

Bees and Wasps (Aculeata) in Young Boreal Forests

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Cover: Female wasps of *Ectemnius cavifrons* (large) and *Crossocerus annulipes* (small) returning to their nest entrance after a foraging trip.
(photo: Jeremy Early)

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Abstract

In Sweden, forest stands younger than 15 years constitute more than 10% of the total forest area. The aims of the research described in this thesis were to investigate how bees and wasps (Aculeata) use young boreal forests as nesting and feeding grounds. Aculeates are sun-loving creatures and do not thrive in closed forest stands. Life history traits of nest-provisioning bees and wasps are characterized by low fecundity and extensive parental care. Their lifestyle differs from most other insects and they exhibit many similarities with breeding songbirds. The offspring are produced in sheltered nests that are stocked with food. Bees collect nectar and pollen and wasps collect insects and spiders. Most of this thesis is about solitary wood-dwelling aculeates that nest in holes made by other wood-boring insects. About 5800 potential nesting holes in deadwood were surveyed and the insect species or genera that had made the hole identified. Less than 2% of these holes were occupied by any bee or wasp. The reason for the low occupancy was probably that the egg-laying females are demanding in their nest choice and rejected many “inferior” holes that would not protect their offspring. Standing deadwood objects had higher occupancy than stumps and tops from harvested trees. Among two bee species, the nest abundance of a pollen-specialist species was predicted only by this species’ specific pollen resource, whereas the nest abundance of a pollen-generalist species was predicted by both pollen (mainly flowers along roadsides) and nesting resources. Tree species, sun exposure and the colonization history of beetles and fungi all contribute to the species assemblage of wood-dwelling aculeates in high stumps. These factors may interact in complex ways. Some exposure to sun seems to be a common requirement for aculeates irrespective of which tree species that were used as nest substrate. The relationship between tree species and aculeate species assemblage seems to be highly dependent on prior colonization history. Bumblebees were more abundant along edges between young and older forest stands than in the middle of the young forest stands. The reason for this is probably associated with the fact that edges represent favorable nesting and mate-finding sites. Based on results in this thesis, it is concluded that young boreal forest stands are important habitats for bees and wasps. Retention and creation of standing deadwood at final fellings is recommended and special care should be taken along forest roadsides to preserve the flora.

Keywords: Aculeata, bees, wasps, deadwood, flowers, saproxylic, solitary, young forest

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Bin och steklar (Aculeata) i boreal ungskog

Sammanfattning

Skogsbestånd yngre än 15 år utgör mer än 10 % av skogsmarken i Sverige. Syftet med denna avhandling var att öka förståelsen för hur insektsgruppen bin och steklar (Aculeata) utnyttjar ungskogar som bo- och födoplatser. Aculeater är solälskande och trivs inte i slutna skogsbestånd. Solitära bin och steklar kännetecknas av att de har låg fekunditet och hög grad av omvårdnad av sin avkomma. Levnadssättet skiljer sig från de flesta andra insekter och liknar på många sätt det hos häckande sångfåglar. Avkomman föds och utvecklas i skyddade bon som förses med mat. Bin samlar pollen och nektar och steklar samlar insekter och spindlar. Stora delar av denna avhandling handlar om solitära vedlevande arter som bygger bon i hål som gjorts av andra insektsarter. Cirka 5800 hål i död ved undersöktes med avseende på vilken insekt som gjort hålet och om det fanns bon av bin eller steklar där. Mindre än 2 % av hålen var utnyttjade som boplats. Anledningen till den låga beläggningen berodde troligen på att de äggläggande bi- och stekelhonorna är kräsna i val av boplats - de flesta hålen var för dåliga för att ge tillräckligt bra skydd för avkomman. Stående dödvedsobjekt hade avsevärt högre andel hål med bon än stubbar och toppar från avverkade träd. Antal bon av två biarter, (rallarbiet och ringcitronbiet) undersöktes och hur antalet berodde på tillgång av föda och naturliga boplatser. Antalet bon av rallarbiet som enbart samlar pollen från mjölkört berodde endast på tillgången av denna växt, medan antalet bon av ringcitronbiet, som samlar pollen från många blomarter berodde både på blomtillgången (främst längs vägkanter) och på boplatser, d.v.s. hål i stående död ved. Trädslag, solexponering, och tidigare förekomst av hålgörande skalbaggar och nedbrytande svampar var viktiga faktorer som påverkade artsammansättning av solitära steklar i högstubbar. Alla dessa faktorer samspelade. Humlor var vanligare längs kanter mellan ungskog och äldre skog än i mitten av ungskogsbeståndet. Avhandlingen visar att ungskogar är viktiga livsmiljöer för bin och steklar. Praktiska råd är att ta hänsyn till befintlig död ved och att skapa ny stående död ved vid avverkning av skog samt att sköta vägkanter längs skogsbilvägar på ett sätt som skonar eller helst gynnar floran.

Nyckelord: gaddsteklar, bin, steklar, död ved, blommor, vedlevande skalbaggar ungskog

Dedication

To Nils and Henry.

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List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

- I Westerfelt, P., Widenfalk, O., Lindelöw, Å., Gustafsson, L. & Weslien, J. (2015). Nesting of solitary wasps and bees in natural and artificial holes in dead wood in young boreal forest stands. *Insect Conservation and Diversity* 8(6), 493-504.
- II Westerfelt, P., Weslien, J. & Widenfalk O. Population patterns in relation to food and nesting resource for a pollen-generalist and a pollen-specialist bee species in young boreal forest stands. (manuscript)
- III Westerfelt, P., Weslien, J. & Stenmark, M. Enhanced abundance and species richness of bumblebees in edge zones between young and older forest. (manuscript).
- IV Westerfelt, P., Lindelöw, Å., Weslien, J. & Lindhe, A. Cut high stumps as nesting substrate for solitary wasps (Aculeata) – the importance of tree species, sun exposure and prior colonization of beetles and fungi. (manuscript).

