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Seasonal phenology and reproductive behaviour of *Dioryctria* species Zeller (Lepidoptera: Pyralidae) in British Columbian seed orchards

by

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Dedication

This thesis is dedicated to my parents, Lloyd and Dianne. As a child, you inspired my passion and curiosity for the natural world. As an adult, you provided me with the unconditional love and support to continue exploring that world. Thank you.

Abstract

Seasonal phenology and mating frequency of moths in the genus *Dioryctria* found sympatrically in north Okanagan Valley, British Columbia seed orchards were assessed. Female moths in the *abietella, auranticella, ponderosae* and *schuetzeella* species groups were trapped in Douglas-fir, lodgepole pine and interior spruce stands. Most species were univoltine based on one peak of flight activity per season. There is evidence that the *abietella* group are bivoltine in this region. Females in the *abietella* and *auranticella* groups are polyandrous; *ponderosae* and *schuetzeella* females are monandrous. The sole *abietella* species, *D. abietivorella*, recorded in British Columbia can have substantial economic impacts on seed production in commercial seed orchards. Factors influencing reproductive behaviour, longevity and fecundity of *D. abietivorella* were investigated. Females are synovigenic and have an income-breeding mating strategy. Reproductive behaviours are delayed post-eclosion and signalling receptivity by females coincides with egg maturation, increasing with age. Female *D. abietivorella* experience trade-offs between reproduction and longevity.

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Table of contents

List of Tables

List of figures

Chapter 1: The biology and management of North American cone-feeding *Dioryctria* species

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Introduction

Dioryctria Zeller (Lepidoptera: Pyralidae) coneworms are destructive pests of conifers throughout the Holarctic. *Dioryctria* species feed on foliage, cambium, and tree wounds, however they are most economically damaging when they consume ovulate cones of genetically-improved trees (Neunzig, 2003). Cone-feeders comprise thirty-five of the seventy-nine species in *Dioryctria*, and these are the most pestiferous Lepidoptera associated with conifer seed cone production (Hedlin *et al.*, 1980; Turgeon *et al.*, 1994). *Dioryctria* infestations cause substantial economic losses to seed orchard production of genetically superior conifer seed for reforestation programs (Hedlin *et al.*, 1980; Zobel and Talbert, 1984).

Despite the pest status of certain cone-feeding *Dioryctria*, their evolutionary ecology is poorly understood. Evolution in this group is likely driven by the temporal and spatial heterogeneity of cone crops and niche separation of sympatric species. Cone-feeding *Dioryctria* that exploit highly variable annual seed crops tend to use a wide range of host genera; *Dioryctria* species that feed on less ephemeral tissue types (*e.g.* cambium) can be be restricted to a single host (McLeod and Daviault, 1963; Neunzig, 2003). Polyphagy, here defined as feeding on more than one conifer genus, is a successful feeding strategy for some *Dioryctria* species and appears to be linked to pest status in the genus. Fir coneworm, *Dioryctria abietivorella* Grote is the most geographically widespread and pestiferous species of *Dioryctria* in Canada. It exhibits polyphagous feeding habits that vary across its wide geographic range in North America and in 2004 caused an estimated $1 million Cdn loss to seed production in southern interior British Columbia seed orchards (Strong, 2005).

Identification of *Dioryctria* species based on morphological characters is difficult and impedes the development of accurate monitoring tools needed in integrated pest management programs targeting these species. Continuing uncertainties about species limits have complicated the ecological literature on *Dioryctria* (Hedlin *et al.,* 1980; Sopow *et al.,* 1996; Du *et al.*, 2005). Recent molecular and morphological studies (Du *et al.,* 2005; Roe *et al.,* 2006; Roe and Sperling, 2007; Roux-Morabito *et al.,* 2008) have begun to clarify the relationships among species within this genus. Continued research on the systematics and the life history of *Dioryctria* will enhance the development of integrated pest management programs for these important pests of conifers (Sopow *et al,* 1996; Roe *et al.,* 2006; Roux-Morabito *et al.,* 2008).

This review presents a synthesis of research completed to date on the systematics, life history, ecology, and management of *D. abietivorella* and other cone-feeding *Dioryctria* species in North America. Turgeon *et al.* (1994) broadly addressed the ecology of cone and seed insects and Neunzig (2003) focused on the morphology-based taxonomy of the genus. Here, we highlight the interaction of evolutionary relationships and ecological phenomena in the genus and identify the biological information required to develop integrated pest management systems that efficiently target *Dioryctria* pest species.

Systematics, taxonomy, and diversity of *Dioryctria*

Dioryctria (Zeller, 1846) is a large, morphologically distinct genus of phycitine moths in the family Pyralidae. Members of the genus are found throughout the Holarctic, with a handful of species in the Neotropical and Indomalayan regions. Currently the genus contains seventy-nine species, although recent studies suggest that additional undescribed species may exist (Du *et al.,* 2005; Roux-Morabito *et al.,* 2008). Recognition of *Dioryctria* species is difficult due to interspecific overlap of diagnostic traits such as wing coloration, genitalic structures, and host association (Sopow *et al.,* 1996; Roe and Sperling, 2007) (Table 1.1; Figs. 1.1, 1.2, 1.3). Species delimitation therefore requires molecular data (Roe *et al.,* 2006) (Table 1.2) or novel morphological traits (Simonsen and Roe, 2009). Seven species groups were initially proposed in *Dioryctria* to improve identification and understanding of the morphological and behavioural diversity within the genus (Mutuura and Munroe, 1972). Since that time, a number of additional species groups have been described (Mutuura and Munroe, 1974; Wang and Sung, 1982; Speidel and Asselbergs, 2000; Neunzig, 2003), and phylogenetic relationships within and between these groups have been examined more extensively (Du *et al.,* 2005; Roe *et al.,* 2006; Roux-Morabito *et al.*, 2008).

The current hypothesis of relationships among seven of the eleven species groups was produced using a parsimony analysis of previously published sequence data from mitochondrial cytochrome c oxidase I and II genes (COI-COII) (Table 1.2; Fig. 1.1). Given the importance of *D. abietivorella* as a pest in Canada, all available representative species in the *abietella* group were included in the analysis, along with representative taxa from the remaining species groups and two species (*D. okui* Mutuura and *D. juniperella* Yamanaka) that have not been assigned to a group (Fig. 1.1). Consistent with previously published phylogenies (Du *et al.,* 2005; Roe *et al.,* 2006), the majority of species groups form well supported monophyletic clades with the exception of the *auranticella* group (although this conclusion is tentative due to incomplete sampling of species). A monophyletic clade, the 'raised scale group', containing three species groups (*zimmermani* gr., *baumhoferi* gr., and *ponderosae* gr.) has also been resolved, while relationships among other species groups have not been confidently resolved (Fig. 1.1).

Cone-feeding *Dioryctria*

Within North America, forty species of *Dioryctria* have been described; seventeen of these, constituting seven species groups, are cone-feeders (Neunzig, 2003) (Table 1.1). In addition to cone-feeding, some of these species also feed on phloem and foliage (Neunzig, 2003) (Table 1.1, Fig. 1.1). Larval hosts for most *Dioryctria* species are in Pinaceae; two species specialize on members of the Cupressaceae (Table 1.1, Fig. 1.1). Many *Dioryctria* species associate with only one or two closely related host plant species, typically in the genus *Pinus* L. (Pinaceae), but other species are polyphagous (Neunzig, 2003; Roux-Morabito *et al.,* 2008). The *ponderosae* group (*D. ponderosae* Dyar, *D. okanaganella* Mutuura, Munroe and Ross, and *D. hodgesi* Neunzig) is the only North American species group that lacks cone-feeders.

The *abietella* group

The *abietella* group contains fifteen species, most of which have either a Nearctic or Palearctic distribution. Larvae of members of this group feed on a range of hosts and host tissues. Cone-feeding is the most prevalent feeding habit in the *abietella* group (Table 1.1, Fig. 1.1) and many of the species are important economic pests. Minor forewing and genitalic characters have been used to identify species, but accurate identification requires information on host plant association or geographic location (Segerer and Pröse, 1997). Recent work has examined the species limits of a number of *abietella* group members using mitochondrial DNA sequences (Roux-Morabito *et al.,* 2008). The combination of all previously published COI-COII sequences for the *abietella* group (Knölke *et al.,* 2005; Du *et al.,* 2005; Roe *et al.,* 2006; Roux-Morabito *et al.,* 2008) shows a range of intra- and interspecific variation among species in the group (Table 1.2). Specifically, *D. abietella* Denis and Schiffermüeller has high intraspecific variation and fails to form a monophyletic group (Roux-Morabito *et al.,* 2008) (Table 1.2, Fig. 1.1), contrasting with the low level of variation in most other species in the group. Phylogenetic results from the European members of the *abietella* group suggest that cryptic species may exist (Roux-Morabito *et al.,* 2008). This issue requires further examination.

The most important species in the *abietella* group in Canada, *D. abietivorella*, has a convoluted nomenclatural history that makes interpretation of the literature difficult. Originally, Grote (1878) described the species as *Pinipestis abietivorella*. Two years later Grote (1880) described a similar species, *P. reniculella* Grote. Subsequent revision of the genus *Dioryctria* by Ragonot (1893) saw these two species reclassified as *D. abietivorella* and *D. reniculella*, respectively. Examination of the *D. reniculella* types by Amsel (1962) and Mutuura and Munroe (1973) demonstrated that both holotypes were in fact specimens of *D. abietivorella*, making *D. reniculella* a junior synonym. Earlier, Heinrich (1956) had synonymized *D. abietivorella* with the European *D. abietella* and misidentified a second distinct Nearctic species as *D. reniculella*. In 1959, Munroe re-examined North American specimens identified as *D. abietella* and recognized them as *D. abietivorella*, distinct from the Palearctic specimens, based on forewing and genitalic characteristics. After clarification of the identity of the *D. reniculella* holotype (Amsel, 1962; Mutuura and Munroe, 1973), the North American specimens considered by Heinrich (1956) to represent *D. reniculella* were named *D. reniculelloides* (Mutuura and Munroe, 1973), while specimens identified as *D. reniculella* prior to Heinrich (1956) were in fact *D. abietivorella*. Finally, a second closely related species, *D. ebeli* (Mutuura and Munroe, 1979), was described from the southeastern United States, and much of the earlier literature on *D. abietella* and *D. abietivorella* from that region actually refers to *D. ebeli* (*e.g.* Ebel ,1965; Fatzinger and Asher, 1971*a*). Given the taxonomic turmoil surrounding *D. abietivorella*, confirmation of the accuracy of taxonomic names used within the literature is particularly important.

In North America, the species group *abietella* includes the seed-feeding *D. abietivorella* and *D. ebeli* (Table 1.1, Fig. 1.1). The geographic range of *D. abietivorella* extends across southern Canada and throughout the western United States (Heinrich, 1956; Lyons, 1957; Munroe, 1959; Prentice, 1965; Neunzig, 2003), whereas the distribution of *D. ebeli* is restricted to the southeastern United States (Mutuura and Munroe, 1979; Neunzig, 2003). These two species have a surprising lack of genetic variation, despite differences in geographic range and host associations (Roux-Morabito *et al.*, 2008) (Tables 1.1-1.2, Fig. 1.1). This lack of genetic variation suggests extensive gene flow between these two species, possibly due to a recent range expansion or a selective sweep that has driven an advantageous mutation through all populations. To clarify species limits between *D. abietivorella* and *D. ebeli*, a more detailed population genetic analysis is needed. Mitochondrial DNA differences between *D. abietivorella* and *D. abietella* are much greater than those between *D. abietivorella* and *D. ebeli*. Du *et al.*, (2005) show a 3.8% uncorrected distance at the COI-COII locus, which further supports the recognition of *D. abietivorella* as distinct from *D. abietella* (Munroe 1959) (Table 1.2, Fig. 1.1).

The *auranticella* group

All North American members of the *auranticella* species group, *D. auranticella* Grote, *D. rossi* Munroe, and *D. disclusa* Heinrich, are cone-miners (Table 1.1, Figs. 1.1, 1.3). *Dioryctria auranticella* and *D. rossi* occur sympatrically over most of their ranges between southern British Columbia and New Mexico, although *D. rossi* is also found in west Texas (Heinrich, 1956; Neunzig, 2003). The economically important *D. disclusa* is found in eastern Canada, and in the eastern and central United States as far west as eastern Texas (Heinrich, 1956; Neunzig, 2003).

The *baumhoferi* group

In North America, ten species are included in the *baumhoferi* group; only two of those species (*D. clarioralis* Walker and *D. pentictonella* Mutuura, Munroe and Ross) infest cones (Heinrich, 1956; Mutuura *et al.,* 1969; Neunzig, 2003) (Table 1.1, Figs. 1.1, 1.3). *Dioryctria clarioralis* is distributed in the southeastern United States while *D. pentictonella* occurs in the west and ranges from southern British Columbia to California and Nevada (Heinrich, 1956; Mutuura *et al.,* 1969; Neunzig, 2003). *Dioryctria clarioralis* larvae are an economically important pest of southern United States seed orchards; *D. pentictonella* is less of an economic issue.

The *erythropasa* group

Dioryctria erythropasa Dyar is the sole North American species in this group. Other species are recorded in Central and South America (Neunzig, 2003) (Table 1.1).

The *pygmaeella* group

The two members of the *pygmaeella* species group, *D. pygmaeella* Ragonot and *D. caesirufella* Blanchard and Knudson (Table 1.1, Fig. 1.3), are unique within *Dioryctria* as cone-feeders on Taxodiaceae (Merkel, 1982; Neunzig, 2003). *Dioryctria pygmaeella* is restricted to the coastal plains of the eastern United States and eastern Texas; *D. caesirufella* is known from east-central Texas and north-eastern Mexico (Blanchard and Knudson, 1983; Neunzig, 2003).

The *schuetzeella* group

The *schuetzeella* group consists of *D. reniculelloides* Mutuura and Munroe and *D. pseudotsugella* Munroe (Table 1.1, Figs. 1.1, 1.3). *Dioryctria reniculelloides* is widely distributed throughout southern Canada and the northern United States; *D. pseudotsugella* is more limited in range, recorded in British Columbia and the northwestern United States. Roe and Sperling (2007) have addressed the diagnosis and delimitation of these two species.

The *zimmermani* group

The *zimmermani* species group contains eighteen species, of which seven infest cones: *D. amatella* Hulst, *D. cambiicola* Dyar, *D. merkeli* Mutuura and Munroe, *D. resinosella* Mutuura, *D. taedae* Schaber and Wood, *D. taedivorella* Neunzig and Leidy, and *D. yatesi* Mutuura and Munroe (Table 1.1, Figs. 1.1, 1.3). Of these species, *D. amatella* and *D. merkeli* are the most pestiferous. As with the *abietella* species group, taxonomic confusion is prevalent within the *zimmermani* group due to the lack of diagnostic features and larval host overlap. Based on the degree of morphological and larval host overlap, an examination of the species limits among members of the *zimmermani* species group is needed.

Dioryctria taedae is an important pest of loblolly pine, *Pinus taeda* L., initially associated with a range from Delaware to Georgia (Schaber and Wood, 1971). This species has been routinely confused with the morphologically similar species *D. amatella* and *D. merkeli*. In fact, the type series for *D. taedae* contains both *D. merkeli* and *D. amatella* material, which adds to the confusion (Hedlin *et al.,* 1980). *Dioryctria amatella* occurs in the southeastern United States (Neunzig *et al.,* 1964; Neunzig, 2003), and is sympatric with *D. taedae* in parts of its range. Although *D. amatella* is considered the primary pest of longleaf pine, *Pinus palustris* Miller, it is known to infest most other pines within its range making it nearly impossible to use larval host as a diagnostic character for species in that region (Hedlin *et al.*, 1980, Neunzig, 2003). *Dioryctria taedivorella* ranges from eastern Virginia and North Carolina to northern Alabama and Mississippi (Neunzig and Leidy, 1989; Neunzig, 2003) and is also a pest of loblolly pine. In the past, this species has been confused with *D. merkeli* and *D. zimmermani* Grote, although the latter is now considered to be a cambial tissue borer (Neunzig, 2003). *Dioryctria merkeli* is morphologically similar to a number of other species throughout its range. The hosts for *D. merkeli* are slash, *Pinus elliottii* Engelmann, and longleaf pine in northern Florida, southern Georgia, and southern Mississippi (Mutuura and Munroe, 1979). Although Mutuura and Munroe (1979) also included Virginia, Maryland, North

Carolina, and eastern Texas as part of the range of *D. merkeli*, these occurrences likely pertain to other species (Neunzig, 2003). *Dioryctria yatesi* is restricted to the mountains of the coastal southeastern United States and Tennessee and is the only member of the *zimmermani* species group to infest table mountain pine, *Pinus pungens* Lambert, (Mutuura and Munroe, 1979; Neunzig, 2003). *Dioryctria resinosella* feeds on red pine, *Pinus resinosa* Aiton, which is found throughout southern Ontario and in the northeastern United States from Maine to Minnesota (Mutuura ,1982; Neunzig, 2003). *Dioryctria cambiicola* is the only known cone-infesting member of the *zimmermani* species group in western North America. Mutuura *et al.,* (1969) reported *D. cambiicola* throughout British Columbia and the western United States. *Dioryctria cambiicola* has been recorded only on lodgepole pine, *Pinus contorta* Douglas ex Loudon . The confusion that exists in the *zimmermani* species group coupled with its economic importance makes a taxonomic revision of this group necessary.

Overall, *Dioryctria* taxa show a wide range of host associations and feeding habits within and between species groups (Table 1.1, Fig. 1.1). Host associations partially determine landscape-level distribution patterns, however the mechanisms driving these patterns remain unexplored. In particular, distribution patterns of polyphagous *Dioryctria* are likely structured by host preferences that differ within and between geographic regions. Within geographic regions, the behaviours and interactions that mediate dispersal into appropriate habitats, and host-finding within such habitats, should be investigated. Information related to landscape-level distribution patterns will contribute to monitoring and prediction protocols that are required by integrated pest management programs (Fig. 1.4).

General biology

Research on the biology of seed-feeding *Dioryctria* has been insufficient to facilitate the development of sophisticated integrated pest management programs in seed orchards. Identification of the processes driving spatial and temporal distributions of populations will provide the foundation for the development of management programs.

This section explores the life history, reproductive traits, and host use of North American *Dioryctria* species and describes knowledge gaps that require further research.

Seasonal and diurnal phenology

Most *Dioryctria* species exhibit protandry on a seasonal basis. The initiation of seasonal activity by *Dioryctria* varies with location, though it commonly extends from early spring to early fall. Multivoltism exists in several species especially those in warmer climates. Adult *Dioryctria* generally eclose at night and are active soon after dark (Fatzinger and Asher, 1971*b*; Trudel *et al.,* 1995). The phenology and location of oviposition and larval development is influenced by host biology. Although the majority of *Dioryctria* pupate within or near the cone, pupation can also occur in the soil proximate to the host tree.

The *abietella* group

Populations of *D. abietivorella* are univoltine in the northern parts of its range (Hedlin *et al.,* 1980) but bivoltine in the north-western United States (Keen, 1952). Capture of adult males in pheromone-baited traps occurs between May and October in the western provinces and states (Roe *et al.,* 2006; unpublished data). It is unclear whether two periods of adult flight, in spring and late summer/fall (Hedlin *et al.,* 1980), correspond to two distinct generations or prolonged development of a single generation. Evidence for overlapping generations is supported by the presence of different larval instars in mid-summer (Lyons, 1957). Alternate developmental pathways may also occur: some *D. abietivorella* larvae develop through mid to late summer while others enter diapause and overwinter (Lyons, 1957). MacKay (1943) reports only one flight period in June throughout its range in Canada.

In contrast to *D. abietivorella, D. ebeli* exhibits five to six generations per year in northern Florida (Ebel, 1965). Multivoltism of *D. ebeli* is facilitated by moderate winter temperatures and larval use of seasonally available tissues (Ebel, 1965). Rust-infected cones are essential habitat for *D. ebeli* in late fall and spring, while second year cones of slash pine are readily infested in summer and early fall (Ebel, 1965).

Male *D. abietivorella* flight in response to sex pheromone begins two hours after sunset, peaks four hours after sunset and ends an hour after dawn (unpublished data). Oviposition by *D. abietivorella* typically begins the night following mating, and can continue for up to two weeks (Trudel *et al.*, 1995). Eggs are laid singly or in small clusters on or between cone scales and on needles (Lyons, 1957; Ruth, 1980; Martineau, 1984). Female *D. abietivorella* lay a maximum of one hundred eggs and an average of twenty-five eggs throughout their lifetime (Trudel *et al.*, 1995) and are less fecund than females of *D. ebeli*, which lay upwards of three hundred eggs (Ebel, 1965). *Dioryctria ebeli* oviposit for approximately one week on substrates that include male flower scales and rust-infected cones (Ebel, 1965).

Dioryctria abietivorella eggs are approximately 1 mm in diameter, oval and flattened with stellate pattern of ridges on the chorionated surface (Lyons, 1957; Ebel, 1965) (Fig. 1.2). As with other *Dioryctria* species (McLeod and Daviault, 1963; Ebel, 1965; Pasek and Dix, 1989), newly-laid *D. abietivorella* eggs are creamy white and turn reddish as development progresses (unpublished data). The dark head capsule of the embryo is discernible through the chorion prior to egg hatch (McLeod and Daviault, 1963; Pasek and Dix, 1989). Egg hatch occurs approximately seven days after oviposition at 25 °C for *D. abietivorella* (unpublished data) and in three to four days at 27 °C for *D. ebeli* (Ebel, 1965). At 25 °C, with a 16L:8D light cycle, *D. abietivorella* larvae develop through five (occasionally six) instars within twenty-three days (Trudel *et al.*, 1995). Once feeding is complete, *D. abietivorella* larvae exit the cone to pupate inside a frass-covered cocoon (Keen, 1952; Lyons, 1957; Trudel *et al.*, 1999*b*). Pupation may occur in the duff (Keen, 1952; Ebel, 1965; Martineau, 1984; Trudel *et al.*, 1999*b*) or in a frass webbing on the exterior of the cone (Keen, 1952). *Dioryctria ebeli* also leave the cone to pupate and adult eclosion occurs in eleven days at 24 °C (Ebel, 1965; Neunzig and Merkel, 1967).

The *auranticella* group

Auranticella species group members are typically univoltine (Neunzig *et al.*, 1964; Pasek and Dix. 1989). Studies conducted in North Carolina and Ontario report one generation of *D. disclusa* with adult flight in early summer in the south (Neunzig *et al.*, 1964; Pasek and Dix, 1989) and mid-summer in the north (Lyons, 1957). *Dioryctria disclusa* overwinter as early instar larvae in Ontario beneath bark scales of red pine (Lyons, 1957) but as late-instars in cones in southern parts of its range (Neunzig *et al.,* 1964). *Dioryctria auranticella* is similarly univoltine with peak adult flight occurring in mid-summer (Pasek and Dix, 1989).

Information on oviposition and fecundity of *Dioryctria* in the *auranticella* species group is limited. Male *D. auranticella* (Pasek and Dix, 1989) and *D. disclusa* (Lyons, 1957) emerge two or three and five days before females, respectively. One *D. auranticella* female reportedly laid twenty-seven eggs in her lifetime (Pasek and Dix, 1989); *D. disclusa* females lay an average of ten to fifty-five eggs, but can produce over one hundred in their lifetime (Lyons, 1957). *Dioryctria disclusa* eggs are laid under the bark scales of needle-free portions of red pine branches (Lyons, 1957). *Dioryctria auranticella* eggs require an incubation period of six to nine days at 26 ± 2 °C (Pasek and Dix, 1989). Larvae of both species feed on staminate flowers in early spring and then disperse to second-year cones later in the season. *Dioryctria auranticella* pupate inside the cone and eclose after fifteen days when held at 23 °C (Pasek and Dix, 1989). *Dioryctria disclusa* also pupate inside or on the cone (Farrier and Tauber, 1953; Neunzig and Merkel, 1967).

The *baumhoferi* group

Information regarding the phenology of the *baumhoferi* group is limited to *D. clarioralis,* which is generally univoltine (Neunzig *et al.,* 1964) but may be multivoltine in the southern reaches of its range (Yates and Ebel, 1975). In Florida, larvae infest buds and first-year cones between November and April (Ebel, 1965). Infestations in second-year cones occur in late winter and spring and pupae are found in early spring (Ebel, 1965). Pupae occur on trees or in the soil and eclose in about fourteen days when held at 24 °C (Neunzig *et al.*, 1964; Ebel, 1965).

The *pygmaeella* group

Dioryctria pygmaeella is multivoltine and can complete up to three generations per year (Merkel, 1982). Eggs are laid in niches between cone scales close to the basal region of the cone. Eggs hatch within a week; neonates eat the chorion and bore into the cone after making exploratory holes (Merkel, 1982). Larval development is complete within twenty-five days and pupation occurs in the cone. Exit holes are created prior to pupation and are closed with a thin, paper-like cover through which adults eclose in approximately two weeks (Merkel, 1982).

The *schuetzeella* group

The majority of phenological information for this group concerns *D. reniculelloides*. *Dioryctria reniculelloides* is univoltine (MacKay, 1943; McLeod and Daviault, 1963). Caged females lay an average of only nine eggs. Oviposition occurs in late summer in various protected locations including niches on stem bark, on lichen, between cone scales, or within frass on damaged foliage (McLeod and Daviault, 1963). Eggs hatch in eleven days under field conditions; early instar larvae enter diapause without feeding (MacKay, 1943; McLeod and Daviault, 1963; Mutuura and Munroe, 1973). Larvae are facultative cone-feeders that migrate between host tissues during development. In mid-spring, larvae feed on needles until cones become available (McLeod and Daviault, 1963). Pupae are present in mid-summer and adults fly in late summer (MacKay, 1943; McLeod and Daviault, 1963; Mutuura and Munroe, 1973).

Dioryctria pseudotsugella larvae are present in late May to late June and adults occur in early July (Prentice, 1965).

The *zimmermani* Group

Phenology of members of the *zimmermani* group has been best studied in *D. amatella*. Voltinism varies between one and four generations per year in Florida (Ebel, 1965); multivoltism is usual in Georgia and North Carolina (Coulson and Franklin, 1970*a*). Adult flight occurs in spring and early fall with less activity in mid-summer (Neunzig *et al.*, 1964; Coulson and Franklin, 1970*a*; Yates and Ebel, 1975; Hanula *et al.*, 1985). *Dioryctria amatella* females oviposit next to or directly on the larval substrate: second-year cones in the summer, and fusiform rust cankers (*Cronartium* Fr.) in the fall (Coulson and Franklin, 1970*a*, 1970*b*). Most eggs are laid three to twelve days after adult emergence with peak oviposition occurring between days five and seven (Hanula *et* *al.,* 1984*a*). Oviposition can continue for up to twenty-three days (Hanula *et al.,* 1984*a*), and lifetime fecundity can be as high as three hundred eggs per female (Ebel, 1965). *Dioryctria amatella* eggs held at 24 °C hatch in about seven days (Ebel, 1965). Egg surface patterns of *D. amatella* are similar to those of *D. abietivorella*: with radially symmetric ridges which are sinuous in *D. abietivorella* and straight in *D. amatella* (Ebel, 1965).

Dioryctria amatella larvae develop until pupation in early summer in various tissues, including fusiform rust cankers, wounds, and second-year cones (Ebel, 1965; Coulson and Franklin, 1970*a*, 1970*b*). Some adults eclose in mid-summer while a portion of the larvae undergo summer aestivation followed by adult eclosion in the fall. Mid-summer adults oviposit to begin a second generation with adult eclosion in November. Second generation adults lay eggs primarily in fusiform cankers or tree wounds; the resulting larvae feed through the winter (Coulson and Franklin, 1970*a*, 1970*b*). Some larvae also overwinter at the base of first-year cones, under unexpanded terminal needles, and in damaged, second-year cones (Neunzig *et al.,* 1964). In North Carolina, most *D. amatella* overwinter as early instar larvae, although older larvae also overwinter (Neunzig *et al.,* 1964). Development recommences in the spring and most adults emerge in early summer when second-year cones serve as suitable oviposition sites. In some cases, adult eclosion occurs earlier in the spring and females must oviposit on other tissues such as branch terminals or first-year cones. The resulting larvae must migrate to second-year cones later in the season to complete development (Coulson and Franklin, 1970*a*).

In conclusion, the development of pest management programs depends on knowledge of phenology and how it is affected by environmental conditions and host interactions. Assessment of temperature thresholds for development and determination of the influence of photoperiod and host phenology on development and mortality are required in order to create management protocols. High-quality oviposition and larval feeding microhabitats need to be identified to increase our understanding of local-scale distribution patterns. Furthermore, the effect of nutrition (larval, adult, and spermatophore-derived) on development and mortality rates should be measured.

Dioryctria display a wide range of overwintering habits, likely defined in part by host tree phenology as well as latitude. Research on overwintering ecology is needed to pinpoint overwintering locations and life stages of pestiferous *Dioryctria*. This information can be used to assess the need for and timing of control techniques. Identification of environmental cues that influence the phenology of *Dioryctria* will increase the understanding of interspecies interactions, population dynamics, and the temporal distributions of various lifestages. We also predict that there are within-species differences in seasonal activity along geographic gradients and with different host associations; this information is necessary for site-specific management.

Reproductive biology

Detailed accounts of reproductive behaviour in some species of *Dioryctria* are available (Fatzinger and Asher, 1971*a*; Phelan and Baker, 1990). In particular, mating behaviour of *D. ebeli* (*abietella* species group) and *D. amatella* (*zimmermani* group) have been thoroughly described (Fatzinger and Asher, 1971*a*; Phelan and Baker ,1990). Intra-species differences in calling behaviour as well as mating frequencies exist. Recent advances have greatly expanded our understanding of sex pheromone composition and intraspecific geographic variation in sex pheromones.

Delayed mating after adult eclosion seems prevalent in *Dioryctria*. Mating behaviour begins three to four, two to three, and two days post-eclosion in *D. abietivorella* (Trudel *et al.*, 1995), *D. amatella* (Ebel, 1965; Fatzinger, 1981; Hanula *et al.*, 1984*a*) and *D. auranticella* (Pasek and Dix, 1989), respectively. At least in *D. abietivorella*, this delay in mating may correlate with egg maturation (unpublished data).

Dioryctria species exhibit polyandrous mating patterns in seed orchards. In southern British Columbia, female *Dioryctria* in the *auranticella*, *abietella*, *ponderosae*, and *zimmermani* species groups mate multiple times throughout the season (unpublished data). This behaviour occurs in stands of Douglas-fir, *Pseudotsuga menziesii*, (Mirb.) Franco (Pinaceae), a spruce hybrid complex collectively termed “interior spruce” (Pinaceae) (Coates, 1994), and lodgepole pine, *Pinus contorta*. Preliminary data indicate that individuals of *D. abietivorella* mate up to eight times; those of other species mate just two or three times (unpublished data). Interspecific differences in benefits accrued by females through multiple matings may explain the differences in mating frequencies. It is unknown if male investment is important to female fitness and receptivity in *Dioryctria*. The effect of male investment may be species-specific, which could influence mating frequency among species.

Like other moths, mate-finding in *Dioryctria* is mediated by female-produced sex pheromones. For many species groups, female pheromone production and release behaviour (calling) have not been described. Calling behaviour of females in the *abietella* species group in North America is known only for *D. ebeli.* Virgin females initiate calling five to six hours after the onset of scotophase under a 12L:12D cycle; calling peaks nine hours after dark and stops before the onset of photophase (Fatzinger and Asher, 1971*a*). Females assume a characteristic calling position with the tip of the abdomen curved upwards between the wings and the pheromone gland extruded from the tip of the ovipositor (Fatzinger and Asher, 1971*a*). At one day post-eclosion, approximately 30% of *D. ebeli* call and are receptive to mating; the number of calling females doubles during the following scotophase (Fatzinger and Asher, 1971*a*). *Dioryctria disclusa* (*auranticella* species group) females begin calling three to five hours after sunset and male moth flight to pheromone follows the same periodicity (DeBarr and Berisford, 1981).

The female-produced sex pheromones of nine *Dioryctria* species are known (Table 3) and synthetic pheromone-baited traps are used to monitor adult activity of various species in seed orchards (Hanula *et al.*, 1984*b*, *c*; Hanula *et al.*, 2002; Strong *et al.*, 2008). For six of the nine species, *Z*9-tetradecenyl acetate (*Z*9-14:Ac) is the major component, although the importance of this component for *D. abietivorella* varies geographically (Grant *et al.*, 2009).

The sex pheromone of *D. abietivorella* contains two major components, (*Z*9, *E*11)-tetradecadienyl acetate (*Z*9, *E*11-14:Ac) and (*Z*3, *Z*6, *Z*9, *Z*12, *Z*15)-pentacosapentaene (C_{25} pentaene), both of which are not typically found in the sex pheromone gland extracts of other *Dioryctria* species (Millar *et al.*, 2005) (Table 1.3). C_{25} pentaene only weakly stimulates male moth antennae in electroantennographic assays but the addition of this component is crucial for attraction of males in field trials in western North America. A third component, *Z*9-tetradecenyl acetate (*Z*9-14:Ac), occurs in small amounts in female gland extracts (Millar *et al.*, 2005). Because these pheromone components have different vapour pressures and belong to different structural classes, it is likely that they are produced through independent biosynthetic pathways (Millar *et al.*, 2005); it is unknown how females emit the precise ratios of the two components. A 1:10 ratio of synthetic *Z*9, *E*11-14:Ac to C_{25} pentaene attracts male *D. abietivorella* in field trials (Table 1.3), but does not reflect the ratio of components stored in the female pheromone gland (Strong *et al.*, 2008).

Male *D. abietivorella* response to female sex pheromones varies geographically (Table 3), which may indicate the presence of different pheromone races (Grant *et al.*, 2009). Lures loaded with a 1:10 ratio of *Z*9, *E*11-14:Ac to C_{25} pentaene are attractive to males in western (Strong *et al.*, 2008) but not eastern Canada (Grant *et al.*, 2009). In eastern populations, the addition of *Z*9-14:Ac is crucial to elicit male response (Grant *et al.*, 2009). Male response to pheromones should be assessed in the populations located in the intervening geographic regions. Geographic variation of pheromone production throughout the large range of this species should be examined also. The minor pheromone component identified in *D. abietivorella* pheromone gland extracts, *Z*9-14:Ac, does not occur in its close European relative, *D. abietella* (Löfstedt *et al.*, 1983) or in *D. ebeli* (Miller *et al.*, 2010) (Table 1.3), the other North American member in the *abietella* group.

Female *D. ebeli* produce *Z*9, *E*11-14:Ac, a component of the *D. abietivorella* sex pheromone. Male *D. ebeli* are responsive to synthetic lures combining *Z*9, *E*11-14:Ac and C_{25} pentaene, the second crucial component of female *D. abietivorella* sex pheromone (Miller *et al.*, 2010) (Table 1.3). Additional work is required to determine whether other pheromone components, such as C_{25} pentaene, are produced by *D. ebeli* females (Miller *et al.*, 2010).

Limited information on pheromone biology is available for other species groups. Field trials that tested the attractiveness of C_{25} pentaene combined with the previously identified sex pheromone components of *D. amatella* (*zimmermani* group) and *D. disclusa* (*auranticella* group) show an increase in male response in both species. Increased male response was not seen in similar studies targeting *D. merkeli* (*zimmermani* group) (Miller *et al.*, 2010). *Dioryctria resinosella* (*zimmermani* group) requires a four-component blend that includes an alcohol, unique within this genus (Grant *et al.,* 1993). The most attractive blend for *D. resinosella* contains *Z*9-tetradecen-1-ol (Z9-14:OH) and *Z*9-dodecenyl acetate (Z9-12:Ac), although the latter component has not been found in female gland extracts (Grant *et al.,* 1993).

Only one pheromone component, *Z*9-14:Ac, has been identified in female gland extracts of *D. reniculelloides* (*schuetzeella* group) (Grant *et al.,* 1987). In electroantennogram assays of male *D. reniculelloides*, antennal responses were elicited by *Z*9-14:Ac, *Z*7-dodecenyl acetate (*Z*7-12:Ac), and *Z*7-dodecenal (*Z*7-12:Ald). The blend most attractive to male *D. reniculelloides* in field assays contained *Z*9-14:Ac as the major component and *Z*7-12:Ac or *Z*7-12:Ac and *Z*7-12:Ald as minor components (Grant *et al.,* 1987). *Dioryctria reniculelloides* is sympatric with *D. abietivorella*, utilizes many of the same hosts (Neunzig, 2003), and has overlapping adult flight activity. Inter-specific differences in pheromone blends may be a mechanism to reduce competition in pheromone communication (Evenden *et al.,* 1999).

