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Cover: Weevils *Cionus scrophulariae* (left and middle) and *C. tuberculosus* (right), sitting on a leaf of figwort *Scrophularia nodosa*. Photo by Petter Andersson.

Quantitative aspects of plant-insect interactions in fragmented landscapes – the role of insect search behavior

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Summary

Insects searching for host plants in the landscape are challenged by habitat fragmentation and heterogeneity. Host plants or habitat are usually distributed in scattered patches that may differ in size, shape and isolation. The ability of finding these patches strongly depends on the insect´s search behavior and the sensory cues used for detecting and locating patches. Here, I describe sensory systems of insects, such as vision, olfaction and taste, in relation to host plant search. I discuss quantitative patterns of insect distributions and density-area relations arising from search behavior. Migration pattern may be strongly affected by the cue used by the insect in the patch detection process. The relation between visual cues and patch size is well known, but we lack knowledge about how olfactory cues are connected to patch size. Since search behavior affects the spatial distribution of insects, I briefly describe consequences for host plants. Finally, I describe the main objectives of my PhD-project.

Sammanfattning

Habitatfragmentering och heterogenitet är försvårande faktorer för insekter som söker efter värdväxter i landskapet. Värdväxter och habitat är vanligtvis fläckvist fördelade och dessa fläckar varierar i storlek, form och isolering. En insekts förmåga att hitta fläckarna beror starkt på dess sökbeteende och vilka signaler den använder för att upptäcka och lokalisera fläcken. I denna uppsats beskriver jag hur insekter använder syn, lukt och smak för att hitta värdväxter. Vidare diskuterar jag kvantitativa mönster hos fördelningen av insekter och täthets-area-förhållanden som uppstår som resultat av insekternas sökbeteende. Migrationsmönster kan påverkas starkt av de signaler som insekterna använder för att finna fläcken. Förhållandet mellan synintryck och fläckstorlek är välkänt, men man vet desto mindre om doftinformation och dess relation till fläckstorleken. Eftersom sökbeteendet kan påverka den rumsliga fördelningen av insekter, beskriver jag kortfattat konsekvenser för värdväxterna. Uppsatsen avslutas med en beskrivning av mitt doktorandprojekt.

Introduction

Many insects are strongly connected to specific host plants, both for feeding and oviposition. In order to be successful in the host-finding process, insects have to detect and locate patches of suitable habitat and thereafter find a suitable host. This host finding process strongly depends on what type of cues insects use and the relative importance of cues at different scales. Most insects use combinations of sensory cues during their host searching process but the relative importance of each sensory system vary among taxa (Schoonhoven et al. 2005). Bukovinszky et al. (2005) distinguished three main groups of herbivorous insects based on their host location behavior; visual searchers, olfactory searchers and contact searchers. This classification is based on sensory cues and alighting behavior used by the insect when searching for host plants. The main difference between a contact searcher and, on the other hand, a visual or olfactory searcher is that the contact searcher assess the plant after landing while visual and olfactory searchers are guided also by sensory cues before landing (Bukovinszky et al. 2005).

In a heterogeneous landscape, habitat and host plants are not uniformly distributed. Instead, habitat and host plants occur in scattered patches varying in size and shape, surrounded by a matrix of less suitable habitat. This scattered distribution of patches has been underlined when studying effects of the ongoing habitat destruction and fragmentation (Bender et al. 1998). Taken together, patch characteristics such as size, shape and isolation are factors that an insect searching for host plants in a heterogeneous landscape has to deal with in order to be successful in host finding (Tscharntke et al. 2002; Tscharntke & Brandl 2004).

In this paper, I present an overview of search behavior of insects. The first part deals with the process of finding a suitable host. I describe the sensory and perceptive abilities of insects, in relation to host plant search. I follow this up by describing density-area relations of insects and discuss quantitative aspects of insect distributions in a patchy landscape. I will highlight the importance of insects search behavior in shaping insect density-area relations, using the classification from Bukovinszky et al. (2005) described above. Since herbivorous insects often are closely associated to their host plants, I will describe consequences arising from the quantitative distribution of insects, from the plants perspective. Finally, I briefly describe what I intend to do the following years, by describing the main objectives of my PhD-project.

The insects – searching for host plants

The majority of herbivorous insects searching for host plants are challenged by habitat heterogeneity and host plants interspersed with non-host plants. The process of finding and accepting a host plant for an insect involves multiple steps from the large scale of landscapes to the fine scale of host-plants (Saint-Germain et al. 2004), and the relative importance of different search mode varies between scales (Schoonhoven et al. 2005; Saint-Germain et al. 2007). The host selection process can be roughly divided into the following three steps; habitat location, host location and host acceptance (Saint-Germain et al. 2004).

Habitat location

When moving between patches in the landscape, the insect first have to locate a suitable habitat. At this scale, the insect may detect and respond to cues at long ranges, and direct movement towards habitat patches. Odors from host habitat or host plants often provide a reliable signal for the long range search process. This long range attraction was experimentally demonstrated for a number of forest-living beetles species (Scolytidae and Cerambycidae), that showed a significantly higher attraction to forest patches with odor baits or patches containing mechanically wounded trees than to control forest patches (Saint-Germain et al. 2007). There are also other habitat cues highly useful for the habitat searching insect. Many insects search for patches by the use of visual cues. For instance, Cant et al. (2005) demonstrated with the use of radar tracking that butterflies orientate and respond to landscape features rather than dispersing at random. In addition, aphids can steer towards green color when migrating between alternative host habitats (Bernays & Chapman 1994). The fact that these insects, at larger scales, are guided by colors or landscape features implies that cues do not have to be directly associated with a specific host plant. Non-host cues may therefore be just as important as host-cues in the habitat location phase of the host finding process of insects, if they provide reliable cues for habitat suitability.

Host location

When arrived at the patch, the insect has to change focus from searching for habitat to searching for host plants, which are usually occurring in-between non-hosts. This change may also imply changing search modality for the insect, since long range cues may no longer provide a sufficient resolution for host plant detection. At this patch scale, host plant size may be of importance, both for insects using olfactory and visual cues. Because of their size, larger plants often rise above surrounding vegetation (Wiklund 1984; Bernays & Chapman 1994) or emit higher quantities of odor and are therefore distinguishable from the surrounding

vegetation. In wind tunnel experiments, females of the beetle *Leptinotarsa decemlineata* significantly discriminated between plants of different size and showed attraction to plants with a height more than 60 cm. When exposed to plants at the height 15-25 cm they responded as they did to clean air (Bolter et al. 1997). A corresponding attraction of *L. decemlineata* to larger plants was also observed in the field (Hoy et al. 2000). Since host plants usually are found among non-hosts the insect also has to discriminate between host and non-host cues. One way for host/non-host discrimination is to use combinations of sensory cues. For instance, some bark beetle species (Scolytidae) was shown to use an integration of visual and olfactory cues. These insects are attracted and guided to coniferous host trees through odors. However, the color of the tree trunk is important in host and non-host discrimination in order not to land on a non-host when following an odor trail (Campbell & Borden 2006).