Paper I is reproduced with the permission of the publisher.

The contribution of Per Westerfelt to the papers included in this thesis was as follows:

- I Main author and fieldwork. Research questions and study design together with Jan Weslien, Åke Lindelöw and Olof Widenfalk. Analyses together with Olof Widenfalk and Jan Weslien.
- II Main author, fieldwork and analysis. Research questions and study design together with Jan Weslien and Olof Widenfalk. Analyses together with Jan Weslien.
- III Main author and fieldwork. Research questions and study design together with Jan Weslien and Magnus Stenmark. Analyses together with Jan Weslien.
- IV Main author. Fieldwork and study design by Anders Lindhe and Åke Lindelöw. Research questions together with Jan Weslien. Analyses together with Jan Weslien.

1 Introduction

In forested regions where the forests are managed for wood production, disturbed areas are common and can represent a significant part of the landscape. In Sweden, there are about 3 million hectares of forest land where the stand age is younger than 15 years, constituting more than 10% of the total forest area. As a biotope for animals and plants, young forests have been considered by many to be a “junk biotope”, i.e. only the most common and least sensitive organisms can survive there. This is not currently true, although their bad reputation was rightly earned during the period about 30 years ago, when harvested forest areas really were clear cut and no trees (other than seed trees sometimes) were left. Regeneration relied on pesticide-treated conifer seedlings and deciduous tree species were killed with herbicides. Environmental activists at that time were probably right – they were “junk biotopes”. During the 1990s, however, a new approach was initiated: retention forestry (Simonsson et al., 2014). Young forest stands harvested under a retention regime have the potential to be valuable habitats for a large variety of organisms that live in sun-exposed environments. Retention also increases the structural complexity of the new young forest (Kruys et al., 2013).

In managed forests, which constitute the majority of forests in northern Europe (Axelsson et al., 2007), we (humans) decide what forests look like. This comes with a responsibility, and we should consider the organisms living in these areas. Before we started to manage forests, many organisms were dependent on natural disturbances such as fires, storms, insect outbreaks or flooding. Such events created large quantities of dead and dying trees, a requisite for a large number of species. Today, the effects of such disturbances are more or less inhibited by forest owners for economic reasons. A significant difference between a naturally disturbed area and a clear cut is the quantity and quality of deadwood that is left. Clear felled areas contain stumps from harvested trees, tops and branches. Many organisms do use these types of dead

wood (Hjältén et al., 2010; Jonsell & Hansson, 2011; Jonsell et al., 2007) but nevertheless such a disturbance creates a relatively homogenous and structurally simple biotope that is poor in biodiversity. Clear felling with retention can counteract such simplification of the habitat by leaving living and dead trees as well as creating dead wood by e.g. girdling or high-cutting. In addition, leaving patches of living trees creates edges and structures in the harvested area and potential wind-fellings, which will add to the quantity of dead wood.

Many insect species, including many red-listed species, are dependent on dead wood in boreal forest ecosystems (De Jong et al., 2004; Gärdenfors, 2010; Tikkanen et al., 2006). Forest management has reduced the amount of dead wood severely during the last 100 years and it is likely that certain types have decreased more than others, resulting in a reduction in habitats for wood-dwelling species to various extents. Saproxylic (wood-dwelling) species and dead wood have been the focus of numerous biodiversity studies (Stokland et al., 2012). In the context of retention forestry, saproxylic insects are overrepresented in studies performed in Scandinavia (Gustafsson et al., 2010).

Bees and wasps (Hymenoptera, Aculeata), are clearly underrepresented among studies on retention forestry. Rubene et al. (2015) found that stands with retained dead wood may have similar species richness and abundance of wood-nesting aculeates as burned forest stands. Today's young forests have great potential to offer nesting and feeding grounds for bees and wasps in the forest landscape. They are sun-loving creatures and do not thrive in cold, closed forest stands, especially not in the chilly boreal forest biome.

In agriculture, bees deliver an important ecosystem service, namely the pollination of many crops. Wasps are top predators among insects and many species hunt sap-feeders such as aphids and leaf-hoppers, which may be pests or vectors of diseases for many crops. In forests, bees and wasps may also be important, e.g. bumblebees are significant pollinators of lingonberry (*Vaccinium vitis-idaea*) and blueberry (*V. myrtillus*) which are picked and sold in large quantities each year.