There is great potential for the use of synthetic sex pheromones to control pestiferous *Dioryctria* species. Seed orchards provide suitable conditions for the application of mating disruption or attract-and-kill formulations that have been widely adopted in fruit orchards (Witzgall *et al.,* 2008). Future research should address the stability of pheromone components under field conditions and determine whether the full pheromone blend is required to disrupt mating behaviour. The identity of sex pheromones of various *Dioryctria* species may serve as a useful trait to include in phylogenetic analyses of this taxonomically difficult group.

Host Use: semiochemicals and larval feeding

Semiochemicals are important cues that mediate host use by female *Dioryctria*, although information beyond basic identification of host cues is limited. Landscape-level distributions could be in part driven by host-cue mediated migration. Pheromone trapping studies indicate that traps placed higher in the canopy (where the highest density of cones and the majority of females occur) capture more male moths than do lower-placed traps (Hanula *et al.,* 1984*c*; Strong *et al.,* 2008). Female and male local-scale distribution may be influenced by cone-derived host cues; male distribution is also likely mediated through female presence.

Oviposition

The monoterpenes myrcene and car-3-ene, released from twigs of eastern white pine, *Pinus strobus* L., elicit both antennal and oviposition responses from female *D. abietivorella* (Shu *et al.,* 1997). Although (-)-limonene is another oviposition stimulant, it does not trigger significant electrophysiological responses from antennae (Shu *et al.,* 1997). These monoterpenes stimulate greater antennal responses from older, mated females than from younger virgins. Increased antennal responsiveness is correlated with increased oviposition, although it is not known if host volatiles actually attract gravid females to oviposition sites (Shu *et al.,* 1997). Male and female *D. ebeli* adults show greater antennal responses to volatiles emitted from the basal and stalk portion of first-year cones of slash pine than to second-year cones and the apical and middle portions of first-year cones, indicating that the basal cone region may be an important oviposition site (Asher, 1970).

In the laboratory, female *D. amatella* (*zimmermani* group) will initiate calling, mating, and oviposition only in the presence of fusiform rust galls (Fatzinger, 1981). *Dioryctria amatella* females use ∝-pinene as an oviposition stimulant; female response is increased by the presence of myrcene and limonene (Hanula *et al.,* 1985). Female *D. amatella* prefer oviposition substrates with high monoterpene content even though feeding by first instar larvae is negatively correlated with monoterpene content.

Host acceptance and oviposition in various species of *Dioryctria* appear to be influenced by host monoterpene emissions; these behaviours could be exploited for pest management. Future research should identify cues used by females for host recognition and acceptance. Migration may also be mediated through host cues; this is another tactic that could be used to deter pest population establishment.

Larval feeding

Larval feeding on cones reduces the reproductive potential of the tree host. In some *Dioryctria* species, larvae migrate between cones as resources are depleted, thus damaging multiple cones during their development (Lyons, 1957; Neunzig, 2003). In addition, larvae can use entry holes created by other insects and thereby act as secondary pests that amplify primary damage (Heinrich, 1956; Lyons, 1957; Ruth, 1980; Fidgen and Sweeney 1996).

Infestations by larval *D. abietivorella* can be detected by an external accumulation of frass, without pitch secretions, on the cone (Fig. 1.2) (Keen 1952; Lyons, 1957; Ross and Evans 1957; Hedlin *et al.*, 1980; Ruth, 1980). In addition to cones, *D. abietivorella* larvae feed on other host tissues including needles, shoots, twigs, and cambial tissue of the tree bole (*e.g.* wounds, galls, and graft unions) (Hedlin *et al.*, 1980; Ruth, 1980). These other tissues appear to provide suboptimal nutrition or greater exposure to natural enemies because larvae feeding on foliage and bark experience higher mortality than those feeding on cones (Trudel *et a.,l* 1999*a*).

Although some *Dioryctria* species are polyphagous, larval performance on the various hosts is unequal. Field-reared *D. abietivorella* larvae have different survival rates when reared on white spruce; black spruce, *Picea mariana* (Miller) Britton, Sterns and Poggenb. (Pinaceae); and jack pine, *Pinus banksiana* Lambert (Trudel *et al.*, 1999*a*). Larvae reared on white spruce, black spruce, and jack pine respectively, show the highest, intermediate, and poorest survival rates. Larval development time is similar on white and black spruce, but is prolonged on jack pine. These differences in larval performance on different hosts likely contribute to a host preference hierarchy that should be identified for monitoring purposes.

In the *zimmermani* group, *D. amatella* larvae feed on different tissue types at different times during the season. In late summer, up to seven different larval stadia can be found feeding in the same cone (Hanula *et al.*, 1985). At the beginning of the season, *D. auranticella* larvae feed on male and female flowers and then migrate to second-year cones. Larvae often require two cones to complete development (Pasek and Dix, 1989). Larvae of *D. disclusa* (*auranticella* group) also damage multiple cones during development (Neunzig *et al.*, 1964).

Host preference hierarchies in polyphagous species of *Dioryctria* remain unexplored, but may govern landscape-level population distributions. Local-scale larval distribution patterns are likely mediated by feeding stimulants and deterrents as well as inter- and intra-specific competition. It is unclear how larval nutrition influences adult fitness, particularly when larvae feed on a less favourable host or tissue type.

Evolutionary ecology

Fluctuating abundance of food resources

Temporal heterogeneity in food resources has likely been a strong driving force in the evolution of *Dioryctria.* Monophagous species of *Dioryctria* (*e.g.* feeding on one conifer genus) such as *D. ebeli* (Table 1.1, Fig. 1.1) are not typically associated with economically damaging levels of infestation. This situation contrasts with polyphagous members of the *abietella* species group, *D. abietivorella* and *D. abietella*, which are significant pests. Host switching by polyphagous species may allow for the maintenance of high population densities despite temporal heterogeneity in the availability of cone crops (Janzen, 1971). The causal mechanisms linking polyphagy and pest status require further clarification. Despite its monophagous lifestyle, *D. amatella* (*zimmermani* group) is a serious pest of pines. *Dioryctria amatella* develops on a variety of host tissues, permitting year-round development and reproduction (Coulson and Franklin, 1970*a*). Continued development during the winter may give *D. amatella* a competitive advantage. This plasticity in tissue use may sustain high population densities in years when cone crops are poor.

Sympatry and interspecific competition

One way in which sympatric species reduce interspecific competition is through resource partitioning and utilization (Grinnell, 1924). This strategy may be another factor in the evolution of the patterns in tissue use and host association of sympatric *Dioryctria* species (Table 1.1, Fig. 1.1). Members of the *pygmaeella* species group are sympatric with some *baumhoferi* group species, and with *D. amatella* (*zimmermani* group) (Table 1.1). *Pygmaeella* group species utilize members of Cupressaceae rather than Pinaceae while *baumhoferi* group and *zimmermani* group species feed solely on *Pinus*. Utilization of *Taxodium* by members of the *pygmaeella* group may permit sympatry of these species. Little genetic information for the *pygmaeella* group is available; its relatedness to the *baumhoferi* and *zimmermani* groups is unknown.

Dioryctria abietivorella and members of the *schuetzeella* group overlap in geographic range and host associations but differ in host tissue use. *Dioryctria abietivorella* are primarily cone-feeders; *schuetzeella* group species are predominantly foliage-feeding. Similarly, the closely related sympatric species, *D. cambiicola* and *D. abietivorella* both feed on lodgepole pine, but *D. cambiicola* feeds primarily on cambium while *D. abietivorella* favours cones. Differential tissue use also occurs in sympatric *ponderosae* group species feeding on ponderosa pine: *D. auranticella* feeds primarily on cones, the others, specialize on healthy and rust-infected cambium.

Between-season differences in tissue use by *Dioryctria* species in the southeastern United States may also facilitate sympatry. A survey of *Dioryctria* species infesting slash and longleaf pine in north Florida highlighted the differences in tissue use between tree hosts and throughout the season (Ebel, 1965). Although *D. amatella*, *D. clarioralis* and *D. ebeli* occur on both pine species, *D. amatella* and *D. ebeli* are most abundant on slash pine, while *D. clarioralis* are more commonly found on longleaf pine. On slash pine, the majority of *D. amatella* occur in fusiform cankers, *D. ebeli* on cones with rust, and *D. clarioralis* on male strobili. On longleaf pine, *D. amatella* and *D. ebeli* are most commonly found on healthy second-year cones while *D. clarioralis* occurs primarily in first-year cones. Spring populations of *D. amatella* larvae are frequently in male and female flower buds, new shoots, overwintering cones, and fusiform rust cankers. Later in the spring, rust-infected cones are also infested by *D. amatella*. In spring, *D. ebeli* can be found on first-year cones and vegetative buds, as well as second-year longleaf pine cones. During the summer, *D. amatella* larvae generally feed on second-year cones, while *D. ebeli* larvae are abundant in second-year slash pine cones. In the fall and winter, *D. amatella* larvae are again located on bud scales, cone stalks, and cankers of longleaf pine. Fall populations of *D. ebeli* larvae frequently infest second-year longleaf cones and overwinter on buds or cankers, similar to *D. amatella*. Year-round, *D. clarioralis* larvae feed on buds and on young cones. *Dioryctria ebeli* larvae feed on tissue with less resin than do *D. amatella* and will often remain within the same tissue to complete development. As well, *D. ebeli* often infest material damaged by *D. amatella*. Although causal mechanisms are unknown, resource partitioning by *Dioryctria* may allow sympatric species to coexist.

Pest status and management

Infestations of seed-feeding *Dioryctria* species can have a significant economic impact on seed production used for conifer propagation. Although infestations are most detrimental in seed orchards, natural stands can also be affected. Knowledge of *Dioryctria* life history and distribution patterns, in both managed and natural stands, will provide the framework for effective pest monitoring and management techniques (Table 1.5, Fig. 1.4). This section describes the pest status, monitoring, and control of seed-feeding *Dioryctria* species considered to be pests, and identifies where further research should be directed.

Impacts in natural forest stands

Little documentation is available on infestation rates of North American *Dioryctria* species in natural forest stands. In the western United States, cones of whitebark pine, *Pinus albicaulis* Engelmann suffer up to 68% infestation by *D. abietivorella*, with 13% seed loss (Kegley *et al.*, 2001). Cones in wild stands of Douglas-fir and hemlock, *Tsuga* Carrière (Pinaceae), are subject to attack by *Dioryctria* species in western North America (Furniss and Carolin, 1977).

Dioryctria abietella, a member of the *abietella* group in Europe, infests cones of at least nine conifer species (Roques, 1983; Lee and Lee, 1994). *Dioryctria abietella* destroys cones, consumes seeds, and reduces germination of Bhutan pine, *Pinus wallichiana* A.B. Jacks (Bhandari *et al.*, 2006*a*). In Switzerland *D. abietella* infestations damage up to 33% of cones of Swiss stone pine, *Pinus cembra* L. (Dormont and Roques, 1999), and 8% of cones of Norway spruce, *Picea abies* (L.) Karst. with 29% seed loss per infested cone (Seifert *et al.*, 2000). Fourteen percent of cones of European silver fir, *Abies alba* Mill. (Pinaceae) in Poland were infested by *D. abietella* (Skrzypczyńska, 2004).

In natural stands, temporal heterogeneity of food sources is an important factor that regulates populations of seed-feeding *Dioryctria* species (Turgeon *et al.*, 1994). Mast seeding occurs in many conifer genera and may have evolved as a tactic to avoid severe seed herbivory (Janzen, 1971; Silvertown, 1980; Kelly, 1994). Mast seeding results in highly variable seed crops between years but synchronous seed production within a year (Silvertown, 1980; Kelly, 1994). During mast years, trees produce abundant seed cone crops which satiate herbivores, allowing a proportion of the seed to escape herbivory. The length of time between mast years is variable; cone yields can be very low during the intervening period (Silvertown, 1980). In the year following a mast seeding event, herbivore population densities increase, in response to the previous year's abundant food sources (Hedlin, 1974; Miller *et al.,* 1984) but then decline between mast years (Miller *et al.,* 1984; Shea, 1989). As a result, the episodic nature of cone production may prevent the establishment of large, stable populations of specialist seed feeders. Polyphagous species such as *D. abietivorella* can feed on alternate tissues and host species between mast crops. Seed feeders can also respond to heterogeneity in cone crops spatially by moth dispersal (Mosseler *et al.,* 1992) or temporally through prolonged larval diapause (Turgeon *et al.,* 1994).

Seed feeders may severely reduce the reproductive success of rare conifer species (Mosseler *et al.*, 1992). In Newfoundland in 1988, a large, geographic masting event occurred in black spruce, white spruce, eastern tamarack (*Larix laricina* (Du Roi) Koch (Pinaceae)), and balsam fir, *Abies balsamea* (L.) Miller followed by a rare three-year mast-seeding event in red pine (Mosseler *et al.*, 1992). The consistently large red pine cone crops coupled with low cone crops in other conifers may have served to concentrate the polyphagous *D. abietivorella* on rarely-exploited red pine. Cone infestation ranged from 8% in lightly infested stands to 98% in highly infested stands. In severely infested trees, the number of full seeds was reduced by 93% compared to 11% in lightly infested trees. Large seed losses two years in a row can negatively impact the reproductive capacity of rare, patchily-distributed conifer populations (Mosseler *et al.,* 1992).

Impacts in conifer seed orchards

In managed forest systems, *Dioryctria* species are most problematic in conifer seed orchards that produce seed for reforestation programs (Pasek and Dix, 1989; Schowalter, 1994). Orchards are managed to increase seed quality and quantity as well as to decrease cone crop variability between years (Zobel and Talbert, 1984; Turgeon *et al.,* 1994). Because seed orchards are monocultures and management practices attempt to circumvent mast seeding, seed orchards provide an abundant and consistent food supply for seed feeders including *Dioryctria* species (Zobel and Talbert, 1984; Turgeon *et al.*, 1994).

Most conifer genera grown in seed orchards are subject to attack by *Dioryctria* species, with the notable exception of *Thuja* L. (Cupressaceae). Historically, up to 15.6% of seeds in Douglas-fir seed orchards in the western United States has been lost to *D. abietivorella* damage (Schowalter *et al.*, 1985). *Dioryctria abietivorella* infestation rates as high as 42% occur in Idaho orchards of western white pine, *Pinus monticola* Douglas ex. D. Don (Shea *et al.*, 1986). Many Pinaceae species grown in seed orchards in Canada, including pines, spruces (*Picea* A. Dietr.), firs (*Abies* Mill.), larch (*Larix* Mill.), and Douglas-fir, sustain losses to seed production by several species of *Dioryctria* (Turgeon and de Groot, 1994, Turgeon *et al.*, 2005). Up to 80% of cones were attacked in some spruce and Douglas-fir seed orchards in central British Columbia in 2004 (Strong, 2005). Norway spruce seed orchards in Sweden are attacked by *D. abietella* larvae with infestation rates between 23 and 77% (Rosenberg and Weslien, 2005).

Seed pests cause direct and indirect damage to cone and seed production. Larval feeding results in smaller cones and lowered seed production per cone (Mosseler *et al.*, 1992). Additionally, pathogens and phytophagous cone insects can promote the presence of secondary pests such as mycophages, saprophages, as well as other phytophages, and thereby amplify primary cone damage (Turgeon *et al.*, 1994). In black spruce and white spruce seed orchards, *D. abietivorella* infestation rates are higher on cones damaged by *Strobilomyia* Michelson (Diptera: Anthomyiidae) cone maggots than on undamaged cones (Fidgen and Sweeney, 1996). Preference for cones infested by cone maggots may be due to pre-existing entry points or the increased nutritive value of infested cones (Fidgen and Sweeney, 1996). Detection of maggot-infested cones by *D. abietivorella* may be mediated by an alteration of the cone monoterpene profile, which acts as a kairomone to attract females for oviposition or larvae for feeding (Fidgen and Sweeney, 1996). Early instar *D. amatella* larvae infest loblolly pine cones previously infested though not killed by *D. disclusa* and the cone midge, *Resseliella silvana* (Felt) (Diptera: Cecidomyiidae) (Hanula *et al.*, 1985).

Dioryctria species magnify the impact of disease damage through a preference for feeding on diseased tissues. Southern cone rust, *Cronartium strobilinum* (Arthur) Hedge and Hahn (Cronartiaceae), affects slash and longleaf pine first-year cones (Merkel, 1958). *Dioryctria amatella* and *D. ebeli* larvae occur in higher abundance on rust-infected, than on disease-free, first-year cones. As *Dioryctria* populations increase on these cones and infected first-year cones die, larvae migrate to second-year cones to continue feeding. Higher larval infestations occur on second-year cones on the same branches as rust-infected first-year cones than on branches with disease-free first-year cones. Seed losses due to rust are amplified by *Dioryctria* infestation on second-year cones (Merkel, 1958).

Cone-boring by *Dioryctria* species also increases cone vulnerability to pathogens. Diplodia tip blight, *Sphaeropsis sapinea* (Fr.) Dyko and B. Sutton (*incertae sedis*), is a common fungal pathogen of conifers that affects shoots, twigs and cones of infected trees (Nicholls and Ostry, 1990). The occurrence of *S. sapinea* in closed red pine cones increased from 9% to 56% when *D. resinosella* (*zimmermani* group) was also present. Boring into closed cones can provide a point of entry for the conidia and cone damage may release the fungus from dormancy (Feci *et al.*, 2003).

The presence of pathogens such as blister rusts may provide polyphagous, facultative cone-feeders with another nutrient source to maintain populations between mast years. *Dioryctria amatella, D. abietivorella*, and *D. cambiicola* attack pines infected with *Cronartium* Fries (Cronartiaceae) species rust diseases (Coulson and Franklin, 1970*a*, 1970*b*; Furniss and Carolin, 1977; Rocchini *et al.*, 1999). The presence of *D. cambiicola* was positively associated with the presence of the *C. coleosporioides* Arthur in lodgepole pine provenance trials in western Canada. Larvae feed at the perimeter of the rust blisters in association with fungal hyphae; the benefits of fungal feeding on *D. cambiicola* fitness are unknown (Rocchini *et al.*, 1999). Measurements of larval and adult survival as well as fecundity are required to ascertain the potential benefits of hyphal feeding.

Monitoring

Management of *Dioryctria* in conifer seed orchards depends on knowledge of the presence of adult or larval stages in the seed production area (Fig. 1.4). The phenology of several pest complexes has been investigated. Schowalter (1994) exposed Douglas-fir cones as oviposition substrates to potential pests for discrete periods throughout the summer in western Oregon. *Dioryctria abietivorella* larval infestations are highest when cones are exposed between mid-April and mid-May, and lower infestations occur from cone exposure through mid-August (Schowalter, 1994). May and June are the primary months of cone infestation by *D. auranticella* larvae (Pasek and Dix, 1989).

Monitoring *Dioryctria* larvae is conducted either by scouting for frass on cones (*e.g.* Rosenberg and Weslien, 2005), or through cone dissections to recover larvae (*e.g.* Dormont and Roques, 1999). No quantitative sampling plans exist for larvae, although indirect estimates of infestation rates can be derived from repeated examinations of cones throughout their development. This method is used in southern United States seed orchards to estimate cone damage and survival (DeBarr *et al.*, 1975). Throughout development, tagged first- and second-year cones are repeatedly checked for damage and mortality, thereby taking into account damage due to *Dioryctria* (DeBarr *et al.*, 1975). Sequential sampling is not economical to quantify stand infestation levels but can be used to determine if cone collection is worthwhile (Kozak, 1964). Larval identification during sampling is critical, and a dichotomous key to the final instars of six eastern North American cone-infesting *Dioryctria* species is available (Leidy and Neunzig, 1989). Morphological keys do not exist for other species or earlier instars, though it should now be possible to identify species groups and most species using molecular techniques (Roe *et al.*, 2006) (Fig. 1.4).

Ultraviolet light is attractive to a broad range of *Dioryctria* species (Fig. 1.4), and adult *Dioryctria* are monitored successfully with light traps. In British Columbia, black light traps are used to monitor flight activity of male and female *D. abietivorella* as well as members from the *auranticella*, *ponderosae*, and *zimmermani* species groups (unpublished data). McLeod and Yearian (1982) deployed blacklight traps to monitor five species of *Dioryctria* in Arkansas. Trap catch of *D. amatella* coincides with adult eclosion from pupae in mature cones. Blacklight traps are also used in Georgia to determine the flight phenology of four *Dioryctria* species (Yates and Ebel, 1975). Roe *et al.,* (2006) used ultraviolet traps to collect adults of the *schuetzeella* group in California.

In all species except *D. pygmaeella*, male moth capture exceeds female catch in light traps (McLeod and Yearian, 1982).

Sex pheromones of several *Dioryctria* species have been developed as monitoring tools. Several commercially-available traps baited with a pheromone attractive to *D. abietivorella* males (Strong *et al.*, 2008) were tested at different positions in the canopy. Diamond traps (ConTech Enterprises Inc., Delta, BC) positioned near the tops of trees capture the largest number of male moths (Strong *et al.*, 2008). Significantly more males are captured when traps are positioned near the tops of trees: 4 m above ground in topped seed orchard trees, 8 m in untopped seed orchard trees, and 22 m in wild-stand trees (unpublished data). The similarity of pheromone components and blends used by four southern Nearctic *Dioryctria* species led to both interspecific cross-attraction and inhibition of adult male attraction to traps baited with synthetic pheromone (Hanula *et al.*, 1984*b*). Attraction of male moths from three different species groups (*D. disclusa, D. merkeli,* and *D. clarioralis*) to one lure allows these species to be monitored with a single lure in a single trap. In the same orchards, *D. amatella* (*zimmermani* group) must be monitored with a different lure in separate traps because of an inhibitory effect on pheromone response of other *Dioryctria* species mediated by one component of the *D. amatella* pheromone. Hanula *et al.* (1984*c*) found pheromone-baited Pherocon 1C traps caught more *D. amatella* than three other trap designs tested. Although adult males are captured in pheromone-baited traps, trap capture has not yet been incorporated into integrated pest management programs targeting these species (Fig. 1.4). Effective monitoring using sex pheromones will depend on the composition of the species assemblages present. It remains to be determined if pheromone-baited trap capture is related to larval damage levels and therefore could be developed as a decision-making tool for orchard pest managers.

Decision-making

Action thresholds based upon monitoring results are typically used to make decisions in integrated pest management protocols (Pedigo, 1996) (Fig. 1.4). Without the development of quantitative methods to monitor for eggs, larvae, or adults, action thresholds cannot be devised for pestiferous *Dioryctria* species. Currently, pesticide applications could be timed based on information known about adult flight phenology, but no such protocols have been developed. A degree-day model has been developed for *D. amatella*, based on accumulations above a threshold temperature of 11 °C initiated with a biofix of five male moths in pheromone traps (Hanula *et al.*, 2002). No other decision-making model for management of seed-feeding *Dioryctria* has been published to date.

Control

Semiochemicals: sex pheromones

Pheromone-based mating disruption is one method that may prove useful to control infestations of seed-feeding *Dioryctria* (Fig. 1.4). Similarity in pheromone composition among species (Table 1.3) may facilitate multispecies mating disruption of sympatric *Dioryctria* species. DeBarr *et al.* (2000) explored the possibility of using pheromone-based mating disruption to control three *Dioryctria* species in loblolly pine seed orchards in Georgia. Three polyvinyl chloride rods releasing a mean of 0.458 mg/ha/d of synthetic pheromone per tree in 1.2-ha plots resulted in 91, 96.7, and 99.5% reductions in trap catches of two *zimmermani* group species (*D. amatella* and *D. merkeli*) and one *auranticella* group species (*D. disclusa*), respectively, compared to untreated plots. Communication disruption of *Dioryctria merkeli* and *D. disclusa* was achieved using *Z*9-14:Ac; disruption of *D. amatella* was achieved using *Z*9-11:Ac. Larval densities and seed loss were not compared between treatments (DeBarr *et al.*, 2000). Large-scale implementation of mating disruption to control *Dioryctria* has not been reported.

Semiochemicals: host plant volatiles

Information about semiochemical cues used by Palearctic *Dioryctria* species for host location and oviposition sites could be exploited for the management of pestiferous North American populations (Fig. 1.4). Host-produced semiochemicals have been used to control *D. mutatella* Fuchs and Fazekas infestations in the French Alps (Dormont *et al.,* 1997). The cones of mountain pine, *Pinus uncinata* Mill. ex Mirb., are more heavily attacked by *D. mutatella* than those of Swiss stone pine and also have different cone volatile terpene profiles (Dormont *et al.,* 1997). Extracts of Swiss stone pine sprayed on cones of mountain pine reduce cone damage by *D. mutatella* from 14.1% to zero, and infestation by all seed-feeding pests from 31% to zero. Large-scale control that utilizes push-pull management strategies will also rely on information derived from research on host preference hierarchies.

Genetic host resistance

Genetic host resistance to *Dioryctria* attack can be exploited in control regimes (Fig. 1.4). Loblolly pine seed orchards show clonal variation in cone attack rates by southern Nearctic *Dioryctria* species (*D. amatella, D. clarioralis, D. disclusa,* and *D. merkeli*) that range from 0 to 67% (Askew *et al.,* 1985). Genetic variation in host resistance allows for the possibility of breeding for resistance, especially because cone infestation rates are not correlated with performance values for tree height or diameter. Even without extensive breeding efforts, sprays could be directed to only the most susceptible genotypes in order to reduce total spray load in an orchard. Fodor (1978) determined the heritability of resistance to *D. abietella* in a Polish pine orchard to be between 0.66-0.86, values that would support the development of a *Dioryctria* resistance-breeding program. However, there is a negative correlation between resistance and cone production, and no breeding effort targeting host resistance to *Dioryctria* has been published.

Parasitoids

Hymenopteran species in the families Braconidae, Eulophidae, Ichneumonidae, Ptermalidae, and Trichogrammatidae, as well as tachinid flies parasitize cone and seed-feeding *Dioryctria* species (Table 1.4). Ichneumonids and eulophids parasitize *D. abietivorella* larvae (Lyons, 1957; Bradle,n 1974). Larvae of seven species of *Elachertus* Spinola (Hymenoptera: Eulophidae) emerged from one mature *D. abietivorella* larva (Lyons, 1957). Though there are few reports, parasitism rates may be as high as 18.8% in *D. amatella* in loblolly pine seed orchards (Mihelcic *et al.,* 2003) and 27.0% in north Florida slash pine (Belmont and Habeck 1983). *Phanerotoma* Wesmael (Hymenoptera: Braconidae) was the most common parasitoid genus associated with *D. ebeli* in slash pine orchards in north Florida (Belmont and Habeck 1983). Forty-eight percent of *D. disclusa* pupae sampled in Ontario red pine orchards were parasitized (Lyons, 1957). Very little biological information is known about the parasitoids of *Dioryctria*; although Belmont and Habeck (1983) did record detailed life history information for *Hyssopus rhyacioniae* Gahan (Hymenoptera: Eulophidae) and a new species of *Pediobius* Walker (Hymenoptera: Eulophidae) reared from *D. amatella*.

The impact of natural enemies in the control of *Dioryctria* populations requires further documentation, including species identification, geographic and host ranges, life history, phenology, and host mortality rates. Parasitoid complexes should be identified and shifts in community composition throughout the season require resolution. Hyperparasitoids, such as *Itoplectis conquisitor* (Say) (Hymenoptera: Ichneumonidae) (Goulet and Huber,1993), *Elasmus meteori* Ashmead (Hymenoptera: Elasmidae) (Merkel, 1982) and a species of *Pediobius* Walker (Belmont and Habeck, 1983), could potentially disrupt biological control efforts, and should be identified. At this time natural enemies have not been incorporated into biological control programmes against *Dioryctria* species (Fig. 1.4).

Pathogens

Pathogenic microorganisms infect several *Dioryctria* species (Table 1.4). In their study of pathogenic microorganisms in *D. amatella*, Mihelcic *et al.* (2003) found that the fungus *Beauveria bassiana* (Balsamo) Vuillemin (Clavicipitaceae), a granulosis virus, and a microsporidian species infected 0.4%, 2.4%, and 5.2% of sampled larvae, respectively. In laboratory trials, *B. bassiana* and the virus were virulent against all larval stages and the microsporidia caused high levels of mortality in early instar larvae. Although natural infection rates of *B. bassiana* were low, a sprayable product is commercially available (Laverlam International Corporation, Butte, Montana USA) and has potential for development as a biopesticide in this system. Additional pathogens, *Hirsutella satumaensis* Aoki (Clavicipitaceae) and *Metarhizium anisopliae* (Mechnikov) Sorokin (Clavicipitaceae), have been recovered from field-collected Palearctic *Dioryctria* species (Mihelcic *et al.*, 2003). More work is needed to fully identify pathogens of North American *Dioryctria* that could be candidates for biological control (Fig. 1.4).

Biopesticides

The commercially available biopesticide, *Bacillus thuringiensis* Berliner subsp. *kurstaki* (Bacillaceae) (Btk), has been tested against various species of *Dioryctria* (Fig. 1.4). *Dioryctria abietivorella* larvae in all stadia are highly and equally susceptible to Btk (Trudel *et al.,* 1997). *Dioryctria amatella* first instar larvae are highly susceptible to Btk in laboratory bioassays; older instars are less susceptible but die more quickly than younger larvae once infected (McLeod *et al.*, 1982). McLeod *et al.* (1984) field-tested Btk sprays in Oklahoma on loblolly pine second-year cones. Btk application one week after *D. amatella* are first caught in pheromone traps increases cone survival by approximately 18% and seed set per cone by 48%. No significant protection from *D. amatella* occurs if Btk is applied two weeks after first trap catch, suggesting that application timing is critical to the success of Btk (McLeod *et al.,* 1984).

The efficacy of Btk has been most thoroughly tested against *D. abietella* (*abietella* group) in Norway spruce seed orchards in Sweden. Three applications, starting within one week of the onset of adult flight, reduce the incidence of infested cones by 65% (Weslien, 1999). Highly susceptible first instar larvae probably ingest Btk as they penetrate cones and older larvae may be exposed as they move between cones (Weslien, 1999). To test the hypothesis that Btk is more persistent within young cones than on exposed cone surfaces, Glynn and Weslien (2004) tested sprays when the female strobili were open. In this trial, *Dioryctria* infestation level was reduced by approximately 50% in sprayed plots. Cone damage can be reduced between 30 and 60% using commercial application equipment in 0.3 ha plots (Rosenberg and Weslien, 2005).

Insecticides

Currently, synthetic pesticides are the main control strategy used to manage *Dioryctria* populations in conifer seed orchards (Fig. 1.4). In laboratory assays comparing contact toxicity of seventeen insecticides against *D. amatella,* eight were more toxic than azinphosmethyl, the only insecticide registered against this species at that time (DeBarr and Fedde, 1980). Two organophosphosphate and three pyrethroid insecticides are ovicidal to *D. amatella* at any point during egg development, while two other organophosphates are ovicidal only to five-day old eggs (McLeod and Yearian, 1983). Timed applications of effective ovicides would be a useful management tool because cone-dwelling larvae escape later contact insecticide applications.

An advantage of systemic insecticides, which can translocate into cones and kill seed-feeding insects, is reduced non-target mortality. Six systemic insecticides tested against *D. amatella* have low contact toxicity in laboratory assays but are effective in the field, which suggests that the mode of action is through ingestion (DeBarr and Fedde, 1980). The efficacy of injection of loblolly pine stems with emamectin benzoate (EB), imidacloprid, or a combination of EB and thiamethoxam was tested in Texas (Grosman *et al.,* 2002). A single application of EB reduced damage from *Dioryctria* species by 94 - 97% over a two-year period; imidacloprid significantly reduced damage only during the season of application. A comparison of injections and dripline drenches of several systemic insecticides against *D. abietella* attacking Himalayan spruce, *Picea smithiana* (Wall.) Boiss. in northern India revealed that stem injections with monocrotophos resulted in 13.5% infested cones, compared with 87.5% in control plots (Bhandari *et al.,* 2006*b*).

Broadcast sprays of contact insecticides are the most commonly used insecticide application technique against a variety of *Dioryctria* species. Treatment of western white pine seed orchards in Idaho to target *D. abietivorella* with one or two, high-volume ground applications of fenvalerate resulted in 13.6% infested cones (and doubled seed yield), compared with 46.6% in untreated control plots (Haverty *et al.,* 1986). Five ground applications of azinphos-methyl, fenvalerate, and permethrin applied by airblast sprayer at monthly intervals reduced seed losses due to *Dioryctria* species in loblolly pine seed orchards by 52-67% (Nord *et al.,* 1985). Aerial applications of fenvalerate increased cone survival from 14% in unsprayed orchards to as high as 86% in treated orchards (Nord *et al.,* 1985). Two ground applications of fenvalerate with an airblast sprayer can significantly reduce cone damage due to *D. amatella*, though a single application does not successfully control the pest (Hanula *et al.,* 2002). Use of a degree-day model to time applications allows for fewer targeted applications of fenvalerate against *D. amatella* (Hanula *et al.,* 2002). Future research on chemical insecticides should identify the effects on non-target species present in seed orchards, including sub-lethal effects and secondary pest upsurges.

Future directions

Research on factors influencing population distributions on spatial and temporal scales is needed to build sound management strategies. Resolution of factors that influence landscape-level distributions of individuals in habitats as mediated by host-finding behaviour, pre and post-mating dispersal, and overwintering behaviour should be a high priority because of their importance in monitoring and management. On a finer scale, at the tree level, it is not fully understood what influences egg or larval distribution. Fine-scale distribution may be moderated by cues that stimulate or deter oviposition and feeding. Intra- and interspecific interactions such as predation and competition could also affect fine-scale distribution.

Research to address the phenological and genetic diversity in *Dioryctria*, including identification of geographic pheromone races, host races, and pesticide resistance, is also necessary to ensure the efficacy of species-specific control methods. Several avenues of phylogenetic research within *Dioryctria*, particularly in the *abietella* group, are needed. First, a thorough population genetic survey of *D. abietivorella* throughout its range is needed to quantify intraspecific variation, given the geographic variability of pheromone response (Grant *et al.,* 2009) and larval host associations. Second, species limits between *D. abietivorella* and *D. ebeli* need to be examined using a variety of molecular (*e.g.*, microsatellites), morphological (*e.g.*, wing pattern variation), and behavioural traits (*e.g.*, larval host plant association) using an integrative approach as described for *D. reniculelloides* and *D. pseudotsugella* (Roe and Sperling, 2007). Third, a well-supported phylogeny of *Dioryctria* species groups would be helpful for forming hypotheses about the diversification of the genus; this will require more comprehensive representation of the known species and their genomic differences.

Successful management of cone-feeding *Dioryctria* relies on sound monitoring protocols, decision-making methods, and appropriate control strategies (Fig. 1.4). Integrated pest management requires the creation of damage prediction methods and monitoring methods, as well as an understanding of population dynamics and density-damage relationships. These measures allow for the development of economic injury thresholds and quantitative decision-making. Integration of predictive methods, such as economic injury thresholds, into control strategies can permit biologically-based timing rather than calendar spray applications.

Pheromone-based control tactics such as mating disruption or attract-and-kill require information derived from reproductive behaviour studies. Additional research on *Dioryctria* reproductive strategies focussing on factors that influence female fecundity (*e.g.* larval feeding, male-derived nutrients), mating frequency, and oviposition are required to design and improve management strategies. The significance of nutrition, including nectar sources for adults, on development rate and reproductive potential is unknown. Semiochemical-based control that exploits important host-finding cues could potentially be used to monitor females and manipulate host-finding and reproductive behaviours. Further development of integrated pest management programs requires research to incorporate pathogens such as Btk into *Dioryctria* management. The effect of natural enemies (insect, avian, and mammal) should be promoted by the development of their habitat.

In conclusion, effective pest control for *Dioryctria* should include multiple methods that serve to manipulate and/or exploit pest behaviour and reduce the current reliance on highly toxic, broad spectrum pesticides to control *D. abietivorella*. This can be achieved through: 1) correct identification of target insects through increased understanding of diagnostic molecular and morphological traits, 2) full documentation of the life history requirements and interactions of *Dioryctria* species within and between trophic levels, and 3) better understanding of the integration of the heterogeneous evolutionary, ecological, and environmental factors that promote the adaptive flexibility of *Dioryctria* coneworms underlying their economic impact.

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Table 1.1. Host and tissue use by *Dioryctria* species organized by species group. Modified from Coulson and Franklin, 1970*a*, Neunzig, 2003.

