

# **Dispersal Ecology of Insects Inhabiting Wood-Decaying Fungi**

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# Introduction

Dead wood has become an increasingly scattered resource in the managed landscape, with the result that many organisms depending on this substrate have become threatened (Gärdenfors 2000; Siitonen 2001). Distribution patterns of several insects associated with dead wood indicate that they are weak dispersers (Økland 1994; Nilsson & Baranowski 1997; Ranius 2000; Siitonen & Saaristo 2000), but few studies have directly assessed the dispersal ability of these species (but see Ranius & Hedin 2001). This thesis is based on investigations in which key features of the dispersal biology of wood-living insects were studied and related to spatial distribution patterns of these species observed in the field.

## Insect movement by flight

Insect movements by flight can be divided into two types (vegetative and migratory) with distinct behavioural characteristics (Dingle 1996; Woiwod et al. 2001). Vegetative movements are essentially explorations for certain resources (e.g. food, shelter, mates, oviposition sites etc.), and are interrupted as soon as the targeted resources are encountered (Dingle 1996; Woiwod 2001). Often, vegetative movements are station-keeping, retaining the individual within its habitat (trivial flights) (Hansson et al. 1992; Dingle 1996; Woiwod et al. 2001). Movements that take an individual away from its previous habitat to search for a new one may be either vegetative, then termed ranging (Dingle 1996), or migratory (Kennedy 1961). A migrating insect does not at first respond to the stimuli from new habitats and the flight is characteristically prolonged, straightened out, and usually undertaken in a specific phase of the life cycle (Kennedy 1961; Hansson et al. 1992; Dingle 1996). However, migratory and vegetative movements often grade into each other so that the same insect may undertake both migratory and vegetative flights (Hansson et al. 1992; Dingle 1996). Dispersal, on the other hand, is a term that has been used broadly to describe movements between habitat patches, without reference to the underlying movement behaviour (e.g. Weisser 2001), (for criticism of this definition of dispersal, see Dingle 1996). In this thesis I generally use the term dispersal to describe insect movements between habitat patches. The term migration is only used for cases where there was clear evidence of migratory behaviour as defined above (e.g. Paper II).

Several factors influence an insect's ability to disperse and colonise new habitats. A good coloniser should 1) be physically capable and willing to take-off and emigrate from a habitat patch, 2) be able to fly far enough to reach a new habitat, 3) be able to locate the new patch, and 4) be able to build up a new population once at the new habitat. A prerequisite for the ability to disperse is a functional flight apparatus. However, many insects show reductions in their flight wings (Roff 1990; Roff & Fairbairn 1991; Wagner & Liebherr 1992), or lack functional flight muscles (Fairbairn & Desranleau 1987; Kaitala 1988; Solbreck, 1986) and are thus physically incapable of flight. Insects also vary both in their flight threshold, i.e. their willingness to take flight (Fairbairn & Desranleau 1987;

Fairbairn & Roff 1990), and in the duration of their flights (Davis 1984; Palmer & Dingle 1989). Migrating insects often fly high above ground downwind and are then carried considerable distances (Solbreck 1980; Gatehouse 1997). To locate a new habitat, flying insects often use a combination of visual and olfactory stimuli (e.g. Hardie et al. 2001). Many insects disperse before mating and reproductive maturation (Johnson 1969). It is then essential for them to locate not only a new habitat but also a mate. In many insects mate-finding is facilitated by the emission of a sexual or aggregation pheromone after arrival at a new patch (Cardé & Baker 1984). Other insects use communication by sound to attract mates to the new habitat (Hoy & Robert 1996).

A good coloniser should not only be able to effectively disperse and locate a suitable new habitat, but also to rapidly build up a population once there (Macarthur & Wilson 1967; Dingle 1972; Safriel & Ritte 1980). Thus, a high rate of reproductive output shortly after arrival at the new patch should be advantageous for a colonist (Southwood 1977; Palmer & Dingle 1989). However, one of the most commonly described costs associated with dispersal in insects is lowered fecundity (Roff & Fairbairn 1991; Rankin & Burchsted 1992; Zera & Denno 1997). Migratory insects therefore show different adaptations to compensate for this cost. Many insects first migrate and then histolyse their flight muscles, using the resources thereby released for egg production (Nair & Prabhu 1985; Zera & Denno 1997), or produce smaller eggs (Solbreck 1986). These measures allow egg production to be concentrated in a short period just after migration (Solbreck 1986; Solbreck et al. 1990). Thus, in some colonist species, selection pressures have resulted in life history traits that maximise both movement ability and reproductive output (Rankin & Burchsted 1992). Simberloff (1981) found that a high proportion of the insect species that successfully colonised mangrove islands were such “super colonists”, i.e. they had both a high immigration rate and a low risk of extinction during their first season in the new habitat.

### **Habitat, dispersal and conservation**

The distribution of suitable habitats in time and space has long been considered the key to the evolution of dispersal strategies, and unpredictable habitats are expected to host species with greater dispersal and colonisation abilities than more predictable environments (Southwood 1962, 1977; Wilson 1995). This is because substantial costs are associated with dispersal (Rankin & Burchsted 1992), so there are generally potent selective forces against dispersal in stable and spatially continuous habitats (Southwood 1977; Wilson 1995). The strongest empirical support for this theory has been provided by studies of wing-dimorphic species, in which ephemeral habitats have been found to harbour a larger proportion of long-winged species (Wagner & Liebherr 1992; Denno et al. 2001).