Host acceptance

Once landed on a plant, the host selection process continues with an assessment of plant quality and suitability. This process usually includes the use of olfactory cues, but gustatory cues from tasting the plant may also be of major importance. Many insects, such as many butterflies, examine plant odors by drumming on the leaf surface with their antennae, palp or tarsi. This chemoreceptive assessment is often combined with certain movement behaviors from which the insect can make a physical inspection of the plant. For instance, females of the cabbage root fly *Delia radicum* walks continuously back and forth on a leaf, followed by a run down the stem to the base, where oviposition might take place in the soil nearby. During this behavioral process, the fly assesses plant quality from hairs on her tarsi (Schoonhoven et al. 2005). Other insects assess plant quality by biting and chewing and determine plant suitability with chemoreceptors located on the mouthparts. Whether the insect accepts or rejects the plant is determined by stimulants or deterrents and the balance between them. The presence of feeding or oviposition stimulants might trigger feeding or ovipositing behavior. On the other hand, sufficient concentrations of deterrents can make the insect leave the plant (Bernays & Chapman 1994; Schoonhoven et al. 2005).

In the following, I will in more detail describe the three main search modalities of insects; visual, olfactory and gustatory search. I will also describe properties of sensory cues and provide examples on insect perception and responses to these cues.

Visual search

Visual cues – properties and constraints

An optical cue originating from a resource such as a host plant is characterized by spectral reflection and dimension and operates on a very fast time-scale, i.e. the speed of light (Prokopy & Owens 1983; Miller & Strickler 1984). In the case of plant populations or habitat patches, distribution patterns are also of importance (Prokopy & Owens 1983). A visual signal is normally not affected by surrounding abiotic factors such as wind and temperature and should be fairly constant at different distances. In addition, visual cues are multi-directional (Briscoe & Chittka 2001; Miller & Strickler 1984). The performance and importance of visual cues is in general more limited at night than during daytime, although some insects have been shown to use color vision also during night conditions (Kelber et al. 2002). In addition, many insects flying at night are capable of seeing the ground as it passes by below the flying insect. This visual capacity enables orientation in other directions than just up- and downwind and is commonly used by insects flying at night, underlining an important aspect of visual cues also during night conditions (Bernays & Chapman 1994).

Insect vision and visual search – light, color and shape

The insect vision differs from, for example, vertebrate vision in several ways. For instance, insects have a fixed focus which implies that the optical performance is optimal only at short distances (Prokopy & Owens 1983; Briscoe & Chittka 2001). Further, the compound eye of insects consists of thousands of similar units, called ommatidia. These ommatidia consist of a light-gathering and a sensory part and contain pigment cells. These pigment cells are of different types responding to light of different wavelengths, most commonly strongest for wavelengths from the ultraviolet, blue and green parts of the spectrum (Bernays & Chapman 1994). These varying types of ommatidia with pigment cells are not uniformly distributed over the compound eye. For instance, many insect species have light receptors with pigment for green color distributed at the ventral side and receptors for blue color on the dorsal side of the compound eye. This distribution of receptors can make the sky and vegetation more clearly visible for a flying insect (Briscoe & Chittka 2001). Further, bees *Apis mellifera* have been shown to be significantly better at discriminating between colors when the colors are presented in the lower half of the bee´s visual field (Lehrer 1998).

Many insects have small groups of ommatidia located at the dorsal part of the compound eye, which are specialized for detecting polarized light (von Philipsborn & Labhart 1990). The use

of polarized light enables the insect to determine the position of the sun during cloudy weather conditions or when the sun is below the horizon. Since many insects rely on sun position for orientation, this ability implies that they can orientate even when they cannot see the sun (Pomozi et al. 2001). However, the ability to detect polarized light can also be used for keeping a straight course, as shown for the fly *Musca domestica* (von Philipsborn & Labhart 1990). Since light reflection from water surfaces is partly polarized, this cue is used by some insects for detecting water, as shown for migrating locusts *Schistocerca gregaria* that avoids flying over the sea (Shashar et al. 2005).

At longer distances many insects use horizon line characteristics for orientation. Along the horizon line the shapes and silhouettes of hosts such as trees and shrubs appear, serving as long distance cues towards which the insect can orientate (Prokopy & Owens 1983). Long-distance visual search is perhaps most studied in diurnal butterflies, which has been shown to orientate towards and distinguish between suitable and unsuitable habitat at distances exceeding 100 m (Conradt et al. 2000; Cant et al. 2005).

Color vision and ability to recognize patterns is probably most important at shorter distances (Briscoe & Chittka 2001; Prokopy & Owens 1983). For butterflies, colors seem to play a significant role in host plant location at short distances. Gravid females of *Pieris brassicae* and *P. napi* show landing responses to green colors from both real and artificial leaf. The color-preference of these species varies from green color to yellow, blue and violet depending on their motivation for oviposition and nectar feeding (Traynier 1986; Schoonhoven et al. 2005). Another example involves the host finding behavior of the leafhopper *Empoasca devastans*. In laboratory experiments, leafhoppers were shown to be equally attracted to host and non-host plants as a result of their similar greenness. The leafhoppers even preferred non-host plants when the plant was presented to the insect in a more intense background light compared to the host plant, demonstrating the importance of light intensity for insect vision (Saxena & Saxena 1975). Also the greenness is important, as demonstrated in a study where *P. brassicae* preferentially alighted on light green substrates in comparison to dark green substrates (Smallegange 2006). A similar preference for light green compared to dark green leaves can be found in the fly *Psila rosae*. The shape of leaves also influences oviposition in this species, and leaf models with a silhouette resembling the host plant leaf received more eggs than leaf models with simple geometric form (Degen & Städler 1997). The Australian butterfly *Eurema brigitta* was also highly discriminative regarding leaf shape. In field studies, it was observed to prefer plants with short, narrow leaves compared to plants with long,

narrow leaves. The preferred leaf shape resembled leaves of the butterfly's host plant (Mackay & Jones 1989).