***Dioryctria* species**	**Larval host**	**Tissue used**	**Citation**
***abietella* gr.**			
abietivorella	Fir species, *Abies* Mill. Spruce species, *Picea* A. Dietr. Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco Jack pine, *Pinus banksiana* Lamb. Lodgepole pine, *Pinus contorta* Douglas ex Loudon Red pine, *Pinus resinosa* Aiton Scotch/scots pine, *Pinus sylvestris* L. White pine, *Pinus strobus* L.	Healthy cones Damaged second year cones Needles Shoots Cambium	Heinrich, 1956; Lyons, 1957; Prentice, 1965; Hedlin *et al.*, 1981; Neunzig, 2003
ebeli	Loblolly pine, *Pinus taeda* L. Longleaf pine, *Pinus palustris* M. Slash pine, *Pinus elliottii* Engelm.	Rust-infested first year cones Healthy second year cones Fusiform rust cankers Vegetative buds and shoots Previously infested material	Ebel, 1965; Mutuura and Munroe, 1979; Hedlin *et al.*, 1981;Neunzig, 2003
***auranticella* gr.**			
auranticella	Austrian pine, *Pinus nigra* Arnold Knobcone pine, *Pinus attenuata* Lemmon Ponderosa pine, *Pinus ponderosa* C. Lawson	Male and female flowers Second year cones	Raizenne, 1952; Heinrich, 1956; Prentice, 1965; Hedlin *et al.*, 1981; Pasek and Dix, 1989; Neunzig, 2003
disclusa	Austrian pine Jack pine Loblolly pine Longleaf pine Mountain pine, *Pinus uncinata* Mill. ex Mirb. Pitch pine, *Pinus rigida* Mill. Red pine Scotch/scots pine Virginia pine, *Pinus virginiana* Mill.	Male and female flowers Second year cones	Farrier and Tauber, 1953; Heinrich, 1956; Lyons, 1957; Munroe, 1959; Neunzig *et al.*, 1964; Prentice, 1965; Hedlin *et al.*, 1981; Pasek and Dix, 1989; Neunzig, 2003
rossi	Arizona pine, *Pinus arizonica* (ngelm. Durango pine, *Pinus durangensis* Martínez Ponderosa pine	Cones	Munroe, 1959; Prentice, 1965; Hedlin *et al.*, 1981; Neunzig, 2003

***baumhoferi* gr.**			
clarioralis	Loblolly pine Longleaf pine Shortleaf pine, *Pinus echinata* Mill. Slash pine	First and second year cones Buds	Heinrich, 1956; Neunzig *et al.*, 1964; Ebel, 1965; Hedlin *et al.*, 1981; Neunzig, 2003
pentictonella	Lodgepole pine Ponderosa pine	Cones Buds	Mutuura *et al.*, 1969; Hedlin *et al.*, 1981; Neunzig, 2003
***erythropasa* gr.**			
erythropasa	Chihuahua pine, *Pinus leiophylla* Schiede and Deppe var. *chihuahuana* (Engelm.) Shaw	Cones	Heinrich, 1956; Hedlin *et al.*, 1981; Neunzig, 2003
***pygmaeella* gr.**			
caesirufella	Bald cypress, *Taxodium distichum* (L.) Rich.	Cones	Blanchard and Knudson, 1983; Hedlin *et al.*, 1981; Neunzig, 2003
pygmaeella	Bald cypress Pondcypress, *Taxodium ascendens* Brongn.	Cones	Heinrich, 1956; Hedlin *et al.*, 1981; Neunzig, 2003
***schuetzeella* gr.**			
pseudotsugella	Douglas-fir	Cones Cambium	Munroe, 1959; Prentice, 1965; Mutuura and Munroe, 1973; Hedlin *et al.*, 1981; Neunzig, 2003
reniculelloides	White spruce, *Picea glauca* (Moench) Voss Sitka spruce, *Picea sitchensis* (Bong.) Carrière Engelmann spruce, *Picea engelmannii* Parry ex Engelm. Black spruce, *Picea mariana* (Mill.) Britton, Sterns & Poggenb. Colorado spruce, *Picea pungens* Engelm. Douglas-fir Western hemlock, *Tsuga heterophylla* (Raf.) Sarg. Alpine fir, *Abies lasiocarpa* (Hook.) Nutt. Amabilis fir, *Abies amabilis* (Douglas ex Louden) Douglas ex Forbes Balsam fir, *Abies balsamea* (L.) Mill. White fir, *Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr. Lodgepole pine	Shoots Foliage Cones	MacKay, 1943; Heinrich, 1956; Munroe, 1959; McLeod and Daviault, 1963; Prentice, 1965; Mutuura and Munroe, 1973; Hedlin *et al.*, 1981; Neunzig, 2003
***zimmermani* gr.**			

amatella	Loblolly pine Longleaf pine Shortleaf pine Slash pine	Rust-infected first year Healthy second year cones Terminal shoots Fusiform canker galls Buds Flowers Wounds	Heinrich, 1956; Neunzig *et al.*, 1964; Ebel, 1965; Franklin and Coulson 1970*a*, 1970*b*; Hedlin *et al.*, 1981; Neunzig, 2003
cambiicola	Coulter pine, *Pinus coulteri* D. Don	Cambium Second year cones Shoots Buds *Peridermium* blister rust canker	Heinrich, 1956; Lyons, 1957; Munroe, 1959; Mutuura *et al.*, 1969; Hedlin *et al.*, 1981; Neunzig, 2003
merkeli	Loblolly pine Longleaf pine Slash pine	Flowers Shoots Cones	Mutuura and Munroe, 1979; Hedlin *et al.*, 1981; Neunzig, 2003
resinosella	Red pine	Lateral and terminal shoots Cones	Hedlin *et al.*, 1981; Mutuura 1982; Neunzig, 2003
taedae	Loblolly pine	Cones	Schaber and Wood, 1971; Hedlin *et al.*, 1981; Neunzig, 2003
taedivorella	Loblolly pine	Cones	Neunzig *et al.*, 1964
yatesi	Table Mountain pine, *Pinus pungens* Lamb.	Cones	Mutuura and Munroe, 1979; Hedlin *et al.*, 1981; Neunzig, 2003

Table 1.2. Members of the *D. abietella* group, with ranges of intra- and interspecific divergence (uncorrected pairwise distance) of mitochondrial cytochrome c oxidase I-II genes shown, when available. Distances in bold indicate species with overlapping intra- and interspecific variation.

Species	**Intra**	**Inter**	**Citation**
D. abietella Denis & Schiffermüller	**0 – 4.8%**	**1.1 – 5.0%**	Du *et al.*, 2005; Roux-Morabito *et al.*, 2008
D. abietivorella Grote	**0 - 0.8%**	**0 - 4.7%**	Du *et al.*, 2005; Roe *et al.*, 2006; Roux *et al.*, 2008
D. ebeli Mutuura & Munroe	n.a.	0 – 4.3%	Roux-Morabito *et al.*, 2008
D. mendecella Staudinger	**0.1 – 1.4%**	**1.2 – 4.8%**	Roux-Morabito *et al.*, 2008
D. pineae Staudinger	0%	1.2 – 4.5%	Roux-Morabito *et al.*, 2008
D. resiniphila Segerer & Pröse	n.a.	0.8 – 4.9%	Knölke *et al.*, 2005
D. simplicella Heinemann (= *D. mutatella* Fuchs & Fazekas)	0%	0.8 – 5.1%	Roux-Morabito *et al.*, 2008

Table 1.3. Sex pheromone blends for North American, cone-feeding *Dioryctria* species. Table modified from Pherolist (www.nysaes.cornell.edu/pheronet/) and updated to include current research.

Species	**Component(s)**	**Female-produced blend**[1]	**Blend attractive to males** (μg)[3]	**Citation**
***abietella* gr.**				
D. abietivorella (eastern)	(*Z*)-9-tetradecenyl acetate[1] (9*Z*,11*E*)-tetradecadienyl acetate[1] (3*Z*,6*Z*,9*Z*,12*Z*,15*Z*)-pentacosapentaene[1]	1:4:10	67:200:2000	Millar *et al.*, 2005; Strong *et al.*, 2008; Grant *et al.*, 2009
D. abietivorella (western)	(*Z*)-9-tetradecenyl acetate[1, 2] (9*Z*,11*E*)-tetradecadienyl acetate[1] (3*Z*,6*Z*,9*Z*,12*Z*,15*Z*)-pentacosapentaene[1]	1:1	200:2000	Millar *et al.*, 2005; Strong *et al.*, 2008
D. ebeli	(9*Z*,11*E*)-tetradecadienyl acetate [1] (3*Z*,6*Z*,9*Z*,12*Z*,15*Z*)-pentacosapentaene	0.51 – 1.58 ng	1:10	Millar *et al.*, 2010
***auranticella* gr.**				
D. auranticella	*Z*9-tetradecenyl acetate [1]	Not reported		Pasek and Dix, 1989
D. disclusa	*Z*9-tetradecenyl acetate[1] (3*Z*,6*Z*,9*Z*,12*Z*,15*Z*)-pentacosapentaene		30-300 1:10	Meyer *et al.*, 1982; Hanula *et al.*, 1984*b*; Miller *et al.*, 2010
***baumhoferi* gr.**				
D. clarioralis	*Z*9-tetradecenyl acetate[1] *E*9-tetradecenyl acetate[1] *Z*11-hexadecenyl acetate	12:88	30:3.6:1.5-3	Hanula *et al.*, 1984*b*; Meyer *et al.*, 1984
***schuetzeella* gr.**				
D. reniculelloides	*Z*9-tetradecenyl acetate[1] *Z*7- dodecenyl acetate *Z*7-docecenal		3:0.15 3:0.15:0.15	Grant *et al.*, 1987
***zimmermani* gr.**				
D. amatella	*Z*11-hexadecenyl acetate[1] (3*Z*,6*Z*,9*Z*,12*Z*,15*Z*)-pentacosapentaene		100 1:10	Hanula *et al.*, 1984*b*; Meyer *et al.*, 1986; Miller *et al.*, 2010
D. merkeli	*Z*9-tetradecenyl acetate *E*9-tetradecenyl acetate		30:0-4.5	Meyer *et al.*, 1984; Hanula *et al.*, 1984*b*
D. resinosella	*Z*9-tetradecenyl acetate[1] *Z*9-tetradecen-1-ol[1] *Z*9- dodecenyl acetate *E*9-tetradecenyl acetate	1:0.2	30:5:10:1.5	Grant *et al.*, 1993

[1] detected in female sex pheromone gland extracts

[2] this component not attractive to males in field trials
[3] μg loaded on rubber septum

Table 1.4. Natural enemies reported from North American cone-feeding *Dioryctria* species.

Dioryctria species	**Natural enemy**	**Citation**
***abietella* gr.**		
abietivorella	*Elachertus* Spinola species [1], *Pediobius* Walker species[1]; *Exeristes comstockii* Cresson[2], *Exochus evetriae* Rohwer[2], *Scambus longicorpus occidentalis* Walley[2], Unidentified tachinid[3]	Lyons, 1957; Bradley, 1974
ebeli	*Hyssopus rhyacioniae* Gahan[1]; *Agathis* Latreille species[4], *Apanteles* Förster species[4], *Apanteles bushnelli* Muesebeck[4], *Macrocentrus* Curtis species[4], *Phanerotoma* Wesmael species[4]; *Trichogramma* Westwood species[5], *Leskiomina tenera* Wiedemann[3], *Phrynofrontina* Townsend species[3], *Xanthophyto* Townsend species[3]	Ebel, 1965; Belmont and Habeck, 1983
***auranticella* gr.**		
auranticella	*Elachertus argissa* Walker[1]; *Exeristes comstockii*[2], *Exochus turgidus* Holmgren[2], *Horogenes* Förster species[2], *Ichneumon brunneri* Rohwer[2], *Scambus* species poss. *annulatus* (Kiss)[2], *Temelucha platynotae* Cushman[2]; *Meteorus* Haliday species[4], *Meteorus indagator* Riley[4], *Habrobracon cushmani* Muesebeck[4]; *Dibrachys cavus* Walker[6], *Nemorilla pyste* Walker[3]	Raizenne, 1952; Bradley, 1974; Pasek and Dix, 1989
disclusa	*Calliephialtes comstockii* Cresson[2], *Coelichneumon* Thomson species[2], *Exeristes comstockii* Cresson[2], *Exochus turgidus*[2], *Horogenes* species[2], *Ichneumon brunneri*[2], *Microtypus* Ratzeburg species[4]; *Apanteles* species[4], *Apanteles bushnelli*[4], *Bracon rhyacioniae* Muesebeck[4], *Meteorus indagator*[4], *Meteorus tetralophae* Muesebeck[4]; *Dibrachys cavus*[6]; *Eupelmus cyaniceps* var. *amicus* Girault[7], Unidentified tachinid[3]	Raizenne, 1952; Lyons, 1957; Farrier and Tauber, 1953; Neunzig *et al.*, 1964; Bradley, 1974
***baumhoferi* gr.**		
clarioralis	*Hyssopus rhyacioniae*[1]; *Campoplex* Gravenhorst species[2]; *Apanteles bushnelli*[4], *Macrocentrus* species[4], *Phrynofrontina* species[3], *Beauvaria bassiana* (Balsamo) Vuillemin[8]	Ebel, 1965; Belmont and Habeck, 1983
***pygmaeella* gr.**		
pygmaeella	*Elasmus meteori* Ashmead[1]; *Calliephialtes grapholithae* (Cresson)[2]; *Apanteles* species[4], *Bracon* F. species[4], *Macrocentrus delicates* Cresson[4], *Macrocentrus dioryctriae* Muesebeck[4]; *Brachymeria molestae* Burks[9], *Genea* Rondani species[3], *Lixophaga* Townsend species[3]	Merkel, 1982
***schuetzeella* gr.**		
reniculelloides	*Pimplopterus* Ashmead species[2], *Pimplopterus parvus* Cresson[2], *Campoplex validus* Cresson[2], *Campoplex* species[2], *Horogenes kiehtani* Viereck[2], *Scambus hispae* Harris[2], *Itoplectis conquisitor* Say[2], *Glypta fumiferanae* Viereck[2], *Phytodietus vulgaris* Cresson[2]; *Apanteles* species[4], *Apanteles canarsiae* Ashmead[4], *Apanteles fumiferanae* Viereck[4], *Bracon politventris* Cushman[4], *Bracon gelechiae* Ashm.[4], *Meteorus trachynotus* Viereck[4], *Phryxe pecosensis* Townsend[3], *Eumea caesar* Aldrich[3]	Raizenne, 1952; McLeod and Daviault, 1963

***zimmermani* gr.**		
amatella	*Hyssopus rhyacioniae*[1], *Pediobius* species[1]; *Campoplex* species[2], *Campoplex conocola* Rohwer[2], *Exeristes comstockii*[2], *Exochus turgidus*[2], unidentified Lissonotini[2], *Lissonota amatella* Townes[2]; *Agathis* species[4], *Bracon* species[4], *Macrocentrus* species[4], *Macrocentrus dioryctriae*[4], *Phrynofrontina* species[3], *Xanthophyto* species[3], *Beauvaria bassiana*[8]; granulosis virus[10]; unidentified microsporidia	Ebel, 1965; Neunzig *et al.*, 1964; Belmont and Habeck, 1983; Mihelcic *et al.*, 2003
cambiicola	*Hyssopus rhyacioniae*[1]; *Campoplex conocola*[2], Unidentified tachinid[3]	Lyons, 1957
taedivorella	*Hyssopus rhyacioniae*[1]	Neunzig *et al.*, 1964

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[1] Hymenoptera: Eulophidae; [2] Hymenoptera: Ichneumonidae; [3]Diptera: Tachinidae; [4]Hymenoptera: Braconidae; [5]Hymenoptera: Trichogrammatidae; [6]Hymenoptera: Pteromalidae; [7]Hymenoptera: Eupelmidae; [8]Clavicipitaceae; [9]Hymenoptera: Chalcididae; [10]Baculoviridae

Table 1.5. Knowledge gaps in the biology and ecology of *Dioryctria* species and pest management applications that could be developed if missing information is resolved.

	Egg	**Larva**	**Pupae**	**Adult**	**Application**
Distribution					
large-scale[1]	Edge effects Important habitat traits	Movement between trees Masting events	Soil composition Meteorological effect on survival	Migration Habitat finding	Habitat management Monitoring techniques
small-scale[2]	Oviposition stimulants/deterrents Effect of density on oviposition	Feeding stimulants/deterrents Predation, competition effects	Predation rates	Predation, competition Synergy of semiochemicals & pheromones Dispersal (*e.g.*, pre/post mating, density effects)	Monitoring techniques Semiochemical-based trapping (monitoring, disruption) Feeding deterrents Predation enhancement
temporal	Development thresholds Photoperiod influence Host phenology Degree day accumulations	Development thresholds Photoperiod influence (overwintering) Host phenology Degree day accumulations	Photoperiod influence	Temperature thresholds for flight/reproduction	Monitoring Timing of biopesticide or insecticide applications
Nutrition	Female diet/spermatophore influence	Performance on secondary host species/ tissue type Cannibalism & predation rates	Size effects on fitness	Nectar source Influence of spermatophore	Kairomone based attract and kill
Natural enemies	Identity and mortality levels Parasitized deter oviposition?	Predators, parasites and diseases Mortality rates	Predators and diseases Mortality rates	Predators	Biocontrol agents
Phenological and genetic diversity	Pesticide resistance Genetic diversity	Pesticide resistance Host races (as related to dispersal distance and gene flow) Genetic diversity Relationship to habitat heterogeneity	Pesticide resistance Genetic diversity	Geographic pheromone races Host races (as related to dispersal distance and gene flow) Genetic diversity Pesticide resistance	Identification for species- and host race-specific monitoring and control strategies

Relationship to habitat heterogeneity

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[1] landscape to tree
[2] on-tree

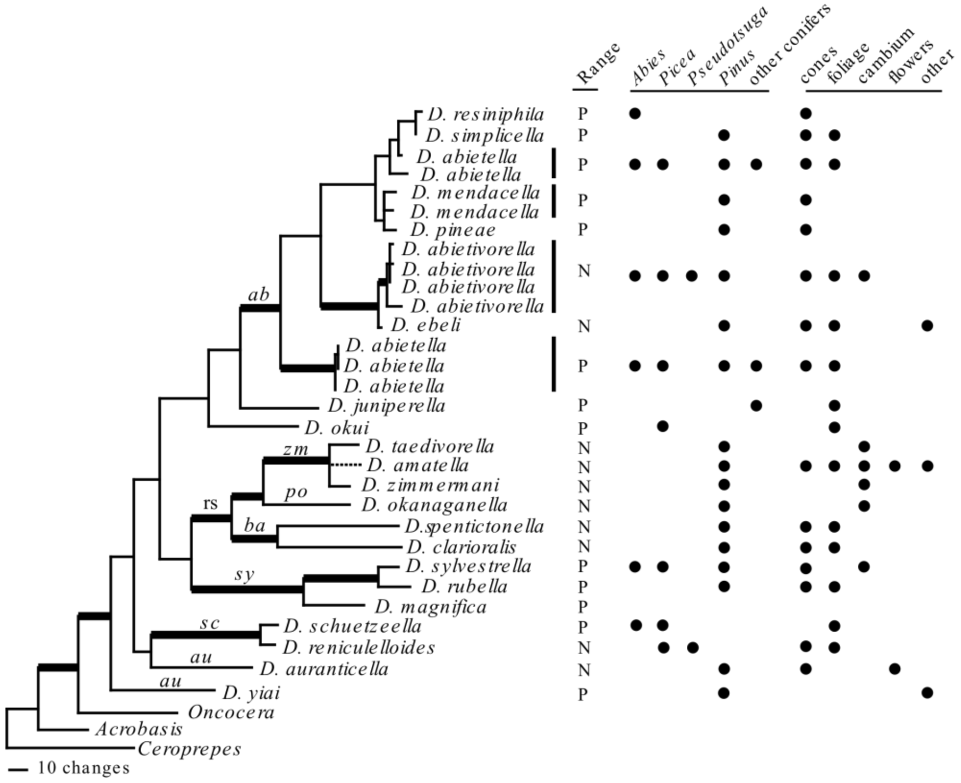

Figure 1.1. One of two most parsimonious phylograms (length = 1444) based on mitochondrial sequences (cytochromes c oxidase I and II – available on GenBank) from exemplar *Dioryctria* species representing major species groups and three outgroups. Thickened branches indicate parsimony bootstrap support of >80% (100 replicates). Labeled nodes are as follows: *ab*, *abietella* group; *au, auranticella* gr.; *ba, baumhoferi* gr.; *po, ponderosae* gr.; rs, raised-scale gr; *sc, schuetzeella* gr.; *zm, zimmermani* gr. *D. amatella* (dashed line) lacks sequence data, but is placed within the *zimmermani* group based on morphological characteristics. Geographic range (Nearctic, N; Palearctic, P), native host place, and host plant tissue are indicated.

Figure 1.2. *Dioryctria abietivorella, abietella* species group: a) fertilized egg, b) larva, c) adult, and d) an infested cone depicting external accumulation of frass.

Figure 1.3. Left fore- and hind-wings of adult *Dioryctria* species: a) *D. auranticella*, *auranticella* species group; b) *D. okanaganella*, *ponderosae* species gr.; c) *D. pseudotsugella*, *schuetzeella* species gr.; d) *D. cambiicola*, *zimmermani* species gr.*;* and e) *D. pygmaeella, pygmaeella* species gr.

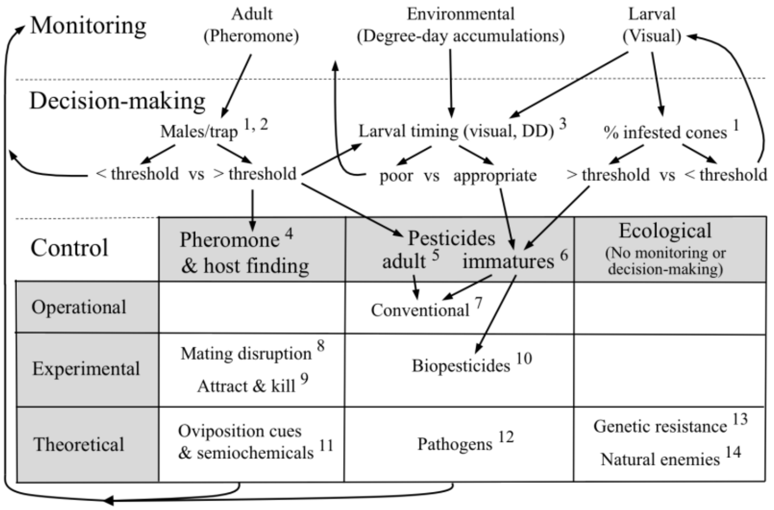
Monitoring
Adult (Pheromone)
Environmental (Degree-day accumulations)
Larval (Visual)
Decision-making
Males/trap 1, 2
Larval timing (visual, DD) 3
% infested cones 1
< threshold vs > threshold
poor vs appropriate
> threshold vs < threshold
Control
Pheromone 4 & host finding
Pesticides adult 5 immatures 6
Ecological (No monitoring or decision-making)
Operational
Conventional 7
Experimental
Mating disruption 8
Attract & kill 9
Biopesticides 10
Theoretical
Oviposition cues & semiochemicals 11
Pathogens 12
Genetic resistance 13
Natural enemies 14

Figure on previous page.

Figure 1.4. Management flow chart for *Dioryctria* species in conifer seed orchards. Results from monitoring protocols (top portion) flow to inform decision-making methods (middle portion) and subsequently to control strategies and tactics (lower table). Control strategies are identified as operational (currently used in managed seed orchards), experimental (show promise and are under active investigation to bring to operational use), and theoretical (conceptually plausible, but not currently under investigation). Success of control actions is determined by a return to monitoring protocols. Points needing further research to enable implementation are identified by numbers as follows:

1. Determine economic or action thresholds for density/damage relationships, value of seed, and cost of controls.
2. Quantify relationship of male trap catches to female density, oviposition and cone damage; dispersal of mated and unmated females within and among areas.
3. Create a degree-day model to predict moth development and to time control efforts.
4. Identification, production, commercialization of pheromones.
5. Rates of immigration and re-invasion; relationship between male trap catches and female densities.
6. Efficacy of ovicidal, long-residual, and systemic insecticides.
7. Efficacy of systemic and new, taxon-specific insecticides.
8. Knowledge of immigration/emigration of mated and unmated females, reproductive behaviour, and an abundant, inexpensive supply of pheromones.
9. Knowledge of immigration/emigration of mated and unmated females, reproductive behaviour, and use of expensive, less readily available pheromone.
10. Operational development of *Bacillus thuringiensis* Berliner subsp. *kurstaki* (Bacillaceae).
11. Clarify roles of visual, tactile, and semiochemical cues in host-finding and oviposition.
12. Identify and culture host-specific viral and bacterial pathogens that could be applied in response to high moth densities.
13. Clonal variation and heritability of *Dioryctria* susceptibility; economics of breeding for resistance.
14. Incidence, taxonomic identity, geographic ranges, and efficacy of predators and parasitoids in controlling *Dioryctria* populations; knowledge of ecological modification to encourage natural enemies.

Chapter 2: Seasonal flight and mating status of *Dioryctria* species

Introduction

Host plant phenology and interspecific competition influence the temporal and spatial distributions of phytophagous insects. The phenology of insect herbivores can be temporally constrained by the plant host, particularly when host tissue is ephemeral, and if the feeding life stage has limited dispersal capability (Denno *et al.*, 1995). Temporal and spatial partitioning of host resources reduces the impact of interspecific competition (Grinnell, 1924). The likelihood of competition is higher for phytophagous insects that feed within host plants (*e.g.* cone or stem feeders) compared to external feeders, like defoliators (Denno *et al.*, 1995). Interspecific competition is more prevalent among closely related species because of similar feeding habits and hosts compared to taxonomically distant species (Denno *et al*., 1995).

Competitive interactions among phytophagous insects may be exacerbated by variation in host tissue abundance. Variation in host tissue abundance can be extreme for insects that feed on conifer cones. In years with low cone availability, competition between cone and seed-feeders is enhanced due to the concentration of individuals that feed in dwindling food sources (Shea, 1989). Competition for cones occurs within the cone- and seed-feeding guild on white fir, *Abies concolor* [Gord. and Glend.] Lindl. (Pinaceae), that is composed of *Dioryctria abietivorella* Grote (Lepidoptera: Pyralidae), *Cydia* prob. *bracteatana* Fernald (Lepidoptera: Oleuthreuidae) and *Barbara* species (Lepidoptera: Oleuthreuidae) (Shea, 1989). High infestation rates of *Barbara* and *Cydia* are associated with low numbers of *D. abietivorella* per cone (Shea, 1989).

The ability of an insect herbivore to shift host associations is influenced by its feeding strategy and may increase its competitive advantage. Polyphagous species have evolved the capacity to shift from primary to secondary hosts or tissue types while maintaining relatively high population levels. Monophagous species that specialize on one host tissue type and host plant are less able to respond to interspecific pressures through a shift in host use than polyphagous species (Denno *et al.*, 1995). In years of low white fir cone crops, *D. abietivorella* and *Barbara* sp. switch from feeding on white fir to red pine, *Pinus resinosa* Aiton (Pinaceae), cones that may reduce interspecific competition (Shea, 1989). Large cone crops in a number of conifer species in

Newfoundland in 1988 led to an increase of *D. abietivorella* populations. Cone crops declined in 1989 except in red pine, which subsequently became heavily infested by *D. abietivorella* (Mosseler *et al.*, 1992). The variable nature of cone production in conifers may have evolved as a strategy to deter cone-feeding insects, but also functions to reduce the level of interspecific competition among herbivores through the reduction of populations between mast years (Shea, 1989). In seed orchards, conifers are managed for large cone crops in which production is relatively stable among years. An artificially constant food source releases cone-feeders from the constraints imposed by unpredictable food sources. This may allow for better establishment of pestiferous cone-feeding insects that out compete other species and results in a reduction of overall species diversity of cone and seed feeders in managed settings (Shea, 1989). The optimal distribution of insect herbivores in space and time should reflect host abundance and quality and minimize interspecific competition (Milinski and Parker, 1991).

Host plant quality is also a factor that can influence reproductive strategies of insect herbivores. Polyandry, the sequential mating of females with different males, is common in Lepidoptera (Arnqvist & Nilsson, 2000). Food quality and its influence on insect size dictate reproductive biology in some species. In some Lepidoptera, the propensity to remate is positively correlated with female size (Drummond, 1984; Bergström *et al.*, 2002; Torres-Vila *et al.*, 2005). Heavy female *Pieris napi* Linnaeus (Lepidoptera: Pieridae) mate more frequently than light females (Bergström *et al.*, 2002). Nutritional quality impacts the size of adult female *Cnephasia jactatana* Walker (Lepidoptera: Tortricidae). Heavy females are polyandrous but poorly-fed, light females experience greater increases in fecundity due to multiple matings than do heavy females (Jiménez-Pérez *et al.*, 2003). Similar weight-related differences in mating frequency occur in *Operophtera brumata* Linnaeus (Lepidoptera: Geometridae) (Van Dongen, 1999) and *Pieris rapae* Linnaeus (Lepidoptera: Pieridae) (Wedell and Cook, 1999). Seasonal differences in the food quality of *Lobesia botrana* (Den. And Schiff) (Lepidoptera: Tortricidae) larvae affects adult female size accompanied by regular seasonal changes in the level of polyandry (Torres-Vila *et al.*, 2005). In addition to food quality, voltinism, population density and sex ratio can affect mating frequency (Drummond, 1984). The benefits of polyandry include release from sperm limitation, stimulation of egg production and fertility, and for some species, nuptial feeding and increased genetic variability of offspring, which is beneficial in unpredictable environments (*e.g.* Drummond, 1984; Arnqvist and Nilsson, 2000; Wiklund *et al.*, 2001). Mating is a costly process in terms of time, energy and risk (Williams, 1966; Roff, 1992), and for polyandrous species the benefits of multiple mating outweigh the costs in terms of overall fitness (Arnqvist and Nilsson, 2000).

There is typically a negative correlation between the degree of polyandry in a population and larval development time (Välimäki and Kaitala, 2007; Larsdotter Mellström *et al.*, 2010). Polyandrous females require more time post adult eclosion than monandrous females to become reproductively mature and produce eggs (Jervis *et al.*, 2005), which impacts subsequent offspring development time (Välimäki *et al.*, 2006). Polyandrous females typically eclose with few mature eggs and require time to complete oögenesis (Välimäki and Kaitala 2007). *Pieris napi* is bivoltine in parts of its range and the two generations exhibit different levels of polyandry, among other reproductive behaviours, which may be linked to larval developmental time (Larsdotter Mellström *et al.*, 2010). Univoltine populations are predominantly monandrous, while bivoltine populations are composed mainly of polyandrous females (Välimäki and Kaitala, 2007). The mating strategy is plastic within season as monandry and polyandry increase in bivoltine and univoltine populations, respectively, between spring and summer (Välimäki *et al.*, 2008). The maintenance of these two mating strategies within a population is attributed to variable season lengths (Välimäki *et al.*, 2008).

In Lepidoptera, much variation exists in relative mating frequencies among and within species (Drummond, 1984; Wiklund and Forsberg, 1991; Kaitala and Wiklund, 1994). Mating strategies of closely-related *Yponomeuta* species (Lepidoptera: Yponomeutidae) vary from monandry in *Yponomeuta padellus* Linnaeus to variable polyandry displayed by female *Y. cagnagella* Hübner. Populations of *Y. cagnagella* contain equal proportions of females that have been mated 1, 2, 3 or 4 times (Bakker *et al.*, 2008). The different mating strategies of these two species may be associated with other life history traits that vary between the two species (Bakker *et al.*, 2008). The monandrous *Y. padellus* is oligophagous, short-lived and reproductively active shortly after adult eclosion. In contrast, the polyandrous *Y. cagnagella* is monophagous, lives longer and is larger as an adult than *Y. padellus* but requires more time to mature sexually after adult eclosion (Bakker *et al.*, 2008). Female *P. napi* in geographically distinct populations mate at varying frequencies (Välimäki and Kaitala, 2005). The prevalence of polyandry differs between northern and southern populations of *P. napi* in Finland; southern populations are polyandrous and northern *P. napi* females are predominantly monandrous due to the constraints of environmental conditions on reproduction (Välimäki and Kaitala, 2005).

This study assessed the seasonal phenology and mating frequency of moths in the genus *Dioryctria* Zeller (Lepidoptera: Pyralidae) found sympatrically in the north Okanagan Valley, British Columbia. Twelve *Dioryctria* species in six species groups (*abietella*, *auranticella*, *baumhoferi*, *ponderosae*, *schuetzeella*, and *zimmermani* groups) have been recorded in British Columbia and are pests on five genera of conifers in the family Pinaceae (Neunzig, 2003; Roux-Morabito *et al*., 2008). This genus shows a wide range of host associations and feeding habits within and between species groups. Some *Dioryctria* species exploit hosts grown in conifer seed orchards in the north Okanagan Valley that grow breeding trees for Douglas-fir, *Pseudotsuga menziesii* Mirb. Franco (Pinaceae), lodgepole pine, *Pinus contorta* Douglas *ex* Loudon (Pinaceae), and *Picea* species for reforestation projects (Hedlin *et al.*, 1980; Zobel and Talbert, 1984). Infestations by *Dioryctria* species in conifer seed orchards can cause substantial economic losses incurred through limb breakage, bud damage and, in particular, seed losses (Hedlin *et al*., 1980; Zobel and Talbert, 1984; Strong, 2005).

In the north Okanagan Valley, several *Dioryctria* species groups are sympatric and overlap in host use. Coexistence by *Dioryctria* species groups may be facilitated by differential host tissue use, which could further impact seasonal flight, voltinism and potentially, the mating frequency of these species. The *abietella* and *schuetzeella* groups are reported to be highly polyphagous and, in this region, both groups readily infest Douglas-fir, lodgepole pine and *Picea* species (Neunzig, 2003). Larvae in the *abietella* group feed primarily on cones though they use needles, shoots and cambium, while *schuetzeella* group larvae primarily infest shoots, foliage and occasionally cones (Neunzig, 2003). Larvae of the *auranticella*, *baumhoferi* and *zimmermani* groups are monophagous and feed on the flowers and second-year cones of lodgepole pine. Infestations of *zimmermani* group larvae can also occur in lodgepole pine galls. In particular, *D. abietivorella* (*abietella* species group) does not perform equally well on all identified hosts and larvae experience differential development times and mortality due to host type (Trudel *et al*., 1999). In this study, I assess the phenology and mating status of *Dioryctria* species in seed orchards in the north Okanagan Valley, British Columbia to address the following questions. (i) How are *Dioryctria* species groups temporally and spatially distributed? (ii) What mating strategies characterize female *Dioryctria* species groups? (iii) Do mating strategies within species group differ within season and among habitat associations?

Methods and Materials

Female *Dioryctria* seasonal flight activity and mating status were monitored by collection of specimens in black light traps (Model 2581A, Bioquip, Rancho Dominguez, CA) in the north Okanagan Valley, British Columbia. Trapping was conducted from 25 June to 26 September 2008 and 4 May to 26 September 2009. In 2008 and 2009, traps were placed in Douglas-fir breeding orchards at the Kalamalka Forestry Centre (KAL) (50º 14’ N, -119º 16’ W), and in two commercial seed orchards: Vernon Seed Orchard (VSOC) (50º 13’ N, -119º 19’ W), and PRT Armstrong (PRT) (50º 26’ N, -119º 12’ W). One trap was placed in each of two blocks at KAL and VSOC separated by at least 500 m, while two traps were located in one continuous block at PRT separated by 250 m to accommodate the different configuration of this orchard. In 2009, *Dioryctria* flight was monitored in these same blocks and in two lodgepole pine and two interior spruce (Pinaceae) (Coates, 1994) blocks at KAL. Traps were hung on a line strung between two trees and positioned in the upper-mid canopy (approximately 2 - 3.5 m above the ground); traps placed high in the canopy capture the most *Dioryctria* adults (Hanula *et al.*, 1984; Strong *et al.*, 2008). Traps were run four nights a week and monitored twice weekly and *Dioryctria* species were removed and were frozen at -18 ºC until species identification could take place. In the commercial seed orchards, insecticides are periodically applied to control *Dioryctria* during the growing season. In these instances, traps were not monitored for two days following pesticide application.

Females collected in light traps were dissected to confirm mating status and species identification. Morphological characters of the *ductus bursae* were used to identify species to taxonomic group (Sopow *et al.*, 1996; Neunzig, 2003). Taxonomic species groups were used in all analyses because of the difficulties in identification of insects in all groups to species. Female mating status was confirmed by the presence of a spermatophore in the *bursa copulatrix* and the number of spermatophores was counted. Wing area was used as a measure of body size for all collected specimens. The right forewing of each female was removed and pasted onto white paper. A digital image of each wing was obtained by scanning (HP Scanjet 4070) the prepared wings. Wing area was measured to 0.1 mm^2 using ImageJ (Version 1.34s, National Institute of Health, USA). Representative voucher specimens from each species group have been deposited at the Strickland Museum, University of Alberta. Male *Dioryctria* captured in light traps were not included in analyses.