2 Thesis aims

The aims of the research described in this thesis were to understand how aculeates (bees and wasps) utilize the resources in young boreal forests and how we can sustain and create suitable habitats for them in young forest stands. Solitary wood-nesting aculeates were the focal group, but bumblebees were considered in one of the studies. The specific questions addressed in the papers were:

- Are high stumps and retained dead trees used more often as nesting substrate by wood-nesting aculeates compared to stumps and lying tops and branches? What qualities does a favored nesting hole possess and are there any wood-boring insects that create preferred nesting holes? (Paper I)
- Is the population size of wood-nesting bees in the forest landscape best explained by their nesting- or food resource, and does it depend on specialization with respect to pollen collection? Is the floral resource found along roadsides important for bees in the forest landscape? (Paper II)
- How does the availability of nesting holes change during the first 15 years after final felling? (Papers I and II)
- Are edge zones in young boreal forests a favored habitat for bumblebees? (Paper III)
- What characterizes a high stump that is inhabited by nesting aculeates? Are these characteristics defined by tree species, sun exposure or prior colonization of hole-making beetles and fungi? Are there similar preferences for aculeates that have the ability to excavate their own nesting holes? (Paper IV)

3 Methods

3.1 Study species

Aculeata is a group within the order Hymenoptera and consists of three super families; Apoidea, Vespoidea and Chrysidoidea. The species differ remarkably in life history traits. This thesis mostly deals with the super family Apoidea, but also considers species within the families Vespidae, Pompilidae (Vespoidea) and Chrysididae (Chrysidoidea); the following description applies to these groups. In addition, only wild species are considered, thus excluding the most well-known aculeate species, the honeybee *Apis mellifera*, which is managed in hives for honey production and pollination services. For simplicity, I refer to these groups as aculeates.

Most aculeate species are solitary, i.e. each female has its own nest, but there are some social species, e.g. bumblebees. Species can be differentiated into nest-provisioning or parasitic species. The females of nest-provisioning species service one or more sheltered nests during their lifetime, where they oviposit and place a food store for the larvae. Parasitic species lay their eggs in the nests of nest-provisioning species and the parasitic larva kills its host (larva or egg) and utilizes the stored food. Most solitary species living in dead wood use holes made by other wood-boring species, but some are wood-burrowing, meaning that they excavate a tunnel in soft wood for the nest themselves.

Aculeates exhibit extensive parental care and the solitary species produce relatively few offspring for insects. Under natural conditions, females of most species lay fewer than 15 eggs during their lifetime (O'Neill, 2001 p. 300-301). Eggs are laid in sheltered nests and provided with a food store which is consumed by the larva after eclosion. Females of some species line the nest with protective material and in all species the nest entrance is sealed by the female with a protective plug. The stored food supply is enough to allow the young to complete their metamorphosis, hence the offspring do not leave their

sheltered nests until the adult stage. This parental care results in high survival rate of the offspring, similar to birds and mammals (Danks, 1971).

For the solitary species, one nest can contain several eggs, but if so, each egg has its own private cell, and the cells are separated by walls built by the female. The food store for bee larvae consists of pollen mixed with nectar. For wasps, the larval food consists of insects or spiders (Figure 1). With a few exceptions, wasp females collect multiple prey individuals for one larva and the number depends on prey size relative to larval size (O'Neill, 2001 p. 80-99). Wasp species which hunt small insects, e.g. dipterans or aphids, can collect more than 80 prey individuals as food for a single larva (Danks, 1970).



Figure 1. Left; a female of *Ectemnius cavifrons* in flight carrying a syrphid fly (*Syrphus vitripennis*). Right; a female of *Pemphredon lugubris* with an aphid between her jaws. The prey items will be placed in their nest holes in dead wood, becoming part of the food store for their larvae. The characteristics of the preferred nest substrate for these two species are described in Paper IV. Photographer: Jeremy Early.

The number of foraging trips required for bees to collect sufficient pollen and nectar for one larva varies greatly between species. Pollen specialists seem to need fewer foraging trips to complete one brood cell, varying between 2 and 12 (Danforth, 1990; Franzén & Larsson, 2007 (and references therein); Larsson & Franzen, 2007; Schäffler & Dötterl, 2011). Pollen generalists seem to need 18-40 foraging trips for brood cell completion (Chun-Ling et al., 2009; McKinney & Park, 2012; Phillips & Klostermeyer, 1978; Strohm et al., 2002).

The food stores are collected during flight trips in the vicinity of the nest. Several studies have examined the foraging range of nest-provisioning solitary bees and a study (including a review) by Gathmann and Tscharntke (2002) found that most species seem to have ranges between 150 and 600 m, with a few exceptions having c. 1 km as their foraging range. Larger species had greater foraging ranges.

Nest-provisioning aculeates are so-called central-place foragers, meaning that females return to their nests after each collection trip. Most probably, the

females have a well-developed sense of location. The homing female uses vision for orientation (Chapman, 1982; Fauria & Campan, 1998; Wcislo, 1992) and can recognize distinctive landmarks in the landscape while navigating back to her nest (Chapman, 1982; Dyer, 1996; Fauria et al., 2004; Kastberger, 1992). These landmarks are learned during so-called orientation flights. Social species can have a sophisticated communication system among the individuals in their society and thereby share information about the locality and quality of nearby food or nesting resources.

3.2 Study sites

The studies described in Papers I, II and III were all performed around Nyhammar, in the southern part of the province of Dalarna in the southern boreal zone (60°N, 14°E) of Sweden. It is a typical managed forest landscape in the boreal coniferous forest belt, with a low proportion of agricultural land and few rural settlements. The dominant tree species in the mature forest stands are Norway spruce *Picea abies* (L.) Karst. and Scots pine *Pinus sylvestris* L., with the former species dominating on rich sites and the latter dominating on poor sites. Broadleaved trees, birch *Betula pubescens* Ehrh. and *B. pendula* Roth, grey alder *Alnus incana* (L.) Moench and aspen *Populus tremula* L., are often vigorously removed during pre-commercial thinning but can still occur as single trees or patches within the conifer-dominated stands.