Olfactory search

<u>Olfaction</u>

Most insects rely upon olfaction when searching for food and oviposition sites and olfaction is also frequently used in sexual and social communication. Chemoreceptors for olfaction are located on hair-like sensilla, predominantly on the insect´s antenna (Schoonhoven et al. 2005). Since the olfactory system of the insect must accomplish several tasks, there are different types of receptors with different functions. For example, large numbers of receptors are specific for pheromones, while other receptors are sensitive to plant odor molecules. In nature, an insect is potentially exposed to many thousand odors from the surrounding environment, forcing the insect´s olfactory system to sort out odors of importance from background noise. There are two major ways an insect can sort out signals from background noise. First, responses to single odorants, such as pheromones, can be processed through labeled-line neural channels, which mean that connected receptors and neurons respond specifically to certain compounds. On the other hand, responses to more complex odor blends, such as plant odors, can operate over large groups of receptors, where the single receptor may respond to several different odors. An important odor mixture for the insect will then be characterized by a specific spatial and temporal activity pattern over these receptor groups and will subsequently activate the neurons connected to the receptors. This process is called cross-fiber patterning (Smith & Getz 1994).

<u>Odor properties and dispersion</u>

In contrast to visual cues, olfactory cues are strongly affected by abiotic factors such as wind and temperature. A visual signal can be detected from multiple directions while an olfactory signal often is possible to detect only from a restricted number of directions. This is because still air is highly uncommon under field conditions and there is more or less always some wind making the olfactory signal travelling downwind from an odor source. Compared to a visual signal, the olfactory signal is moving slowly and the dispersal of odors strongly depends on wind velocity. This implies that receivers (e.g. insects) located downwind from an odor source (e.g. a host plant) have a higher probability of detecting and finding the source than receivers located upwind from the source (Miller & Strickler 1984; Murlis et al. 1992; Bernays & Chapman 1994).

Dispersing from a point odor source, the odor typically adopts the shape of a plume. Within this plume, odors travel in packages or filaments interspersed with odor-free air. These filaments reach highest concentrations near the odor source and, as they travel downwind, gets elongated and torn apart by eddies and wind turbulence. Consequently, the concentration within filaments usually decreases as they disperse downwind. The distance between filaments should also increase with increasing distance from the odor source. This implies that the interval between filaments and the concentration within filaments may provide important information for insects trying to locate odor sources. There are two major physical dispersal mechanisms of odors; molecular diffusion and turbulent diffusion caused by wind and local turbulence. In molecular diffusion, random movement of molecules gradually makes them move away from each other with increasing time. In the field, this normally occurs at very short time-scale as the molecular diffusion only acts before the filaments reaches the size of the smallest eddies after which turbulent diffusion takes over. At a larger time-scale, this type of dispersion requires ideal conditions with no wind and should consequently be rare in the field. Turbulent diffusion, on the other hand, is common and should be the most frequent odor dispersal feature an insect has to prevail in order to find its host plant (Murlis et al. 1992; Bernays & Chapman 1994; Murlis et al. 2000; Farrell et al. 2002).

Anemotaxis

Olfactory responses have been extensively studied in several insect species. Moths, in particular, are well known for their exceptionally sensitive antennas, especially regarding responses to sex pheromones. Like many other insects, moths display a behavior called anemotaxis which implies flying upwind using the current wind direction in order to orientate towards the odor source (Fig. 1A) (David et al. 1983; Willis & Arbas 1991; Mechaber et al. 2002). One species using this behavior is the hawk moth *Manduca sexta*. Once in contact with the odor the moth starts flying upwind demonstrating a zigzag flight in which it tries to maintain inside the plume. If the interval between the antennal responses becomes too long and the moth loses contact with the plume it starts with a widely counter-turning flight pattern moving more across the wind followed by a slow downwind regression (Fig. 1B). If new odor filaments are detected by the moth, it starts the zigzagging flight again until locating the odor source. Studies have shown that this behavior is practiced both by males searching for females emitting sex pheromones and by females searching for host plants (Fig. 1A) (Willis & Arbas 1991; Mechaber et al. 2002).
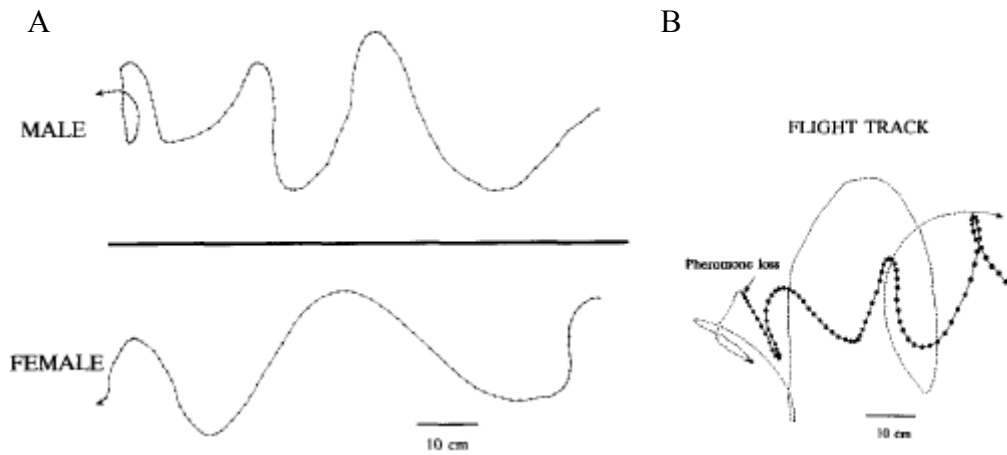
Figure 1. Flight tracks of moths practicing upwind anemotaxis in a wind tunnel, seen from above. Wind-direction is from left to right. (A) Male moth flying upwind towards a pheromone source and a female flying upwind towards a host plant. (B) The behavioral response with counter-turning flight followed by a down-wind regression after the moth lost contact with the plume. Thick dots in (B) mark the flight track of the moth flying inside a pheromone plume, thin dots mark the flight after the pheromone source was removed. From Willis & Arbas (1991).

Upwind anemotaxis also seems to play an important role in the host searching behavior of larger parasitoids. Wind tunnel studies have shown the use of anemotaxis of a parasitoid wasp (Zanen & Cardé 1996). Further, a recent field experiment produced evidence suggesting that parasitoid wasps practice upwind anemotaxis also under field conditions (Williams et al. 2007). However, the type of odor cue differs between parasitoid species. There are examples of parasitoids responding to host feces (Zanen & Cardé 1996) and to odors from the host larva's host plant (Williams et al. 2007). The variation in odor cue use among parasitoids indicates that there are constraints connected to the host finding process. Odor from host individuals should be highly reliable cues correctly indicating a suitable resource, but these cues normally occur at low amounts and concentrations in the field. In contrast, plant odors are more detectable but are instead poor predictors of host individual presence. Some species track hosts by the host's aggregation- or sex pheromones since these cues usually are emitted in high quantities and has a potential to disperse longer distances (Vet & Dicke 1992). However, it has also been suggested that parasitoids have to track an odor blend from the host organism and the host organisms host plant (Murlis et al. 1992).