Male *D. abietivorella* flight was monitored weekly between 4 May to 21 September 2008 and 4 May to 24 September 2009 with sex pheromone-baited diamond traps (Contech Inc., Delta, BC) in the same blocks where light trapping occurred. In 2008 and 2009, two pheromone-baited traps were located in each block at KAL, PRT and VSOC, except for one block in VSOC where only one trap was monitored in 2009. The traps were baited on site with a grey septum loaded with (9*Z*,11*E*)-tetradecadienyl acetate and (3*Z*,6*Z*,9*Z*,12*Z*,15*Z*)-pentacosapentaene in a 200:2000 µg dosage (ChemTica International, Heredia, Costa Rica). Traps were hung at a height of 2 m above the ground and situated at least 10 m from the edge of the block. Pheromone and light traps were separated by at least 50 m to minimize trap interference. Pheromone trap catch was enumerated and moths were removed from traps every seven days and lures were replaced at 3-week intervals.

Statistical analyses

For the purposes of analysis, trapping data was divided into three time periods that corresponded to early-, mid- and late- season of each year based on degree-day accumulations ($DDA_{12\,°C}$) beginning on 1 January for both 2008 and 2009. Developmental thresholds for *Dioryctria* species in the north Okanagan Valley have not been determined. The 12 °C threshold for degree-day accumulation used in this study is based on the developmental threshold determined for *Dioryctria amatella* Hulst in the southern United States (Hanula *et al.*, 1984). The cut-off dates used to delimitate early-, mid- and late- season trapping were chosen based on alignment of DDA between 2008 and 2009 to minimize the effect of environmental differences on analyses between years. Early-season trapping for females was not conducted in 2008, while mid- and late-season catches occurred between 21 June – 2 August 2008 (258 – 673 DDA) and 9 August – 20 September 2008 (673 – 1034 DDA), respectively. In 2009, early-season trapping occurred between 11 May – 8 June 2009 (44 – 227 DDA), and mid- and late-season between 15 June – 27 July 2009 (227 – 695 DDA) and 3 Aug – 21 September 2009 (695 – 1204 DDA), respectively.

2.1. Seasonal flight phenology of Dioryctria species

Seasonal flight phenology of the different *Dioryctria* species groups was assessed from trap catch in 2008 and 2009 in Douglas-fir stands at KAL. Due to non-normality, a non-parametric Kruskal-Wallis test (Zar, 1984) was used to detect differences in trap catch among the *Dioryctria* species groups. Post-hoc analysis was conducted using Dwass-Steel-Critchlow-Fligner (DSCF) pairwise comparisons (Critchlow and Fligner, 1991). To test for differences in mean trap catch within *Dioryctria* species groups due to host stand type a Kruskal-Wallis test (due to non-normality) was used and post-hoc analysis was conducted with DSCF comparisons. Contingency table analyses were used to test for an effect of trapping period (early-, mid- and late-season) on the relative proportion of females from each species group captured in light traps positioned in Douglas-fir stands in 2008 and 2009. To test for differences in the proportion of females from each species group captured in light traps positioned in stands of different hosts (Douglas fir, lodgepole pine and interior spruce), contingency table analyses were conducted on females captured in 2009 at KAL. To investigate the influence of season on females captured in traps positioned in stands of different hosts, Fisher’s exact tests compared the proportion of females captured in each species group in traps positioned in Douglas-fir, lodgepole pine and interior spruce, separately. Contingency table analysis was used to test for an effect of trapping period on the relative proportion of male *D.*

abietivorella trapped in the three host stand types. To test the hypothesis that moth size differed throughout the season, correlation between weekly and mean wing area for *abietella* in 2008 and 2009 and *auranticella, ponderosae* and *schuetzeella* in 2009 was calculated using Pearsons product moment correlation (Zar, 1984). Species group wing area was pooled for all host types to increase sample size.

2.2. Mating status of Dioryctria species females

To determine if mating frequency varied among females in different species groups, a one-way ANOVA was used to compare the mean (± SE) number of spermatophores among females in each species groups, within each year. Post-hoc analysis was conducted using Student-Newman-Keuls (SNK) (Zar, 1984). These means (± SE) were visually compared to a contol mean of 1.4, an average mating frequency used to distinguish polyandry from monandry (Arnqvist and Nilsson, 2000). Species with an average mating frequency that exceeds 1.4 are considered polyandrous, while those at or below this level are considered monandrous (Arnqvist and Nilsson, 2000). To assess the effect of season on the occurrence of polyandry, I visually compared mean spermatophore number (± SE) by species within each trapping period within each year to 1.4 (polyandry threshold). To test for an effect of female size on mating frequency, weekly average spermatophore numbers throughout the season and correlations between wing area and total spermatophore number in each species group were calculated using Spearman R (Zar, 1984). Within each species group, mating frequency was categorized (0, 1-2, 3-4, 5-8 spermatophores). Contingency table analysis was used to determine if relative proportions of females in each mating frequency category varied by species. The effect of trapping period within season on the proportion of females in each mating frequency category was assessed using contingency table analysis to compare the proportion of females in each category within each species group.

To assess the effect of host on the occurrence of polyandry, I visually compared mean spermatophore number by species within each host type to1.4 (polyandry threshold). To test for an effect of host on the proportion of females in each mating frequency category (0, 1-2, 3-4, 5-8 spermatophores) Fisher’s exact test was used on each species group separately.

All statistical analyses were completed using R version 2.11.1 (R Core Development Team, 2010).

Results

2.1. Seasonal flight phenology of Dioryctria species

In 2008 and 2009, species from the *abietella*, *auranticella*, *baumhoferi*, *ponderosae*, *schuetzeella*, and *zimmermani* groups were trapped at KAL, PRT Armstrong and VSOC (Tables 2.1, 2.2; Fig. 2.1). Females in the *abietella* group were the first to fly in the spring and were initially caught in light traps in late-May in 2009 and were not caught after mid/late-August in either year (Fig. 2.1). This group did not show a peak in trap catch of females in light traps as similar numbers were caught throughout the season (Fig. 2.1). Between 2008 and 2009, the number of females in the *abietella* group recovered from light traps decreased, while the number of *auranticella* group females increased dramatically. Female *auranticella* were caught in late-July 2008 and early-July 2009; trap catch remained consistently low in 2008 but in 2009 catch peaked in late-July and decreased thereafter (Fig. 2.1). Female *ponderosae* were trapped between late-June and early-August 2008, though they only occurred in traps in July 2009 (Fig. 2.1). The mean number of *ponderosae* group females caught increased dramatically between 2008 and 2009, though this increase may have been due to the inclusion of traps in lodgepole pine stands (Table 2.2). Females in the *schuetzeella* group were the most commonly captured of any species group and the mean trap catch was greater in 2009 than 2008 (Table 2.1, Fig. 2.1). In both years, *schuetzeella* females were trapped between late-June and mid/late-August and trap catch peaked in late-July/early August (Fig. 2.1). Initial trap catches for all groups occurred at similar degree-day accumulation, between 300-500, in 2008 and 2009 (Fig. 2.1). In general, *baumhoferi* and *zimmermani* group females were either rarely or never caught in Douglas-fir stands in 2008 or 2009 and due to low catch numbers these groups were excluded from further analyses. There was no evidence for seasonal changes in wing area for *abietella* group females in 2008 ($r_{abi} = -0.1110$, $P = 0.7930$) (Fig. 2.2A) or for any *Dioryctria* species group females in 2009 ($r_{abi} = 0.4050$, $P = 0.2900$, $r_{aur} = -0.0980$, $P = 1.000$; $r_{pond} = 0.3740$, $P = 0.4660$; $r_{shz} = -0.1220$, $P =$

0.7380, for *abietella, auranticella, ponderosae* and *schuetzeella* groups, respectively) (Fig. 2.2B).

Male *D. abietivorella* (*abietella* species group) were caught in pheromone-baited traps from mid-May to late-September in 2008 and 2009 (Fig. 2.3). Mean captures were low after late-August, and decreased from an average of four males per week to one male per week from late August to late-September. The first flight peak occurred in early-July and early-June in 2008 and 2009, respectively (Fig. 2.3). A second peak in moth capture occurred in early-August 2008 but this was not evident in 2009 when there was an extended period of high trap catch between July and August (Fig. 2.3).

There is an effect of time within season on the proportion of females of each *Dioryctria* species group trapped in Douglas-fir stands. The ratio of females captured among different *Dioryctria* species groups varied significantly between trapping periods in 2008 ($P < 0.0001$) and in 2009 ($P < 0.0001$). In both years, females were most commonly captured in light traps during mid-season trapping (Fig. 2.4). This difference was primarily driven by *abietella* females, which comprised almost 20% of the overall trap catch in the mid-season but only 2% in late- season 2008 (Fig 2.4A). Other groups occurred in fairly similar proportions between the two trapping periods in 2008. In 2009, *abietella* group females comprised very little of the overall trap catch but were present during all trapping periods (Fig. 2.4B). The significant difference in the distribution of females captured during different trapping periods in 2009 is driven by *auranticella* and *schuetzeella* group females. Females in the *auranticella* group were not present in early- or late-season trapping but were abundant during mid-season, comprising 20% of the total 2009 catch (Fig. 2.4B). A similar pattern occurred in *schuetzeella* group, which comprised 0, 42 and 29% of total trap catch during early-, mid- and late-season trap catches, respectively (Fig. 2.4B).

Season also affects the trap catch of male *D. abietivorella* ($P = 0.0161$). The proportional trap catch of male *D. abietivorella* in Douglas-fir orchards differed significantly among the three trapping periods but ratios were similar between 2008 and 2009 (Fig. 2.5). In 2008 and 2009 trap catch increased between early- and mid-season and remained similar during late season trapping. Overall, males represented 4, 17 and 17% in early-, mid- and late-season in 2008 and 13, 22 and 27% in 2009 (Fig. 2.5).

In 2009 at KAL, *abietella*, *auranticella*, and *schuetzeella* group females were caught in all three stand types, Douglas-fir, interior spruce and lodgepole pine (Table 2.2). All groups, except *schuetzeella* (P = 0.886) varied significantly in the average number caught in traps within stand type ($P_{abietella} < 0.001$, $P_{auranticella} < 0.001$, $P_{ponderosae} < 0.001$) (Table 2.2). Female *abietella* and *auranticella* were found in traps positioned in all host types. Female *ponderosae* were captured in traps in lodgepole pine and interior spruce (Table 2.2). Although *ponderosae* group females were also caught in interior spruce, they were most commonly recovered from traps in lodgepole pine (Table 2.2). Females in the *schuetzeella* group were the most abundant in all three stand types.

There is a relationship between host stand type and the proportion of females in different *Dioryctria* species recovered from light traps positioned in each host type stand ($\chi^2 = 8034158$, $df = 6$, $P < 0.0001$) (Fig. 2.6). This relationship is driven by the presence of *schuetzeella* species group females in all host stand types and the low proportion of the other species groups found (Fig. 2.6). Females in the *abietella* group were present in lodgepole pine and Douglas-fir; *ponderosae* females only occurred in traps positioned in lodgepole pine, while *auranticella* females were not present in any of the different host stands at KAL in 2009 (Fig. 2.6). There were significant differences in habitat association by moths in different species groups throughout the season ($P_{\text{douglas-fir}} < 0.0001$, $P_{\text{lodgepole pine}} < 0.0001$, $P_{\text{interior spruce}} = 0.0012$) but this relationship was driven by the dominance of *schuetzeella* females captured during the mid- and late-season in all three stand types. In all three stand types, the greatest activity occurred during the mid-season.

There is no effect of trapping season on the occurrence of male *D. abietivorella* in pheromone-baited traps positioned in stands of Douglas-fir, lodgepole pine and interior spruce (P = 0.7948). A similar proportion of male *D. abietivorella* were present in the three different host stands throughout the trapping season (Fig. 2.7).

2.2. Mating status of female Dioryctria species

The average frequency at which *Dioryctria* females mate varies among the species groups ($P_{2008} < 0.001$, $P_{2009} < 0.001$). Females in the *abietella* and *auranticella* groups are polyandrous and both displayed a similar spermatophore number in 2009 but not 2008 (Fig. 2.8). Average spermatophore number for *abietella* and *auranticella* females exceeded the polyandry threshold of 1.4 in 2008 and in 2009. Female *ponderosae* and *schuetzeella* average mating frequency were at or below the threshold of 1.4, although the *schuetzeella* group just exceeds the threshold in 2009 (Fig. 2.8). The number of spermatophores found in *abietella* females varies with time in the season but this is more evident in 2009 than in 2008. There is an increase in spermatophore number from first catch until late-June; later in the season females captured have fewer spermatophores (Fig. 2.9). Average spermatophore number remains similar throughout the season for *auranticella*, *schuetzeella* and *ponderosae* females (Fig. 2.9). Average mating frequency of *abietella* females is not different from the polyandry threshold of 1.4 in early-season trapping but does exceed the threshold in mid- and late- season (Fig. 2.10). Female *auranticella* average mating frequency exceeds the threshold in mid- and late- season 2008 and 2009 (Fig. 2.10). Female *schuetzeella* average mating frequency just exceed the threshold of 1.4 during mid-season but was below the threshold during late-season in 2009 (Fig. 2.10). Female *ponderosae* spermatophore number did not differ from the threshold of 1.4 in mid-season, the only trapping period that they were recovered from the light traps (Fig. 2.10).

Correlations between wing area and mean spermatophore number varied among species groups (Fig. 2.11). Wing area is not correlated with mean spermatophore number for *abietella* (2008: $r = -0.1040$, $P = 0.3870$; 2009: $r = -.01170$, $P = 0.6170$), *ponderosae* (2009: $r = 0.0222$, $P = 0.891$) and *schuetzeella* group females ($r_{2009} = -0.07$) (Fig. 2.11). Interestingly, there is a negative correlation between wing area and spermatophore number in *auranticella* (2009: $r = -0.5450$, $P = 0.0286$) and *schuetzeella* (2009: $r = -0.0926$, $P = 0.0010$) indicating that large females were less polyandrous in this species (Fig. 2.11B).

Few virgin females from any species group were captured in light traps (Fig. 2.12). The proportion of females within each mating frequency category varied among species groups ($P_{2008} < 0.0001$, $P_{2009} < 0.0001$). The significant relationship was driven primarily by the large proportion of *schuetzeella* females that mated only 1-2 times in 2008 and in 2009 (Fig. 2.12). In 2008, relatively similar proportions of *abietella* females occurred in each mating frequency category (Fig. 2.12A). In 2009, *ponderosae* group females occurred in each mating frequency category but the greatest proportion mated 1-2 times.

The distribution of females in each mating frequency category was variable among the species groups during early-, mid- and late-season trapping in 2009 (Fig. 2.13). Female *abietella* group members trapped in early-season 2009 had mated between 0 and 8 times, with the largest proportion mating 1-2 times. Early-season trapping was the only time period within season that virgin *abietella* females were captured (Fig. 2.13A). The ratio of species groups occurring in each mating frequency category differed significantly ($P < 0.0001$) during mid-season trapping in 2009 (Fig. 2.13B). This relationship is primarily driven by the occurrence of many *schuetzeella* females that mated 1-2 times. Most *auranticella* group females mated 1-2 times although some females there were occurrences of females mating between 3-4 and 5-8 times (Fig. 2.13B). Most *schuetzeella* females captured in light traps late in the season were mated 1-2 times, with relatively few females mating 3-4 times (Fig. 2.13C).

The average mating frequency of female *abietella* exceeds the polyandry threshold in Douglas-fir and lodgepole pine but not in interior spruce stands. Female *auranticella* average mating frequency exceed the 1.4 polyandry threshold in lodgepole pine but not in Douglas-fir or interior spruce. Female *ponderosae* and *schuetzeella* average mating frequencies do not exceed the polyandry threshold in any of the host stand types (Fig. 2.14). Host stand type has variable influence on the occurrence of *Dioryctria* species group female distribution among mating frequency categories (Fig. 2.15). The occurrence of *abietella* females in each mating frequency category did not differ among host types ($P = 0.4851$), although 21% of females collected mated up to 8 times in Douglas-fir stands (Fig. 2.15A). The proportion of *auranticella* females in each mating frequency category did not vary by host type ($P_{auranticella} = 0.8788$) (Fig. 2.15B) while the proportion of *ponderosae* females did ($P_{ponderosae} < 0.0001$) (Fig. 2.15C). The ratio of females in the various mating frequency categories in the *schuetzeella* group varied significantly with host stand in which the females were captured ($P < 0.0001$), although there appears to be little variation in ratio among host types (Fig. 2.15D). The significant relationship may be driven not by host type but by mating frequency category. Almost 93% of *schuetzeella* females trapped occurred in the 1-2 mating frequency category relative to the other categories (Fig. 2.15D).

Discussion

2.1. Seasonal flight phenology of Dioryctria species

Female moths in the *abietella, auranticella, ponderosae* and *schuetzeella* species groups were caught in significant numbers in light traps positioned in seed orchards located near Vernon, British Columbia. *Dioryctria abietivorella* is the only *abietella* group species member recorded in British Columbia, and *D. okanaganella* Mutuura, Munroe and Ross is the only *ponderosae* species group member recorded from British Columbia (Neunzig, 2003). Therefore, I am confident that females categorized in each of these species groups actually comprise a single species per group. Two species, *D. reniculelloides* Mutuura and Munroe and *D. pseudotsugella* Munroe, that are classified in the *schuetzeella* group occur sympatrically and utilize the same hosts in British Columbia (Neunzig, 2003). It is difficult to differentiate these two species even based on genitalic characters (Sopow *et al.*, 1996) and it is likely that my *schuetzeella* group catches were a combination of these two species. Two species are recorded in the *auranticella* group from British Columbia, *D. auranticella* Grote and *D. rossi* Munroe. Although these two species can be separated based on wing characters, wing wear was prevalent among females caught in light traps which made it difficult to differentiate these species (Neunzig, 2003). *Dioryctria* present in seed orchards in the north Okanagan Valley exhibit overlapping flight periods and habitat use. Females in the *abietella* species group had the longest flight period of any *Dioryctria* and were the only females recovered from light traps in spring (Fig. 2.2). Females in the other species groups are present from early July through to mid-August while *schuetzeella* was trapped until late-August (Fig. 2.2). The phenology of trap catch did not vary between Douglas-fir, lodgepole pine and interior spruce.

My data suggest that voltinism varies among the *Dioryctria* species groups that I monitored in the northern Okanagan Valley. It appears that *abietella* (*D. abietivorella*) has two generations, with adult flight occurring in early-spring and again in mid-summer.

There are two peaks in the male *D. abietivorella* flight activity in 2008 (Fig. 2.3), although this is not apparent in female trap capture in light traps (Fig. 2.1). However, the mating frequency of *abietella* females suggests the presence of two generations. Spermatophore numbers per female increased from spring to summer and then decreased in late July (Fig. 2.9). The recovery of females that secured few matings late in the season suggests the occurrence of a second, though non-discrete, generation of newly eclosed females. Development from first instar larvae to pupae requires approximately 22-days at 25°C in the laboratory (Trudel *et al.*, 1995) and approximately another 7-10 days are required to adult eclosion (personal observation). It is quite possible for spring-eclosed females to produce a second generation whose offspring overwinter as mature larvae. This evidence supports some early work on the voltinism of *D. abietivorella* (Keen, 1952) but is contrary to other reports suggesting this species is univoltine (MacKay, 1943; Hedlin *et al.*, 1980). These reports were based on periodic survey work that may not have captured voltinism differences between geographically-distant populations. Males were trapped until late September, when female *abietella* were no longer recovered from light traps. I am unable to discern whether females are still present and not being trapped or if they are no longer flying after mid-August. Bias towards light-trap captures of gravid and mated females searching for oviposition sites has been reported (Landolt and Curtis, 1991; Cowan and Gries, 2009). It would appear that little reproductive activity occurs during the late-season period as few mated females are trapped. These males could represent a small proportion of individuals that did not enter diapause.

It is likely that the two *abietella* generations experience different seasonal environments that impact life history traits such as mating frequency. Such differences in mating frequency by generation occur in the bivoltine species *Pieris napi* that overwinter as pupae. Reproduction is constrained in time and mating frequency is reduced for the generation of moths that does not overwinter compared to the polyandrous overwintering generation (Larsdotter Mellström *et al.*, 2010). Delayed mating by females that undergo diapause leads to females that are reproductively mature at their first mating and that achieve higher realized fecundity over a longer oviposition period than females that do not delay mating post adult eclosion (Larsdotter Mellström *et al.*, 2010). Although there are two distinct generations of *P. napi* per year, the prevalence of monandry increases from spring to summer (Välimäki *et al.*, 2008). The decrease in the number of spermatophores recovered from *abietella* females at the end of the season may indicate that females are constrained in time to mate and produce offspring later in the season, so that larvae can mature to overwinter (Trudel *et al.*, 1999).

Female *auranticella* were present solely during mid-season with a single peak in flight activity in mid- to late-July (Fig. 2.9), which indicates the occurrence of one generation as reported from other parts of its range (Neunzig *et al.*, 1964; Pasek and Dix, 1989). Female *ponderosae* also appear to be univoltine as females were only trapped during a short three-week period in July (Fig. 2.9). Little is known about the flight activity of moths in the *ponderosae* group although adult specimens have been collected in June in California (Roe *et al*., 2006) and July and early August in western Canada (Mutuura *et al*, 1969). Univoltinism of the *schuetzeella* group trapped in my study is supported by a single peak in flight activity and by consistency of mating frequency of trapped females throughout the season (Figs. 2.9, 2.13). Species in the *schuetzeella* group are univoltine in other parts of their range (MacKay, 1943; McLeod and Daviault, 1963; Mutuura and Munroe, 1973). It is important to note that most females in all species groups trapped had already mated, therefore it may be that females do not readily disperse until mated and do not encounter the light traps. As such, trap captures may not truly reflect the flight period of the entire population but only that of the reproductively-active individuals.

In both years of my study, the *schuetzeella* group dominated female trap catches in light traps located in all three host types (Figs. 2.6, 2.15) and their presence is likely linked to their feeding ecology. Species within this group predominantly feed on shoots and foliage (Mutuura and Munroe, 1973; Neunzig, 2003), which are abundant and reliable food sources compared to cones. A feeding strategy that targets a reliable food source could facilitate the establishment of large and stable populations. Species in the *schuetzeella* group are also highly polyphagous (Neunzig, 2003) as is supported by their presence in large numbers in the Douglas-fir, lodgepole pine and interior spruce stands monitored in this study (Fig. 2.15). The relatively high and equal trap catch of *schuetzeella* among the three host types suggests that this group is achieving similar success regardless of host type though this requires further investigation into the effect of host on fitness.

Species in the *schuetzeella* group also feed on cones, particularly those of Douglas-fir (Mutuura and Munroe, 1973; Neunzig, 2003). No *schuetzeella* larvae were found in the ~3000 Douglas-fir cones that I collected at KAL. It is possible that in this region, this group solely feeds on foliage and cambium and does not use cones. The variable nature of cone-crop production may also limit the population size of *abietella* compared to *schuetzeella*. Although *abietella* are highly polyphagous on species within Pinaceae (Neunzig, 2003), females were captured in very low numbers in traps positioned in lodgepole pine and interior spruce stands and this may reflect a local female preference for Douglas-fir. This pattern was not evident for male flight activity, as male trap catch was equal in pheromone-baited traps positioned in each host stand type.

Females in the *auranticella* group were trapped in Douglas-fir stands and *ponderosae* in lodgepole pine in considerable numbers in 2009 (Tables 2.1, 2.2). These results are surprising as *auranticella* is not reported to infest Douglas-fir, nor is *ponderosae* previously recorded on lodgepole pine (Neunzig, 2003). Both species have only been recorded on ponderosa pine, *Pinus ponderosa* C. Lawson (Pinaceae), in this region (Neunzig, 2003). These females could be migrating into stands from other host stands within the study sites or from surrounding forested areas. This seems unlikely due to the relatively large trap catch of females from these species groups in stands of trees that are not known to serve as hosts. Specimens from the *auranticella* species group have also been reared from cones of alternate conifer hosts grown in seed orchards in the region, such as western white pine, *Pinus monticola* Douglas *ex* D. Don (Pinaceae) and lodgepole pine (J. Corrigan, pers. comm.), which are both new host records for species in this group. The small size of the orchards and host stand blocks where I performed light trapping does not exclude the possibility that transient moths dispersing throughout the seed orchards were trapped. Larval rearing from Douglas-fir, lodgepole pine and interior spruce cones should be performed to substantiate these predicted habitat associations based on light trapping surveys.

2.2. Mating status of Dioryctria species females

Dioryctria females in different species groups vary in their mating strategies. Females in the *abietella* group are highly polyandrous while *auranticella* females are polyandrous but to a lesser degree. Females in the *ponderosae* and *schuetzeella* groups are predominantly monandrous. A certain degree of variation in mating frequency exists within each group and it is difficult to tease apart the reasons for this variation. In polyandrous species, females acquire more matings as a function of time post adult eclosion (Drummond, 1984) as in *Acrobais nuxvorella* Neunzig (Lepidoptera: Pyralidae) (Calcote *et al.* 1984). Others have found a certain amount of intraspecific variation in mating frequency (Van Dongen, 1999; Wedell and Cook, 1999; Jiménez-Pérez *et al.*, 2003; Torres-Vila *et al.*, 2005). Mating frequency is a heritable trait for some Lepidoptera (Torres-Vila *et al.*, 2001; Wedell *et al.*, 2002) and selection for different mating frequencies may be maintained through year-to-year differences in season length (Välimäki *et al.*, 2008). Seasonal changes in average mating frequency occur in *abietella* females but not in the other species groups investigated in which the relative mating frequency remains similar throughout the season. There is a clear increase in the mating frequency of *abietella* females from early- to mid-season, after which time the average spermatophore number per female decreases (Fig 2.9). As previously discussed, this pattern could be due to the emergence and flight of a second generation of female *abietella*.

The correlation between spermatophore number and wing area is variable across *Dioryctria* species groups. Large *auranticella* and *schuetzeella* females secure fewer matings than small females. It is unknown if these females accrue benefits such as male-derived nutrients through multiple mating. In some Lepidoptera species, smaller females benefit disproportionally from multiple mating (Jiménez-Pérez *et al.*, 2003). There may also be longevity costs associated with repeated matings (Roff, 1992). Large females may be less motivated to remate than small females that may be energetically deficient. There was no support for a correlation between wing area and spermatophore number in females recovered from the *abietella* and *ponderosae* species groups. It is possible that another measure of body size, such as pupal or adult weight could be a better indicator of mating frequency in these species.

There was no effect of the host stand in which females were captured on the number of matings achieved by *Dioryctria* females. Females are either able to find mates in all stand types or disperse some distance after mating. Mating frequency differs among species groups collected in the different host stand types. Though not significant, highly polyandrous *abietella* females occurred in high frequency in lodgepole pine and Douglas-fir stands but less commonly in interior spruce stands. This may be due to a lack of mating opportunities at the low population densities in these stands, as similar proportions of males were caught in pheromone-baited traps in all stand types.

Dioryctria species groups occur sympatrically and overlap in their host associations in northern Okanagan seed orchards in British Columbia. Females in the *abietella*, *auranticella*, *ponderosae* and *schuetzeella* species groups were present in Douglas-fir stands though relative abundances varied between 2008 and 2009. *Dioryctria abietivorella* (*abietella* species group) appear to be bivoltine, which is unique among the species groups. The two generations are exposed to different seasonal environments that may apply different selection pressures on life history traits to create polyphenism in mating frequencies between the generations. Female *schuetzeella* dominated trap capture in Douglas-fir, lodgepole pine and interior spruce stands and their impact on host trees is unknown at this time. The capture of *auranticella* in Douglas-fir and *ponderosae* in lodgepole pine stands was surprising as both are known only from ponderosa pine in this region. *Dioryctria* species group females exhibited different mating strategies in these seed orchards. Female *abietella* and *auranticella* were polyandrous while *ponderosae* and *schuetzeella* are monandrous and each group presents a certain amount of variation in the mating frequency. *Dioryctria* species groups provide an interesting opportunity to study the impact of different mating strategies on fitness because of their close taxonomic relationship, their sympatric occurrence and overlap in host associations.

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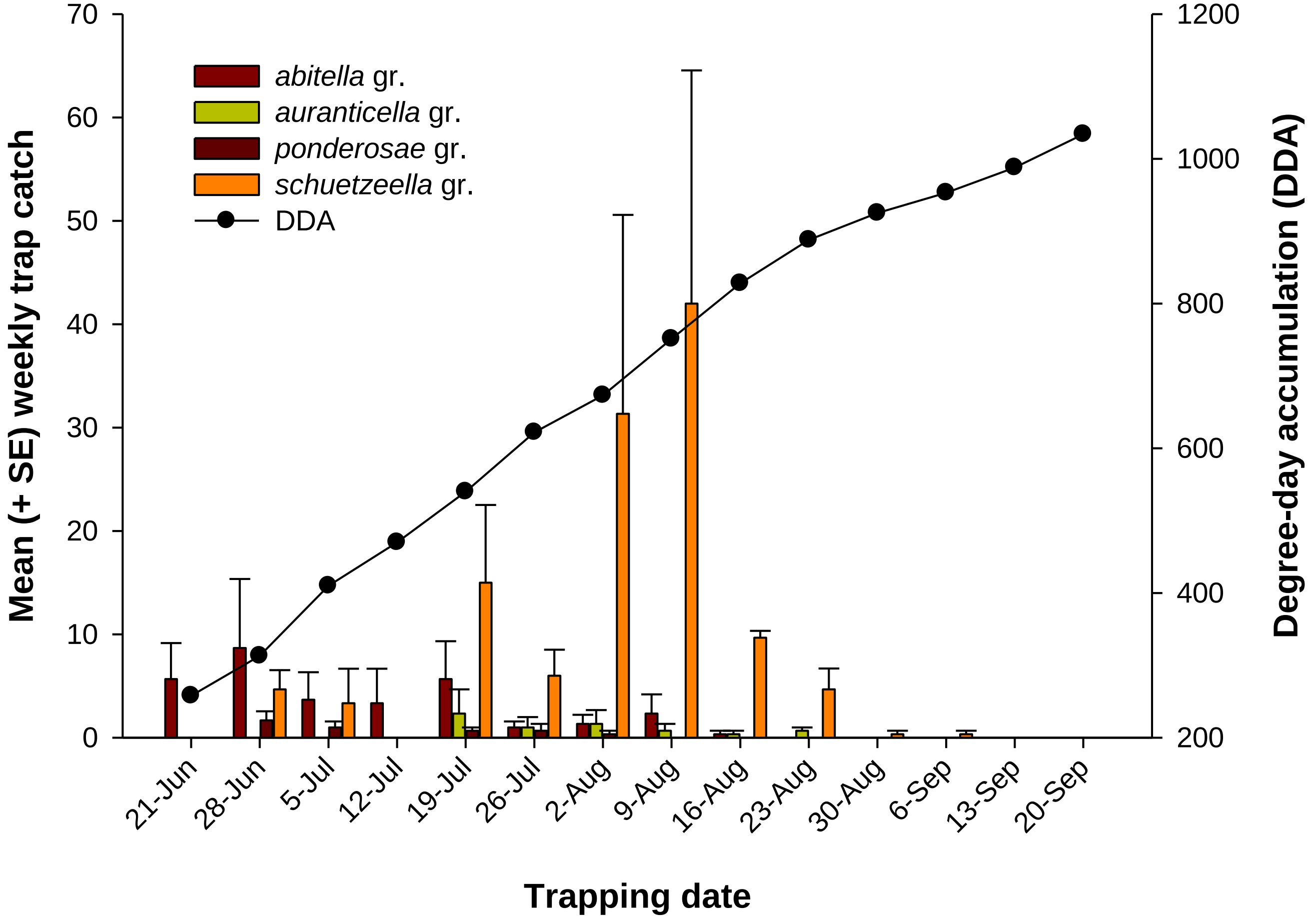
Table 2.1. Mean (+ SE) number of females in each *Dioryctria* species group caught in light traps placed in Douglas-fir blocks at Kalamalka Forestry Centre, Vernon Seed Orchard, and PRT Armstrong (n=3) in 2008 and 2009. Within each year, means followed by the same letter are not significantly different (DSCF multiple comparisons, *P* > 0.05). Females captured in 2008 were recovered from traps positioned in orchards during the mid- and late-season only.

	2008	2009
abietella gr.	32.00 + 23.03a	8.33 + 4.45a
auranticella gr.	6.33 + 5.84b	100.00 + 96.50ab
ponderosae gr.	4.33 + 1.20b	3.00 + 3.00a
schuetzeella gr.	117.33 + 55.80c	422.00 + 304.53b
zimmermani gr.	1.67 + 1.67b	3.00 + 0.33a

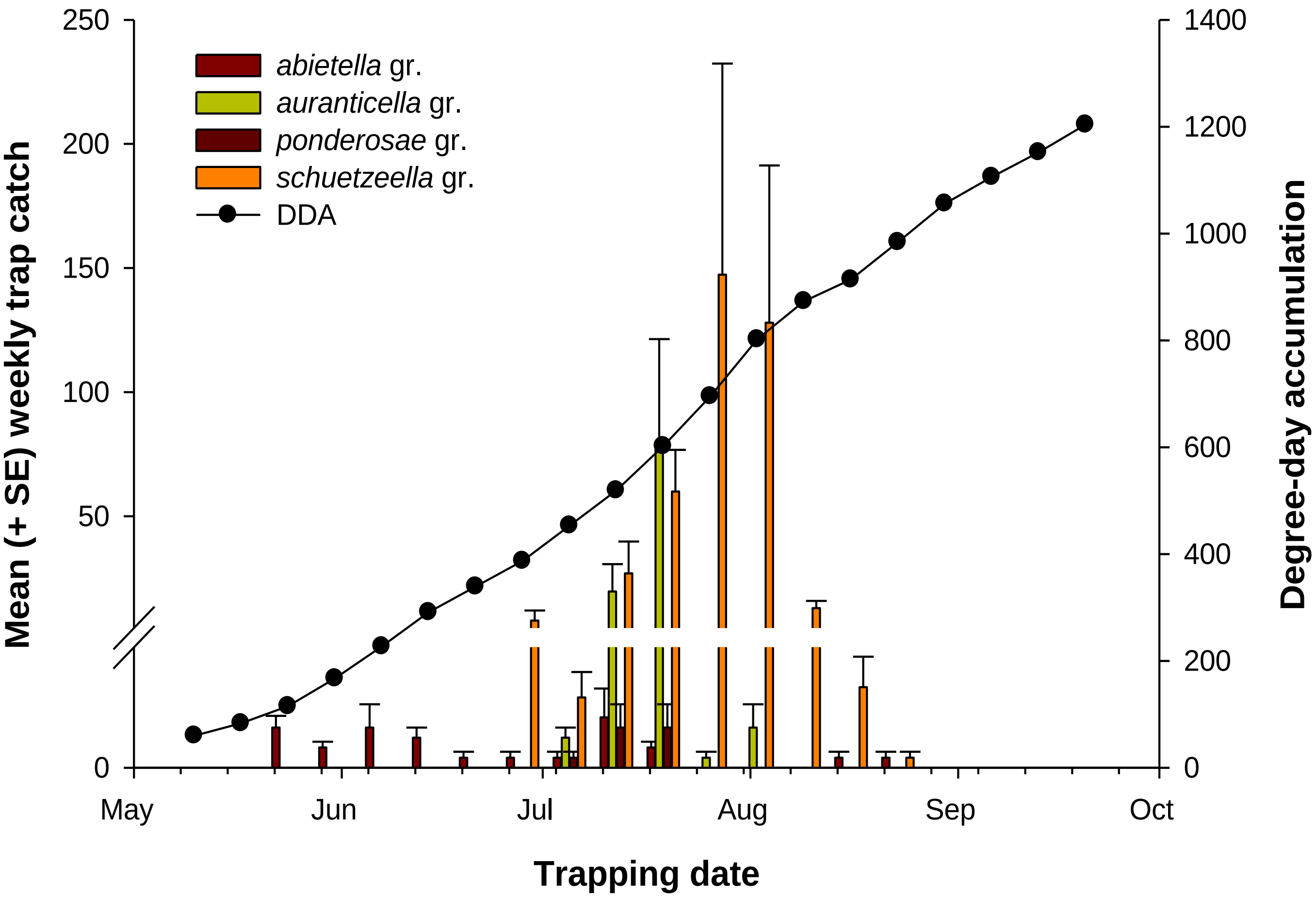
Table 2.2. Mean (+ SE) number of females in each *Dioryctria* species group caught in light traps placed in Douglas-fir, interior spruce and lodgepole pine stands (n = 2 blocks per stand) at Kalamalka Forestry Centre in 2009. Within each species group, means followed by the same letter within a row are not significantly different (DSCF multiple comparisons, *P* > 0.05). Species groups without letters were not tested statistically.

