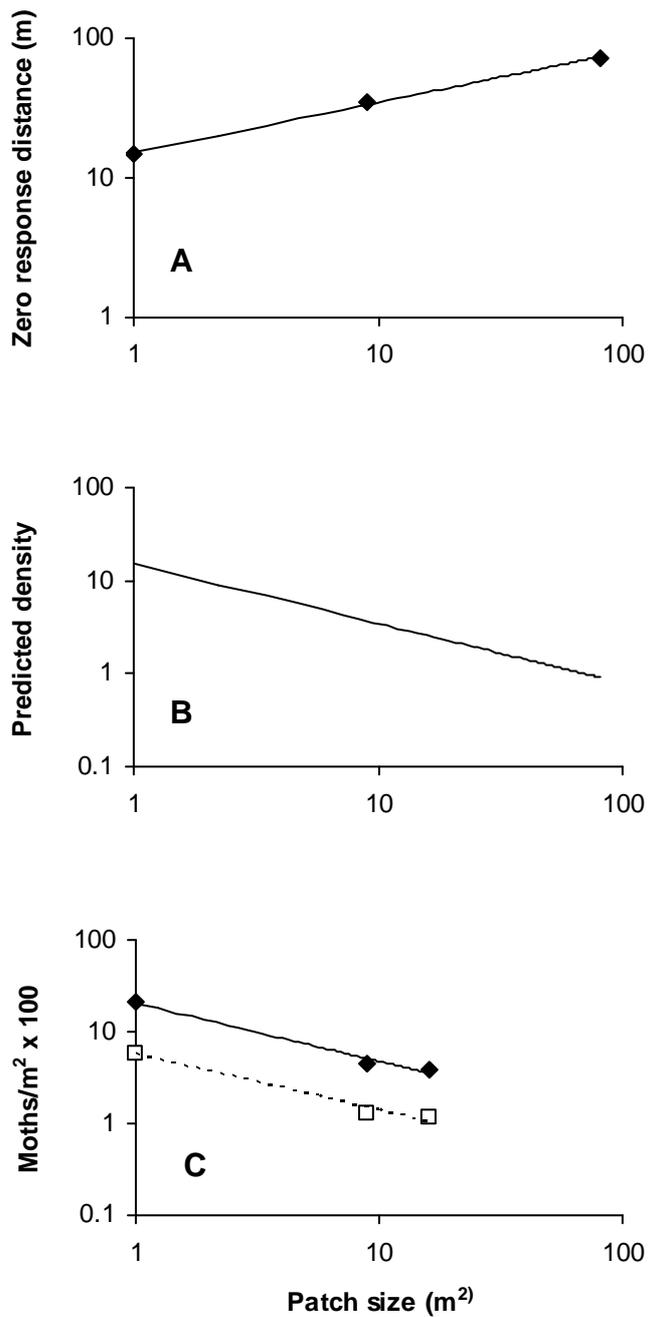


Figure 4. (a) Attraction radius (the estimated distance (m) where antennal responses intercepted the x-axis) plotted against patch size. (b) Prediction from field experiment of DAR for olfactory searching insects. (c) The relation between moth density and area resulting from simulations. Black diamonds (solid line) denote moths with a random initial distribution and white squares (dotted line) denote moths that were released downwind. Note the log-scale in all figures.

However, at a smaller scale, as in my experiment (Paper I), an edge effect occurs where the number of odor sources per area is proportionally higher in small patches (Fig 1 in Paper II). Consequently, the DAR-slope differs depending on the way to define density. These differences in slope disappear when increasing the scale, and are negligible at large scales (Paper II). In Paper I, I analyzed the scaling of olfactory information in response to patch area, and the reason was that I explicitly aimed at investigating the scaling of olfactory cues to patch area and to compare to known scaling properties of visual cues. At this stage, it therefore seems reasonable to suggest a diameter-dependent scaling of odor attraction to patch size, since the slope is fairly close to the slope predicted from a diameter-dependent scaling. However, studies that aim at separating the effect of patch area and the number of odor sources are clearly needed.