Another upwind search behavior is the jumping approach practiced by the flies *Delica radicum* and *D. antique*. These insects jump short steps towards the wind when stimulated by

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host plant odor. Between every step the fly sit and wait on the ground until it encounters the odor again. This behavior will eventually lead the insect to the host plant (Bernays & Chapman 1994; Finch & Collier 2000).

The upwind anemotaxis behavior is also used by walking insects. This behavior has been studied in the chrysomelid beetle *Leptinotarsa decemlineata*. During the first days as adults, individual beetles are not capable of flying and therefore have to find their host plant by walking. In experiments, beetles were strongly attracted to odors from host plants and showed an almost straight walk towards the odor source when exposed to an airstream carrying host plant odor (Visser 1986; Schoonhoven et al. 2005). Walking towards host plants using odors have also been observed in the field for the chrysomelid beetle *Trirhabda canadensis* (Puttick et al. 1988).

Herbivore-induced responses

Plants are well-known for their production of secondary compounds following herbivore damage (Karban & Baldwin 1997). These induced responses of plants often serve as information for insects searching for hosts, both natural enemies and herbivores. It has been shown that parasitoid wasps locate their host using induced responses of damaged plants. For instance, the parasitoid *Cardiochiles nigriceps* locate its host, the larvae of the moth *Heliothis virescens,* from the volatile blend emitted from the host plant. These volatiles are also host specific, making the parasitoid capable to distinguish between their specific host larvae and other similar, closely related moth larvae (De Moraes et al. 1998). Further, the plant *Nicotiana attenuata* releases volatile organic compounds following attack from herbivores. These volatiles attract predators that feed on eggs of these herbivores, thus leading to reduced damage to the plant (Kessler & Baldwin 2001; Halitschke et al. 2007). However, the flea beetle *Epitrix hirtipennis* was also attracted to green leaf volatiles emitted from damaged *N. attenuata* plants (Halitschke et al. 2007). Another example is the chrysomelid *Galerucella calmariensis* which is strongly attracted to plants colonized by conspecifics (Grevstad & Herzig 1997). This attraction results both from induced emission of volatiles from the plants and released aggregation pheromones from conspecifics (Bartelt et al. 2006; Hambäck submitted manuscript).

Olfactory images of host plants

In some cases, insects respond to a single volatile during the host plant search (labeled-line processing, see Olfaction). This single volatile attraction usually occurs in cases when plant

odor is highly specific and when odor is not found in surrounding, unrelated species (Visser 1986). On the other hand, many plant compounds, such as green leaf volatiles, are widely found in unrelated plant species. Thus, volatiles emitted from host plants can be a mixture of compounds occurring in species-specific relative proportions. For the host plant searching insect, this type of odor blends can be perceived as an olfactory image (cross-fiber patterning, see Olfaction) (Visser 1986; Roseland et al. 1992) and there are quite many species that respond and orientate to host plants by tracking blends of volatiles. This response was demonstrated in the weevil *Smicronyx fulvus* which showed strongest attraction to a mixture of five volatiles from its host plant. In fact, when volatiles were exposed separately some of them acted as deterrent for the weevils (Roseland et al. 1992). A similar pattern was found in the beetle *Leptinotarsa decemlineata*, where specific concentration ratios were highly important for attraction and orientation of beetles (Visser 1978). However, an obvious constraint on olfactory images of insects is that volatile emission of host plants usually are preserved only for quite short distances (Schoonhoven et al. 2005).

The role of background odor

When searching for a resource in the landscape, the olfactory searching insect has to face not only the resource odor. This signal has to be detected against a background of non-informative odors. An obvious constraint on the odor-finding process is when the resource-indicating odor becomes masked by other odors or complex odor blends (Schröder & Hilker 2008). This masking of host produced volatiles has been applied in modern silviculture by mixing conifers and angiosperms and thereby reducing attack from bark beetles (Scolytidae) (Zang & Schlyter 2004). Just as there are examples of background odors masking host odors, there are also examples of background odors containing repellent components, overriding the attractiveness of resource odor (Schröder & Hilker 2008). There are also several studies demonstrating the enhancing effect from background odors on the olfactory search of insects. For instance, the moth *Heliothis virescens* was significantly more attracted to the combination of host plant odor and one additional sesquiterpene in comparison to odors from undamaged host plants (Mozuraitis et al. 2002). As with odor masking, the enhancing effect can act both through single volatile components and more complex odor blends. The use of complex odor blends is practiced by parasitoids when searching for oviposition sites. The egg-parasitoid *Chrysonotomyia ruforum* responds to odors from pine twigs containing egg masses from its host, the sawfly *Diprion pini* (Hilker et al. 2002). The response was even stronger when the

odor blend from the pine twig was combined with an additional sesquiterpene (Mumm et al. 2003).

Gustatory search

While the role of visual and olfactory cues is highly important before landing on the plant, the importance of taste, or gustatory cues, increases once the insect has landed on the plant. The functions of gustatory sensilla are similar to the olfactory, but mainly differ in their location. While the olfactory sensilla predominantly are located on antennas, the gustatory sensilla are situated in the oral cavity and also on the external mouthparts, tarsi, ovipositor and antennae. While insects evidently use the mouthparts for taste, the other extremities are also used for gustatory evaluation, often by a repeated tapping on the plant surface (Bernays & Chapman 1994; Schoonhoven et al. 2005). This behavior is frequently practiced by the butterfly *Pieris brassicae*, showing a drumming with tarsae on the surface of the plant (Chun & Schoonhoven 1973). However, just as this behavior is important for assessment of host plant suitability for oviposition, it can also provide information about the presence of eggs from conspecific females. For instance, the marking of host plants with host-marking pheromones or other species-specific compounds after oviposition is frequently used by insect females and decreases competition for her progeny (Schoonhoven et al. 2005).