	Douglas-fir	Interior spruce	Lodgepole pine
abietella gr.	8.50 + 0.50a	2.00b	4.50 + 1.50b
auranticella gr.	4.00a	1.50 + 0.50b	5.00a
baumhoferi gr.	0	0	1.00
ponderosae gr.	0	2.00 + 1.00a	25.50 + 11.50b
schuetzeella gr.	511.50 + 310.50a	416.50 + 78.50a	558.50 + 165.50a
zimmermani gr.	1.00	0	2.50 + 0.50

A. 2008


70
60
50
40
30
20
10
0
1200
1000
800
600
400
200
abitella gr.
auranticella gr.
ponderosae gr.
schuetzeella gr.
DDA
Mean (+ SE) weekly trap catch
Degree-day accumulation (DDA)
21-Jun
28-Jun
5-Jul
12-Jul
19-Jul
26-Jul
2-Aug
9-Aug
16-Aug
23-Aug
30-Aug
6-Sep
13-Sep
20-Sep
Trapping date

B. 2009



250
200
150
100
50
0
1400
1200
1000
800
600
400
200
0
abietella gr.
auranticella gr.
ponderosae gr.
schuetzeella gr.
DDA
Mean (+ SE) weekly trap catch
Degree-day accumulation
May
Jun
Jul
Aug
Sep
Oct
Trapping date

Figures A) and B) on previous two pages.

Figure 2.1. Flight phenology for *Dioryctria* females caught in light traps positioned at the Kalamalka Forestry Centre, Vernon Seed Orchard and PRT Armstrong in (A) 2008 and (B) 2009. On the primarly y-axis, bars represent the weekly mean (+ SE) trap catch which is based on the pooled captures for the four-night trapping period at each orchard (n = 3). On the secondary y-axis, each point represents the number of degree-days ($DDA_{12\,°C}$) accumulated to-date beginning on 1 January for both 2008 and 2009.

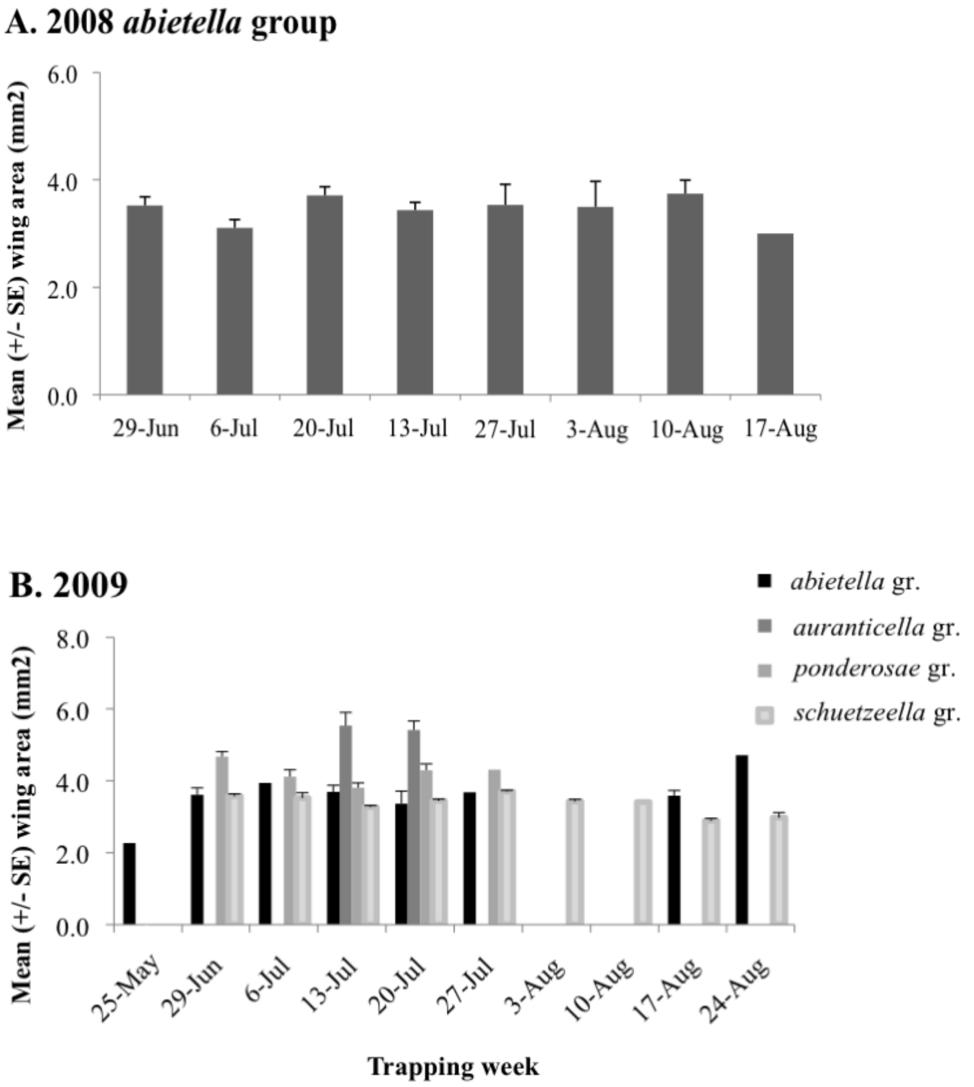


Figure 2.2. Mean (+ SE) wing area (mm^2) for *Dioryctria* females caught in light traps positioned at the Kalamalka Forestry Centre, Vernon Seed Orchard and PRT Armstrong over time within season in (A) 2008 *abietella* gr.: r = -0.1110, *P* = 0.7930; (B) 2009 (data include females captured in traps positioned in all host stand types). Correlations between date and wing area calculated using Pearsons. *abietella* gr.: r = -0.1110, *P* = 0.7930, *auranticella* gr.: r = -0.0980, *P* = 1.000; *ponderosae* gr.: r = 0.3740, *P* = 0.4660; and *schuetzeella* gr.: r = -0.1220, *P* = 0.7380.

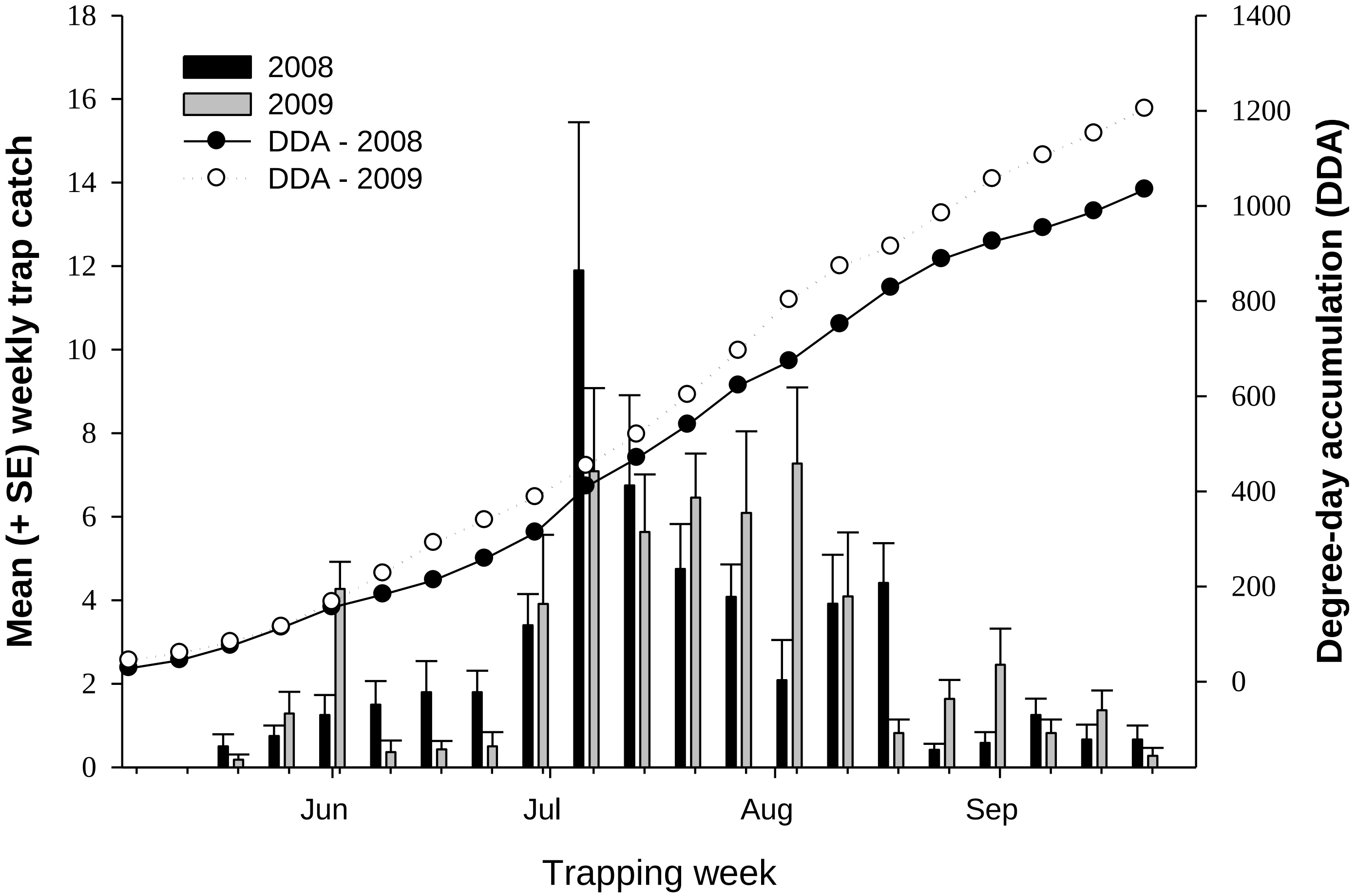

18
16
14
12
10
8
6
4
2
0
1400
1200
1000
800
600
400
200
0
2008
2009
DDA - 2008
DDA - 2009
Mean (+ SE) weekly trap catch
Degree-day accumulation (DDA)
Jun
Jul
Aug
Sep
Trapping week

Figure on previous page.

Figure 2.3. Flight phenology for male *Dioryctria abietivorella* captured in pheromone-baited traps positioned in Douglas-fir blocks in 2008 and 2009. On the primarly y-axis, bars represent the weekly mean (+ SE) trap catch based on the pooled weekly-trap captures in Douglas-fir blocks at the Kalamalka Forestry Centre, Vernon Seed Orchard and PRT Armstrong (n = 3). On the secondary y-axis, each point represents the number of degree-days ($DDA_{12\,°C}$) accumulated to-date beginning on 1 January for both 2008 and 2009.

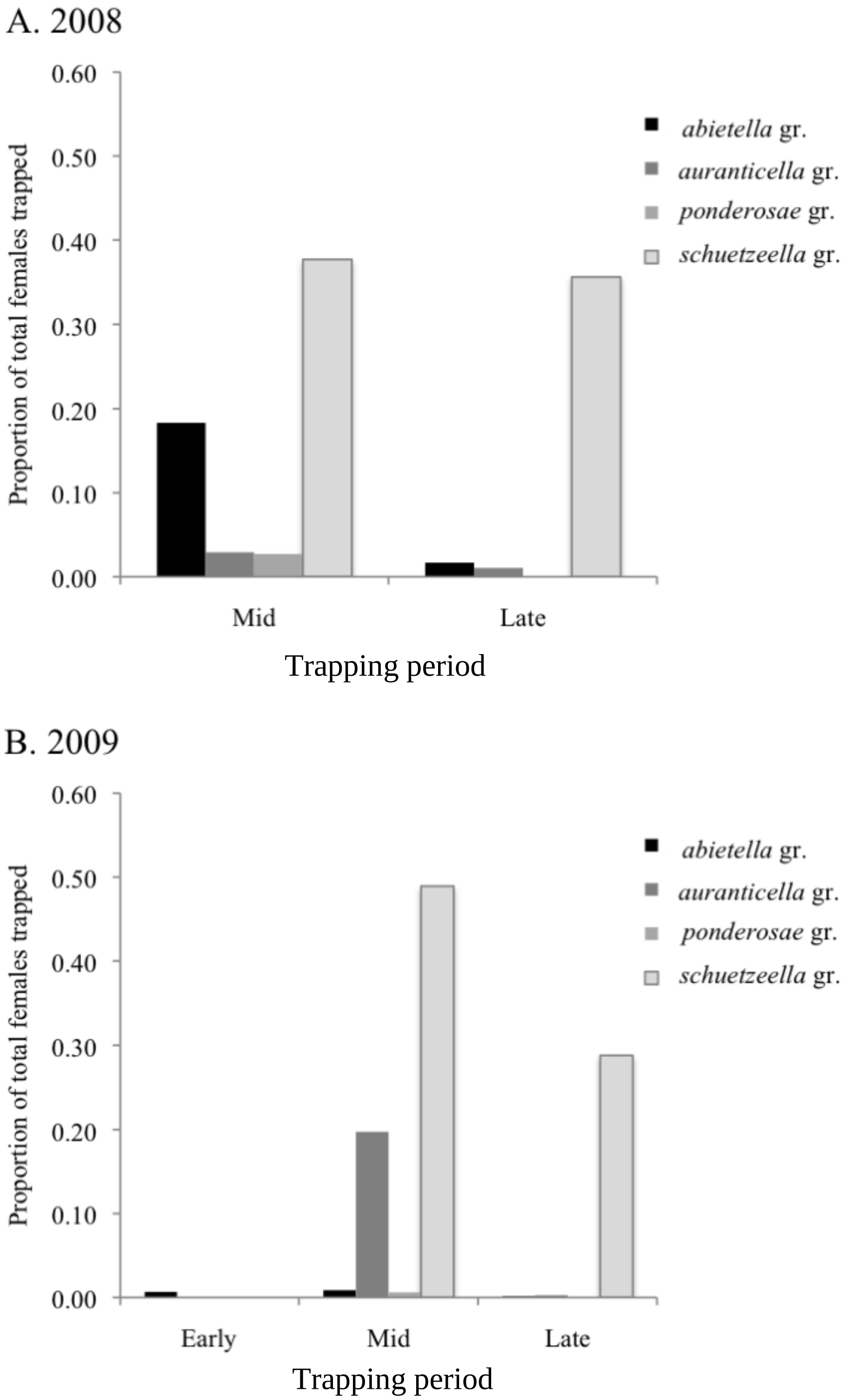


Figure 2.4. The proportion of females from each *Dioryctria* species group captured throughout the flight season in light traps placed in Douglas-fir stands at the Kalamalka Forestry Centre, PRT Armstrong and the Vernon Seed Orchard (n=3) in (A) 2008 (χ^2 = 61.4248, df = 3, P < 0.0001) and (B) 2009 (χ^2 = 746.5846, df = 6, P < 0.0001).

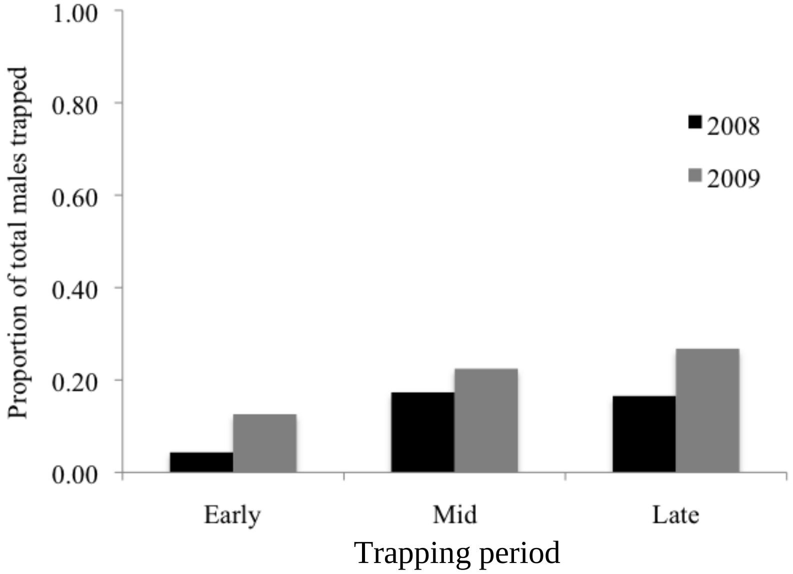


Figure 2.5. The relative proportion of *Dioryctria abietivorella* (*abietella* species group) males caught in pheromone-baited traps positioned in Douglas-fir stands at the Kalamalka Forestry Centre, PRT Armstrong and the Vernon Seed Orchard in 2008 and 2009 ($\chi^2 = 8.2637$, $df = 2$, $P = 0.0161$).

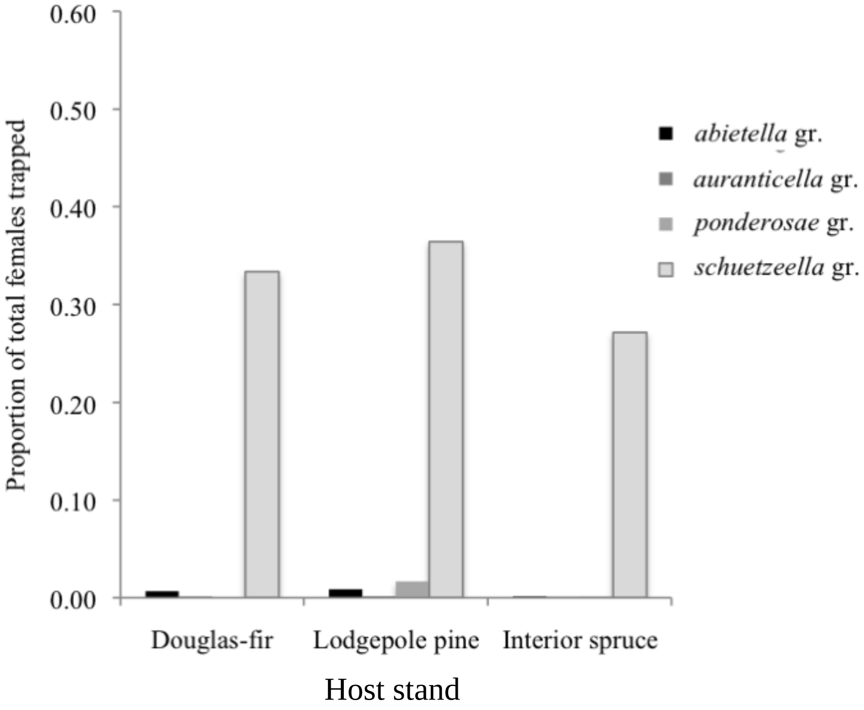


Figure 2.6. The relative proportion of females in various *Dioryctria* species groups caught in light traps placed in Douglas-fir, lodgepole pine, and interior spruce stands at the Kalamalka Forestry Centre in 2009 ($\chi^2 = 80.4158$, $df = 6$, $P < 0.0001$).

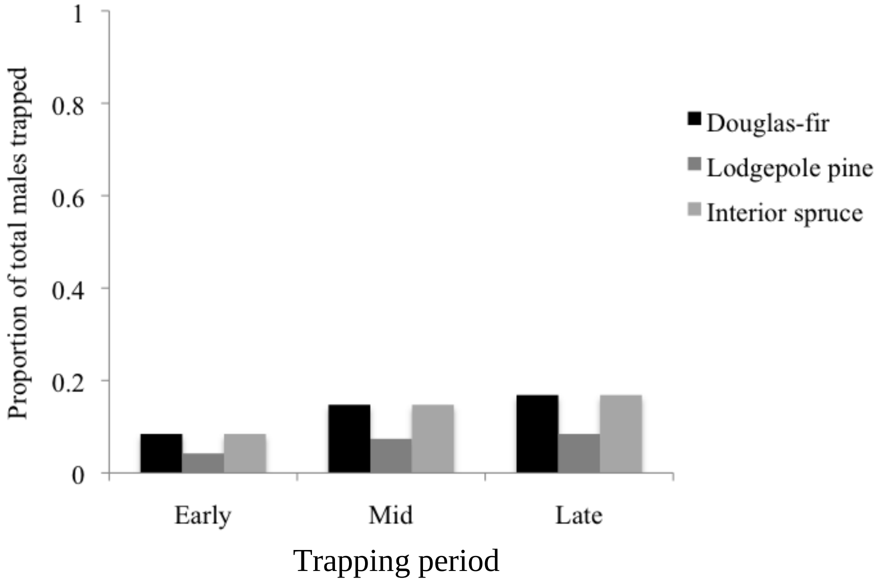


Figure 2.7. The relative proportion of male *Dioryctria abietivorella* (*abietella* species group) caught in pheromone-baited traps placed in Douglas-fir, lodgepole pine, and interior spruce stands at the Kalamalka Forestry Centre in 2009 (χ^2 = 1.6775, *df* = 4, *P* = 0.7948).

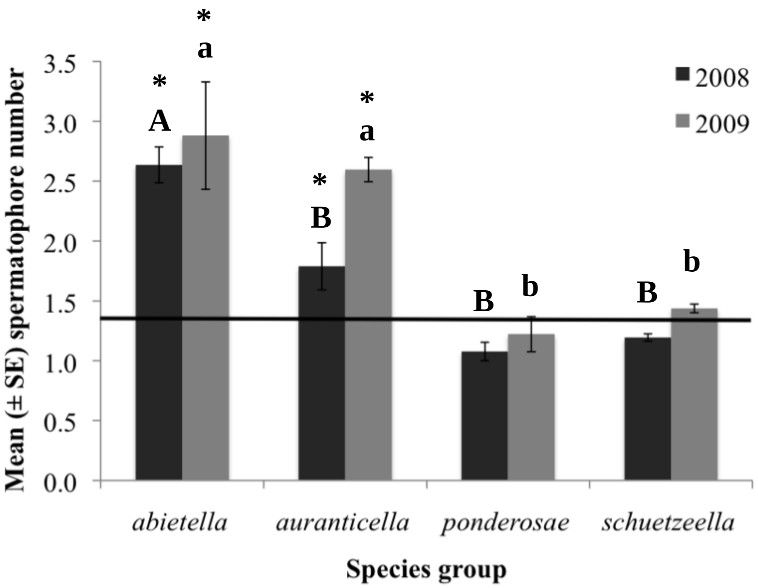
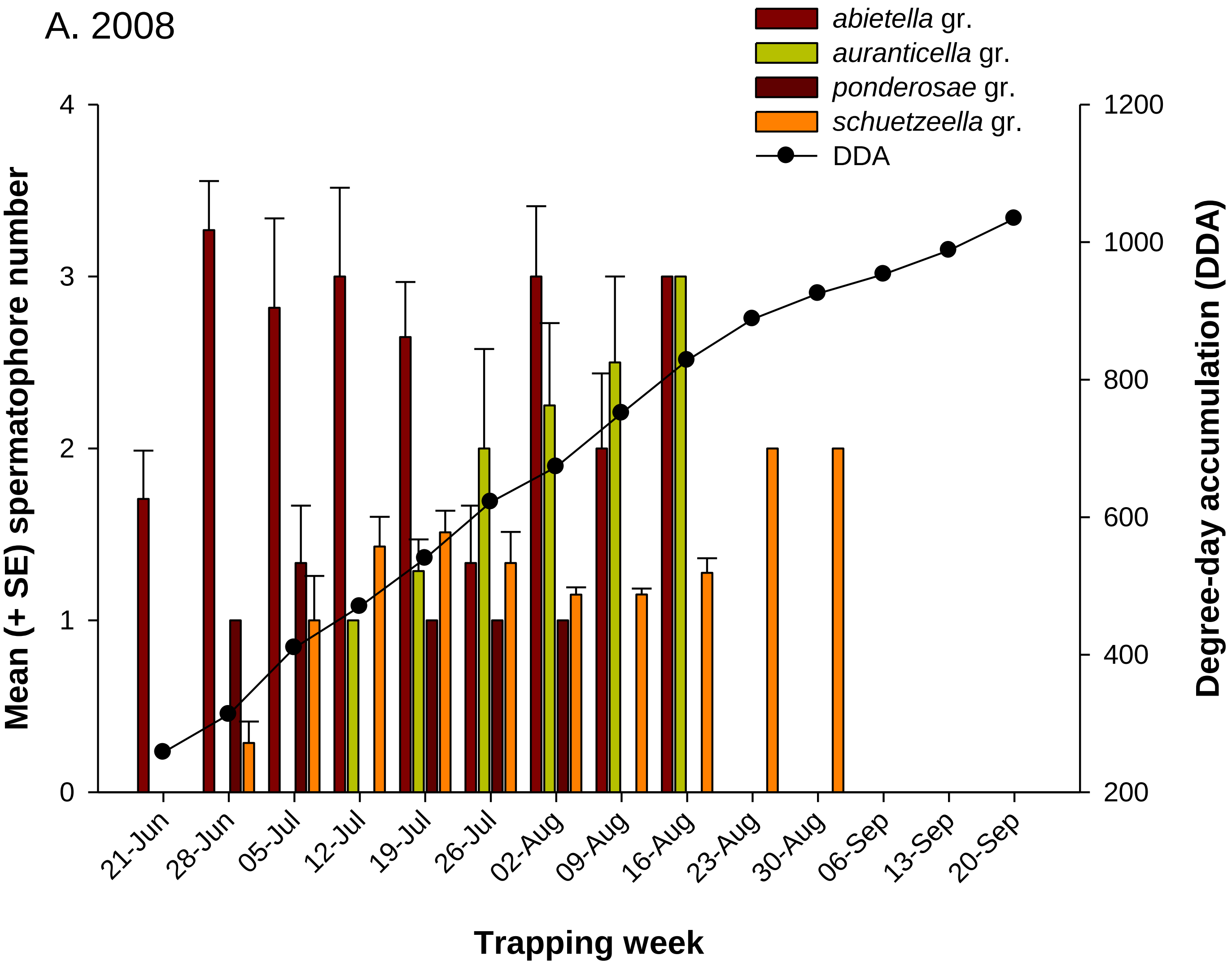
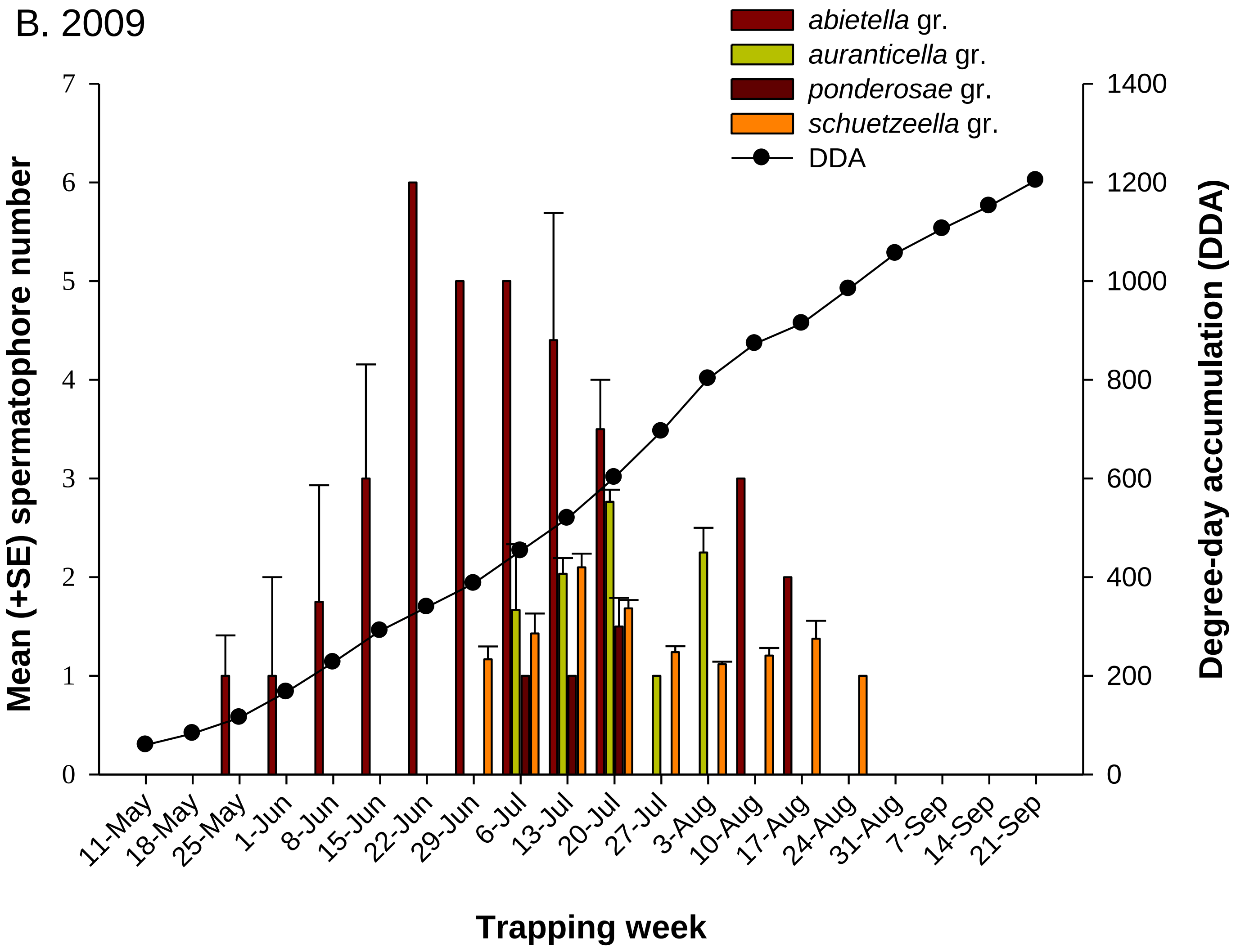


Figure 2.8. Mean spermatophore number (± SE) recovered from female *Dioryctria* caught in light traps positioned at the Kalamalka Forestry Centre, Vernon Seed Orchard and PRT Armstrong in 2008 and 2009. Bars, within year, marked with the same letter are significantly different (SNK, $P < 0.05$). Bars marked by * exceed (visual assessment) the polyandry threshold of 1.4 denoted by the horizontal line (Arnqvist and Nilsson, 2000).


A. 2008
abietella gr.
auranticella gr.
ponderosae gr.
schuetzeella gr.
DDA
Mean (+ SE) spermatophore number
0
1
2
3
4
Degree-day accumulation (DDA)
200
400
600
800
1000
1200
21-Jun
28-Jun
05-Jul
12-Jul
19-Jul
26-Jul
02-Aug
09-Aug
16-Aug
23-Aug
30-Aug
06-Sep
13-Sep
20-Sep
Trapping week


B. 2009
abietella gr.
auranticella gr.
ponderosae gr.
schuetzeella gr.
DDA
Mean (+SE) spermatophore number
0
1
2
3
4
5
6
7
Degree-day accumulation (DDA)
0
200
400
600
800
1000
1200
1400
11-May
18-May
25-May
1-Jun
8-Jun
15-Jun
22-Jun
29-Jun
6-Jul
13-Jul
20-Jul
27-Jul
3-Aug
10-Aug
17-Aug
24-Aug
31-Aug
7-Sep
14-Sep
21-Sep
Trapping week

Figures A) and B) on previous two pages.

Figure 2.9. Seasonality of mating frequency for *Dioryctria* females caught in light traps positioned at the Kalamalka Forestry Centre, Vernon Seed Orchard and PRT Armstrong in (A) 2008 and (B) 2009. On the primary y-axis, bars represent the mean (+ SE) spermatophore number is the number of spermatophores per individual in each species group from four trap nights per date at each orchard. On the secondary y-axis, each point represents the number of degree-days ($DDA_{12\ °C}$) accumulated to-date beginning on 1 January for both 2008 and 2009.

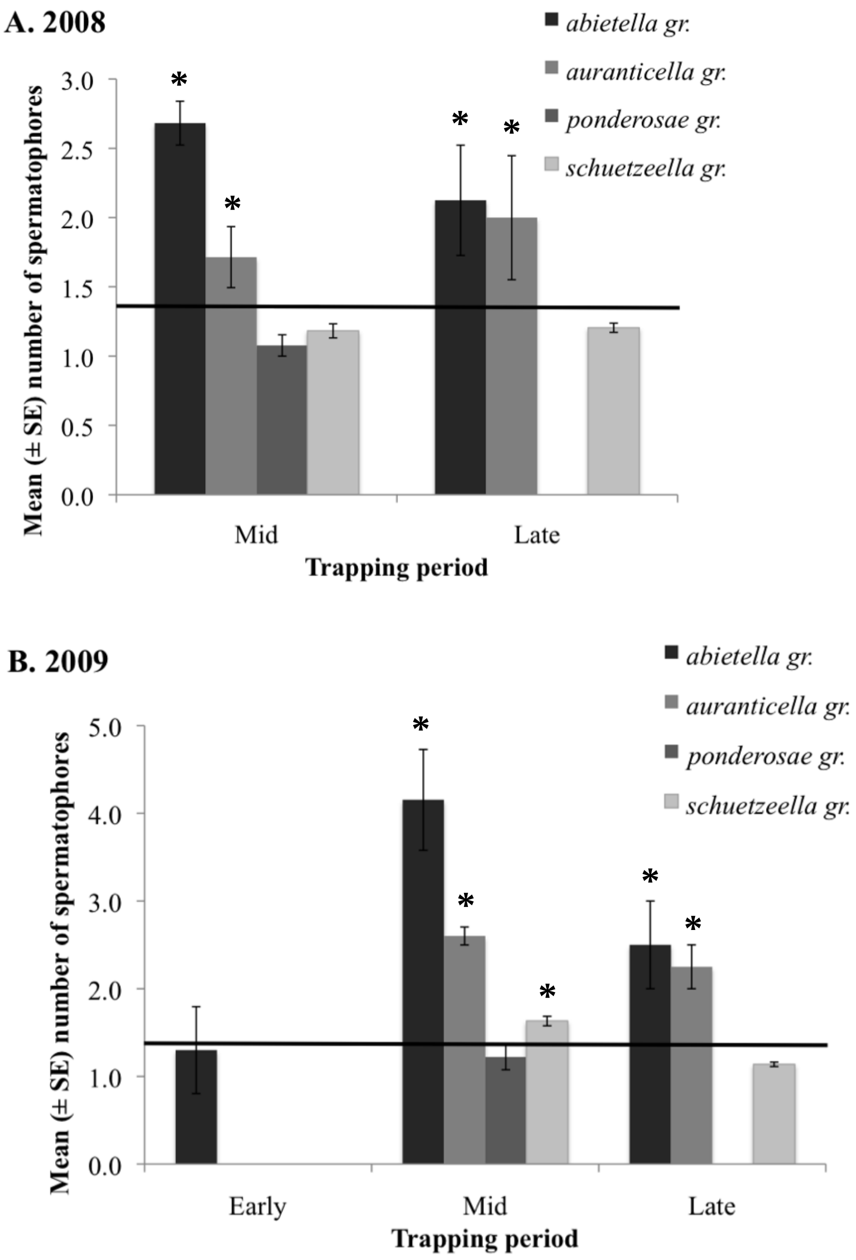


Figure 2.10. The mean spermatophore number (± SE) recovered from *Dioryctria* females caught in light traps positioned at the Kalamalka Forestry Centre, Vernon Seed Orchard and PRT Armstrong over the flight season in (A) 2008 and (B) 2009. Bars marked by * exceed (visual assessment) the polyandry threshold of 1.4 denoted by the horizontal line (Arnqvist and Nilsson, 2000).