Human activities often tend to make habitats less predictable in time and space (Gaston 1994), by both fragmenting them, and disturbing the remaining habitat patches. Thus, many species that are adapted to stable, natural conditions are likely to have too weak dispersal abilities to persist in intensively managed

landscapes. Dispersal in relation to habitat distribution is therefore also of great importance in the field of spatial ecology. In a classical metapopulation there is a moderate rate of dispersal between the patches, so extinctions of local populations are compensated by colonisations (e.g. Hanski 1997). If the dispersal rates decrease as an effect of, for example, habitat fragmentation, the whole metapopulation will be doomed to extinction. Although classical metapopulations may be uncommon in nature (Doak & Mills 1994; Harrison & Taylor 1997; Thomas 2001), this theory highlights the importance of dispersal for the long-term survival of species. Dispersal enables the colonisation of new habitat patches (or those of extinct populations) and lowers extinction risks via rescue effects (Stacey et al. 1997). In addition, dispersal promotes gene flow, which can counteract loss of genetic variability and inbreeding (e.g. Hartl & Clark 1997).

### **Dispersal ability of saproxylic insects**

Saproxylic insects are species that depend on dead wood during some part of their lifecycle (Speight 1989). Saproxylic species account for much of the species richness in Fennoscandia (Hanski & Hammond 1995). In Sweden, for instance, about 1,000 species of beetles are saproxylic (Esseen et al. 1997): almost a quarter of the total number of beetle species found in the country (Lundberg & Gustafsson 1995). However, modern forestry has led to a decline in most kinds of dead wood, by as much as 90% or more in managed forests (Fridman & Walheim 2000; Siitonen 2001), with the consequence that many species have become threatened (Gärdenfors 2000; Rassi et al. 2000). In addition, a large proportion of the species now present may continue to decline and in the future become extinct (Hanski 2000). Knowledge about the dispersal ability of these species is essential to understand why they have become threatened, and what measures that are necessary to preserve them.

Habitat predictability is probably an important indicator of the dispersal ability of saproxylic insects. Evidence for this hypothesis was provided by Wikars (1997), who studied morphological traits related to the dispersal ability of three buprestid beetles associated with habitats differing markedly in persistence. The fire-adapted beetle *Melanophila acuminata* De Geer had the lowest wing load and largest flight muscle mass, whereas the reverse was true for *Phaenops formaneki* Jacobson, which inhabits pines on stable bogs (Wikars 1997). *Phaenops cyanea* (Fabricius), which is associated with habitats of intermediate persistence, was also intermediate with respect to both of these morphological characters (Wikars 1997). Further evidence was provided by Nilsson & Baranowski (1997), who sampled red-listed species in two types of substrate differing in stability: hollow beeches (more stable) and downed dead beeches (less stable). They found a higher number of red-listed species in hollow trees in nearly primaeval stands than in formerly managed stands, but no difference in the number of red-listed species associated with downed logs in the two types of stand. They concluded that the differences in these patterns were probably due to the species inhabiting old hollow trees having poorer dispersal abilities compared with those in downed logs.

Many studies of the dispersal ecology of saproxylic insects have been carried out on bark beetles. These beetles depend on substrates (recently dead or weakened trees) that occur unpredictably in time and space, that can usually be used for breeding in just one breeding season, and are scattered in the landscape. Accordingly, bark beetles have been found to be good dispersers that can cover distances of many kilometres in flight (Botterweg 1982; Forsse & Solbreck 1985; Forsse 1989; Jactel & Gaillard 1991). The genetic structure of *Ips typographus* (L.) also suggests that this bark beetle is a good disperser (Stauffer et al. 1999).

Old tree hollows, on the other hand, comprise a particularly stable type of dead wood substrate that could be expected to host saproxylic species with poor dispersal abilities (Nilsson & Baranowski 1997). One such insect that has been studied recently is *Osmoderma eremita* Scopoli, a threatened saproxylic beetle associated with hollow oaks (Ranius & Nilsson 1997; Ranius 2000; Ranius 2001; Ranius & Hedin 2001). Using a mark-recapture experiment and a simulation model, Ranius & Hedin (2001) found that the majority of *O. eremita* individuals remain in the same oak tree for their entire lives. Dispersing beetles were recaptured at distances ranging between 30 and 190 m from the release point (Ranius & Hedin 2001). The occupancy of *O. eremita* per tree was found to be higher in large stands than in smaller stands, but there was no correlation between the occupancy per stand and the isolation of stands (Ranius 2000). Based on these results it was suggested that *O. eremita* has a metapopulation structure within stands, and a poor dispersal ability that makes it vulnerable to habitat fragmentation (Ranius 2000; Ranius & Hedin 2001). In a later study, Ranius (2002) found evidence suggesting that two other saproxylic beetles associated with hollow oaks, *Tenebrio opacus* Duftschmid and *Elater ferrugineus* L., are even more vulnerable to habitat fragmentation than *O. eremita*.

Many types of logs, snags and stumps, and the microhabitats associated with them are intermediate in terms of predictability between recently dead trees and old tree hollows. Several authors have presented indirect evidence that some of the insects inhabiting these substrates are weak dispersers.