Insects in the landscape

Animal density and abundance in heterogeneous environments are not spatially or temporally constant. This observation has lead to an extensive research effort in investigating the impact of habitat area on animal abundance and density. A general view is that the abundance of organisms is almost always reduced, as a consequence of habitat fragmentation. However, the effects of area on the density of organisms is much more variable and has been of central interest for conservation ecologists studying fragmentation and habitat loss (e.g. Debinski & Holt 2000) and for applied issues in control of pest insects (e.g. Root 1973). The local density of a population that inhabits a habitat patch is determined by local growth, i.e. births and deaths, and migration between patches (Fig. 2) (Hambäck & Englund 2005) and these processes will influence animal density responses to patch size. In the following part of this paper, I will introduce the concept of density-area relations. Further, I describe processes that determine insect densities in heterogeneous landscapes, such as migration, local growth, edge effects and species interactions. Since migration patterns, as we shall see, might differ between insect groups depending on their search mode, migration will be described using the

classification of Bukovinszky et al. (2005), dividing insects into visual, olfactory and contact searchers.
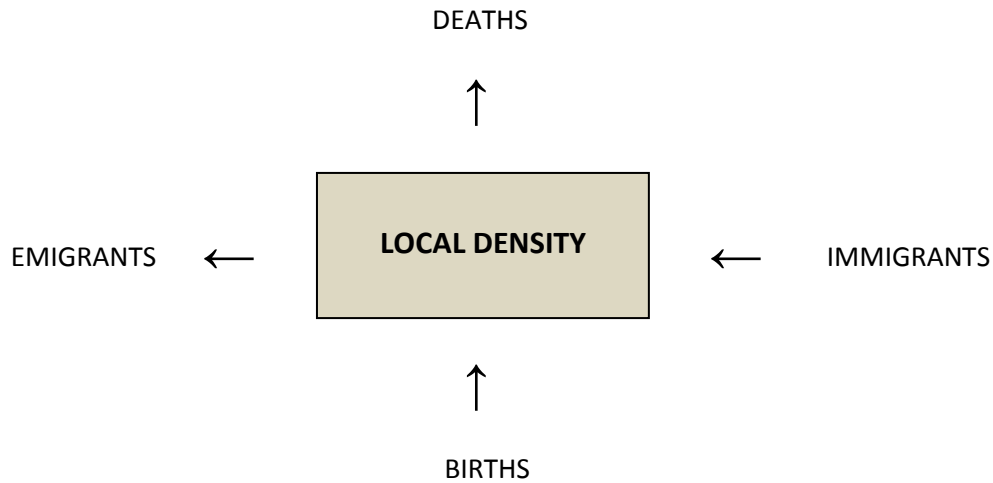
Figure 2. Processes determining the local density within a patch.

Density-area relations

A general prediction regarding insect populations exposed to habitat fragmentation has for a long time been that population density should increase with increasing patch size (Root 1973). This prediction was originally stated by Root (1973) and according to his "resource concentration hypothesis", densities of insects should increase with increasing patch size as a result of higher immigration and lower emigration rates for large in comparison to small patches. However, this hypothesis has not gained any general support from field studies and experiments and the relation between organism density and patch size can show almost any relation – positive, negative, no relation (Kareiva 1985; Bach 1988; Grez & Gonzalez 1995; Bender et al. 1998; Bukovinszky et al. 2005; Hambäck et al. 2007) or a hump-shaped relation with highest densities in patches of intermediate size (von Zeipel et al. 2006; Hambäck et al. 2007). Therefore, it seems like the resource concentration hypothesis is not sufficient in explaining insect densities in the field (Grez & Gonzalez 1995; Bowman et al. 2002; Bukovinszky et al. 2005). In fact, it has been argued that the resource concentration hypothesis is based on wrong assumptions, since a higher number of immigrants into larger patches not necessarily lead to higher densities, for the reason that immigrants are diluted over a larger area, which often has the consequence that the relative density is lower in larger patches (Hambäck & Englund 2005).

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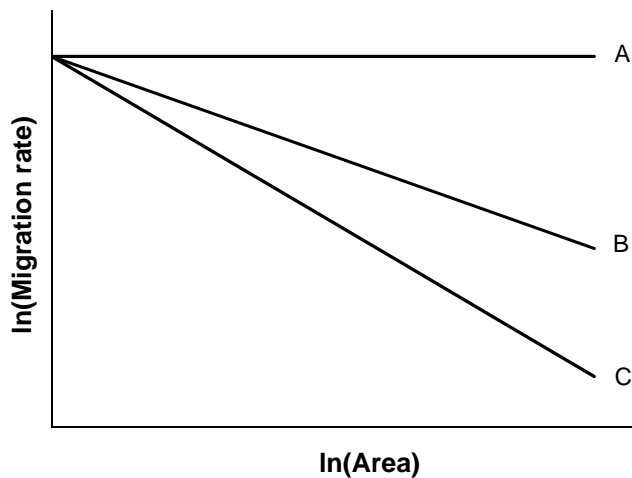
Figure 3. Scale-dependent migration rates of insects. A) area-dependent, B) perimeter-dependent and C) diameter-dependent migration.

The scaling of migration rates

Migration patterns may differ between organisms based on their movement and search behavior and can give rise to different scaling of migration. This has been noted by several authors (e.g. Bowman et al. 2002; Bukovinszky et al. 2005) and Hambäck & Englund (2005) distinguished three general cases of migration scaling. First, area-dependent migration occurs when organisms are likely to arrive or leave from anywhere in the patch. As a consequence, migration will scale independently of area (Fig. 3A). Second, perimeter-dependent migration occurs when migrants enter or leave patches from edge or boundaries. This type of migration will scale to the perimeter-to-area ratio of the patch and leads to a negative migration-area relation (Fig. 3B). Third, diameter-dependent migration results from organisms locating patches at a distance and orienting towards it. In this case, migration scales to the diameter-to-area ratio and is more negatively related to area than perimeter-dependent migration (Fig. 3C) (Hambäck & Englund 2005). Although these three broad categories of migration behavior can explain many insects migration behaviors, still many insect groups deviate from those categories. As we shall see later in this paper, some insects show other density-area relations which indicate that their search behaviors may differ from the above-mentioned and that scaling of migration rates remains to be investigated.

Migration – visual searching insects

Diurnal butterflies often show a negative density-area relation (Fig. 4) (Välimäki & Itämies 2003; Bukovinszky et al. 2005; Hambäck & Englund 2005; Hambäck et al. 2007; Rabasa et al. 2008). This has previously been suggested to be a consequence of their search behavior. Many butterflies detect habitat patches from boundary characteristics, which scale immigration roughly to the perimeter-to-area ratio. Bukovinszky et al. (2005) found a negative relation between *Pieris rapae* egg densities and patch size. They suggested both from field results and from a modeling analysis based on insect search mode that immigration from these butterflies was perimeter-dependent (Fig. 3B) (Bukovinszky et al. 2005). However, butterflies have also been suggested to detect suitable habitat from distances exceeding 100 m (Conradt et al. 2000; Cant et al. 2005) which implies that they can show a directed movement towards a suitable habitat patch once it has been detected. Since the visual impression of a patch is proportional to the patch diameter, it leads to an immigration that is proportional to the patch diameter, i.e. diameter-dependent immigration (Fig. 3C) (Hambäck & Englund 2005; Englund & Hambäck 2007).