The results on the scaling of olfactory information to patch size could not explain why many olfactory searching insects show a more positive DAR than visually searching insects (Fig 2) (Hambäck et al. 2007). It is important to remember that the DARs in the large dataset analyzed by Hambäck et al. (2007) were not the result of immigration only. Other factors that could affect the slope in the relations are local growth and emigration behavior (Hambäck & Englund 2005), which also have the potential to differ between olfactory and visually searching insects (Bukovinszky et al. 2005). For instance, an insect that mainly uses visual cues may also be able to detect other patches while still inside the patch. This has the consequence that the insect can leave patches from anywhere inside the patch. On the other hand, an olfactory searching insect may be unable to perceive patch edges once located inside the patch, with the consequence that the insect may have problems to leaving the patch. Further, it may be difficult for the insect to distinguish odors from other patches from odors inside the patch. This behavior can therefore lead to a higher patch residency of olfactory searchers compared to visual searchers (Bukovinszky et al. 2005). These differences in patch residency between visually and olfactory searching insects may play a role in shaping density-distributions of insects, since the local population density partly depends on the balance between emigration and immigration rates. Hence, the differences in DARs between butterflies and moths, as showed in the study by Hambäck et al. (2007), may not result only from differences in the way these groups locate patches, but rather from differences in the way that they leave them.

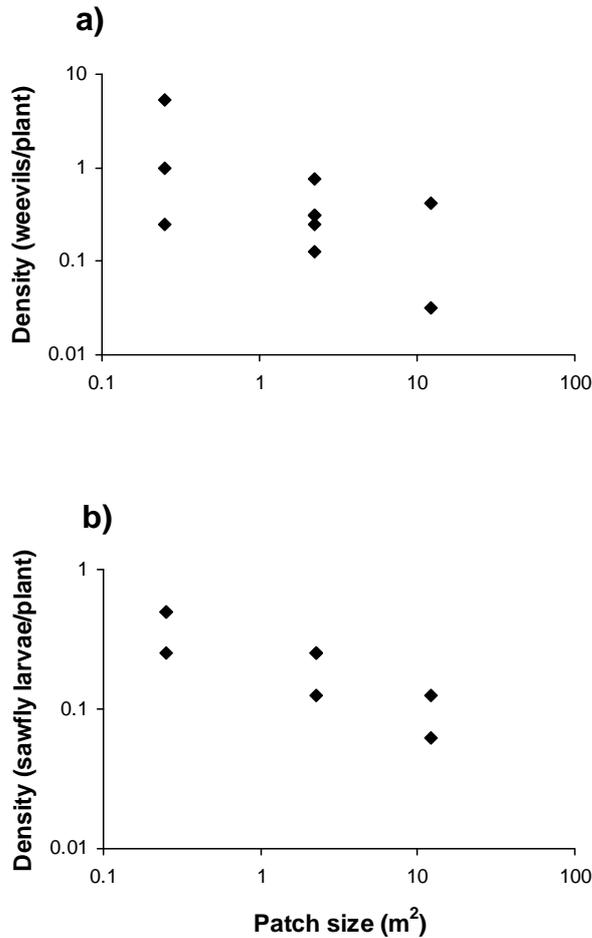


Figure 5. (a) The regression between $\log(\text{density})$ and $\log(\text{patch size})$ for weevils in the colonization field experiment. The scaling relation roughly matched the predicted slope. (b) The relation between $\log(\text{density})$ and $\log(\text{patch size})$ for figwort sawfly larvae. The slope in the relation was less negative than the slope for weevils. Note that some patches had the same densities, which makes some data points overlap in the two figures. Also note that some patches were not colonized (see Results in Paper II) and are not included in the figures, but are included in the statistical analyses (see Methods in Paper II).