In North America, the tenebrionid beetle *Bolitotherus cornutus* (Panzer), which inhabits fruiting bodies of *Fomes fomentarius* (L.:Fr.) and *Ganoderma applanatum* (Pers.), has been studied by several authors. Kehler & Bondrup-Nielsen (1999) found patterns of isolation by distance in the occurrence of this beetle at three different scales: between fruiting bodies within clusters of trees, between clusters of trees, and between forest patches. Although *B. cornutus* is capable of flight (Teichert 1999), mark-recapture studies have indicated that its movement between trees is rather limited (Heatwole & Heatwole 1968; Whitlock 1992).

Nilsson (1997b) carried out a mark-recapture study on the tenebrionid beetle *Bolitophagus reticulatus*, which inhabits fruiting bodies of the wood-decaying fungus *F. fomentarius*, within a forest site of about 50 x 200 m. He found that beetles moving between trees preferred to settle on trees close by, and suggested that they often moved by walking (Nilsson 1997b). Rukke & Midtgaard (1998) and Sverdrup-Thygeson & Midtgaard (1998) found isolation patterns in the occurrence of this beetle between trees within forest sites, but no such patterns

between groups of trees and forest islands (Rukke & Midtgaard 1998). Furthermore, the average incidence of *B. reticulatus* per tree within a fragmented forest was shown to be lower than in a continuous one (Rukke & Midtgaard 1998; Sverdrup-Thygeson & Midtgaard 1998). Based on these trends, several authors have suggested that *B. reticulatus* has a relatively weak dispersal ability (Nilsson 1997b; Rukke & Midtgaard 1998; Sverdrup-Thygeson & Midtgaard 1998; Knutsen et al. 2000). However, in a recent study it was suggested that the dispersal ability of *B. reticulatus* may have been underestimated previously (Jonsson et al. 2001).

Colonisation rates of insects inhabiting *F. fomentarius* and *Fomitopsis pinicola* (Schwartz:Fr.) at different distances from a source area were studied by Jonsell et al. (1999). They found several beetle species to be more effective in colonising distant patches than species of flies and parasitic wasps, and beetles belonging to the genus *Dorcatoma* (Anobiidae) seemed to be better colonisers than beetles of the family Cidae.

Different authors have found various saproxylic insects to be mainly associated with stable, long continuity habitats (Økland 1994; Nilsson & Baranowski 1997; Siitonen & Saaristo 2000; Jonsell & Eriksson 2001; Jonsson et al. 2001; Jonsell & Nordlander 2002). Such patterns could have been caused by low dispersal abilities, which makes colonisation of new habitat patches slow. Siitonen & Saaristo (2000) found that *Pytho kolwensis* (Coleoptera: Pythidae) was restricted to spruce mire forests with a high density and long continuity of dead wood. Since the microhabitat conditions did not seem very specific for this species, the authors suggested that *P. kolwensis* was restricted to long continuity sites because it has a poor dispersal ability (Siitonen & Saaristo 2000). Similarly, Økland (1994) found that several species of Mycetophilidae (Diptera) were associated with long continuity forests, and suggested this was due to poor dispersal ability.

*Oplocephala haemorrhoidalis* (F.) (Coleoptera: Tenebrionidae) and *Scardia boletella* (F.) (Lepidoptera: Tineidae), both inhabiting fruiting bodies of *F. fomentarius*, was found to be most common at sites having a high density of substrate assumed to have been available continuously for more than 100 years (Jonsson et al. 2001; Jonsell & Nordlander 2002). The cited authors also found *Cis quadridens* Meille (Coleoptera: Cidae) to be associated with sites with a high density of suitable substrate (but not with continuity). All three species were present in fruiting bodies that differed markedly in various respects, such as sun exposure, size, and successional stage (Jonsell et al. 2001; Jonsson et al. 2001), implying that suitable fruiting bodies would also have been available in the managed forests. It was therefore suggested that these species have particularly weak colonisation abilities (Jonsson et al. 2001; Jonsell & Nordlander 2002). Another species inhabiting fungal fruiting bodies that seem restricted to old-growth conditions is *Dorcatoma minor* Zahradnik (Coleoptera: Anobiidae) (Jonsell & Eriksson 2001; Jonsell & Nordlander 2002).

Komonen et al. (2000) studied the guild of insects inhabiting fruiting bodies of *Fomitopsis rosea* (Alb. & Schwein.: Fr), a fungus that mainly occurs in old growth boreal forests in Fennoscandia. These authors found that both the fungus and an associated tineid moth, *Agnathosia mendicella* (Denis & Schiffermüller), were less

common in forest fragments than in continuous forests. The tachinid fly, *Elfia cingulata* (Robineau-Desvoidy), which parasitises the moth, was completely absent in 12-32 year old forest fragments (Komonen et al. 2000). The observed patterns could be due to these species having poor colonisation abilities.

To conclude, very few authors have directly studied the dispersal ecology of rare saproxylic insects. However, several studies have found distribution patterns indicating that some of these insects may have poor dispersal abilities, although such patterns may be due to other mechanisms in some cases. For example, Nordén & Appelkvist (2000) argued that many of the insect species associated with long continuity stands probably have specific microhabitat demands that are only fulfilled in old-growth forests. Other authors have shown that many red-listed saproxylic insects can colonise clear-cuttings if suitable substrate is left, and have suggested that these species do not require old-growth forests to survive in the landscape (Ahnlund & Lindhe 1992; Kaila et al. 1997; Martikainen 2001). To evaluate the extent to which dispersal limits the occurrence of saproxylic species in managed landscapes, more direct studies of their dispersal ecology are needed.