The emigration behavior of butterflies, however, can be a combination of area- or perimeter-dependent emigration (Fig. 3B). For instance, if individuals decide to leave a patch when encountering the patch edge the relative emigration rate would decrease with increasing patch size because the probability of encountering edges decreases with increasing patch size. On the other hand, if butterflies once inside a habitat patch are able to detect other patches at longer distances, then the emigration would be dependent on the patch area for the reason that they can decide to leave the patch from anywhere inside the patch (Hambäck & Englund 2005).

Migration – olfactory searching insects

Nocturnal moths in general show the opposite density-area relation as diurnal butterflies (MacGarvin 1982; Bukovinszky et al. 2005; Hambäck & Englund 2005; Hambäck et al. 2007). Bukovinszky et al. (2005) found that densities of the moth *Plutella xylostella* were higher in large compared to small patches. Further, when performing an analysis on a large dataset of density-area relations of moths in fragmented landscapes, Hambäck et al. (2007) found an average positive relation between moth densities and patch size (Fig. 4). This positive relation between insect density and patch size was suggested to be a result of the moths olfactory search behavior, thus leading to different density-area relations than for visual searchers (Bukovinszky et al. 2005; Hambäck et al. 2007). The scaling of olfactory

information to area has not been studied under field conditions but models suggest that the olfactory impression of a patch should increase faster with increasing patch size than the visual impression (Bossert & Wilson 1963; Balkovsky & Shraiman 2002). From this, a prediction could be that immigration rates of olfactory searching insects should be higher in large compared to small patches. Interestingly, in the analysis the diurnal burnet moths (Zygaenidae) showed a negative relation between density and area, i.e. a similar pattern as observed for butterflies (Fig. 4) (Hambäck et al. 2007). Phylogenetically, burnet moths belong to the moths, but are ecologically more similar to butterflies. This finding most certainly underlines the importance of search behavior in predicting and explaining density-area relations of insects.
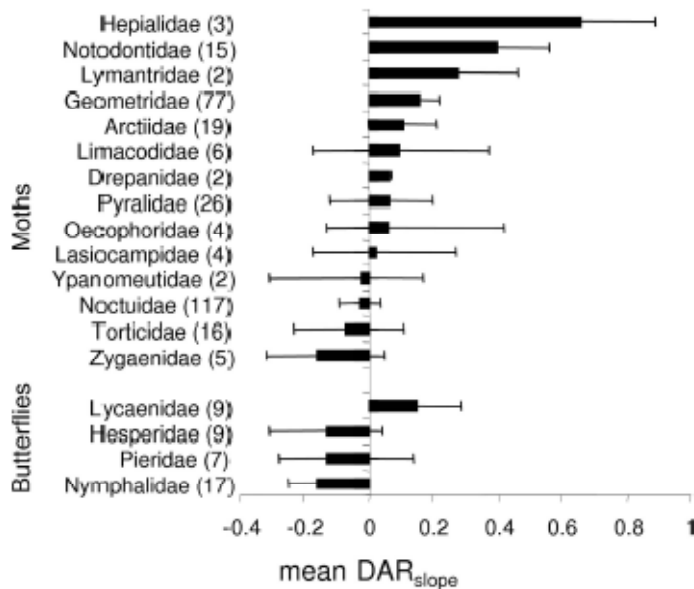
Figure 4. Comparisons of density-area relations between butterflies and moths. DAR_{slope} denotes the slope in the density-area relation. From Hambäck et al. (2007).

An important difference between olfactory and visual searchers is their ability to detect other patches once located in a patch. A visual searcher can detect another patch at large distances and make a decision to leave. In contrast, a searcher relying upon olfactory cues cannot detect other patches from inside a patch or can have difficulties to detect the patch edges (Hambäck et al. 2007). The probability that an olfactory searcher leaves a patch is possibly more depending on the individual´s state and motivation. Further, a common feature of olfactory searching insects is the arrestment response which implies that the insect, once finding its host

plant, is restricted to movement only within a small area and therefore is unable to leave the patch once it is colonized (Schoonhoven et al. 2005). Although the arrestment response is important for the individual insect´s host plant selection it has the consequence that the insect may be prohibited to emigrate from the patch thus influencing the local density of the host plant patch. Models suggest that an increased arrestment response makes larger patches retaining a higher number of individuals than small ones, for the reason that large patches loses less individuals through emigration compared to small patches (Bukovinszky et al. 2005).

Primary and secondary attraction – importance for migration
The olfactory search for host plants can be divided into primary and secondary search. Primary attraction could be defined as a positive response from insects to host-produced volatiles from undamaged plants (Saint-Germain et al. 2007). In contrast, secondary attraction refers to insects that are attracted to odors from previously damaged plants or to aggregation pheromones released by conspecifics (Hambäck et al. 2003: Wertheim et al. 2005). The beetle *Epilachna varivestis* serves an example of this secondary attraction by aggregating on already colonized plants. Turchin (1987) demonstrated in experiments that it was the actual presence of conspecifics that attracted beetles. Otherwise it could be argued that these insects aggregate on high quality plants through primary attraction (Turchin 1987).

This secondary attraction can be important for density-area relations of olfactory searching insects because it creates a positive feedback for patches that are already colonized. Kareiva (1985) studied immigration and densities of the leaf beetle *Phyllotreta cruciferae* in patches consisting of *Brassica oleracea* and found a positive relation between density and patch size in patches where no reproduction occurred during the study. These densities occurred after a time-period of 20 days. However, an immigration experiment conducted at shorter timescale (ca 24h) revealed a clear negative scaling of the initial immigration with highest immigration rates into small patches (Kareiva 1985). This suggests that during the initial phase of colonization, beetles shows perimeter- or diameter-dependent immigration. Once the patch is colonized it serves as a magnet attracting conspecifics through odors and since the probability of being colonized is highest for large patches, feedbacks will be strongest there. This feedback subsequently creates a positive relation between density and patch size (Hambäck & Englund 2005; Englund & Hambäck 2007). The positive scaling is most likely the result of the beetles responding to odors through secondary attraction. The exact mechanism for the

secondary attraction is not clear since it is known that these beetles can respond to both plant odors (Feeny 1970 in Visser 1986) and to aggregation pheromones (Peng & Weiss 1992).

Migration – contact searching insects

Contact searching refers to insects that respond to host plant cues only after landing on the plant. One insect group that belongs to this category is the aphids. These insects often show a scaling of immigration with no relation to patch size (Bukovinszky et al. 2005; Hambäck & Englund 2005; Englund & Hambäck 2007), i.e. area-dependent immigration (Fig. 3A). This implies that there is an equal probability of landing in any part of the patch and is most probably an outcome of their host-shifting behavior. Many aphid species in temperate areas spend the cold season on alternative host plants and migrates to summer hosts drifting as passive travelers in the air column. Densities within patches arising from this passive immigration are thus unrelated to the patch area. Further, this aphid "rain" makes individuals land outside habitat patches and aphids landing in the vicinity of the patch can orientate towards it and consequently show perimeter-dependent immigration (Fig. 3B) (Hambäck et al. 2007). This perimeter-dependent immigration should also apply to ground-searching contact searchers (Bowman et al. 2002).