For studies in Papers I and II, 15 young forest stands were selected within an area of approximately 300 km² with the help of stand databases, to deliver the following criteria: 1) > 4 years and < 15 years old to ensure some variation of hole types in the dead wood; 2) not pre-commercially thinned; 3) about half of the stands replanted with Norway spruce, and half with Scots pine; 4) at least 500 m apart, separated largely by older forest stands; and 5) intermediate fertility (increment 4.3 – 6.6 m³ ha⁻¹a⁻¹).

For the study described in Paper III, 25 young forest stands were selected within an area of approximately 500 km² with the help of stand databases, to deliver the following criteria: 1) > 7 years and < 15 years old to ensure some concealment of the pan traps; 2) not pre-commercially thinned; 3) about half of the stands replanted with Norway spruce, and half with Scots pine; 4) at least 500 m apart, separated largely by older forest stands; and 5) intermediate fertility (increment 4.0 – 7.5 m³ ha⁻¹a⁻¹).

The research described in Paper IV was performed on Fagerön, a six hundred hectare island on the Baltic coast in the province of Uppland, Sweden (60°12'N – 18°27'E). The area falls within the northern part of the hemi-boreal

zone (Ahti et al., 1968). Coniferous forest with Norway spruce and Scots pine dominate, but there are also open pastures and areas of lush, mixed forest growing on former meadows. A nature reserve containing some of the forests and pastures was established in 1993 and it is known to support a high diversity of organisms from various taxa.

3.3 Surveys

3.3.1 Dead wood

In Paper I, dead wood was surveyed to find nests of wood-nesting aculeates. The nests are constructed in holes in dead wood and the presence of a nest is indicated by a plug which covers the hole opening (Figure 2). It was possible to attribute the plug to one or several genera of aculeates based on the plug material (Table 1).



Figure 2. Left; A retained dead pine with two holes made by *Anoploclera sanguinolenta/reyi*, one has a resin-plug which indicates a nest of the aculeate genus *Passaloecus*. Right; A high stump of pine with two holes made by *Asemum striatum*, one them has a plug made from wooden chips, which indicates a nest of *Pemphredon*, *Megachile* or *Hoplitis*.

Table 1. Emerged adult bees and wasps by genus and plug type from Paper I. The table is based on the catch in trap nests with predrilled holes of four diameter classes: 3, 5, 7, 10 mm.

Plug type	Genus	Super family	Utilized hole diameter (mm)
Clay	<i>Trypoxylon</i> Latreille	Apoidea	5
	<i>Ancistrocerus</i> Wesmael	Vespoidea	5, 7
Resin	<i>Passaloecus</i> Shuckard	Apoidea	3
Cellophane-like membrane	<i>Hylaeus</i> Fabricius	Apoidea	3, 5, (7)
Soil/Wood	<i>Pemphredon</i> Latreille	Apoidea	5, 7
	<i>Megachile</i> Latreille	Apoidea	7, 10
	<i>Hoplitis</i> Klug	Apoidea	5, 7

All holes, even empty ones that could potentially be used as a nesting hole by the aculeates, were counted on all surveyed dead wood objects, making it possible to estimate the proportion of the potential nesting holes actually used. The nesting holes are seldom made by the aculeates themselves, but are excavated by other wood-boring insects, mostly beetles. All holes were attributed to the insect species or genera that had made the hole (Figure 2) and preferences for certain insect holes among the recorded aculeate species were investigated. To analyze preferences among the wood-nesting aculeates for specific types of dead wood, three dead wood types were distinguished: Standing Dead Wood (SDW), stumps and Lying Dead Wood (LDW). The sampling effort per stand was 10 SDW objects, 90 stumps and LDW object along three 80 m transects.

In Paper II, the relative importance of nesting resource (i.e. holes in dead wood) and food resource (i.e. flowers) was considered. Part of the dataset from the dead wood surveys described in Paper I was used, including only hole types and deadwood types that were used by the two bee species studied. To obtain a measure of the amount of standing dead wood for each young stand, all standing dead wood objects were counted and their tree species identified within a radius of 300 m from the trap nests. Note that these standing dead wood objects were not surveyed for potential nesting holes nor aculeate nests.

3.3.2 Insect Traps

Hole-nesting aculeates were surveyed using trap nests (Papers I and II). Three traps were placed in each study stand (n=15) with a mean spacing of 90 m. The trap nests consisted of wooden poles (height 1.5 m, width 10 cm) with predrilled holes of different diameters. Different species of hole-nesting aculeates are known to prefer certain hole diameters, so a trap nest with a variety of hole sizes will attract a range of species. After exposure in the field (c. 70 days), the

trap nests were brought to the laboratory for the aculeates to be reared. This allowed plug–aculeate association for this area (Table 1). A standardized survey method, such as this, also allows for assessment of the relative abundance of the species caught (Paper II). Trap nests only attract hole-nesting aculeates, meaning that few species are caught compared to other survey methods e.g. pan traps (Rubene et al., 2014). The focal group in Papers I and II was the wood-nesting aculeates and therefore this survey method seemed appropriate.

In Paper III the focal group was bumblebees. For this study, we used traps consisting of colorful pans combined with a plexiglass sheet (Figure 3). This trap type is a combination of a passive flight interception trap (window) and an active trap (pan). The brightly colored pan attracts flower-visiting species and the window acts as a stopper, which increases catch efficiency. This trap type caught a variety of insects, to a high degree dominated by flower-visiting species e.g. bumblebees. We sampled bumblebees at one edge and in the middle of each young forest stand. This allowed for within-stand comparisons, which provides a way to control for differences between the studied stands.



Figure 3. Left; trap nest (wooden pole with pre-drilled holes). Right; yellow pan trap.