### **Scope of this thesis**

The overall aims of the studies presented in this thesis were to increase our knowledge concerning the dispersal ecology of saproxylic insects, and to get a better understanding of how it relates to their spatial distribution in nature. My general approach has been to compare key aspects of dispersal biology in species that differ in distribution patterns.

My study system has been insects inhabiting fruiting bodies of the polypore fungi *F. fomentarius* and *F. pinicola*. The predictability of these kinds of substrate is considered intermediate between those of old tree hollows and recently dead trees. We would therefore expect them to host insects with intermediate dispersal and colonisation abilities (Jonsell et al. 1999). However, some reported distribution patterns indicate that these species differ in their colonisation abilities (Jonsson et al. 2001; Jonsell & Nordlander 2002). For example, it has been suggested that the tenebrionid beetle *O. haemorrhoidalis* has weaker dispersal ability than *Bolitophagus reticulatus* (Jonsson et al. 2001). In the first paper (I) included in this thesis we compared the genetic structure within and between localities of these two species. The main aims were to determine whether *O. haemorrhoidalis* and *B. reticulatus* differ with respect to gene flow between their respective populations, and to examine their levels of genetic variability. In the next study (II) I compared a number of different life history traits between *O. haemorrhoidalis* and *B. reticulatus* that should influence their colonisation abilities. The traits compared were: presence of flight wings and flight muscles, willingness to take off, flight duration, and the size and number of mature eggs in the females' abdomens.

Many insects disperse before mating and reproductive maturation (Johnson 1969). It is then not only necessary for them to locate a new patch while dispersing, but also to find a mate. Among many insects, pheromones are used to facilitate mate-finding (Cardé & Baker 1984). In the study described in Paper III, I



investigated whether some representatives of the beetle genera *Cis* (Coleoptera: Cisidae) and *Dorcatoma* (Coleoptera: Anobiidae) inhabiting *F. fomentarius* and *F. pinicola* use pheromones to communicate with conspecific insects. The results indicate that these two species rely on two different strategies to find a mate. Using a simulation model (Paper IV), I then compared the efficiency of these two strategies of mate-finding at various densities of conspecific insects and substrates. The primary goal was to find out if species with different mate-finding strategies differ in sensitivity to habitat fragmentation and are likely to experience Allee effects at different population densities.

## Study system

### *Biology of O. haemorrhoidalis and B. reticulatus*

In studies described in the first two papers included in this thesis (I & II) I compared different aspects of the dispersal ecology of the threatened tenebrionid beetle *O. haemorrhoidalis* and its common relative *B. reticulatus*. Both species feed and breed exclusively inside fruiting bodies of the polypore fungus *F. fomentarius* (Palm 1951, 1959), which in Sweden predominantly grows on decaying birches. In areas where both species occur, they are often found together in the same fruiting bodies and often in high numbers (Palm 1951, 1959). They have overlapping generations and hibernate both as adults and larvae (Nilsson 1997a). *Bolitophagus reticulatus* can reach a high age, surviving up to at least three winters as an adult (Nilsson 1997a). *Oplocephala haemorrhoidalis* is categorised as Near Threatened (NT) on the Swedish red-list (Gärdenfors 2000), whereas *B. reticulatus* is not red-listed.

*Oplocephala haemorrhoidalis* has been considered to be associated primarily with sun-exposed fruiting bodies (Jonsson et al. 2001). However, no clear association of *O. haemorrhoidalis* with sun-exposed fruiting bodies per se was detected in inventories published by Jonsell et al. (2001) and Jonsson et al. (2001), although an association was found with fruiting bodies high above ground, indicating that sun-exposure may have some importance. In any case, *O. haemorrhoidalis* seems to be able to utilise fruiting bodies in a variety of conditions with respect to, for example, size, successional stage, exposure and height above ground, as well as stem diameter of the inhabited trees (Jonsell et al. 2001; Jonsson et al. 2001). The occurrence of *B. reticulatus* has been reported to be positively correlated with sun exposure (Rukke & Midtgaard 1998), and with the number and size of brackets on the host tree (Midtgaard et al. 1998; Rukke & Midtgaard 1998). Jonsson et al. (2001) found that the microhabitat association of *B. reticulatus* was slightly less specific than that of *O. haemorrhoidalis*.

*Oplocephala haemorrhoidalis* is primarily restricted to forest stands and wooded pastures with a high density of suitable breeding substrate that have probably been available continuously for a long time (Jonsson et al. 2001; Jonsell & Nordlander 2002). *Bolitophagus reticulatus*, on the other hand, is also common in many forests with lower density and shorter continuity of suitable substrate (Jonsson et al. 2001; Jonsell & Nordlander 2002; Jonsell et al. unpubl.). However, within forest stands *B. reticulatus* occurs at higher densities where trees with

fruiting bodies stand close together (Nilsson 1997b; Rukke & Midtgaard 1998; Sverdrup-Thygeson & Midtgaard 1998).