The emigration behavior of contact searching insects can vary between taxa. Aphids disperse from plants during summer both as wingless individuals (apterous) through walking (Roitberg et al. 1979) and as winged (alate) individuals that leave the patch in flight (Kring 1972). The consequence of these dispersal behaviors is that the scaling of emigration would be perimeter-dependent as the probability of leaving a patch in this case increases when they encounter patch edges and the likelihood of detecting the edge decreases with increasing patch size (Hambäck & Englund 2005).

Local growth

One important process that determines population density within a patch is local growth, expressed as the impact of births and deaths of individuals within the population. This can be understood in terms of source-sink dynamics, where sources imply populations where birth rates exceed death rates and sinks refer to populations where death rates exceed birth rates. Still, a sink population can be sustained by individuals immigrating into the patch from source patches in the surroundings (Pulliam 1988). A general pattern is that migration is more important in small patches whereas local growth dominates in large patches. Therefore, local processes are more important in large patches and regional processes are more important in

small patches (Hambäck & Englund 2005; Hambäck et al. 2007). This has consequences for insect densities at a temporal scale because growth rates will be strongest in larger patches making the density-area relation become more positive with increasing time. For instance, for a species with a positive area-scaling of immigration rates the density-area relation will be more positive as time increases. Further, if the area-scaling of immigration rates is negative, the slope of the density-area relation will subsequently become less negative (Hambäck & Englund 2005; Hambäck et al. 2007).
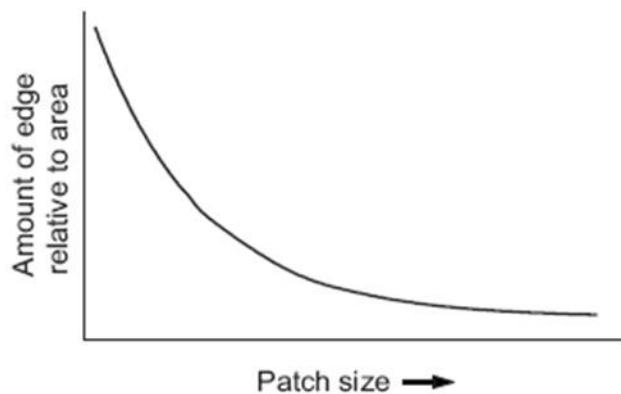
Figure 5. The relation between the edge-area relation and patch size. Modified from Fletcher et al. (2007).

Edge effects

Except for the effect of the patch size, the edge of the patch can have strong direct impacts on the density and abundance of animals (Fletcher et al. 2007; Ewers & Didham 2008). A consequence of habitat fragmentation is that it usually leads to smaller and more isolated habitat patches. As the size of patches decreases, the importance of the edge increases (Fig. 5). This in turn can have profound influences on processes such as local growth and migration. This is partly because edges enhance the flow of energy and nutrients, leading to a higher productivity. There is also a potential for increased species interactions, such as predation and competition, at the patch boundaries. All these processes may affect the local growth of species and can lead to different density-area relations. For instance, a species specialized on patch edges will reach the highest density in small patches whereas a patch core specialist will reach the highest density in large patches since the edge effect decreases with increasing patch size (Fig. 5) (Fletcher et al. 2007). Dispersal and movements may also

be affected by edges, leading to a decreased emigration probability with increasing area and therefore a weakened scale-dependence in smaller patches (Englund & Hambäck 2004).

The shape of the patch may also affect the impact of edge effects on animals. A patch with a complex shape will have a higher perimeter-area ratio and therefore a more edge-affected area, compared to a simpler shaped patch. This patch complexity can have effects on dispersal and migration since a more complex shaped patch will have a higher number of migrants, as a consequence of the longer perimeter than a circular patch (Ewers & Didham 2006).

Species interactions – natural enemies
Interactions between herbivores and their natural enemies can have consequences on density-area relations. For instance, larvae of the moth *Eupithecia immundata* showed highest densities in host plant populations of intermediate size. The reason for this pattern was that a guild of parasitoids attacked moth larvae at highest rates in the largest host plant populations. Therefore, the moth showed a hump-shaped relation between density and host plant population size, and top-down effects of parasitoids were strongest in the largest populations (von Zeipel et al. 2006). Another example is the planthopper *Prokelisia crocea* which showed the opposite density-area relation to its natural enemies, a predator guild consisting of cursorial and web-building spiders. While spiders declined with increased patch size the planthoppers instead increased with patch size. Through experiments the authors demonstrated that an increase in the density of spiders had a negative effect on the planthoppers. This was not exclusively an effect on planthopper mortality caused by spider predation. In fact, the main effect of an increase in spiders within patches was an induced dispersal and emigration of planthoppers (Cronin et al. 2004). In addition, if the herbivore and its predator show divergent search strategies for host location, their relative immigration into patches will differ thus leading to a varying predation rate along the patch size gradient (Hambäck et al. 2007).

Consequences for plants

Antagonistic and mutualistic interactions
From the plant´s view, antagonistic interactions such as attacks from herbivorous insects may cause severe damage, both for the individual plant and for its progeny. If the density of herbivores can vary between patches of different size, the relative rate of herbivory should also vary between small and large patches. The perennial plant *Silene latifolia* is attacked by

an herbivore, the noctuid moth *Hadena bicruris*. These moths oviposit in the ovary and the larvae then feeds on the ovule and developing seeds, thereby mediating an obvious reduction in individual plant fitness. Attack rates from moths on *S. latifolia* were studied in both natural populations and in experimental patches and there was a significantly higher attack rate on plants growing in small compared to large populations. Thus, an increased population size brought an increase in the individual fitness of plants (Elzinga et al. 2005). The opposite pattern of seed predation was found in a study of the perennial herb *Vincetoxicum hirundinaria*. This plant is mainly attacked by the tephritid fly *Euphranta connexa*, and to some extent also by the lygaeid bug *Lygaeus equestris*. In a three-year study, seed predation significantly increased with plant population size in two out of three years. In the third year almost all seeds were consumed (Ågren et al. 2008).