3.3.3 Flowers

In Paper II, the relative importance of nesting resource (i.e. holes in dead wood) and food resource (i.e. flowers) was studied. To obtain a measure of the available flowers, 1 ha (divided into three squares situated adjacent to the trap nests) of each stand was surveyed for all flowering plants. In addition, all roadsides within 300 m of the trap nests were surveyed for flowering plants. Different measurements were used for different plant species depending on the metric that was most convenient to evaluate in the field. For the species

belonging to Asteraceae, Dipsacaceae, *Campanula* spp. L. and *Hypericum* spp. L., the metric was the number of individual blossoms. For species belonging to Rosaceae and Fabaceae as well as *Vaccinium* spp. L., *Melampyrum* spp. L. and *Calluna vulgaris* (Hull), the metric was the ground area covered. For *Epilobium* spp., *Chamerion angustifolium* and species belonging to Lamiaceae, Boraginaceae and Scrophulariaceae, the metric was the number of stems.

3.3.4 Net-enclosed high stumps

For Paper IV, the data originated from an earlier field experiment (Lindhe, 2004). Sixty high stumps were surveyed for emerging insects by enclosing each with a large fine-meshed nylon net sack. Insects emerging from the high stumps were caught in stem-mounted window traps within the enclosures. These traps, since they were enclosed by the net, only target insects emerging from the high stumps (and not insects attracted to them), which is important for the assumptions made in this study. Sixty high stumps of four tree species; spruce (15), birch (16), aspen (15) and oak (14) were assessed. The high stumps were situated in three treatments: clear cut, thinned and intact forest, resulting in varied sun exposure which was measured individually for each stump based on water-evaporation from glass vessels.

The field experiment proceeded over several years and the enclosure altered between years, so that each individual high stump was open to egg-laying females one season and enclosed the next. The high stumps in our study were enclosed for three seasons (1995, 1997 and 2000). Data from hole-making beetles come from all years of enclosure but aculeate data were only available for the year 2000. In addition, the high stumps were surveyed for the presence of fungal fruit bodies in 5 years: 1995, 1996, 1997, 1998 and 2000.

This study design and sampling method made it possible to correlate individuals and species of wood-nesting aculeates with prior emergence of hole-making beetles and presence of wood-decaying fungi. Positive correlations indicate priority effects, i.e. wood-making beetles and/or saproxylic fungi facilitate aculeate nesting.

3.4 Analyses

All statistical analyses were performed in R, version 2.14.2.(R Development Core Team, 2012).

To compare different dead wood types and age classes (Paper I) with respect to each type of potential nesting hole, presence/absence as well as number of holes per dead wood object were considered. The statistical unit was a dead wood object since this was assumed to be the spatial scale at which

nest-seeking females select holes. For presence/absence data, generalized mixed models controlled for the random effect of site were used, assuming a binomial distribution with logit link. For the number of potential nesting holes, general mixed models assuming a negative binomial distribution were used due to overdispersed data with log link.

In Paper II, aculeate measurements were considered at stand level and ln-transformation ensured that the data fulfilled the criteria for linear models, i.e. normally distributed residuals, homoscedasticity and equal leverage. For analyses of plants species' correlations with bee abundance, generalized linear models were used because the data did not meet the homoscedasticity requirement. The distribution was assumed to be a negative binomial since this gave the best model fit due to over-dispersed data.

In Paper III, linear models were used to analyze how stand size and tree cover at stand level affected bumblebees. Linear models were also used when analyzing how bumblebees were affected by the relative openness within a stand. Paired t-tests were used in all comparisons between edge and middle traps: for the whole dataset, for shady stands and for open stands. All linear models were checked for normal distribution, homoscedasticity and equal leverage. When paired t-tests were used, the differences between the pairs were checked to determine whether the data were normally distributed. The variables were ln-transformed if this improved the model fit.

In Paper IV, the statistical unit was a high stump. When comparing different high stumps (tree species, exposure), aculeate density (hatched aculeate individuals and species per square meter of wood surface) was used as the response variable. In analyses of aculeates and hole-making beetles from the same stump, the number of individuals per high stump was used since both would be affected by surface area in the same way. The response variables, number and density of aculeate individuals and species, did not fulfill the criteria for linear models. Hence, generalized linear models were used, assuming a negative binomial distribution due to over dispersion. Analyses concerning the correlation between some explanatory variables did fulfill the criterion for linear models. All correlations between two continuous variables were visually inspected for non-linear trends.

3.5 Spatial scales

This thesis covers nesting and foraging of aculeates across three spatial scales: nesting hole, nesting substrate and forest stand (Table 2).

Table 2. *The four papers by the studied spatial scale and aculeate taxa. (F) denotes food resource, N denotes nesting resource*

Paper	Nesting hole	Nesting substrate	Stand	Bees	Wasps
I	X	X	X (N)	X	X
II			X (F, N)	X	
III			X	X	
IV	X	X	X (N)		X

4 Results and Discussion

4.1 Spatial scale - nesting hole

Hole diameter was an important factor explaining aculeate occupancy of a certain aculeate species (Paper I). They seemed to choose nesting holes just big enough for their bodies and rejected larger holes. No plug type was exclusively associated with one specific hole-maker in the dead wood, but certain plug types were more common in some hole types (Table 2). One advantage of selecting a hole just large enough is that it reduces the risk of predation or parasitism, as has been shown for cavity nesting birds (Zhu et al., 2012). A small hole is easier to defend against nest-entering predators/parasites and is also faster to seal with a plug (Fricke, 1995).