### *Biology of Cis and Dorcatoma*

In Papers III and IV, I consider the way in which some beetle species of the *Cis* (Cisidae) and *Dorcatoma* (Anobiidae) genera locate mates while flying. The studied species all inhabit fruiting bodies of either the wood-decaying fungus *F. fomentarius* or *F. pinicola* (Jonsell et al. 2001). Species of *Cis* often utilise the same fruiting body for more than one generation, whereas species of *Dorcatoma* probably spend only one generation in each fruiting body (Palm 1951). Results from a colonisation experiment indicated that species of *Dorcatoma* are better colonisers than species of *Cis* (Jonsell et al. 1999). In inventories of different forest sites, *Cis quadridens* Meille was found at higher incidence per fruiting body where the substrate density was high (Jonsell & Nordlander, 2002). Accordingly, *C. quadridens* is categorised as near threatened (NT) on the Swedish red list (Gärdenfors 2000).

Two species that specialise on *F. pinicola*, *Cis glabratus* Meille and *C. quadridens*, are specifically attracted to the odour of their host fungus (Jonsell & Nordlander 1995). Similarly, Guevara et al. (2000a) found that several other cisid beetles were able to discriminate between odours from host and non-host species, and even between different successional stages of the fruiting body (Guevara et al. 2000b). The anobiid beetles, *Dorcatoma punctulata* Muls & Rey and *D. robusta* Strand also showed tendencies to be attracted to the odour of their hosts, but the trends were not statistically significant (Jonsell & Nordlander 1995). However, both *Dorcatoma* species were caught in considerable numbers in traps located beneath living fruiting bodies of their host (Jonsell & Nordlander 1995). The cited authors therefore suggested that these insects might have been attracted by pheromones released by conspecific individuals that were already present on the fungus.

## **Results and discussion**

### **Genetic structure of *O. haemorrhoidalis* and *B. reticulatus* (Paper I)**

In the first paper included in this thesis (I), we studied the genetic structure of *O. haemorrhoidalis* and *B. reticulatus* with allozyme and RAPD genetic markers. Analysis of genetic structure can give information about dispersal rates between habitat patches, provided there is equilibrium between gene flow and genetic drift (Wright 1943; Weir & Cockerham 1984; Slatkin 1985). Although the use of genetic structure analysis for estimating gene flow has been criticised because the underlying assumptions are unrealistic (Whitlock & McCauley 1999), genetic differentiation is usually strongly influenced by dispersal (Peterson & Denno 1998; Bohonak 1999). We found a high level of genetic differentiation between sites in *O. haemorrhoidalis*, whereas it was considerably weaker in *B. reticulatus*.

Furthermore, the RAPD-marker analyses suggested a state consistent with what would be expected at equilibrium between gene flow and genetic drift (Hutchison & Templeton 1999) in *B. reticulatus*, and a state close to equilibrium in *O. haemorrhoidalis*. Similar trends were indicated by the allozyme-markers. As population sizes were probably similar between the species at the sites sampled, the observed differences in genetic structure have probably been largely shaped by differences in gene flow. Thus, our results suggest there were considerably lower levels of gene flow between the populations of *O. haemorrhoidalis* in the past than between those of *B. reticulatus*.

A closer look at the RAPD-data revealed a steeper increase in genetic differentiation with distance between a few neighbouring sites than when all inhabited sites were included in the analysis. Therefore, it is possible that a new equilibrium between gene flow and drift is developing within this area, following fragmentation, which has not had enough time to fully develop over larger geographic distances. This indicates that *O. haemorrhoidalis* may have experienced a recent decrease in gene flow levels due to habitat fragmentation. For *B. reticulatus*, on the other hand, levels of genetic differentiation between inhabited sites were generally low, suggesting high levels of gene flow.

Between trees, within sites, we found the levels of genetic differentiation to be highly variable in both *O. haemorrhoidalis* and *B. reticulatus*. Whitlock (1992) studied the genetic structure and dispersal of the related fungivorous beetle *Bolitotherus cornutus* (Panzer) at a similar scale to the one we investigated. He showed that colonisation and deterministic extinctions increased genetic differentiation between patches to greater levels than those seen in populations at equilibrium between genetic drift and gene flow. The pattern of genetic differentiation between trees in our study could thus have been caused by founder events rather than by restricted gene flow. The fact that pairwise estimates of  $F_{ST}$  were low when relatedness estimates were around zero supports this hypothesis. It is also consistent with the results of Knutsen et al. (2000), who suggested that differences in genetic differentiation between trees in *B. reticulatus* were likely to have been caused by differences in the numbers of founders.

Small, isolated populations are likely to lose genetic variability due to genetic drift. In our study, the level of genetic variability in the allozymes was not particularly low in either species, both of which showed heterozygosity levels similar to average levels for insects compiled from the literature by Nevo (1978). However, it seems likely that levels of genetic variability will decrease in *O. haemorrhoidalis* in the future because of lag effects following habitat fragmentation.

## **Colonisation ability of *O. haemorrhoidalis* and *B. reticulatus* (Paper II)**

A number of life history traits that should influence the colonisation ability of an insect were compared between *O. haemorrhoidalis* and *B. reticulatus* in studies reported in Paper II. More specifically, the presence of flight wings and flight muscles was examined by dissecting individuals, willingness to take off was tested

in a field experiment, duration of flight was tested in a flight-mill study, and the number and size of mature eggs in females were studied by dissection.

The results of the dissections indicated that both *O. haemorrhoidalis* and *B. reticulatus* usually have fully developed flight muscles as young adults, but they histolyse later and are therefore usually absent in older specimens. Mature eggs are almost absent in young females, but more common in samples including also older females. Thus, it is likely that both *O. haemorrhoidalis* and *B. reticulatus* generally conform to the oogenesis-flight syndrome, with dispersal preceding reproduction (Johnson 1969). Overall, fewer individuals of *O. haemorrhoidalis* than *B. reticulatus* had flight muscles.