This thesis demonstrates the importance of considering traits, such as search mode, when studying insect responses to habitat heterogeneity. When I write this thesis in January 2010, the year proclaimed as the “International year of biodiversity” (UN Convention on Global Diversity 2008) has just begun. Despite this attempt to raise awareness of the global biodiversity loss, a vast numbers of species are still exposed to degradation and fragmentation of suitable habitats worldwide (Debinski & Holt 2000; Prugh et al. 2008). A thorough

understanding of insect species traits, and how these traits are connected to population responses, may both increase knowledge and improve predictions about insect responses to habitat fragmentation (e.g. Hambäck et al. 2007; Hambäck et al. 2010). My work is part of an ongoing research program that has focused at developing a predictive theory for insect density-responses (Englund & Hambäck 2004, 2007; Hambäck & Englund 2007). Despite that the result in the thesis provides an important building block for this general theory, further questions on the olfactory search process arise. The olfactory search process should be highly dependent on the perceptual range of the insect, but knowledge is quite limited (reviewed in Schoonhoven et al. 2005). Hence, studies on the perceptual range of olfactory searching insects in combination with information on odor landscapes (Atema 1996) in the field could improve predictions of density-distribution of insects and their response to habitat fragmentation and heterogeneity.

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References

- Atema, J. (1996) Eddy chemotaxis and odor landscapes: exploration of nature with animal sensors – *Biological bulletin* 191: 129-138.
- Bernays, E. A. & Chapman, R. F. (1994) Host-plant selection by phytophagous insects. Chapman & Hall, USA.
- Bossert, W. H. & Wilson, E. O. (1963) The analysis of olfactory communication among animals. – *Journal of theoretical biology* 5: 443-469.
- Bowman, J., Cappucino, N. & Fahrig, L. (2002) Patch size and population density: the effect of immigration behavior. – *Conservation ecology* 6.
- Brisco, A. D. & Chittka, L. (2001) The evolution of color vision in insects. – *Annual review of entomology* 46: 471-510.
- Bukovinszky, T., Potting, R. P. J., Clough, Y., van Lenteren, J. C. & Vet, L. E. M. (2005) The role of pre- and post- alighting detection mechanisms in the responses to patch size by specialist herbivores. – *Oikos* 109: 435-446.
- Cant, E. T., Smith, A. D., Reynolds, D. R. & Osborne, J. L. (2005) Tracking butterfly flight paths across the landscape with harmonic radar. – *Proceedings of the royal society* 272: 785-790.

- Conradt, L., Bodsworth, E. J., Roper, T. J. & Thomas, C. D. (2000) Non-random dispersal in the butterfly *Maniola jurtina*: implications for metapopulation models. – *Proceedings of the royal society* 267: 1505-1570.
- Debinski, D. M. & Holt, R. D. (2000) A survey and overview of habitat fragmentation experiments. – *Conservation biology* 14: 342-355.
- Denno, R. F., McClure, M. S. & Ott, J. R. (1995) Interspecific interactions in phytophagous insects: competition reexamined and resurrected. – *Annual review of entomology* 40: 297-331.
- Englund, G. & Hambäck, P. A. (2004) Scale dependence of emigration rates. – *Ecology* 85: 320-327.
- Englund, G. & Hambäck, P. A. (2007) Scale dependence of immigration rates: models, metrics and data. – *Journal of animal ecology* 76: 30-35.
- Farrell, J. A., Murlis, J., Long, X., Li, W. & Cardé, R. (2002) Filament-based atmospheric dispersion model to achieve short time-scale structure of odor plumes. – *Environmental fluid mechanics* 2: 143-169.
- Fletcher, R. J., Jr., Ries, L., Battin, J. & Chalfoun, A. D. (2007) The role of habitat area and edge in fragmented landscapes: definitely distinct or inevitably intertwined? – *Canadian journal of zoology* 85: 1017-1030.
- Hambäck, P. A., Pettersson, J. & Ericson, L. (2003) Are associational refuges species-specific? – *Functional ecology* 17:87-93.
- Hambäck, P. A. & Englund, G. (2005) Patch area, population density and the scaling of migration rates: the resource concentration hypothesis revisited. – *Ecology letters* 8: 1057-1065.
- Hambäck, P. A., Summerville, K. S., Steffan-Dewenter, I., Krauss, J., Englund, G. & O. Crist, T. (2007) Habitat specialization, body size, and family identity explain lepidopteran density-area relationships in a cross-continental comparison. – *Proceedings of the national academy of sciences* 104: 8368-8373.
- Hambäck, P. A., Bergman, K. -O., Bommarco, R., Krauss, J., Kuussarri, M., Pöyry, J. & Öckinger, E. (2010). Allometric density responses in butterflies: The response to small and large patches by small and large species. – *Ecography* in press.
- Kelber, A., Balkenius, A. & Warrant, E. J. Scotopic colour vision in nocturnal hawkmoths. – *Nature* 419: 922-925.
- Kruess, A. & Tschardtke, T. (1994) Habitat fragmentation, species loss and biological control. – *Science* 264: 1581-1584.