Table 3. *The abundance of clay- resin- and cellophane-like membrane plugs in different hole types in standing dead wood (SDW). The percentages of holes occupied are shown in brackets.*

Hole-maker	No. of holes in SDW	Clay	Resin	Cellophane-like membrane
<i>Anoploclera sanguinolenta/reyi</i>	623	23 (3.7%)	7 (1.1%)	5 (0.8)
<i>Hylecoetes dermestoides</i>	294	7 (2.4%)	9 (3.1%)	4 (1.4%)
<i>Monochamus sutor</i>	132	3 (2.3)	0	3 (2.3)
<i>Arhopalus rusticus</i>	115	1 (0.9%)	0	0
<i>Acanthocinus aedilis</i>	114	0	0	1 (0.9%)
<i>Anobium thomsoni</i>	23	0	1 (4.3%)	0
<i>Camponotus spp.</i>	438	2 (0.5)	0	0
<i>Sirex spp./Xeris spectrum</i>	54	1 (1.9%)	0	0
Total		37	17	13

Preferences for certain hole diameters have been shown previously in trap nests (Budrienė et al., 2004; Gathmann et al., 1994), but this is the first time that natural holes have been surveyed and assessed as suitable nesting holes for

aculeates. In artificial trap nests, the egg laying females can pick the appropriate hole size and position in relation to sun-exposure and ground level. Such a wide range of options seldom or never exists in natural substrates. Apparently, however, the hole diameter was also important when selecting from natural holes in the dead wood.

In Paper IV, we report that high stumps that had been used by many wood-boring beetle species had more wood-nesting aculeate species than high stumps used by few beetle species. This further strengthens the hypothesis that each aculeate species has specific demands with respect to their nesting hole.

Some aculeate genera have been considered to be wood-burrowers (Ehnström & Axelsson, 2002; Lomholdt, 1975), i.e. they make their own nesting hole in the dead wood. Our result (Paper IV) suggests that there are primary and secondary wood-burrowers among the aculeates, just as in cavity-nesting bird communities (Cooke & Hannon, 2011); *Ectemnius cavifrons* is a primary hole-maker and *Pemphredon lugubris* is a secondary hole-maker, modifying holes made by other species.

4.2 Spatial scale - nesting substrate

Wood-nesting aculeates seem to be highly favored by dead wood retention (Paper I). Retained dead trees and cut high stumps, in this thesis called standing dead wood (SDW), supported a higher density of nesting aculeates than stumps and lying dead wood (LDW) (Figure 4). It is notable that stumps possessed a similar density of potential nesting holes as SDW but half of the plug types were absent from the stumps. Lying dead wood (LDW), which was mostly tree tops and branches, had a low density of potential nesting holes and few nesting aculeates. The same species that were absent from stumps were also absent from LDW.

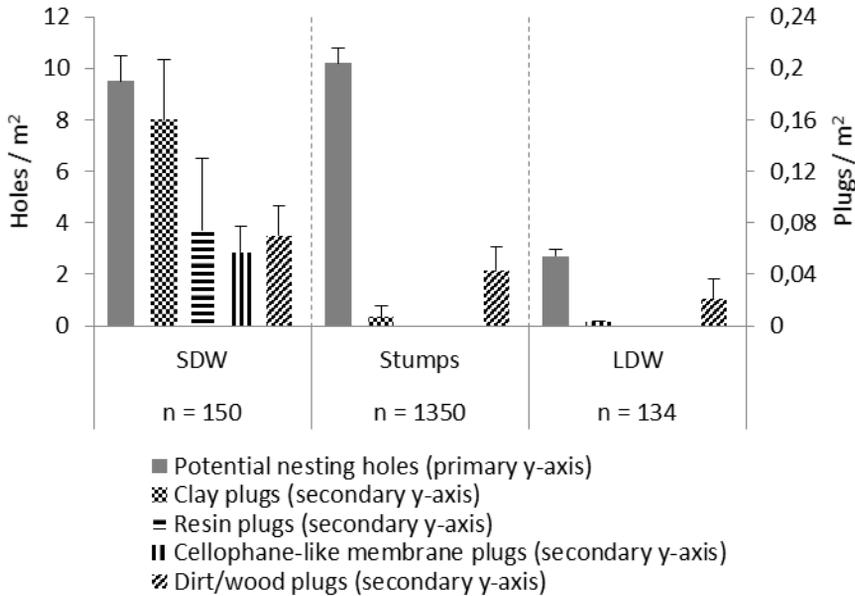


Figure 4. The density of potential nesting holes (primary y-axis, holes/m²) and four different plug types (secondary y-axis, plugs/m²) in three different dead wood types. SDW = Standing dead wood, LDW = Lying dead wood. The mean surface area per object for the surveyed parts of the dead wood types were: SDW (bottom 2 m) = 1.51 m², Stumps = 0.21 m², LDW = 2.12 m². Bars show the standard error, n indicates number of surveyed objects.

It was apparent during the dead wood survey that SDW objects were generally harder and dryer than stumps and LDW, especially in older stands. The holes in the wooden poles (trap nests) had much higher occupancy than the holes in the natural dead wood. The wooden poles were dry and fresh, characteristics that were very rare among the natural dead wood objects. Another example of aculeates' preference for dryer and harder wood concerned the birch high stumps. Compared to conifers, birch high stumps were softer and more decayed. However, parts of birch high stumps where the bark was absent could be hard and dry. Holes made by *Hylecoetes dermestoides* in birch had much higher occupancy by aculeates when situated in wood without bark (11%) than in wood with bark (2.5%).