The number of eggs was larger in *B. reticulatus* than in *O. haemorrhoidalis*. This indicates that *B. reticulatus* has a higher potential rate of population increase than *O. haemorrhoidalis*, which should be favourable during colonisation (Southwood, 1977; Palmer & Dingle 1989). However, despite having smaller bodies, the eggs of *O. haemorrhoidalis* beetles were twice as large as those of *B. reticulatus*. The large eggs of *O. haemorrhoidalis* may be advantageous under crowded conditions with high levels of competition, as the larvae that hatch from them are also larger. Furthermore, our results indicate that *O. haemorrhoidalis* females invest more in egg production than do females of *B. reticulatus*. The lower incidence of flight muscles in *O. haemorrhoidalis* may allow for this reproductive investment.

*Bolitophagus reticulatus* was considerably more willing to take off than *O. haemorrhoidalis*, both in the take-off experiment and in the flight-mill study. However, the flight-mill experiment showed that both species, especially *O. haemorrhoidalis*, are very strong fliers once on their wings. The total duration of flight of both species was of the same magnitude as corresponding figures for certain saproxylic pest species recognised as good fliers (Solbreck 1980; Forse 1989; Jactel & Gaillard 1991; Akbulut & Linit 1999). Calculations of flight distances suggest that the median flier of *O. haemorrhoidalis* is able to fly more than 12 kilometres, whereas the median flier of *B. reticulatus* flies almost seven kilometres. *Oplocephala haemorrhoidalis* generally tended to make fewer flights, but of longer duration, than *B. reticulatus*. It seems very likely that many of the flights of *O. haemorrhoidalis* and some flights of *B. reticulatus* were migratory in character, according to criteria set by authors such as Dingle & Evans (1987), Rankin et al. (1994) and Kent & Rankin (2001). In addition, results of the take-off study suggest that at least some individuals of *B. reticulatus* are able to travel long distances downwind by flying above the tree canopies. This is a common pattern among migrating insects (Solbreck 1980; Gatehouse 1997).

The life history traits of *O. haemorrhoidalis* indicate that it is primarily adapted to life in a relatively stable environment, where dispersal and colonisation by flight is seldom needed (Fig. 1a). This could explain why *O. haemorrhoidalis* occurs mainly at sites with both a high density and long continuity of suitable breeding substrates (Jonsson et al. 2001; Jonsell & Nordlander 2002). The deciduous forest phase following forest fires and wooded pastures are types of habitat where large densities of deciduous trees with fruiting bodies of *F. fomentarius* are often present and *O. haemorrhoidalis* has probably thrived in the

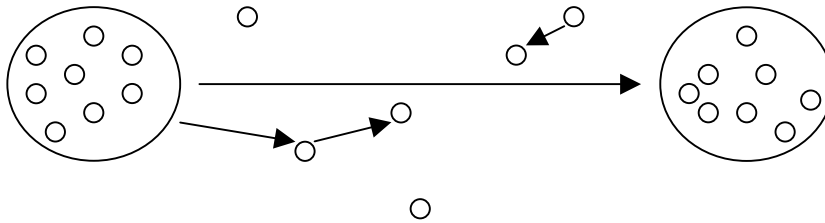
A



Large, stable patch  $\Rightarrow$  Dispersal by flight less often, but  $\Rightarrow$  *O. haemorrhoidalis* then of long duration. Colonisation of new patches less often.

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B



Both large, stable, and small, unstable patches.  $\Rightarrow$  Dispersal by flight more often, flights both of long and of shorter duration. Colonisation of new patches more often.  $\Rightarrow$  *B. reticulatus*

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Fig. 1. Principal sketch showing the kinds of habitat that I suggest *O. haemorrhoidalis* (A) and *B. reticulatus* (B) are adapted to. In (A) only patches with a high density of substrate is considered habitat (large circle), in (B) both high density patches and more isolated, single trees are considered habitat (large and small circles).

past (Esseen et al. 1997; Jonsson et al. 2001). Such habitats have always been more or less patchily distributed in the landscape. Therefore, occasional long-distance dispersal was presumably necessary to colonise new habitats. This might explain the long flight durations of *O. haemorrhoidalis* once on its wings. Similarly, Forsse (1989) found a high incidence of long migratory flights in bark-beetle species utilising substrates that often occur in large, but widely scattered patches.