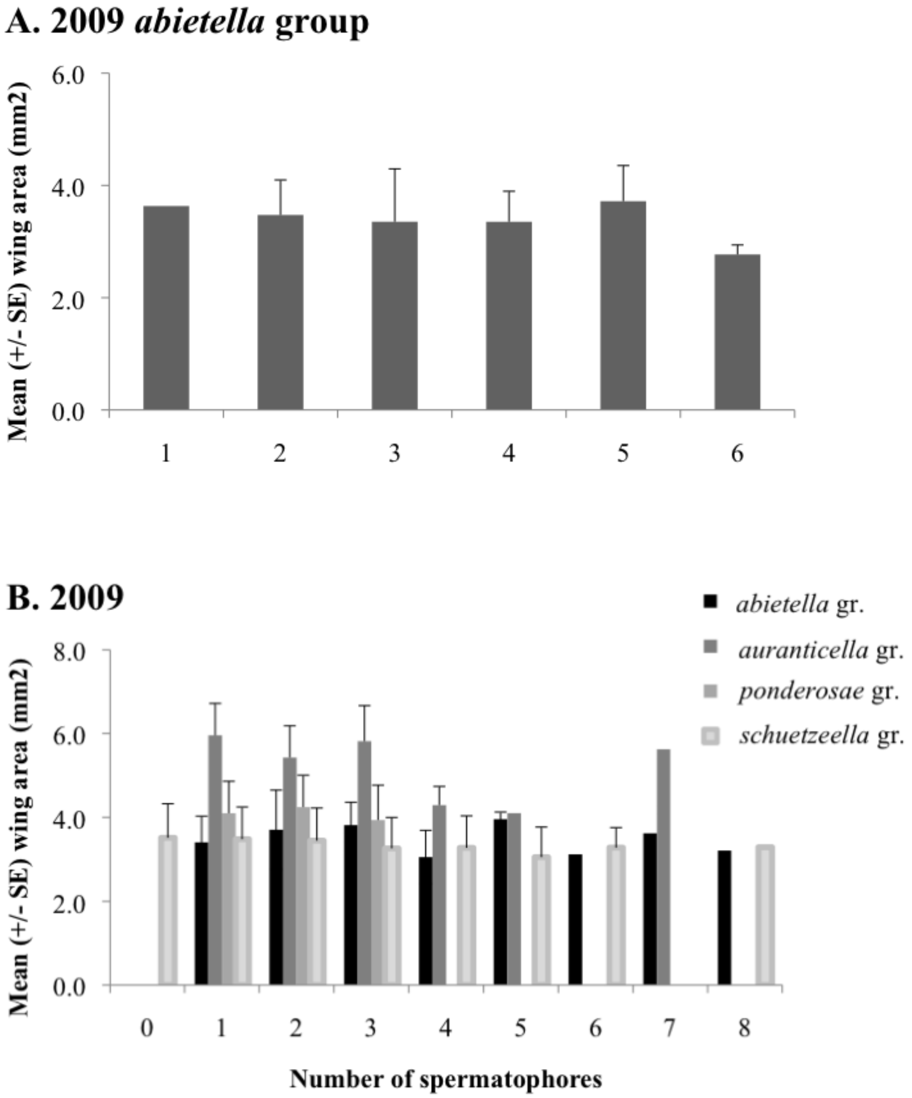


Figure 2.11. Mean (+ SE) wing area (mm^2) of female (A) *abietella* species gr. in 2008 and (B) all females from all species groups in 2009 (includes data of females captured in traps positioned in all host stand types) caught in light traps positioned at the Kalamalka Forestry Centre, Vernon Seed Orchard and PRT Armstrong. Correlations between spermatophore number and wing area were calculated using Spearman's r. *abietella* gr. (2008: r = -0.1040, *P* = 0.3870; 2009: r = -.01170, *P* = 0.6170), *auranticella* (2009: r = -0.5450, *P* = 0.0286), *ponderosae* gr. (2009: r = 0.0222, *P* = 0.891), and *schuetzeella* (2009: r = -0.0926, *P* = 0.0010).

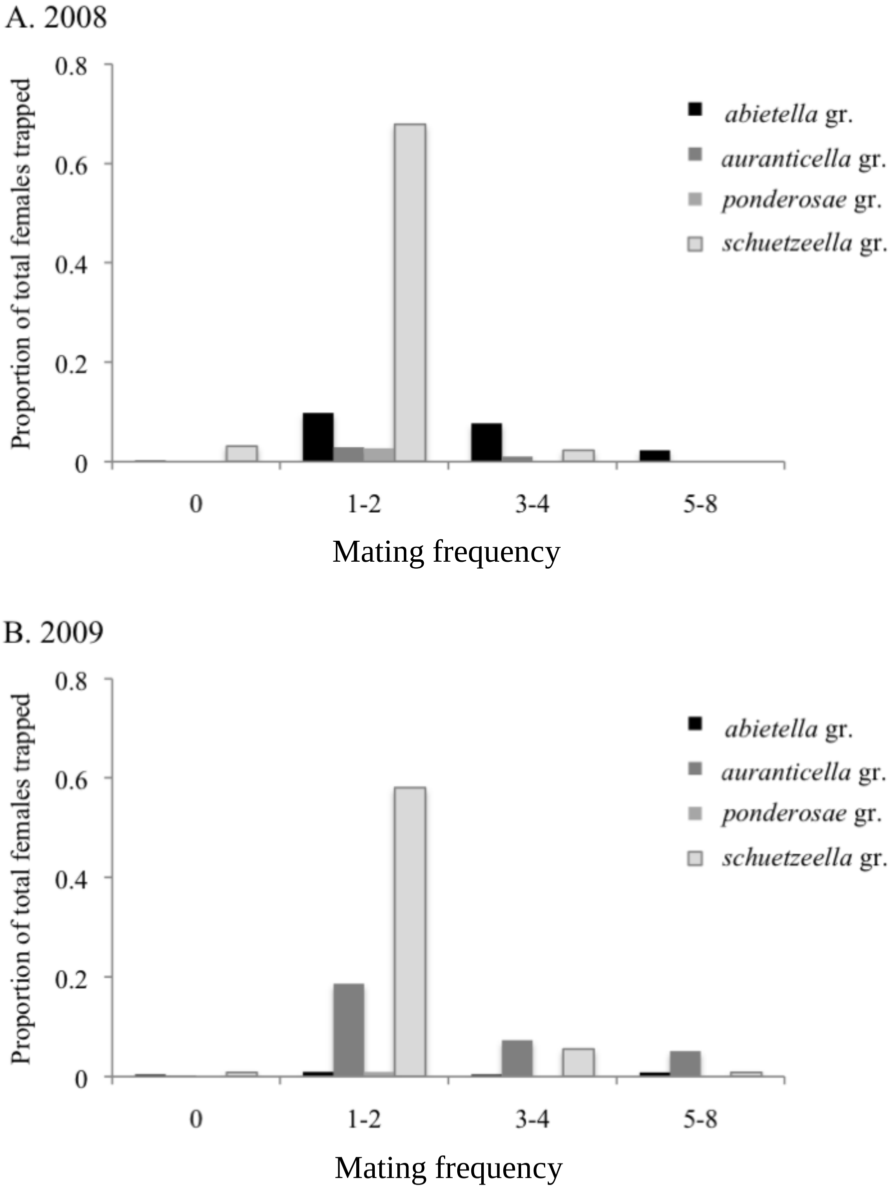
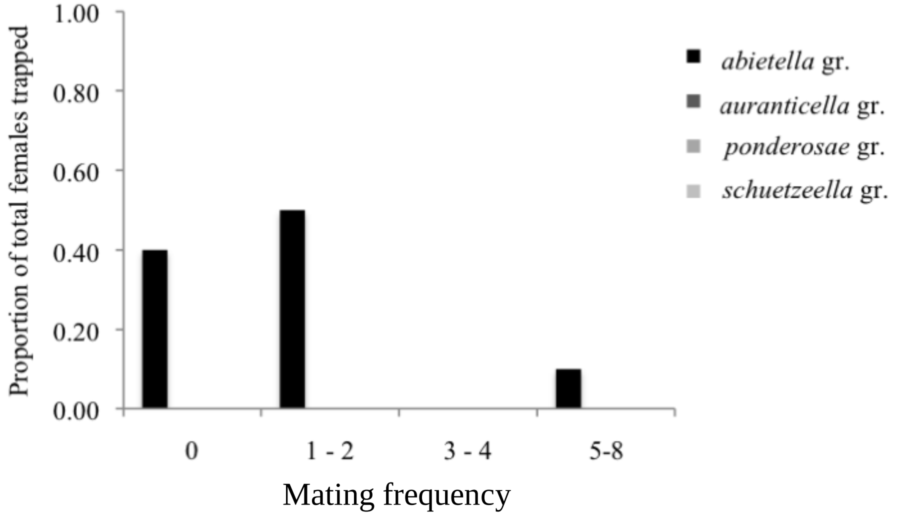
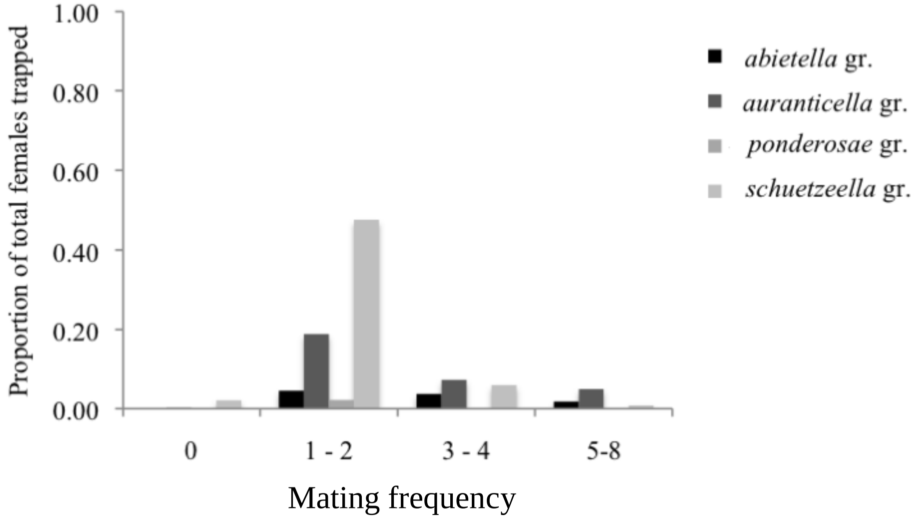


Figure 2.12. The distribution of *Dioryctria* females in each mating frequency category caught in light traps positioned in Douglas-fir stands at the Kalamalka Forestry Centre, PRT Armstrong and the Vernon Seed Orchard in (A) 2008 (χ^2 = 156.5654, df = 9, $P <$ 0.0001) and (B) 2009 (χ^2 = 194.1309, df = 9, $P < 0.0001$).

A. Early


Proportion of total females trapped
1.00
0.80
0.60
0.40
0.20
0.00
0
1 - 2
3 - 4
5-8
Mating frequency
abietella gr.
auranticella gr.
ponderosae gr.
schuetzeella gr.

B. Mid


Proportion of total females trapped
1.00
0.80
0.60
0.40
0.20
0.00
0
1 - 2
3 - 4
5-8
Mating frequency
abietella gr.
auranticella gr.
ponderosae gr.
schuetzeella gr.

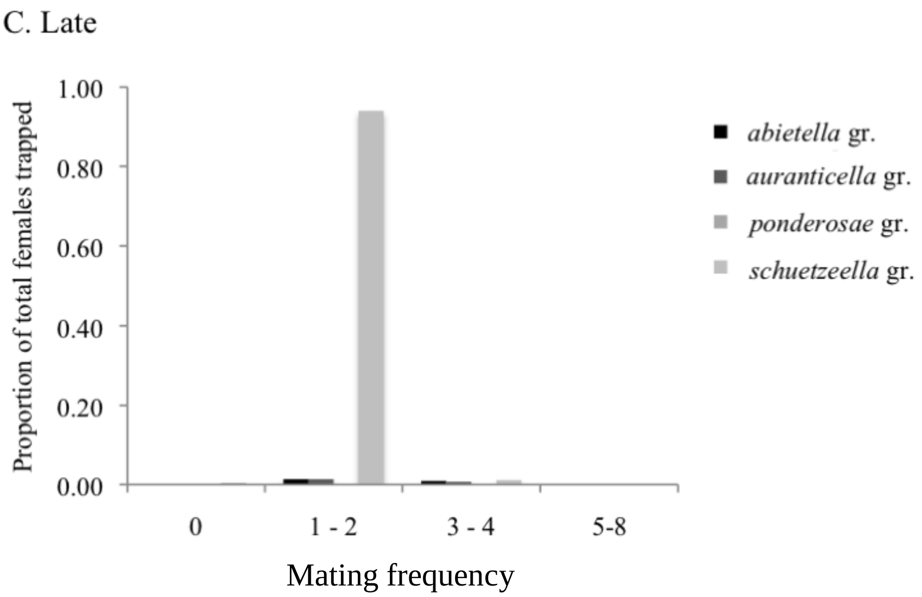

C. Late

Figure 2.13. The distribution of *Dioryctria* flight in each mating frequency category caught during (A) early-, (B) mid- ($\chi^2 = 162.4708$, $df = 12$, $P < 0.0001$) and (C) late-season in light traps positioned in Douglas-fir stands at the Kalamalka Forestry Centre in 2009. Analyses were not completed for early and late trapping periods due to low trap catch in some species groups.

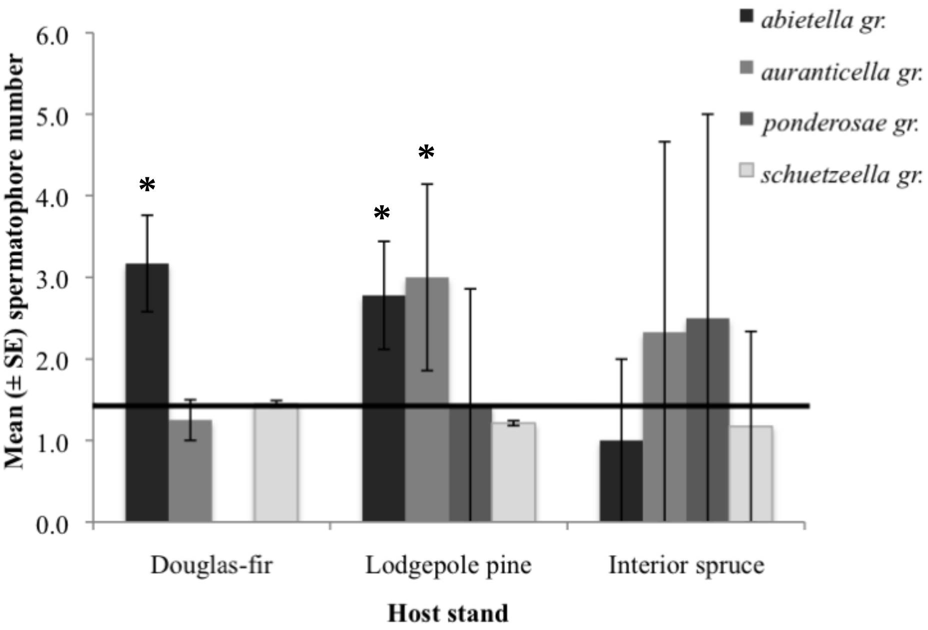
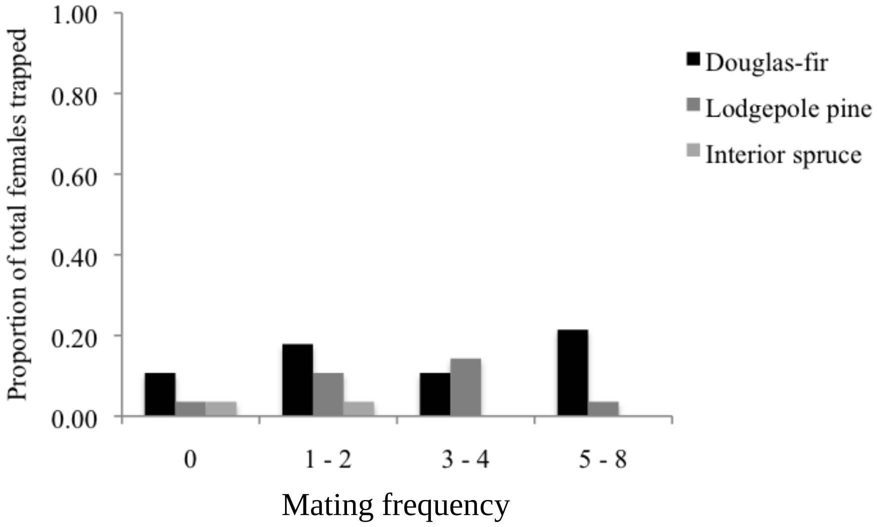
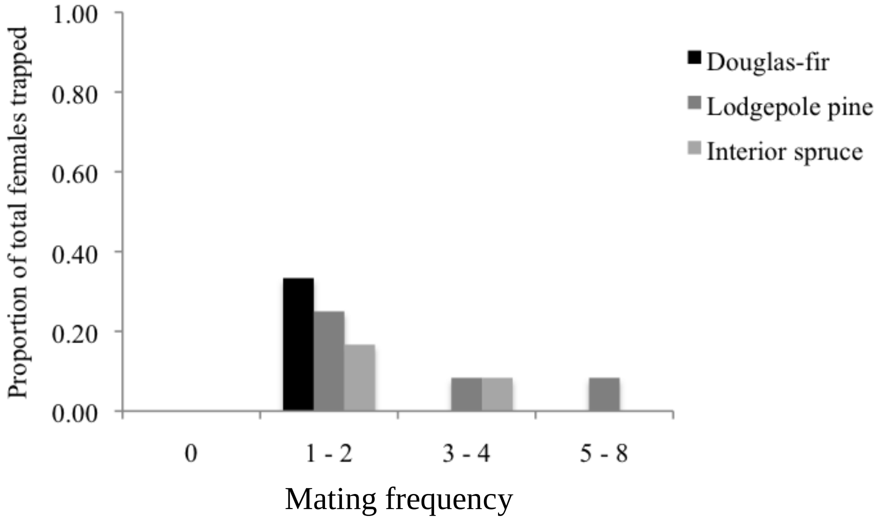


Figure 2.14. The mean (± SE) spermatophore number recovered from female *Dioryctria* caught in light traps positioned in Douglas-fir, lodgepole pine and interior spruce stands at the Kalamalka Forestry Centre in 2009. Bars marked by * exceed (visual assessment) the polyandry threshold of 1.4 denoted by the horizontal line (Arnqvist and Nilsson, 2000).

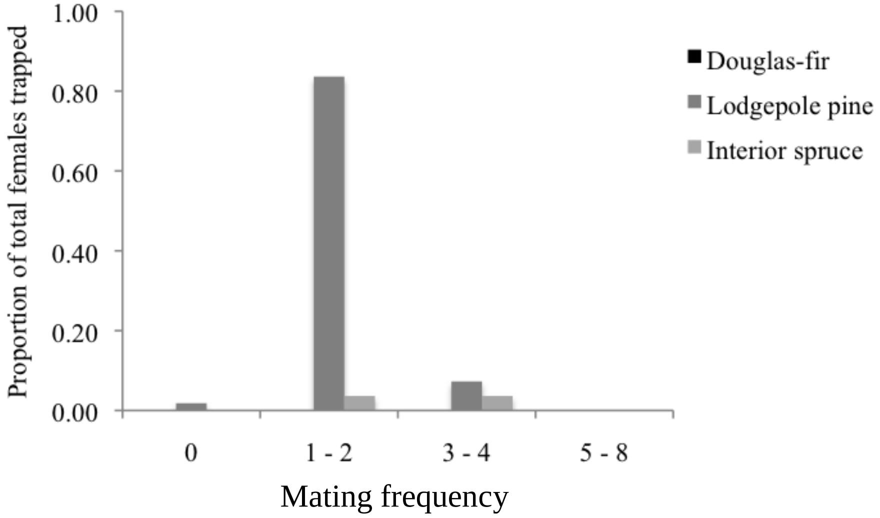
A. *abietella gr.*



B. *auranticella* gr.



C. *ponderosae* gr.



D. *schuetzeella* gr.

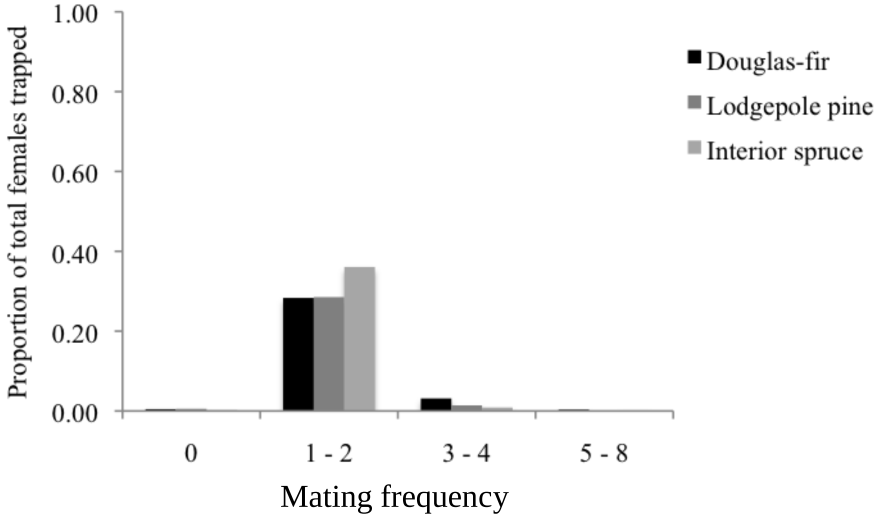


Figure 2.15. The distribution of female *Dioryctria* in each mating frequency category captured in light traps positioned in Douglas-fir, lodgepole pine and interior spruce at the Kalamalka Forestry Centre in 2009. Proportions were compared using Fisher's exact test (A) *abietella* gr. ($P = 0.4851$), (B) *auranticella* gr. ($P = 0.8788$), (C) *ponderosae* gr. ($P < 0.0001$) and (D) *schuetzeella* gr. ($P < 0.0001$).

Chapter 3. The reproductive biology of *Dioryctria abietivorella*

Introduction

In Lepidoptera, reproductive strategies can be broadly classified as capital versus income breeding depending on the degree to which larval- and adult-acquired nutrients are directed towards gametogenesis and somatic maintenance. Pure capital breeders do not feed as adults but rely solely on resources sequestered as larvae or derived from maternal factors (Stearns, 1992; Jönsson, 1997; Boggs, 2009). Alternatively, true income breeders continue to acquire nutrients during adulthood, which subsidize larval resources directed to somatic maintenance and gametogenesis (Stearns, 1992; Jönsson, 1997). Capital breeding females concentrate their reproductive effort soon after adult emergence and eclose with their full egg complement while income breeders spread out their reproductive effort by completing oögenesis after eclosion, which can occur continuously during adulthood (Ramaswamy *et al.*, 1997). True capital and income breeding strategies represent extremes of the resource allocation spectrum but many species exhibit an intermediate state along this spectrum. Life-history traits, like the timing of sexual receptivity, lifespan, fecundity and reproduction can be studied within the framework of resource allocation strategies, and can ultimately contribute to the understanding of population dynamics of a species (Miller, 1996; Tammaru and Haukioja, 1996; Jervis *et al.* 2005; Varpe *et al.*, 2009).

In moths, sexual receptivity is signaled by females to potential mates through the release of a species-specific, sex pheromone that mediates scramble competition among males for mates (Wyatt, 2003). To release the signal, females assume a characteristic posture known as calling (Phelan and Baker, 1990). It is adaptive for females to confine calling behavior to a time when they are sexually mature (*e.g.* are capable of maturing eggs) and under environmental conditions that promote mate finding (Anton *et al.*, 2007). Response to pheromone by male moths can occur over long distances and be energetically costly (Cardé and Haynes, 2004). Male response should coincide with female sexual receptivity to reduce energetic and exposure costs associated with mate location (Anton *et al.*, 2007). Female moths optimize pheromone biosynthesis and release in response to appropriate physiological and environmental cues to coordinate sexual activity with egg maturation and oviposition on an appropriate substrate (Hillyer and Thorsteinson, 1969; Traynier, 1983; Tammaru and Javois, 2000; Åsman and Ekbom, 2006). The release of pheromone is regulated by, among other endogenous and exogenous factors, female age post-eclosion (*e.g.* Valles *et al.*, 1992; del Mazo-Cancino *et al.*, 2004; Rafaeli and Bober, 2005), exposure to host plant volatiles (*e.g.* Raina *et al.*, 1992; Yang *et al.*, 2004) and environmental cues such as photoperiod (*e.g.* Webster and Cardé, 1982; Delisle and Royer, 1994; Iglesias *et al.*, 1999; Zhou *et al.*, 2000) and temperature (*e.g.* Delisle, 1992; Webster and Yin, 1997; Zhou *et al.*, 2000).

The initiation of calling behavior post-female eclosion coincides with egg maturity in several moth species (Howlander and Gerber, 1986). *Ephiphyas postivittana* Walker (Lepidoptera: Tortricidae) females are synovigenic; the percentage of females that call increases with female age post eclosion, as does the number of mature eggs contained within the ovaries (Lawrence and Bartell, 1972). Female *Mamestra configurata* Walker (Lepidoptera: Noctuidae) do not begin calling until the second scotophase post-eclosion when they also begin to accumulate mature eggs (Howlander and Gerber, 1986). Alternatively, pro-ovigenic *Lymantria dispar* Linnaeus (Lepidoptera: Lymantriidae) females (Davis *et al.*, 1990) initiate calling during their first scotophase post eclosion and the percentage of females that call does not increase dramatically as they age (Tang *et al.*, 1992).

Moth age post eclosion influences the diurnal onset of calling similarly in capital and income breeding female Lepidoptera. Older, virgin *Estimene acrea* Drury (Lepidoptera: Arctiidae) females call earlier in the scotophase than do younger virgins (del Mazo-Cancino *et al.*, 2004) and a similar advance in calling onset occurs in virgin female *M. configurata* as they age (Howlander and Gerber, 1986). In some species, older females have lower pheromone titres and are less attractive to males than young females (Webster and Cardé, 1982; Howlander and Gerber, 1986; Delisle and Royer, 1994; del Mazo-Cancino *et al.*, 2004). Calling earlier in the scotophase is thought to compensate for reduced attractiveness of older females compared to younger conspecifics and allows older females to compete for high quality mates (Swier *et al.*, 1977).

Lepidoptera are phytophagous and rely on plants as oviposition substrates and for larval development. Many species integrate host plant cues into their reproductive strategy; some are stimulated to release sex pheromone only in the presence of volatile chemicals released by the host plant (McNeil, 1991; Landolt and Phillips, 1997; Reddy and Guerrero, 2004). Income breeding *Heliocoverpa zea* (Boddie) (Lepidoptera: Noctuidae) females do not release pheromone until they are in proximity of their corn host when volatile compounds released from corn silk stimulate pheromone release (Raina *et al.*, 1992). Moths in the genus *Yponomeuta* Latreille delay calling post adult eclosion and more females call when exposed to host semiochemicals (Hendrikse and Vos-Bünnemeyer, 1987). In the presence of the host plant *Brassica juncea* (Brassicaseae) females of the income breeder *Plutella xylostella* Linnaeus (Lepidoptera: Plutellidae), are induced to call at a younger age, initiate calling earlier in the scotophase and increase the duration of calling as compared to females positioned in clean air (Pittenrigh and Pivnivk, 1993).

There is a great degree of variation in the sexual receptivity at adult emergence in Lepidoptera, which is reflected in the egg maturation strategy of species and correlated with resource acquisition and allocation strategies (Ramaswamy *et al.*, 1997; Jervis *et al.*, 2005). After ovariole development and follicle formation, the process of oögenesis consists of two major stages: vitellogenesis and postvitellogenic development (Telfer, 2009). Broadly, vitellogenesis involves yolk deposition in the oöcyte and postvitellogenesis includes the formation of the protective chorion (Telfer, 2009). In pure capital breeding species, the entire process of egg development occurs prior to adult eclosion. In pure income breeding systems, egg maturation is restricted to the adult stage, with vitellogenesis and choriogenesis occurring after adult eclosion. In all species, oögenesis is controlled by the endocrine system; although the hormones involved (*e.g.* juvenile hormone and/or ecdysteroids) vary with the egg maturation strategy (Ramaswamy *et al.*, 1997; Telfer, 2009). Hormonal control of oögenesis is affected by factors such as adult feeding, the presence of an appropriate oviposition substrate, mating status and age (Ramaswamy *et al.*, 1997).

Oögenesis is stimulated by mating in many income breeding Lepidoptera that do not eclose with their full egg complement and exhibit delayed reproduction (Ramaswamy *et al.*, 1997). Along with sperm, males transfer accessory gland compounds that can stimulate egg production. These compounds may include male-derived hormones or nutrients that promote egg production (Boggs and Gilbert, 1979; McNamara *et al.*, 2008).

Cydia pomonella Linnaeus (Lepidoptera: Tortricidae) females complete choriogenesis after emergence. After mating, the juvenile hormone titre of females increases, which is associated with elevated choriogenesis (Webb *et al.*, 1999). Male *H. virescens* accessory sex glands contain juvenile hormone, which is transferred to the female during mating and stimulates egg production (Zeng *et al.*, 1997; Shu *et al.*, 1998; Pzczolkowki *et al.*, 2006). *Lanacobia oleracea* Linnaeus (Lepidoptera: Noctuidae) exhibits delayed mating and oviposition (Corbitt *et al.*, 2009) and female juvenile hormone titre spikes after mating to stimulate oögenesis and oviposition and decreases with age thereafter (Edwards *et al.*, 1995).

For female Lepidoptera, delays in mating post eclosion can significantly reduce fecundity. Females that do not mate may resorb eggs (Proshold *et al.*, 1982; Boggs and Ross, 1993) and/or halt oögenesis (Zeng *et al*, 1997; Shu *et al.*, 1998). Capital breeders have little flexibility in oögenesis compared to income breeders that exhibit extended oögenesis during the adult stage. Income breeding females may preserve their longevity and increase the opportunity for future matings through the retention of reserves that might otherwise be allocated to egg production (Williams, 1966; Proshold *et al.*, 1982; Leather, 1988; Arnqvist & Nilsson, 2000). Female Lepidoptera with various resource allocation and reproductive strategies experience the detrimental effects of delayed mating on oögenesis (Torres-Vila *et al.*, 2002).

Reproduction is a costly process and trade-offs between reproduction and longevity are common in Lepidoptera (Williams, 1966; Roff, 1992). Costs are incurred through the act of mating and the production of gametes. These costs negatively impact lifespan or decrease reproductive capacity and carry similar costs for both income and capital breeders. Mating requires time and exposes insects to predation (Acharya and McNeil, 1998), disease and parasites (Hurst *et al.*, 1995). Additionally, female reproductive organs can be damaged during mating (Crudington & Siva-Jothy, 2000). Due to sperm competition in species that mate multiple times, male ejaculate may contain substances that decrease female receptivity, lengthen post mating refractory time or reduce the fertility of the previous mate's sperm (Wedell, 2005; Fischer, 2007). These antiaphrodisiacs can have a significant negative effect on female health and lifespan (Chapman *et al.*, 1995; Fischer, 2007).

Trade-offs between reproduction and longevity occur when energetic reserves are shunted from the soma to gametogenesis. The allocation of these resources to reproductive processes by mated individuals can result in reduced survival compared to virgins (Roff, 1992). Capital breeding females' use energy reserves as an adult solely for somatic maintenance, while these reserves are allocated to both somatic maintenance and future reproduction in income breeding species. In Lepidoptera, adult longevity heavily influences fecundity (Leather, 1988). Among species, the relationship between longevity and fecundity varies depending on the ability to resorb tissue, age at first mating, the degree of multiple mating, as well as with the resource allocation strategy (Leather, 1988; Arnqvist and Nilsson, 2000; Jervis *et al.*, 2005). The fecundity of capital breeders *Cleorodes lichenaria* Hufnagel (Lepidoptera: Geometridae) (Pöykkö, 2009) and *Streblote panda* Hübner (Lepidoptera: Lasiocampidae) (Calvo and Molina, 2005) is closely linked to pupal mass but not adult longevity. Alternatively, body weight is correlated with realized fecundity and longevity in the capital breeder, *Lobesia botrana* Denis and Schiffermüller (Lepidoptera: Tortricidae) (Torres-Vila *et al.,* 2002). In the income breeding species *Mnesampela privata* Guenée (Lepidoptera: Geometridae) weight and realized fecundity are not correlated but longevity is correlated with the number of eggs laid (Walker and Allen, 2010). Increased fecundity is linked with adult feeding and there is a lack of correlation between fecundity and weight in the income breeder, *Panolis flammea* Denis and Schiffermüller (Lepidoptera: Noctuidae) (Leather, 1984). Mated *Caudra cautella* Walker (Lepidoptera: Pyralidae) females die sooner than virgins but larger females live longer than smaller females in this income breeding species (McNamara *et al.*, 2008). Lifespan increases for mated females that receive only prespermatophoric seminal compounds compared to females that receive prespematophoric compounds and a spermatophore (McNamara *et al.*, 2008). Higher fecundity is achieved by females that receive both a spermatophore and prespermatophoric compounds (McNamara *et al.*, 2008).

This study focuses on the reproductive biology of *Dioryctria abietivorella* Grote (Lepidoptera: Pyralidae), an economically important cone-feeder with a wide geographic range in North America (Heinrich, 1956; Neunzig, 2003). *Dioryctria abietivorella* is a highly polyphagous cone feeder on *Abies*, *Picea*, *Pseudotsuga* and *Pinus* trees (Heinrich, 1956; Neunzig 2003) and infestations can cause substantial economic losses for conifer seed orchards that produce seed for reforestation programs (Hedlin *et al*., 1980; Strong, 2005). Although some research has been conducted on the reproductive biology of this moth, several aspects remain unexplored. *Dioryctria abietivorella* adults are long-lived and delay mating until three to four days after adult eclosion, which is followed by an extended oviposition period that lasts approximately two weeks in the laboratory (Trudel *et al*., 1995). These behaviours suggest that *D. abietivorella* is an income breeder, though it is unknown if females eclose with their full egg complement, nor what affect mating has on oögenesis and the lifespan of both sexes. Female *D. abietivorella* respond to monoterpenes (Shu *et al*., 1997) but the role of host volatiles in their reproductive behaviour has not been clearly delineated. In these experiments, I evaluate the effects of age and host material on calling behaviour, as well as the effect of age and mating on egg production. Further to this, I consider the trade-off between reproduction and longevity in both males and females of this species, along with the potentially mitigating affects of body size on reproduction and longevity. The results are discussed within the framework of resource allocation in *D. abietivorella.*

Methods and Materials

3.1. Insect collection and handling

Infested cones that contained mature *D. abietivorella* larvae were collected from a Douglas-fir seed orchard located at the Kalamalka Forestry Centre in Vernon, British Columbia (50º 14’ N, 119º 16’ W) from 13 June to 31 July in 2008 and 30 June to 3 August in 2009. Insects were housed in an environmental chamber (Conviron E-15, Conviron, Winnipeg, MB) and held at 24ºC, 30% RH under a 16:8 (L:D) h photoregime. Each larva was transferred individually upon emergence from the cone to a 29.6 ml Solo® cup (Cleanway Supply Inc., Kamloops, BC) that contained casein and wheat germ-based diet (McMorran, 1965; Trudel *et al*., 1995). Insects were separated by sex as pupae (Trudel *et al*., 1995), placed in a 15.4 L opaque plastic bucket (Container Supply Company, Garden Grove, California) and observed daily for adult eclosion. Representative voucher specimens from each species group have been deposited at the Strickland Museum, University of Alberta.

3.2. Calling behaviour of female D. abietivorella

3.2.1. Effect of age on female calling behaviour

Experiments to test the hypothesis that female moth age influences pheromone release behaviour (calling) were conducted in August 2008 and 2009 in Douglas-fir blocks at the Kalamalka Forestry Centre. In 2008, females were assigned to one of three age groups: young (0-1 day old), middle-aged (5-7 days) and old (10-12 days). In 2009, the young age class was further split into 0 and 1-day old treatments in addition to the middle-aged and old treatments. Newly eclosed females were held communally in a 15.4 L opaque plastic bucket allocated to each age group. No more than twenty individuals were held in each bucket at a time. Females were provided with 10% sugar water through a cotton wick (Patterson Dental Supply Inc., Richmond, BC). On the morning of the bioassay, moths were placed individually in a mesh-capped 207.0 ml translucent plastic Dixie® cup (Zellers, Vernon, BC) in the 2008 experiment and in 74.0 ml plastic vials (Fisher Scientific) with both ends covered in mesh in 2009. Each cup was suspended from a Douglas-fir branch at a height of approximately 1.5 m. Females were spaced at least 15 m apart in one of two blocks with females from each age group randomly distributed in the two blocks. Female behaviour was monitored every 30 minutes for 24 h starting at noon, approximately eight hours before sunset. Between two and twenty-two females per age class were observed on each of three days in 2008 and between two and ten females per age class were observed on each of three days in 2009.

Logistic regression was used to compare the proportion of calling females by age group for experiments conducted in 2008 and 2009. Data for 2008 and 2009 were analyzed separately using the main effects of trial date and age group and an interaction between the two variables. Backwards-stepwise regression was used to find the most parsimonious models. ANOVA was used to test the hypothesis that age affects calling behaviour. The mean time of initiation, cessation and the duration of calling were compared among female age groups tested in 2008 and 2009. In 2008, the analysis was blocked by trial date, a significant variable in the regression model. In 2009, the analysis was not blocked by trial date because this variable was not significant in the regression model. Individual differences among treatments were compared with Tukey's honestly significant difference test. All statistical analyses were completed using R version 2.11.1 (R Core Development Team, 2010).