Tree species (of high stumps) had a significant effect for three out of six aculeate species analyzed (Paper IV), but none of these species were found in only a single tree species. On the same stumps as in this study, Lindhe et al. (2005) showed that each tree species (spruce, birch, aspen and oak) supported a unique set of beetle species. Aculeates do not consume the dead wood nor the associated fungal hyphae, which most saproxylic beetles do. Instead, it is

merely a structure where they construct their sheltered nest for offspring development from egg to adult. Therefore, it was surprising that solitary hole-nesting aculeates exhibited preferences for tree species. Some tree species were probably preferred over others because they differed in density of suitable nesting holes. Birch supported few hole-making beetles with respect to both abundance and species and, therefore, hosted fewer wood-nesting aculeates than the other tree species. Prior presence of white-rot fungi, in combination with sun exposure, determined a high stump's suitability as a nesting substrate for the primary wood-burrowing species *E. cavifrons*. Facilitation by fungi has been shown for many other organisms utilizing dead wood e.g. beetles (Weslien et al., 2011), woodpeckers (Cooke & Hannon, 2012; Harestad & Keisker, 1989; Pasinelli, 2007) and other fungi (Ottosson et al., 2014).

4.3 Spatial scale - stand level

In Paper II we showed that the food resource at stand level for the pollen specialist (*M. lapponica*) was the single most important predictor of bee abundance. The abundance of the pollen generalist (*H. annulatus*) was predicted by both food- and nesting resource at stand level in the studied landscape where both these resources occur naturally. Hence, we demonstrated that pollen specialization among solitary bees affects their different dependences on food- and nesting resource. This result is discussed in the context of trade-offs between specializations in pollen or nesting resource. Forest roadsides offered different flowering plant species compared to young forests and this flora predicted abundance of the pollen generalist better than the flora in the young forest stand.

It was apparent that sun-exposed stands contained more wood-nesting aculeates (Paper IV). Among 28 species in this study, 21 were collected on stumps situated in the treatment with highest tree canopy removal and 14 of these species were unique to this situation (Fig. 5). Sun exposure had no apparent effect on the hole-making beetles that facilitated aculeate nesting, indicating that it is the warm microclimate that comes with high sun exposure that is favorable. Note that we analyzed only a small fraction of the whole beetle fauna. In Lindhe et al. (2005), where many more beetle species were included in the analyses, there was a positive effect of sun exposure.

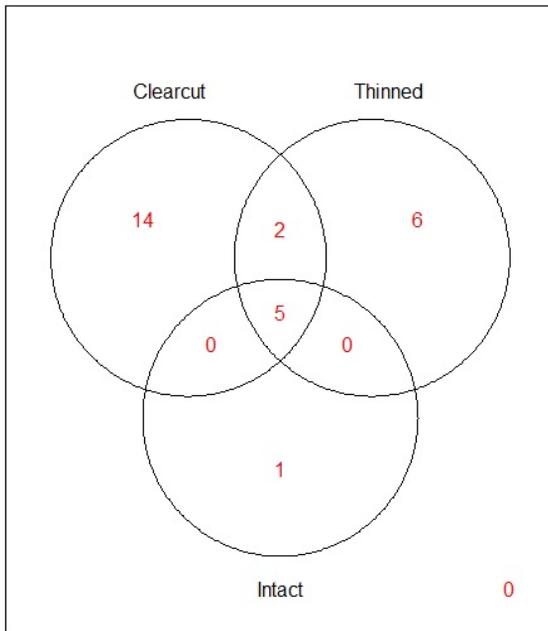


Figure 5. Venn diagram – unique and shared species of hole-nesting aculeates among high stumps in three different cutting intensities: clear cut, thinned and intact forest.

It has been shown in other studies that many insect species are favored by removal of the tree canopy in forests (Korpela et al., 2015; Taki et al., 2010). Beetle species specialized on oak and aspen were found at much higher frequencies on sun-exposed high stumps than on shaded ones (Lindhe et al., 2005).

The first decades after clear felling are associated with many changes to the vegetation structure and composition. Most apparent is the growth of trees and shrubs, turning a more or less two-dimensional clear cut into a three-dimensional young forest. Dead trees from the old stand will gradually decompose and become more shaded over time. These changes will, hypothetically, decrease the habitat quality for many solitary hole-nesting aculeates as time progresses. On the other hand, the number of holes and hole types in the dead wood will increase with the succession of wood boring species over time as the decay stage reaches the threshold for more wood boring species. Most aculeates are favored by sun-exposed dead wood as a nesting substrate (Paper IV) but still many wood-nesting aculeates were positively affected by aging during the first 15 years after cutting. This was probably because the nesting resource increased (Figure 6) (Papers I and II).