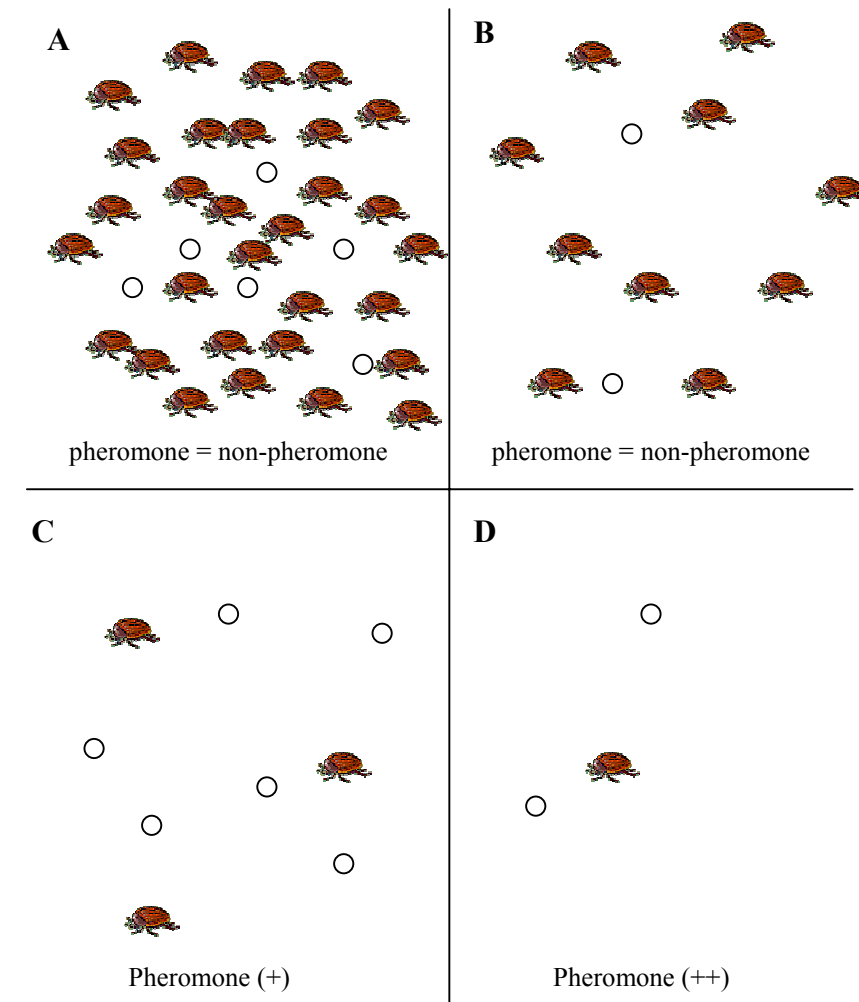
I suggest that *Bolitophagus reticulatus* is better adapted to colonise single scattered trees with fruiting bodies than *O. haemorrhoidalis* (Fig. 1b). This may explain why *B. reticulatus* is common also in many managed forests (Jonsell et al. manuscript). A higher proportion of *B. reticulatus* beetles had flight muscles, they were more prone to take off, and the females had more (but smaller) mature eggs

in their abdomens than *O. haemorrhoidalis*. In addition, its tendency to make many flights of shorter duration suggests that it is well adapted to fly around within a forest searching for single trees with fruiting bodies. However, within sites one or a few hectares large, *B. reticulatus* tends to be more common where trees with suitable fruiting-bodies are located close to each other (Nilsson 1997b; Rukke & Midtgaard 1998; Sverdrup-Thygeson & Midtgaard 1998). Several authors have suggested that these small-scale isolation patterns indicate that *B. reticulatus* has a relatively poor dispersal ability (Nilsson 1997b; Rukke & Midtgaard 1998; Sverdrup-Thygeson & Midtgaard 1998; Knutsen et al. 2000). My results, however, clearly show that most *B. reticulatus* beetles would be able to fly far beyond even the most isolated of the trees in the cited studies.

### **Pheromones among beetles inhabiting wood-decaying fungi (Paper III)**

Many insects disperse before reproductive maturation and mating (Johnson 1969). To successfully colonise a new habitat it is not only necessary for such insects to locate a suitable site while flying, but also to find a mate. Pheromones are commonly used to facilitate mate-finding among insects (Cardé & Baker 1984). Therefore, as described in Paper III, we studied the presence of pheromones in a few species of beetle inhabiting *F. fomentarius* and *F. pinicola*. This was done in a field experiment by comparing catches in traps baited with either females or males together with a piece of fruiting body, and traps with only a piece of fruiting body as controls. Although responses to acoustic signals cannot be completely excluded in beetles (Hoy & Robert 1996), we interpreted any attraction observed as being odour-mediated. The results clearly demonstrated the presence of a female sex pheromone attracting males of *D. robusta*, a species inhabiting fruiting bodies of *F. fomentarius*. Since only two individuals (both females) of the related species, *D. punctulata*, were caught in the experiment, no clear conclusions could be drawn about whether it used pheromones like its relative. However, as only females of this species were attracted to host odours in an experiment by Jonsell & Nordlander (1995), we suggest that *D. punctulata* possesses a similar pheromone system to *D. robusta*. Functionally similar pheromones have also been described in other anobiid species (Kuwahara et al. 1975, Levinson & Levinson 1987, White & Birch 1987).

The trap catches of *C. glabratus* did not indicate the involvement of any pheromone. However, both females and males of this species were caught in relatively high numbers in the traps baited with fruiting bodies of *F. pinicola* both in our study and in the investigation by Jonsell & Nordlander (1995). We therefore suggest that both sexes of *C. glabratus* fly and locate breeding substrates by their odour, and once at a new substrate they find mates without the aid of a long-range pheromone. A similar strategy of mate-finding has been suggested for other species of Cisidae (Guevara et al. 2000a,b) as well as for the bark beetle *Tomicus piniperda* (L.) (Byers 1991). The trap catches of *C. Jacquemartii* and *B. reticulatus* were too low to draw any conclusions about the possible involvement of pheromones.