Mutualistic interactions between insects and plants, such as pollination, are also potentially affected by insect search behavior and patch size. A significant relation between pollination or reproductive susceptibility and patch size is in general considered strongest when plants are pollen-limited. Pollen-limitation usually occurs as a result of self-incompatibility (i.e. when the plant cannot pollinate itself) or when the plant-pollinator interaction is highly specialized. In both cases, the plant depends completely on the insect´s capability in finding the plant (Aguilar et al. 2006). The perennial plant *Lythrum salicaria* is self-incompatible and therefore strongly depends on an array of flower-visiting insects, such as bumblebees, syrphid flies and butterflies, for successful reproduction. In a study from northern Sweden, seed set of *L. salicaria* was found to be positively correlated with plant population size, and a hand-pollination experiment revealed that seed production was strongly pollen-limited (Ågren 1996).

Induced resistance and defense
Since herbivores may have strong impacts on plant performance and fitness, plants commonly produce compounds to reduce or resist damage. The use of indirect defenses and the attraction of natural enemies to the herbivores have previously been discussed in this paper (see Herbivore-induced responses), but there are also many examples of plants producing direct defenses following herbivory. Induced responses are usually divided into two main categories. First, induced resistance occurs when plants reduce survival, reproductive output and preference of herbivores (Karban & Baldwin 1997). This response was demonstrated in a study of the perennial plant *Filipendula ulmaria* conducted in an archipelago in northern Sweden. The study area is subject to an ongoing land lift, leading to a number of islands of

different successional stage. It was shown that levels of tannins and phenolic compounds in *F. ulmaria* were closely correlated to island height, thus reflecting the historic exposure to the leaf-feeding beetle *Galerucella tenella*. For the leaf beetles, the increased levels of defensive compounds resulted in lower egg densities and leaf feeding (Stenberg et al. 2006) and also an increased diet breadth (Stenberg et al. 2008). Induced defenses, on the other hand, are responses that decrease negative fitness connected to herbivore attack. This type of response may not necessarily affect herbivore fitness and performance at all. The type of defense can also vary, ranging from defenses that reduce damage to defenses that increase tolerance (Karban & Baldwin 1997). An example of a plant using an induced defense in response to herbivory is *Asclepias syriaca*. The plant contains a viscous latex secretion which is exudated when an herbivore starts feeding on the leaves. This secretion serves as a defense, especially for generalist herbivores which avoid feeding on the plant (Dussourd & Eisner 1987).

A   B
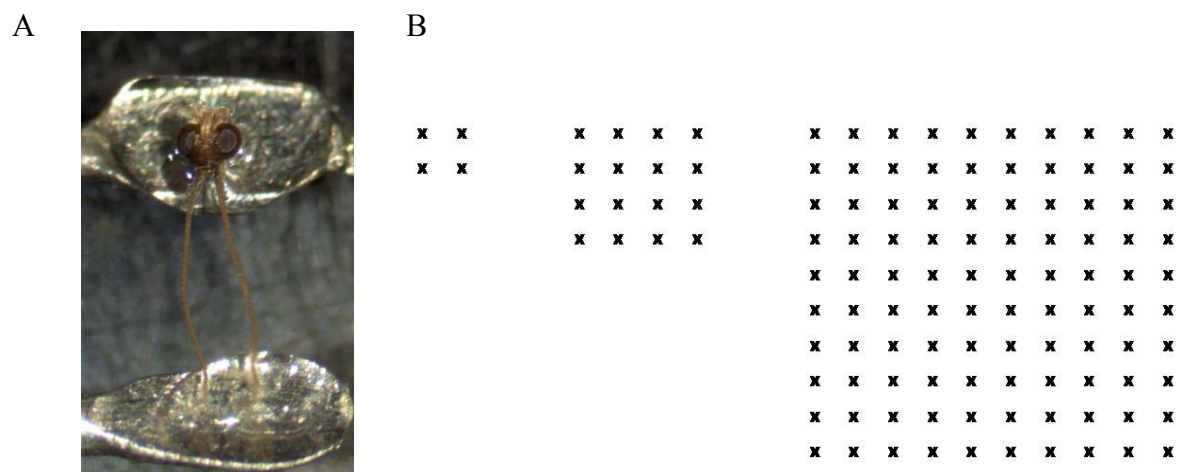
Figure 6. (A) EAG-preparation of head and antennas of a male *Plodia interpunctella*. Photo by Petter Andersson. (B) Setup for field experiment.

My project

As we have seen, there is a gap in our knowledge about the scaling of olfactory information to patch size. We know that the visual impression of a patch scales to the patch diameter, but how does the olfactory impression of a patch vary in a patch size gradient? Can the scaling of olfactory information explain observed immigration rates of olfactory searching insects? What is the role of olfactory search in plant-insect interactions? As an overall objective, my project will deal with olfactory information and search behavior of insects. As a first step, I

will try to understand the scaling of olfactory information in relation to patch size. This work will involve measuring odor dispersion under field conditions. As this part of the project aims at understanding general principles about the movement and dispersion of molecules under field conditions, I will not use plant odors as these usually occurs at very low concentrations. Instead, I will perform an experiment with synthetic sex pheromones of moths and measure pheromone concentrations using an electroantennogram (EAG). The EAG-method implies using insect antennas and measure electronic impulses as pheromone filaments hits the antennae (Fig. 6A). In the field, I will establish patches of various sizes consisting of evenly distributed dispensers loaded with moth sex pheromones (Fig. 6B). This setup has the intention to mimic a patch consisting of host plants and I will measure the attractive distance downwind from the patch.

As the next step, I will quantify immigration of olfactory searching insects. This will be done by studying experimental plant populations. As the study system, I will work with common figwort *Scrophularia nodosa*, which is a plant associated with several insect herbivores. *S. nodosa* has a highly characteristic odor and the weevils *Cionus scrophulariae* and *C. tuberculosus* (see front cover of this paper) are of special importance as they are attracted to plant odor and feed and oviposit on the plant. Both adults and larvae of *Cionus* spp. mainly feed on leaf tissue but also on flower buds and may have strong impact on plant fitness (Read 1977). In the lab, I will investigate primary and secondary attraction of the weevils to host plants. Further, I will repeat the experimental setup from the pheromone experiment, exchange pheromone dispensers to *S. nodosa* plants (Fig. 6B), and observe immigration of weevils into patches. The colonization rates of weevils will then be compared with observed scaling relations from the pheromone experiment.

Attack from herbivores may change the odor emission of plants and this emission can potentially attract natural enemies. Larvae of both *C. scrophulariae* and *C. tuberculosus* are frequently attacked by hymenopteran parasitoids. My work will include studying the induced odor emission of *S. nodosa*, and also examining the olfactory search of parasitoids. Further, *S. nodosa* is specialized to pollination of wasps, such as *Dolichovespula sylvestris* (Devos 1983). In the research field of pollination ecology, flower-visiting pollinators are traditionally considered to be guided by visual cues (Raguso 2008). However, I have the intention to investigate the role of olfactory search in the pollination process of *S. nodosa*, both from lab experiments and field studies.

Acknowledgements

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