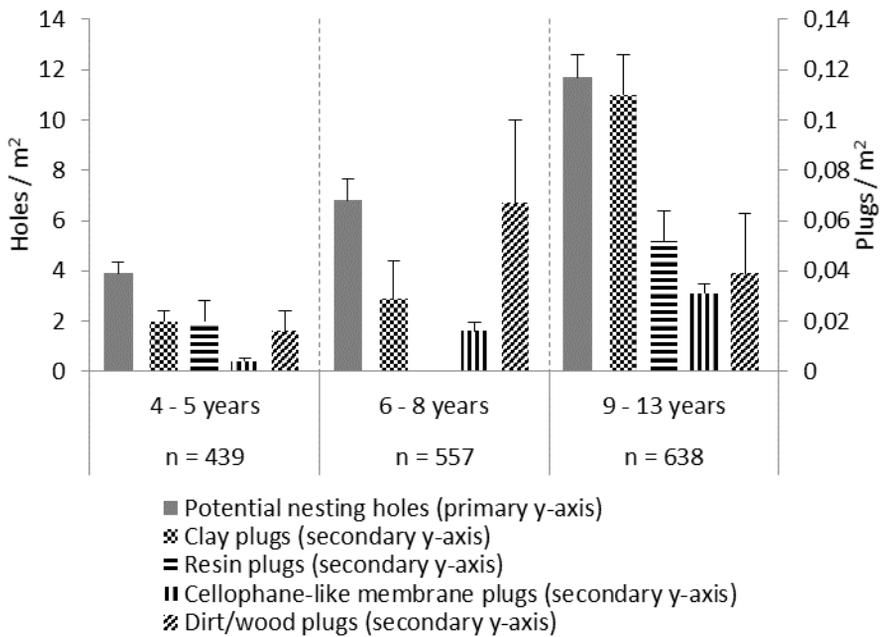


Figure 6. The density of potential nesting holes (primary y-axis, holes/m² and four different plug types (secondary y-axis, plugs/m²) in three age categories (after final felling). Bars show the standard error, n indicates number of surveyed objects (SDW, stumps and LDW).

M. lapponica, which was highly dependent on fireweed *Chamerion angustifolium*, for pollen declined with forest age as did its specific pollen resource (Paper II).

In Paper III, we showed that edge zones between young forests and older forest stands may be essential bumblebee habitats in managed boreal forest landscapes. The two abundant species in this study that were significantly more common along edges, *B. pratorum* and *B. pascuorum*, are known to use edge zones as mating structures (Mossberg & Cederberg, 2012). Males and cleptoparasites were more abundant along edges in our study. This further supports the suggestion that edges are used for nesting and mating since males and cleptoparasites do not collect pollen and nectar and mostly move around nesting sites (Eickwort & Ginsberg, 1980). Another possible advantage with edges is that they may facilitate homing during foraging trips and decrease the time spent on orientation flights. Such orientation flights can occupy a large part of a flight trip if a bumblebee gets lost. From this perspective, it is easy to conceive that the long and distinct edges between young and old managed forests stands may facilitate navigation between foraging and nesting sites.

5 Conclusions and implications for conservation

Wood-nesting aculeates have high demands with respect to their breeding substrate and they choose carefully where to construct their nests. We (humans) have great opportunities to create suitable nesting substrates for this group of organisms in young forests through tree retention. By retaining dead trees and cutting high stumps in sun-exposed locations, we can create dead wood that has characteristics which favor wood-nesting aculeates.

- Dead wood structures originating from retention measures, i.e. retained dead trees and high stumps, are used to a much higher degree as nesting substrate by solitary wood-nesting bees and wasps than stumps and logging waste. Many species rejected stumps and lying tops and branches. A suitable nesting hole for most wood-nesting bees or wasps should be just large enough for their body to fit into and situated in hard and dry wood. Most holes in dead wood do not possess these qualities, resulting in a low occupancy by aculeates: less than 2% in our study.
- If a wood-nesting bee species has the ability to nest in holes in stumps, the nesting resource is virtually unlimited and population size is solely explained by its food resource in young boreal forest stands. If a wood-nesting bee species rejects stumps, lying tops and branches as nesting substrate, the population size is best explained by both its food- and nesting resource. It seems reasonable that a strong dependence on a specific food resource could be associated with limited demands on nest characteristics. This suggests that one needs to consider specialization with respect to both nesting and pollen resources to make a sound assessment of a bee species' habitat requirements. Forest roadsides may provide a stable food resource for solitary bees in managed forested landscapes. Flower density along

forest roadsides explained the abundance of the generalist bee *H. annulatus* to a greater extent than the flower density in young forests.

- The number of potential nesting holes in the dead wood increases with time during the years following final felling as the decay stage reaches the threshold for more wood boring species, resulting in an accumulation of holes. Thus the availability of nesting holes for solitary aculeates increases over time. Still, sun-exposed, hard and dry wood is favored by the wood-nesting aculeate fauna. Thus, wood-boring species that use newly dead wood are likely to be of great importance to facilitate aculeate nesting in recently cut forest stands.
- Edge zones between young forests and older forest stands are favorable bumblebee habitats in managed boreal forest landscapes. The reason for this is probably that edge zones provide suitable nesting sites for bumblebees because they 1) possess a favorable microclimate, 2) facilitate mate-finding and 3) facilitate navigation between the nest and the foraging site.
- A high stump acting as a nesting substrate for many wood-nesting aculeates is characterized by being sun-exposed and having a high diversity of hole types, i.e. has been used by many species of wood-boring beetles. Aculeate species that are primary wood-burrowers do not favor high stumps with many pre-existing holes but prefer those with appropriate decay of white-rotting fungi.

The findings presented in thesis contribute to our understanding of the habitat requirements of forest-dwelling bees and wasps. However there are still large gaps in our knowledge. More research is needed, specifically on the following topics

- The importance of forest roadside flora as a food resource for a variety of bee species.
- Forest edges – why are they favored by bumblebees? What is their relative importance for foraging, orientation, nesting and mating?
- Food resources for solitary wasps – how important are food resources for species that collect insects and spiders for their brood? What environments offer high densities of preferred prey?
- And, finally, the role of forests in a changing landscape – can young forests offer suitable habitats for bees and wasps that are threatened by changes in the agricultural landscape?

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