- Kunin, W. E. (1999). Patterns of herbivore incidence on experimental arrays and field populations of ragwort, *Senecio jacobaea*. – *Oikos* 84: 515-525.
- Jansson, E. -M. (2004) Interactions between two weevil species attacking common figwort. Degree thesis, Swedish university of agricultural sciences
- Miller, J. R. & Strickler, K. L. (1984) Finding and accepting host plants. In Bell, W. T. & Cardé, R. T. (eds.) *Chemical ecology of insects*, Chapman and Hall Ltd, London.
- Morris, M. F. (1992) The effects of natural enemies, competition, and host plant water availability on an aphid population. – *Oecologia* 90: 359-365.
- Morris, M. G. (1991) Weevils. *Naturalist's Handbook* 16. Richmond Publishing Co. Ltd, Slough
- Murlis, J., Elkinton, J. S. & Cardé, R. T. (1992) Odor plumes and how insects use them. – *Annual review of entomology* 37: 505-532.
- Murlis, J., Willis, M. A. & Cardé, R. T. (2000) Spatial and temporal structures of pheromone plumes in fields and forests. – *Physiological entomology* 25: 211-222.
- Nieminen, M. (1996) Migration of moth species in a network of small islands. – *Oecologia* 108: 643-651.
- Prokopy, R. J. & Owens, E. D. (1983) Visual detection of plants by herbivorous insects. – *Annual review of entomology* 28: 337-364.
- Prugh, L. R., Hodges, K. E., Sinclair, A. R. E. & Brashares, J. S. (2008) Effect of habitat area and isolation on fragmented animal populations. – *Proceedings of the national academy of sciences* 105: 20770–20775.
- 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.
- Saint-Germain, M., Drapeau, P. & Hebert, C. (2004) Landscape-scale habitat selection patterns of *Monochamus scutellatus* (Coleoptera: Cerambycidae) in a recently burned Black spruce forest. – *Environmental entomology* 33: 1703-1710.
- Schoonhoven, L. M., van Loon, J. J. A. & Dicke, M. (2005) *Insect-plant biology* (2nd ed). Oxford University Press, USA.
- Tscharntke, T., Steffan-Dewenter, I., Kruess, A. & Thies, K. (2002) Characteristics of insect populations on habitat fragments: a mini review. – *Ecological research* 17: 229-239.
- UN Convention on Global Diversity (2008) Draft strategy for the preparations for the International Year of Biodiversity 2010. – Conference of the parties to the convention on biological diversity.

- Voskamp, K. E., Den Otter, C. J. & Noorman, N. (1998) Electroantennogram responses of tsetse flies (*Glossina pallipides*) to host odors in an open field and riverine woodland. – *Physiological entomology* 23: 176-183.
- Wiklund, C. (1984) Egg-laying patterns in butterflies in relation to their phenology and the visual apparency and abundance of their host plants. – *Oecologia* 63: 23-29.
- Wright, A. (1990) British sawflies (Hymenoptera: Symphyta) A key to adults of the genera occurring in Britain. – *Field studies* 7:531-593.

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