A third experiment tested the hypothesis that female age influences their attractiveness to males. Delta traps with sticky inserts were baited with a single virgin female in one of three age groups: young (0-1 day old), middle (5-7 days) and old (10-12 days). Females were contained within a 6 x 6 cm black mesh (Central Tarp & Awning, Vernon, BC) bag. Each of three to four traps baited with a female from each age group and at least one synthetic pheromone-baited trap (a positive control) were located in each of three Douglas-fir blocks at the Kalamalka Forestry Centre. Traps were positioned at mid-canopy at least 15 m apart in random order by treatment. Traps were checked every 60 minutes beginning one hour prior to sunset and ending one hour past sunrise and captured male moths were counted. Three to four traps from each treatment group were observed on each of the two bioassay nights. Too few male moths were captured in this experiment to conduct statistical analysis on the data.

3.2.2. Effect of host material on female calling behaviour

To test the hypothesis that exposure to host plant material influences calling behavior, virgin females were held in 74.0 ml plastic chambers (Fisher Scientific) with both ends covered in mesh in close proximity to one of three treatments: 1) Douglas-fir cones (~ 6 cm long); 2) Douglas-fir foliage (branch and needles, ~ 6 cm long); or 3) no host material. Females aged 5-7 days were used in this trial because in previous trials middle-aged females showed the greatest propensity to call. Cones and foliage with no visible signs of insect or fungal infestation were harvested in July 2009 and immediately frozen at -20ºC until initiation of the experiment in August 2009. The host material was defrosted just before the initiation of each bioassay. Observations of females were conducted indoors on each of three nights under a 16:8 (L:D) photoregime at 21ºC. Females were monitored at 30-minute intervals starting one hour before the onset of scotophase until the end of the first hour of the photophase. Moths exposed to the three treatments were located in separate rooms during the bioassay to reduce the potential for cross contamination among treatments. Treatments were rotated between rooms on different observation nights. Ten insects from each treatment group were observed on each of three nights.

Logistic regression was used to test the hypothesis that the presence of host material will affect the proportion of calling females compared to the control group. The saturated model included the main effects of trial date and treatment and an interaction between the two variables. Backwards-stepwise regression was used to reduce the model. ANOVA was used to test the hypothesis that the presence of host material affects the mean time of initiation, cessation and the duration of calling with trial date included as a blocking factor. Trial date and the interaction between trial date and treatment were not significant and so dates were pooled. Individual differences among treatments were compared with Tukey's honestly significant difference test. All statistical analyses were completed using R version 2.11.1.

3.3. Female D. abietivorella egg production

3.3.1. Effect of female mating status on egg production

To test the hypothesis that mating status affects egg production in *D. abietivorella* females, realized (eggs laid) and potential (eggs laid + eggs remaining in the ovaries) fecundity over a 10-day period were measured in mated and virgin females. Adult females were weighed to 0.1 mg (Mettler AE240) within 24-hours of eclosion and placed either individually or with a male in a 0.54 L translucent plastic container (Container and Packaging Supply, Eagle, Idaho) with a mesh lid. Moths were fed a 10% sugar solution through a cotton wick (Patterson Dental Supply Inc., Vernon, BC) and the containers were misted daily with distilled water. Preliminary observations showed that the presence of Douglas-fir cones encouraged reproductive behavior; uninfested cones were placed on top of each container and were replaced every three days throughout the bioassay. Moth pairs were maintained in an environmental chamber (Conviron E-15) held at 24ºC, 30% RH under a 16:8 (L:D) h photoregime. Eggs laid in the containers were counted and removed 1, 5 and 10 days after pairing and moths remained together during the 10-day bioassay. At 10 days of age, females were frozen at -18ºC and preserved for dissection in 70% ethanol. The ovaries were dissected in Ringer's solution and the number of chorionated eggs in each ovariole was counted using a dissecting microscope (Leica MZ9.5) at 40 x magnification. Mating status was confirmed by the presence of a spermatophore in the *bursa copulatrix* and the number of spermatophores was counted. Wing area was used as a measure of body size for all collected specimens. The right forewing of each female was removed and pasted onto white paper. A digital image of each wing was obtained by scanning (HP Scanjet 4070) the prepared wings. Wing area was measured to 0.1 mm^2 using ImageJ (Version 1.34s, National Institute of Health, USA).

Three-way ANOVAs were used to test the influence of mating on egg production in *D. abietivorella* females. The first model assessed realized fecundity and the number of eggs laid was specified as the dependent variable with wing area, body weight, and mating status as independent variables. Interaction terms between wing area and mating status, and body weight and mating status were also included in the model. The second model assessed potential fecundity with the total number of eggs as the dependent variable with wing area, body weight, and mating status specified as independent variables. Interaction terms between wing area and mating status, and body weight and mating status were also included in the model. The potential for collinearity between wing area and body weight as independent variables was assessed with Pearson's correlation coefficients and variance inflation factors for each variable. Individual treatment differences were compared with Tukey's honestly significant difference test.

3.3.2. Effects of female age on egg production

The effect of female age on egg production was tested by assessment of chorionated eggs in the ovaries of virgin females in experiments conducted in 2008 and 2009. Adult females were placed individually within 24-hours of eclosion in a 0.54 L translucent plastic container fitted with a mesh lid. Uninfested Douglas-fir cones were placed on top of each container and replaced every three days. The moths were fed a 10% sugar solution through a wick (Patterson Dental Supply Inc., Richmond, BC) and containers were misted daily with distilled water. The age categories compared in 2008 were young-0 (0 day old, n = 5), old (10-12 days, n = 15), and oldest (16-18 days, n = 11). In 2009, the age groups were young-0 days (n = 30), young-1 days (n = 34), middle-aged (5-7 days) (n = 33), old (10-12 days) (n = 32) and oldest (16-18 days) (n = 30). When females reached the appropriate age, they were frozen at -18ºC and preserved in 70% ethanol. The reproductive tract was removed in Ringer's solution and the number of chorionated eggs was counted using a dissecting microscope (Leica MZ9.5) at 40 x magnification. A digital image of each wing was obtained by scanning (HP Scanjet 4070) the prepared wings. Wing area was measured to 0.1 mm^2 using ImageJ (Version 1.34s, National Institute of Health, USA).

Three-way ANOVAs were used to test that the effect of female age on egg production in virgin *D. abietivorella* females. The number of chorionated eggs was specified as the dependent variable and wing area, body weight, and mating status were included as independent variables. Interaction terms between wing area and mating status, and body weight and mating status were also included in the model. The potential for collinearity between wing area and body weight as independent variables was assessed with Pearson's correlation coefficients and variance inflation factors were calculated for each variable. Individual treatment differences were compared with Tukey's honestly significant difference test. Data from experiments conducted in 2008 and 2009 were analyzed separately.

3.4. Trade-offs between reproduction and longevity

This experiment tested the hypothesis that mating status influences adult longevity. Adult moths were weighed to 0.1 mg (Mettler AE240) within 24-hours of eclosion and placed either individually or in mating pairs in 0.54 L translucent plastic containers (Container and Packaging Supply, Eagle, Idaho) fitted with a mesh screen lid and held at 24ºC, 30% RH under a 16:8 (L:D) h photoregime. Moths were provided with a supply of 10% sugar solution through a cotton wick (Patterson Dental Supply Inc., Richmond, BC) and cages were misted daily with distilled water. Adult mortality was checked daily. Eggs laid in the container were counted and removed every five days until the female died. Pairs remained together until death and females were preserved in 70% ethanol for dissection of the ovaries. The reproductive tract was removed in Ringer's solution and the number of chorionated eggs was counted using a dissecting microscope (Leica MZ9.5) at 40 x magnification. Female mating status was confirmed by presence of at least one spermatophore in the *bursa copulatrix* and the number of spermatophores was counted. A digital image of the right wing of each moth was obtained by scanning (HP Scanjet 4070) the prepared wings. Wing area was measured to 0.1 mm^2 using ImageJ (Version 1.34s, National Institute of Health, USA).

To assess the potential of collinearity between wing area and body weight as independent variables the Pearson's correlation coefficients and variance inflation factors were calculated separately for males and females. To determine if mating influences egg production in female moths, a Welch's T-Test (to account for unequal variances) (Welch, 1947) was used to assess whether realized and potential fecundity varied with mating status. A backwards-stepwise generalized linear regression procedure was used to predict adult *D. abietivorella* longevity and determine if there is a trade-off between longevity and reproduction. The data were heterogeneous and the ratio of residual errors to degrees of freedom indicated that the data were overdispersed. Application of a negative binomial distribution compensated for the overdispersion of the errors. The first model predicted the longevity of adult moths using wing area, body weight, mating status, sex, and all possible two-way interactions as independent variables. Longevity was then modeled separately for females and males because sex was a significant factor in the first model. To predict female longevity, two separate models were used with different reproductive measures (realized and potential fecundity) in each model. The first model included the independent variables eggs laid, wing area, body weight, mating status, and all two-way interactions. An additional model predicted female longevity based on potential fecundity, wing area, body weight, mating status and all two-way interactions as independent variables. Male longevity was modeled using wing area, body weight, mating status and all possible two-way interactions as independent variables. In each model, the most parsimonious model was selected by automatic sequential removal of insignificant variables based on analysis of deviance tests and Akaike information criteria (AIC) (Burnham and Anderson, 2002).

All statistical analyses were completed using R version 2.11.1. In models that contained categorical independent variables, contrasts were conducted by treatment resulting in the arrangement of factor levels alphabetically. The factor with the first letter occurring in the alphabet is made into the intercept to which all other factors are compared. With factors that contain more than one level, comparisons are made only between the intercept and each level and are not made between the levels of individual factors.

Results

3.2. Calling behaviour of female D. abietivorella

3.2.1. Effect of age on female calling behaviour

Female *D. abietivorella* released pheromone only after sunset and ceased prior to sunrise. There is a delay in calling behaviour and sexual receptivity post adult eclosion. The proportion of calling females was significantly greater in the middle-age group than in the young and old groups in the experiment conducted in 2008 ($z = 2.713$, $P = 0.0067$) (Fig. 3.1A) (Appendix 1, Table A1.1). A significantly greater proportion of females called in the middle- ($z_{middle} = 3.152$, $P = 0.0016$) and old- ($z_{old} = 3.216$, $P = 0.0013$) age groups as compared to young-0 females in the 2009 experiment (Fig. 3.1B) (Appendix 1, Table A1.2). The proportion of young-0 and young-1 females that called was similar ($z = 0.902$, $P = 0.3663$) in 2009 (Fig. 3.1B). Trial date was significantly associated with the proportion of females that called in 2008 (Appendix 1, Table A1.1) but not 2009. The effect of trial date on calling behaviour was likely the result of variable temperatures throughout the study in 2008: 31 August - 12.3 °C; 18 August -25.3; and 28 August-18.5 °C.

There was a significant effect of female age on the initiation of calling behaviour within the scotophase in 2008 ($F_{2,11} = 5.0843$, $P = 0.0273$) (Fig. 3.2A) and 2009 ($F_{3,61} = 4.3987$, $P = 0.0072$) (Fig. 3.2B). Middle-aged females initiated calling within 2 hours after sunset in 2008 and within 5 hours of sunset in 2009. In 2008, middle-aged females initiated calling earlier than the other age groups (Fig. 3.2A). In 2009, middle- and old-aged females initiated calling significantly earlier than young-0 day-old females and young-1 day-old females were intermediate in their initiation of calling (Fig. 3.2B). Calling by younger females in both years did not begin until 5.5-7 hours after sunset. The average time of initiation varied with date of observation in 2008 ($F_{2,11} = 9.9027$, $P = 0.0035$) but not in 2009 ($F_{2,61} = 1.2033$, $P = 0.3072$). Female age had a significant effect on the time in the scotophase when females ceased to call in 2008 ($F_{2,11}$ = 4.1503, P = 0.0454). Middle-aged females stopped calling earlier in the scotophase than the other age groups in 2008 (Fig. 3.2A). Conversely, the time within the scotophase when calling stopped did not differ among the differently-aged females in 2009 ($F_{3,61}$ = 1.4541, P = 0.2360) (Fig. 3.2B). Females of all ages generally called until dawn. The day of observation did not affect time at which calling ceased in 2008 ($F_{2,11}$ = 0.2262, P = 0.8012) or in 2009 ($F_{2,61}$ = 2.5061, P = 0.0900).

The duration of calling in experiments conducted in both 2008 and 2009 did not differ among the variously-aged females (2008: $F_{2,11}$ = 2.4464, P = 0.1321; 2009: $F_{3,61}$ = 2.2310, P = 0.0936). The day of observation did not influence calling duration in 2008 ($F_{2,11}$ = 2.4464, P = 0.1321) but did in 2009 ($F_{2,61}$ = 7.6243, P = 0.0011).

Female age does appear to affect the attractiveness of the pheromone signal and/or the propensity of females to call based on the number of male moths captured in traps baited with females of varying age. Although too few males were attracted to female-baited traps to analyze the data statistically, older females attracted more males earlier in the scotophase than females in the younger age groups (Table 3.1). Traps baited with older females caught the largest number of males with the exception of traps baited with synthetic pheromone lures (Table 3.1). Males were not recovered from traps baited with young-1 day-old females. Males were found in synthetic pheromone traps earliest in the evening and these traps also caught the most males (Table 3.1).

3.2.2. Effect of host material on female calling behaviour

The presence of host material did not have an effect on female calling behaviour but the proportion of calling females did differ by date in this experiment ($z_{Aug\ 21}$ = 3.157, P = 0.0016; $z_{Aug\ 23}$ = -2.481, P = 0.0131; $z_{Aug\ 31}$ = -3.562, P = 0.0004) (Appendix 1, Table A1.3). Females exposed to host material initiated calling six hours after dark ($F_{2,41}$ = 0.7229, P = 0.4914) and ceased calling ten house after dark ($F_{2,41}$ = 0.4591, P = 0.6351), the same time as the control group that were not exposed to any host material. The average duration of calling also did not vary among females exposed to the various host material treatment groups ($F_{2,41}$ = 2.0711, P = 0.1382).

3.3. Female D. abietivorella egg production

3.3.1. Effect of female mating status on egg production

Mating increases egg production by *D. abietivorella* females. Mated females have higher realized ($F_{1,41}$ = 12.7631, P = 0.0004) and potential fecundity ($F_{1,41}$ = 31.7293, P < 0.0001) than virgin females (Fig. 3.3). Realized fecundity was affected by an interaction between wing area and mating status ($F_{1,41}$ = 15.8048, P = 0.0003). Weight is not an important factor in predicting realized female fecundity (weight * mating status: $F_{1,41}$ = 1.5435 P = 0.2212; weight: $F_{1,41}$ = 3.4956, P = 0.0687); but does influence potential fecundity ($F_{1,41}$ = 9.4751, P = 0.0037) (Fig. 3.4). Realized fecundity is also influenced by the individual effects of wing area ($F_{1,41}$ = 6.3398, P = 0.0158) and mating status ($F_{1,41}$ = 31.7293, P < 0.0001) (Fig. 3.3). Wing area and adult body weight were slightly correlated (r = 0.6915) but these parameters did not display collinearity (GVIF_{wing} = 1.9229, GVIF_{weight} = 2.0081) and both body size parameters were used in the analyses.

3.3.2. Effect of female age on egg production

Age influences egg production in *D. abietivorella*. Females eclose with few chorionated eggs, but begin to mature eggs within 24-hours of eclosion. In 2008, the mean number of eggs laid varied significantly with female age ($F_{2,25}$ = 7.1389, P = 0.0035) and total egg production increased with age (Fig. 3.5A). Significantly different numbers of chorionated eggs were contained within the ovaries of differently-aged females ($F_{2,25}$ = 6.2796, P = 0.0062). Egg number in the ovaries peaked in 10-12 day old females in 2008 (Fig. 3.5). Total egg production increased with age in 2008 ($F_{2,25}$ = 15.8326, P < 0.0001) (Fig. 3.5A) and 2009 ($F_{4,149}$ = 23.0338, P < 0.0001) (Fig. 3.5B). The interaction between wing area and age was a significant factor that predicted the potential fecundity in 2009 ($F_{2,25}$ = 4.2118, P = 0.02652).

3.4. Trade-offs between reproduction and longevity

There is a trade-off between longevity and reproduction in *D. abietivorella*. Virgin female and male *D. abietivorella* live significantly longer than mated moths (Fig. 3.6) (Appendix 1, Table A1.4). The relationship between longevity and adult body weight is influenced by mating as demonstrated by the significant interaction between body weight and mating status ($z = 2.718$, $P = 0.0066$) (Fig. 3.7). Larger virgins lived longer than smaller virgins but there was no effect of body weight on the longevity of mated moths. The individual main effects of sex ($z = -2.379$, $P = 0.0174$) and mating status ($z = -2.142$, $P = 0.0322$) significantly predicted adult longevity. Adult body weight ($z = -0.571$, $P = 0.5682$) was not significant as a main effect but remained in the model because of the significant interaction with mating status. In this data set, wing area and adult body weight were not highly correlated ($r_{male} = 0.3201$, $r_{female} = 0.1643$) and did not display collinearity ($\text{GVIF}_{male} = 1.1142$, $\text{GVIF}_{female} = 1.0277$), therefore both body size parameters were included in the longevity models. Wing area was not a significant factor in the model and the fit of the model was improved when this factor was removed.

Mating significantly increased both realized ($t_{35.017} = 2.3498$, $P = 0.0246$) and potential ($t_{40.3387} = 2.3498$, $P = 0.0051$) fecundity of female *D. abietivorella* (Fig. 3.8). An interaction between realized fecundity and mating status was significant to predict female longevity (Appendix 1, Table A1.5). Realized fecundity was positively correlated with mated female longevity, but negatively correlated with virgin female longevity ($z = -3.147$, $P = 0.0017$) (Fig. 3.9). There was a significant interaction between realized fecundity and female body weight ($z = -2.128$, $P = 0.0333$) that negatively influenced female longevity. The interaction term between wing area and mating status ($z = 1.963$, $P = 0.0500$) was also significant and the lifespan of virgins increased with wing area but decreased for mated females.

Female longevity was significantly affected by interactions between mating status and potential fecundity ($z = -3.147$, $P = 0.0017$) (Fig. 3.10) (Appendix 1, Table A1.6). Potential fecundity increased with longevity in mated females but decreased for virgin females. Weight and potential fecundity also produced a significant interaction ($z = -2.128$, $P = 0.0333$) to affect female longevity. Heavier females had a higher potential fecundity than lighter females. The interaction between wing area and mating status ($z = 1.963$, $P = 0.0500$) was significant to predict female longevity.

Male longevity was predicted solely based on the individual effect of adult body weight ($z = 2.553$, $P = 0.0107$) (Fig. 3.11) (Appendix 1, Table A1.7). Adult weight was positively correlated with male longevity. The main effects, wing area and mating status, and all interaction terms were not significant in the original model and these factors were removed to improve model fit and statistical power.

Discussion

Many aspects of the reproductive behaviour displayed by *D. abietivorella* in this study suggest that this species has evolved an income breeding mating strategy (Jönsson, 1997; Jervis, *et al.*, 2005). As occurs in other synovigenic Lepidoptera (Lawrence and Bartell, 1972; Howlander and Gerber, 1986), female age affects calling behaviour, which coincides with egg maturity in *D. abietivorella*. Females delay the expression of sexual receptivity post-eclosion and calling activity is greatest in middle- and old-aged *D. abietivorella* females (Fig. 3.2). More females in older age groups call and do so earlier in the evening than younger females but it is not known if the quality of the signal differs with female age. In other species of Lepidoptera, older females call earlier than young females (Webster and Cardé, 1982; Howlander and Gerber, 1986; Delisle and Royer, 1994; del Mazo-Cancino *et al.*, 2004) to compensate for the reduced pheromone titre in older females (Swier *et al.*, 1977). Female *D. abietivorella* are afforded flexibility of signal release during the scotophase as males are active and respond to pheromone throughout the scotophase. Male moths are captured earliest in the scotophase in traps baited with synthetic pheromone (Table 3.1) probably because females have not commenced calling at this time. Peak male activity occurs later in the scotophase (W. Strong, pers. comm.), which coincides with the peak calling activity of sexually-mature females. Few young female *D. abietivorella* call and those that do, call later in the scotophase and attract fewer males than older females (Fig. 3.2). Further work is necessary to support these observations which are based on few captured individuals.

In the current study, female calling behaviour was not affected by the presence of Douglas-fir cones or foliage in close proximity to female moths (Appendix 1, Table A1.3). *Dioryctria abietivorella* is polyphagous and may not use a specific host plant cue to initiate calling behaviour. Female response to host volatiles may be more important for host location or close-range host selection for oviposition. The perception of host plant cues stimulates pheromone release and induces egg production in some moth species. Calling behaviour of *P. xylostella* females is increased (Pittenrigh and Pivnivk, 1993) and egg production is stimulated (Pivnick *et al.*, 1990) when females are exposed to brassicaceous host plants. The perception of host plant cues may serve as a mechanism by which income breeding moths can coordinate signal production with sexual maturation. Female *D. abietivorella* can detect volatile monoterpenes released from eastern white pine, *Pinus strobus* Linnaeus (Pinaceae) and perception of these cues induces oviposition behaviour (Shu *et al.*, 1997). Host material used in this study was previously frozen and this may have altered the volatile profile emitted by the material that rendered it unattractive to the moths tested and further research using fresh host material is required to substantiate the observation that the presence of host material does not influence calling behaviour.

Calling experiments held indoors produced results that slightly differed from those conducted outdoors. Middle-aged females initiated calling approximately 4-hours after sunset outside but not until 6-hours after dark inside. In both the indoor and outdoor trials, females generally ceased to call at first light. Results from calling trials conducted indoors may not be representative of behaviours observed under natural conditions.

My data suggest that female *D. abietivorella* require time after eclosion to become sexually mature and signaling receptivity through pheromone release coincides with egg maturation. Females do not eclose with mature eggs, but production of chorionated eggs is evident 24-hours after eclosion. Egg maturation continues throughout the adult stage and females in the older age groups oviposit more eggs and have a greater number of chorionated eggs in their ovaries than younger females (Fig. 3.5). Age-related differences in oögenesis are common in income breeding Lepidoptera (Ramaswamy *et al.*, 1997). The number of mature eggs increases with age in the income-breeding species *M. privata* (Walker and Allen, 2010). In my study, the presence of chorionated eggs in the ovaries increased with female age but decreased in the ovaries of the oldest *D. abietivorella* females tested in 2009 (Fig. 3.5). In some moth species, the first eggs are more costly to produce (Rosenheim, 1996) and may be larger than eggs produced by older females (Harvey, 1977). Alternatively, old virgin female *D. abietivorella* may extend their longevity through egg resorption. Reallocation of energy through egg resorption is a common strategy in insects that produce eggs continuously throughout the adult stage (Rosenheim *et al.*, 2000). A positive interaction between female *D. abietivorella* wing area and age predicts the number of chorionated eggs produced and suggests that female size probably contributes to female fecundity. For income breeding species, the effect of body size on fecundity is likely an indirect effect through increased longevity (Leather, 1988; Honëk, 1993).

Female *D. abietivorella* are subject to life history trade-offs between reproduction and longevity as is predicted to occur in species with continuous egg production in the adult stage (Jervis and Ferns, 2004). Mating reduced the longevity of adult moths (Fig. 3.6) but increased the realized and potential fecundity (Fig. 3.8) of female *D. abietivorella*. Mating-stimulated increases in fecundity are common in synovigenic Lepidoptera (Ramaswamy *et al.*, 1997) and have been linked to changes in hormone titres after mating that promote choriogenesis in *C. pomonella* (Webb *et al.*, 1999) and *L. oleracea* (Corbitt *et al.*, 2009). Male-derived resources passed to the female during mating can also stimulate egg production (Smedley and Eisner, 1996; Czesak and Fox, 2003). Females of the income-breeding moth *C. cautella* receive accessory gland compounds from males during mating that stimulate egg production (McNamara *et al*, 1998). The fact that mated *D. abietivorella* females do not live as long as virgins suggests that paternal contributions are negligible in this species. Male *D. abietivorella* ejaculate could in fact contain elements that negatively impact female longevity due to selection pressures imposed through sperm competition (Chapman *et al.*, 1995; Fisher, 2007) in this polyandrous species. Reduced longevity of mated individuals may also be due to costs associated with the physical act of mating (Crudington and Siva-Jothy, 2000), or disease and parasites (Hurst *et al.*, 1995) transmitted through copulation. Most of the females that successfully mated in this study did so only once. There were small additional reductions in the average lifespan of the few females that remated. Females mating once lived on average 25 days while those that mated twice lived approximately 22 days. In nature, female *D. abietivorella* can mate up to eight times (Chapter 2) and the costs associated with mating detected in the current study may severely underestimate those experienced by wild moths, which could also include mate-finding flight for males and dispersal to oviposition sites for females.

Virgin females oviposited in my study even though they had not mated, as occurs in many insects (Engelmann, 1970). Egg production is costly and egg-dumping by virgins seems counterintuitive. Females may produce a baseline number of mature eggs that cannot be resorbed once they enter the posterior region of the reproductive tract as observed in *Callosobruchus maculates* Fabricius (Coleoptera: Bruchidae) (Wilson and Hill, 1989).

Longer-lived, mated *D. abietivorella* females have higher realized fecundity than shorter-lived mated females (Fig. 3.9). The importance of adult female longevity on fecundity is common to Lepidoptera (Leather, 1988) and, in particular, this relationship is prevalent in income breeders like *M. privata* (Walker and Allen, 2010) and *P. flammea* (Leather, 1984) that produce eggs throughout their adult life. Interestingly, there is a negative interaction between female body weight and realized fecundity that significantly predicts female longevity in *D. abietivorella* (Appendix 1, Table A1.6). This finding suggests that larger females lay fewer eggs than smaller females. It is possible that large *D. abietivorella* females lay fewer but larger eggs than small females as occurs in *Utetheisa ornatrix* Linnaeus (Lepidoptera: Arctiidae) (Iyengar and Eisner, 2002). The production of large eggs results in better protection from harmful environmental conditions during the egg stage and may produce larger offspring that develop faster (Iyengar and Eisner, 2002). Egg size was not measured in this study but could explain the observed pattern of differential realized fecundity based on female body weight.

Surprisingly male lifespan was predicted only by adult body weight (Fig. 3.11) in this study. This is a trait more commonly observed in capital breeding females (Leather, 1988). There is no effect of male mating status on longevity. Though this may be an experimental artifact as males generally mated only once and those males that remated did not exhibit reductions in lifespan. On average, males that mated once lived 21 days while those that mated twice lived 20 days. Female *D. abietivorella* mate multiply in nature (Chapter 2) and theory predicts that male fitness should increase with the number of matings achieved (Arnqvist and Nilsson, 2000). This study did not assess the energetic costs associated with mate finding, which could change the relationship between male moth longevity and body weight. Lipid content of male *Choristoneura* *conflictana* Walker (Lepidoptera: Tortricidae) is reduced after flight and the fat reduction is correlated with the distance flown (Elliott and Evenden, 2009). Reallocation of energy to flight may decouple the relationship between male body weight and longevity observed in the current study (Boggs and Ross, 1993).

Dioryctria abietivorella can be considered an income breeding moth. Reproductive activities are age-specific and females require time after eclosion to initiate reproduction. Research is needed to address the effect of age and diurnal periodicity on female pheromone titre and signal quality. Host plant volatiles do not appear to influence calling behavior but are important for oviposition behavior (Shu et al., 1997) and may provide a mechanistic link between signal production and sexual maturity. Mating increases both potential and realized female *D. abietivorella* fecundity but the mechanism mediating this effect is undetermined. There is a trade-off between longevity and reproduction in *D. abietivorella*. Long-lived females lay more eggs than short-lived females but mated individuals have reduced adult longevity. Adult longevity may be further impacted by the multiple matings that occur in this polyandrous species. Future research should assess the impact of multiple mating on the fecundity and lifespan of both sexes, while incorporating other energetic costs such as flight. Moths in this study were provided with sugar water *ad libitum* but variation in adult nutrition may further influence allocation of energy and trade-offs among the life history traits studied here.

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Table 3.1. Male attraction to traps baited with differently-aged virgin female *D. abietivorella* and synthetic pheromone. Female age categories tested were: young-0 (0 day old), young-1 (1 day old), middle (5-7 days) and old (10-12 days). Statistical analysis was not conducted on these data due to the small number of males trapped.

Treatment	N	Number of males trapped	Proportion of traps in which males were observed
Young-0	11	1	0.09
Young-1	10	0	0.00
Middle	10	2	0.10
Old	12	2	0.17
Pheromone	12	3	0.25

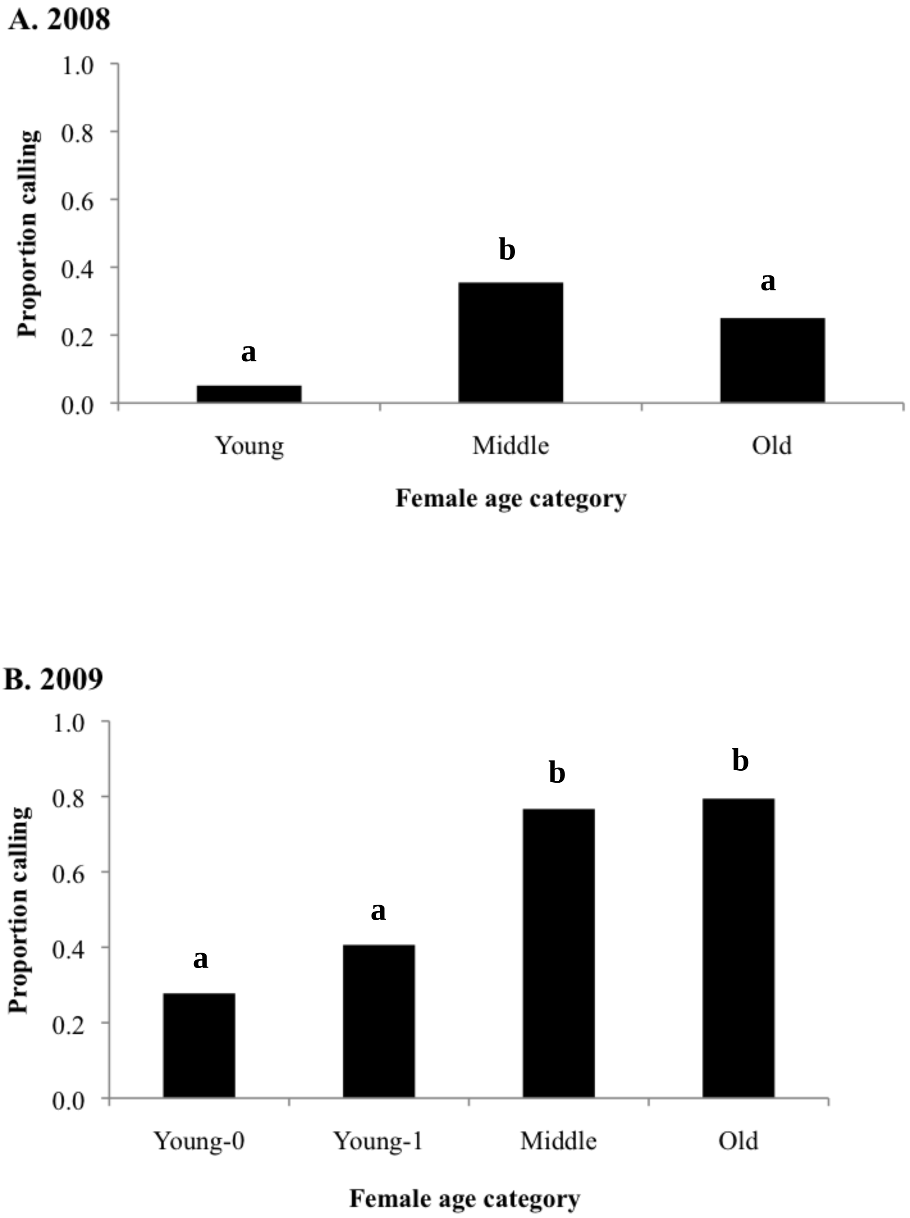

Figure 3.1. The proportion of variously-aged female *D. abietivorella* that exhibited calling behaviour in experiments conducted in Douglas-fir blocks at KAL in A) 2008 and B) 2009. Points represent the proportion of females calling on each night. Female age groups tested in 2008: young (0-1 day old), middle (5-7 days) and old (10-12 days). Additional female age groups added in 2009: young-0 (0 day) and young-1 (1 day). Within each year, female age categories marked with the same letter are not significantly different (Logistic regression, $P > 0.05$).

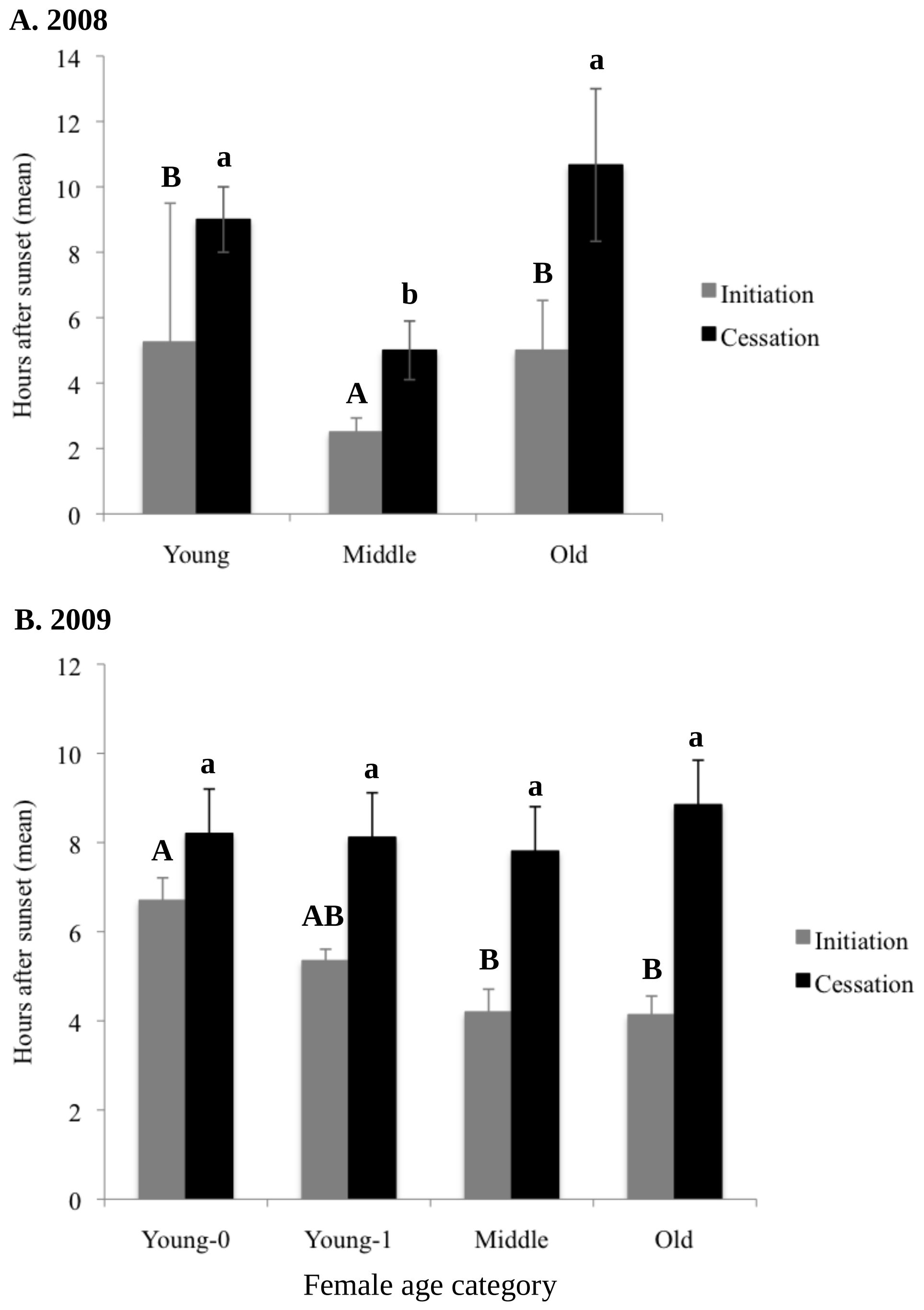

Figure 3.2. The mean number of hours (+ SE) after sunset when variously-aged female *D. abietivorella* initiated and ceased calling behaviour in experiments conducted in Douglas-fir blocks at KAL in A) 2008 and B) 2009. Female age groups tested in 2008: young (0-1 day old), middle (5-7 days) and old (10-12 days). Additional female age groups added in 2009: young-0 (0 day) and young-1 (1 day). Data include only those females that did call, therefore SE is based on the number of calling females rather than N. Within each year, bars marked with the same letter are not significantly different (Tukey's HSD, $P > 0.05$).