*Fig. 2.* Different types of simulated scenarios where the pheromone strategy for mate-finding (used by *Dorcatoma*) and the non-pheromone strategy (used by *Cisidae*) was compared. The most efficient strategy is marked with (+). The different scenarios are: (A) high relative density of females, high density of substrate, (B) high relative density of females, low density of substrate, (C) low relative density of females, high density of substrate, and (D) low relative density of females and low density of substrate. (Note that the relative densities of females and substrate shown in this figure does not exactly correspond to the simulated ones!).

## The efficiency of different mate-finding strategies (Paper IV)

Finding mates is an essential process for all animals, but it can be especially problematic for those living in heterogeneous environments. At high population densities sufficient mate-finding opportunities may be provided by random encounters of the opposite sex (e.g. Byers 1991), but as population densities decline an efficient mate-finding strategy becomes increasingly important. A low rate of mate encounter may cause Allee effects, in worst-case scenarios, leading to population extinction (Boyce 1992). With a simulation model, we compared the efficiency of the mate-finding strategies adopted by *Cisidae* and *Dorcatoma* at different densities of substrate and conspecific individuals (Paper IV). In the *Cisidae* both sexes are attracted to the odour of their host fungus, but no pheromone is used (non-pheromone strategy), whereas in *Dorcatoma* only the females are attracted to host odour, but having found a fruiting body they attract males with a sexual pheromone (pheromone strategy).

In the modelling, the movement paths of a specified number of insects were simulated simultaneously within an imaginary forest landscape with a specified density of trees supporting the host fungus. An individual was considered to have found a tree with fruiting bodies or, for males of *Dorcatoma*, a pheromone-emitting female, if the distance to it was smaller than a specified radius of attraction. The efficiency of the strategies was measured in terms of the median number of time steps needed to reach 50 % mated females in 100 replicates. The comparisons were carried out at ranges of relative densities of insects and densities of trees with fruiting bodies corresponding to conditions that *C. quadridens* and *D. punctulata* commonly encounter in natural and managed forests (Jonsell & Nordlander 2002, Jonsson unpubl.). The attraction radius of trees with fruiting bodies (1.5 m) was set by calculating the effective attraction radius (EAR) (Byers et al. 1989) of *C. glabratus* towards fungal host odour (Jonsell & Nordlander 1995). As pheromones may have a larger attraction radius than host odours (Byers 1995; Hardie et al. 2001), we tested pheromone attraction radii of both 3 m and 1.5 m. For the non-pheromone strategy, we included the possibility that insects may leave a tree lacking potential mates after a while. We therefore estimated the optimal probability for insects leaving an empty tree for all combinations of relative female density and tree density, and included the derived figures in comparisons of the two strategies.

The non-pheromone strategy was equally efficient to the pheromone strategy, regardless of the attraction radius of the pheromone, when the relative female density was at the highest level (Fig. 2a,b), corresponding to the densities of *C. quadridens* found in natural forests. However, when the relative insect densities decreased the pheromone strategy became more efficient than the non-pheromone strategy (Fig. 2c,d). This indicates that the mate-finding strategy used by *Dorcatoma* is more efficient than that used by *Cisidae* at natural densities of *D. punctulata*. At the lowest relative insect densities (corresponding to densities of *C. quadridens* in managed forests) the advantage provided by the pheromone strategy was even larger. This indicates that species with a non-pheromone strategy are likely to be more sensitive to habitat fragmentation and experience Allee effects at higher population densities than species with a pheromone strategy. The low



efficiency of its mate-finding strategy under present conditions may be one reason for the rarity of *C. quadridens* in managed forests of Sweden.

## Implications for conservation

The studies outlined in this thesis have revealed great differences in the way various insect species inhabiting similar kinds of saproxylic substrate disperse and colonise new habitats. Firstly, I have shown that even rare saproxylic insects may cover several kilometres by flight, implying that large spatial scales should be considered in studies of population dynamics and in management strategies designed to conserve *O. haemorrhoidalis*, as well as many other threatened saproxylic insects. I suggest, however, that *O. haemorrhoidalis* is adapted to a life in a relatively stable environment where colonisation by flight is seldom needed. This could explain why *O. haemorrhoidalis* today occurs mainly at localities with a high density and long continuity of suitable substrate (Jonsson et al. 2001; Jonsell & Nordlander 2002), and why there is a high level of genetic differentiation between its populations. Other saproxylic insects that are primarily restricted to old growth conditions (e.g. Økland 1994; Siitonen & Saaristo 2000; Jonsell & Nordlander 2002) may also possess suites of life history traits that make exploitation of the scattered resources in managed forests inefficient.

To preserve *O. haemorrhoidalis* it is probably necessary to retain sites with a high density of substrate for extended periods to allow colonisation. A recent theoretical model suggests that leaving dead wood concentrated in certain localities is likely to be a more efficient strategy for preserving saproxylic species than spreading the substrate more thinly, but evenly, over larger areas (Hanski 2000). *Oplocephala haemorrhoidalis* clearly constitutes an example of a species that would benefit from such a concentrated conservation approach. However, considering the flight ability of this species it is not necessary to ensure that sites with a high density of suitable substrates are located absolutely adjacent to already populated sites.

Many insects disperse before mating and reproductive maturation (Johnson 1969). For successful colonisation it is essential for such insects to find a mate at the new site. I found that the strategy used to find a mate could be important for the efficiency of this process under fragmented habitat conditions and at low population densities. This might be one reason for the rarity of *C. quadridens* in managed forests. Consideration of mate-finding behaviour is therefore relevant to population viability analysis of saproxylic (and other) insects.

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