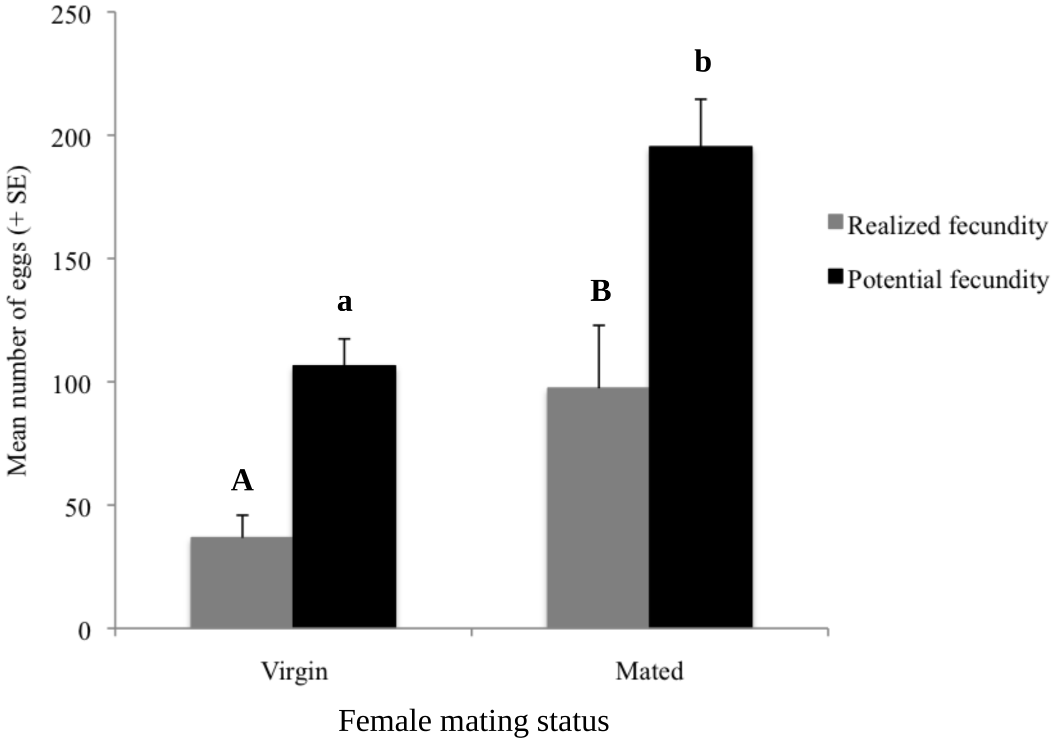

Figure 3.3. Mean (+ SE) realized (eggs laid) and potential lifetime fecundity (total eggs) of virgin and mated *D. abietivorella*. Within each fecundity category, bars marked with the same letter are not significantly different (Tukey's HSD, *P* > 0.05).

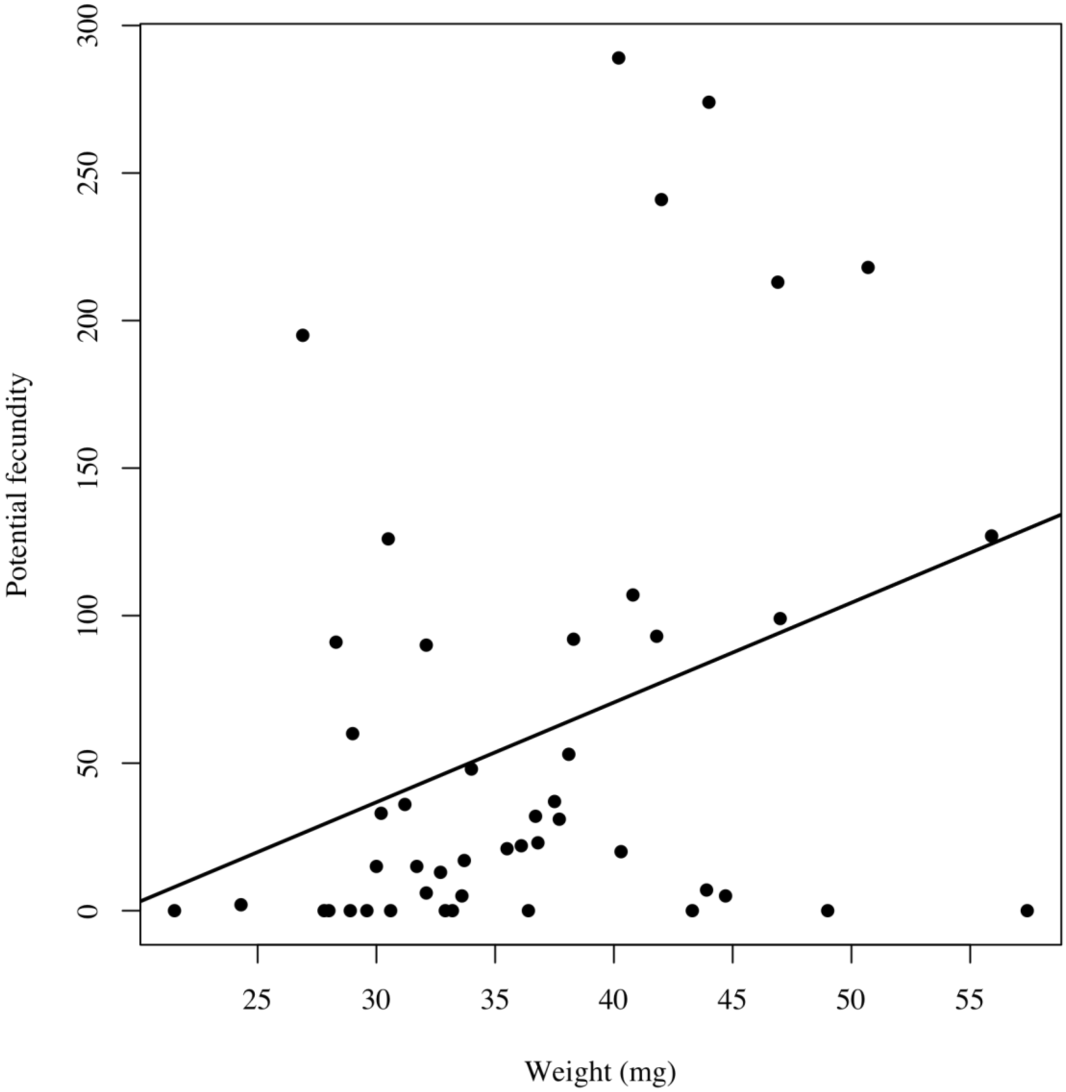

Figure 3.4. The relationship between adult weight and the potential fecundity (total eggs) of female *D. abietivorella* during the ten-day experiment. Negative binomial generalized linear regression: weight $F_{1,41} = 9.4751$, $P = 0.0037$.

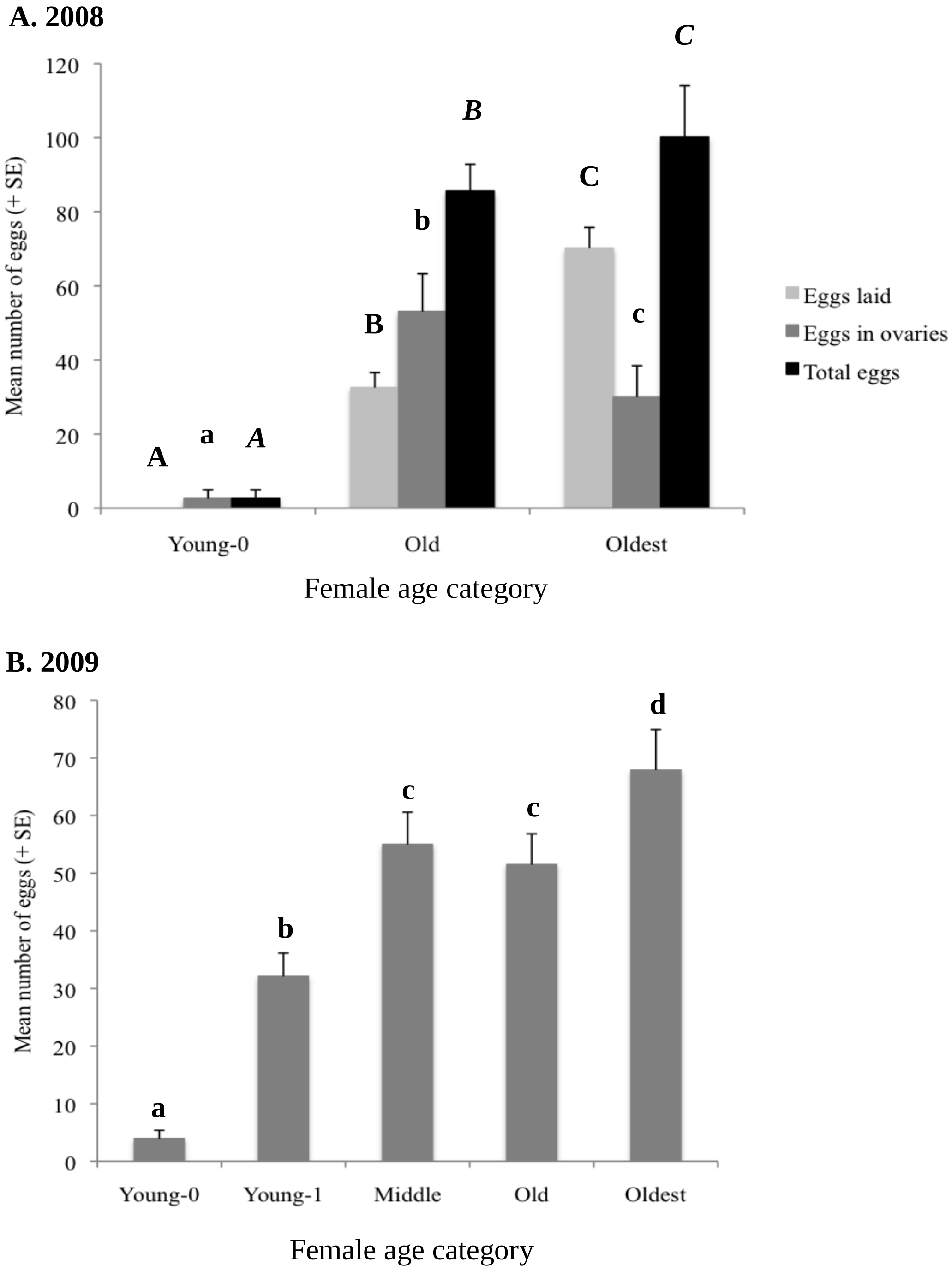

Figure 3.5. Mean (+ SE) A) eggs laid, eggs in ovaries and total eggs of young-0 (0 day), old (10-12 days) and oldest (16-18 days) females in 2008 and B) eggs in ovaries of young-0 (0 day), young-1 (1 day), middle (5-7), old (10-12 days) and oldest (16-18 days) *D. abietivorella* females in 2009. Within each year and category, bars marked with the same letter are not significantly different (Tukey's HSD, *P* > 0.05).

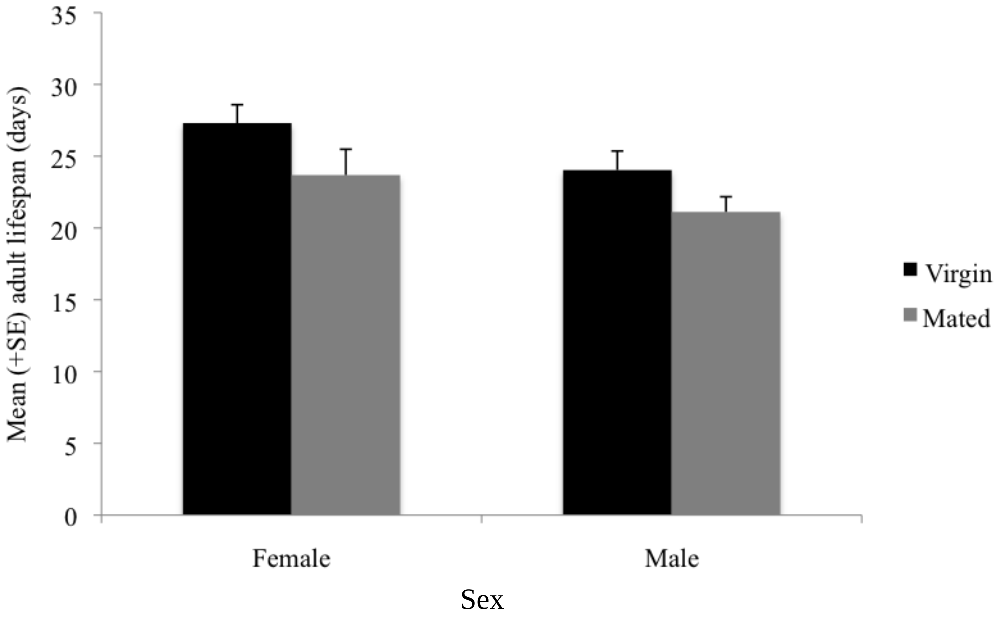

Figure 3.6. Mean (+ SE) lifespan of virgin and mated male and female *D. abietivorella* adults. Negative binomial generalized linear regression: z_{sex} = -2.379, *P* = 0.0174 and $z_{mating\ \mathrm{status}}$ = -2.142, *P* = 0.0322.

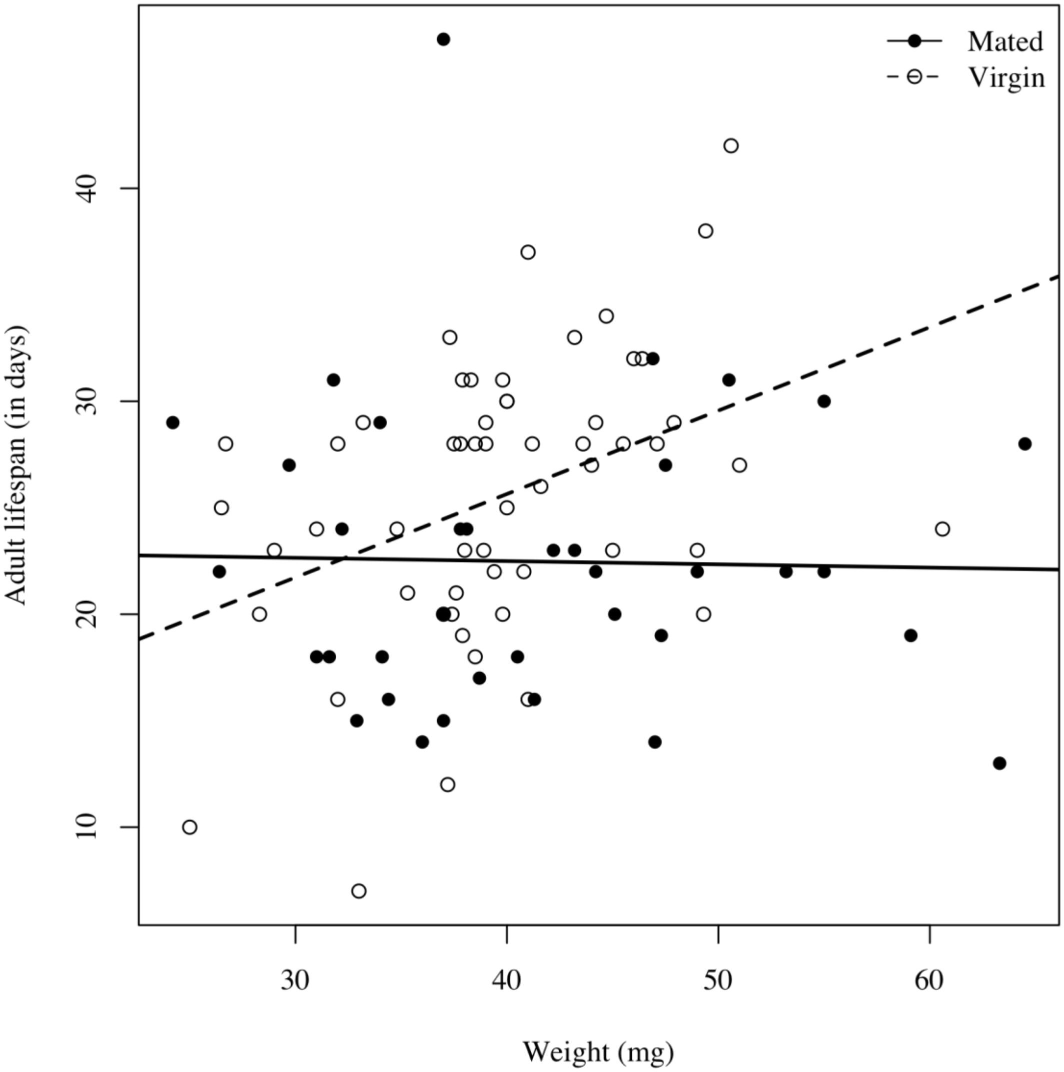

Figure 3.7. The relationship between adult body weight and longevity for mated and virgin, male and female *D. abietivorella* adults. Negative binomial generalized linear regression: weight * mating status *z* = 2.718, *P* = 0.0066.

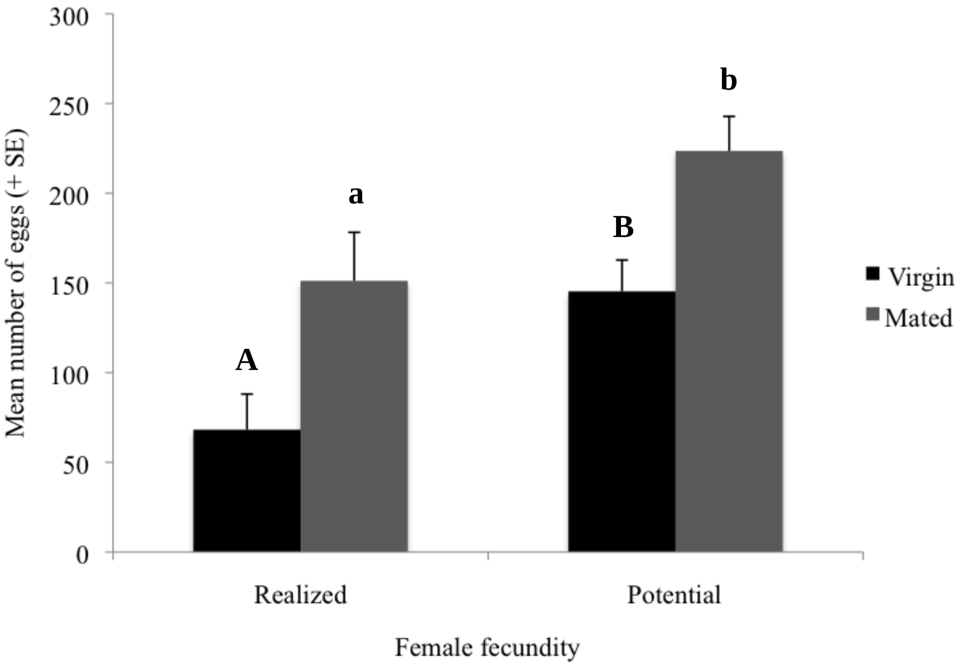

Figure 3.8. Mean (+ SE) number of eggs laid (realized fecundity) and total eggs (potential fecundity) of virgin and mated *D. abietivorella* females. Within each fecundity and mating status category, bars marked with the same letter are not significantly different (Welch's two-sample T-test, $P > 0.05$). Eggs laid: $t_{35.017} = 2.3498$, $P = 0.0246$; total eggs $t_{40.3387} = 2.3498$, $P = 0.0051$.

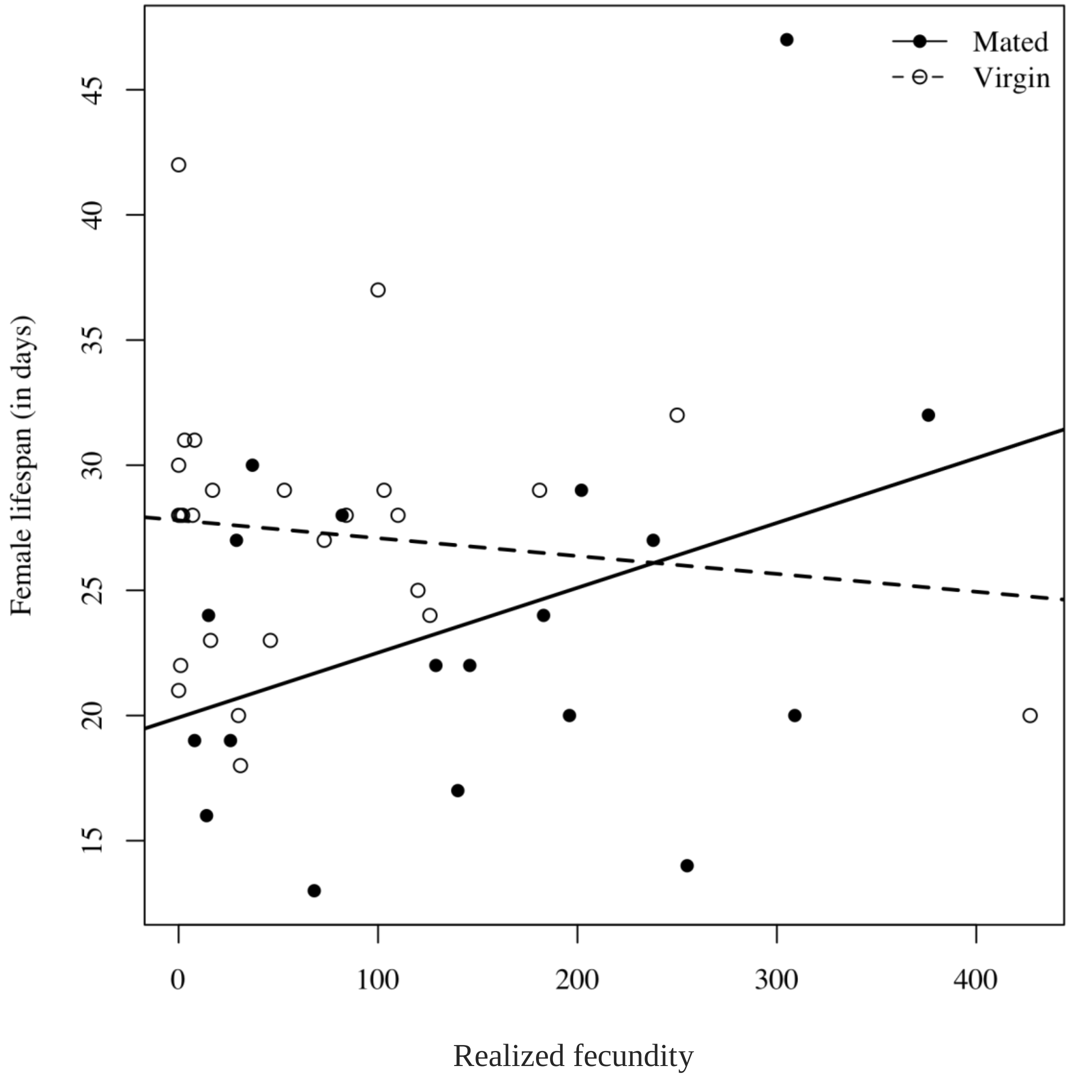

Figure 3.9. The effect of mating status on the number of eggs laid (realized fecundity) by and longevity of female *D. abietivorella*. Negative binomial generalized linear regression: eggs laid * mating status z = -3.405, P = 0.0007.

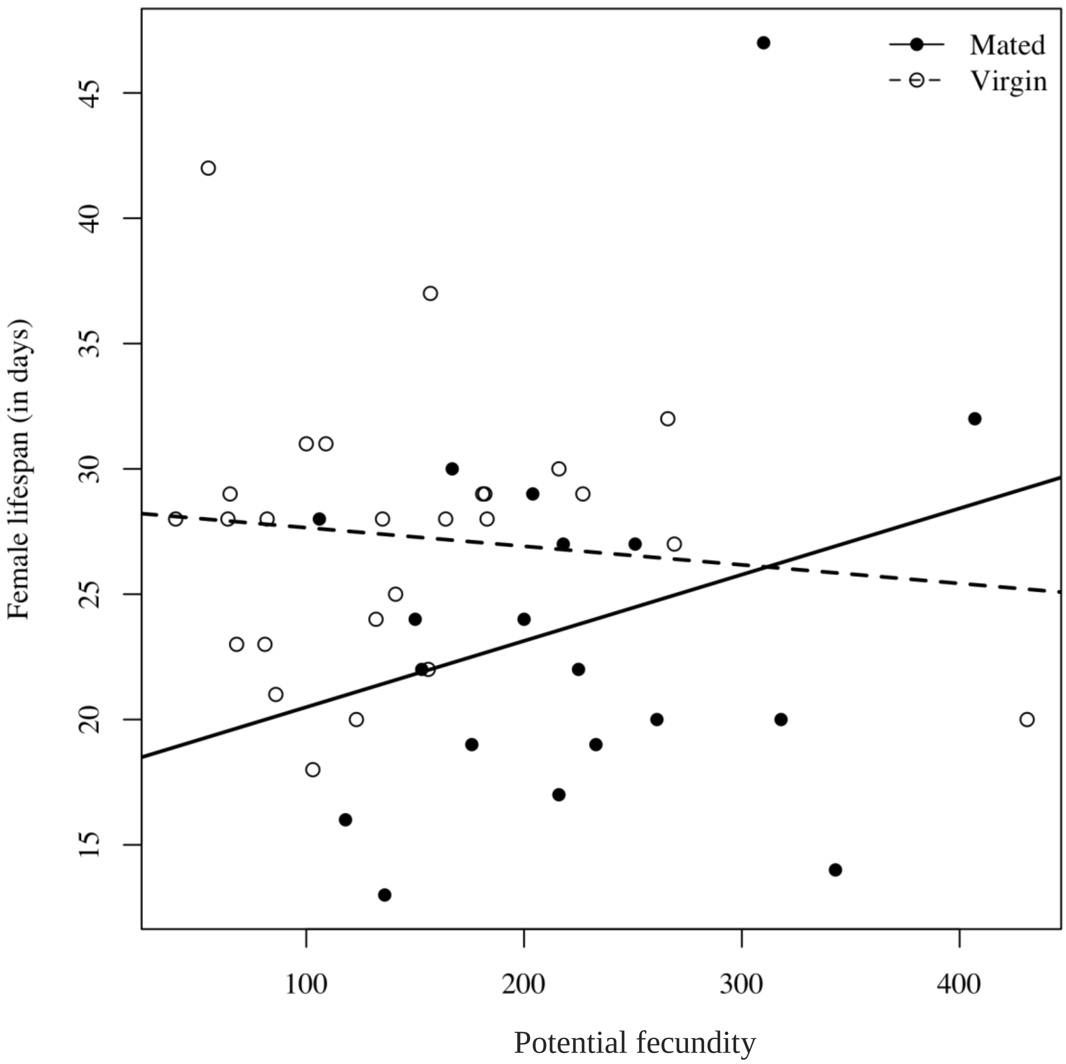

Figure 3.10. The relationship between mating status, potential fecundity (total eggs) and longevity of female *D. abietivorella*. Negative binomial generalized linear regression: mating status x total eggs $z = -3.514$, $P = 0.0004$.

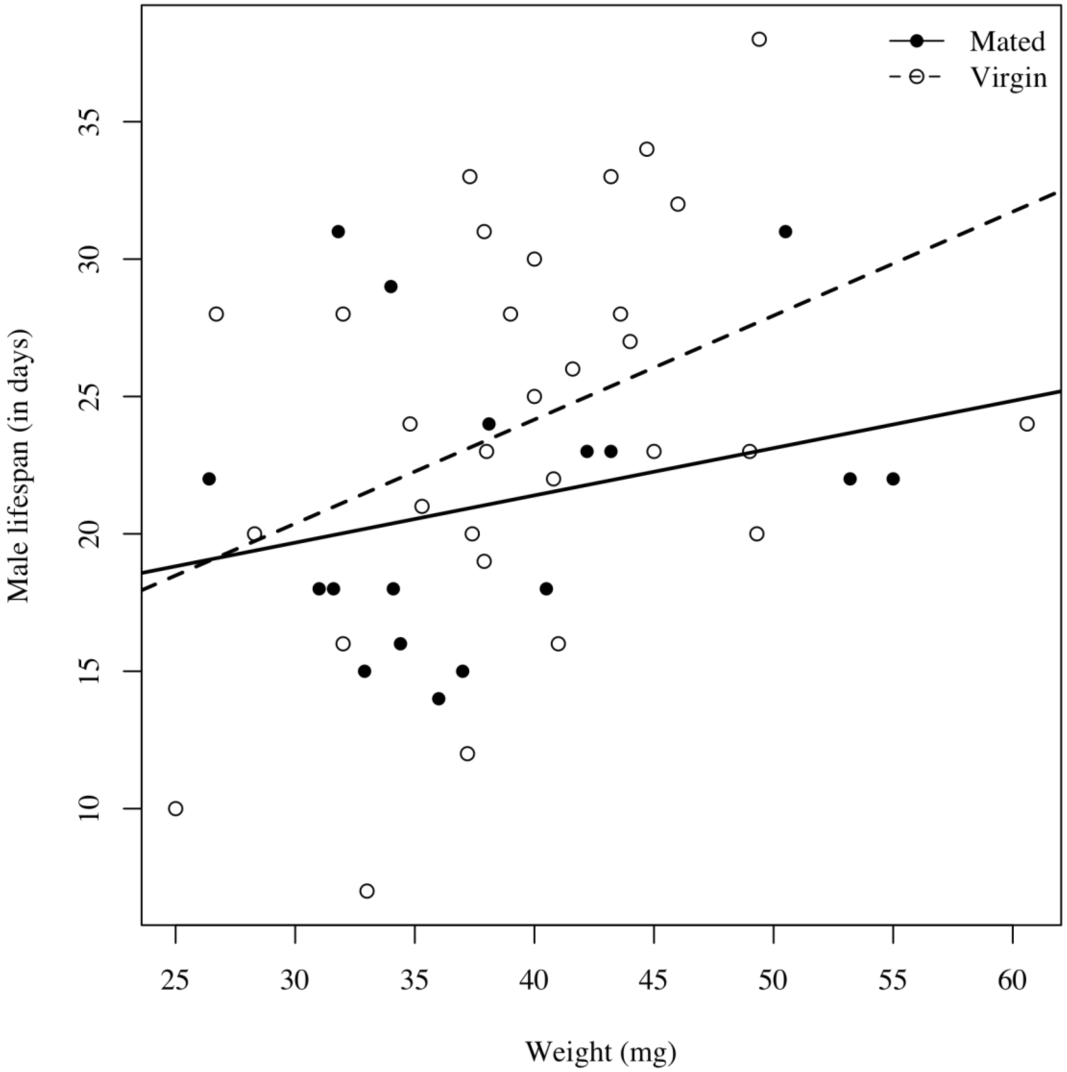

Figure 3.11. The relationship between male body weight and longevity for mated and virgin male *D. abietivorella*. Negative binomial generalized linear regression: weight x mating status $z = 2.553$, $P = 0.0107$.

Chapter 4: Research summary and future research

Research highlights and future directions

This research assessed the seasonal phenology, habitat use and mating frequency of moths in the genus *Dioryctria* Zeller found sympatrically in the north Okanagan Valley, British Columbia. Light-trap monitoring demonstrated that females in the species groups *abietella*, *auranticella*, *ponderosae* and *schuetzeella* occur in Douglas-fir, lodgepole pine and interior spruce stands in seed orchards in this region. In particular, infestations of the cone-feeder *D. abietivorella* Grote, the sole *abietella* species recorded in British Columbia, can have substantial economic impacts on seed-cone production in these orchards (Strong, 2005). I investigated the reproductive behaviour of *D. abietivorella* to better understand the effects of age and mating on calling behaviour and egg production. Further to this, I considered the occurrence of life history trade-offs between reproduction and longevity in *D. abietivorella*. Results of this research are dicussed within the framework of resource allocation strategies. The results of this thesis provide documentation on the factors that contribute to the fecundity of *D. abietivorella,* which may be exploited to develop integrated pest management tactics against this pest in the future (Whitehouse *et al.*, 2011). Data on the occurrence and phenology of *abietella*, *auranticella*, *ponderosae* and *schuetzeella* will inform seed orchard managers of the presence of other species of *Dioryctria* that could impact seed orchard productivity (Hedlin, *et al.*, Zobel and Talbert, 1984). These results also provide a framework on which to base future research to better understand how reproductive strategies influence population dynamics and pest status in this group.

Two years of monitoring female flight with light traps and male *D. abietivorella* flight with pheromone-baited traps throughout the season has not only allowed me to assess the diversity of *Dioryctria* in seed orchards but also to understand their flight phenology. Females in the species groups *auranticella*, *ponderosae* and *schuetzeella* fly from early summer to mid- or late- August in the north Okanagan Valley. First trap captures occurred at similar degree-day accumulations between years within each species group. Male and female *D. abietivorella* (*abietella* species group) were the first to be recovered from traps and exhibited an extended flight period. Surprisingly males are present until late September even though females were not captured after the end of August in both years. The lack of female moths at the end of the season could indicate that they are not present or not actively able to fly. Alternatively, late season females may not be mated and may not orient to light traps. Virgin *D. abietivorella* females represented only 1% of the total 2008 and 2009 season-long trap catch and other studies have demonstrated trap catch bias for mated moths (*e.g.* Landolt and Curtis, 1991; Cowan and Gries, 2009). The presence of males late in the season may represent a small cohort of the population that does not enter diapause to overwinter.

Univoltinism of moths in the *auranticella* (Neunzig *et al.*, 1964; Pasek and Dix, 1989), *ponderosae* (Mutuura *et al*, 1969; Roe *et al*., 2006) and *schuetzeella* (MacKay, 1943; McLeod and Daviault, 1963; Mutuura and Munroe, 1973) species groups have been previously reported. The data from my light-trap monitoring support that moths in these species groups are univoltine in the north Okanagan Valley of British Columbia. In contrast, my findings on the *abietella* group flight and mating frequency indicate the occurrence of a second generation of *D. abietivorella* in the mid-season at my study sites. I propose that the overwintering population ecloses in the spring and produces a generation that completes development within the season and become reproductively active in early summer. The offspring of early summer adults develop to mature larvae that enter diapause and overwinter. Two peaks in male *D. abietivorella* flight activity support this conclusion. The mating frequency of female *D. abietivorella* (*abietella* species group) also suggests the presence of two generations. Mean spermatophore number per female increases from spring to summer but decreases thereafter. Newly eclosed second generation females would be expected to have fewer spermatophores as they are just beginning to acquire matings. Other research in the western United States (Keen, 1952) supports my findings of a bivoltine life cycle of *D. abietivorella*. Although other surveys indicate that this species is univoltine in parts of its range (MacKay, 1943; Hedlin *et al.*, 1980). It is likely voltinism is plastic in this species but identification of bivoltine populations is important as seasonal polyphenism can arise from differential selection pressures on insects at different times of the season (Larsdotter Mellström *et al.*, 2010). Various differences in life history traits can arise from polyphenism, which include differences in larval development time, fecundity (Välimäki *et al*., 200) and mating frequency (Välimäki *et al.*, 2008), all are life history traits that are important to consider when developing integrated pest management programs (Whitehouse *et al.*, 2011). Future research to confirm the occurrence of bivoltine populations of *abietella* in the north Okanagan Valley are required and should involve determination of the overwinter stage so clarify early-season population structure. A better tool to monitor female flight would be useful to ensure that the entire female population is being assessed and not just the reproductively active individuals captured in light traps in this study. Light wavelengths in the blue/violet-light range attract significantly more virgin female *P. interpunctella* Hübner (Lepidoptera: Pyralidae) moths than (Cowan and Gries, 2009) and future research could be directed towards evaluating *D. abietivorella* attraction to different wavelengths of light.

Females in *schuetzeella* were the most abundant group recovered from light traps in Douglas-fir, lodgepole pine and interior spruce. Larvae in the *schuetzeella* group infest shoots and foliage, which are relatively stable food sources and this stability could lead to the establishment of the large population observed in the current study. Moths in the *auranticella* and *ponderosae* species group were captured in light traps positioned in stands of trees that have not previously been recorded as hosts. In 2009, 90% of the *ponderosae* female trap catch at KAL occurred in ponderosae pine, a previously unrecorded host (Neunzig, 2003). Also in 2009, 98% of *auranticella* females recovered from light traps were in Douglas-fir stands. Previously recorded hosts for *auranticella* moths are restricted to the genus *Pinus* (Neunzig, 2003). These may represent new host associations but require further monitoring and rearing larvae from cones to substantiate this conjecture.

Dioryctria species groups present in the north Okanagan Valley exhibit differences in mating strategies. Polyandry is prevalent in the *abietella* and *auranticella* groups, while monandry is common in the *ponderosae* and *schuetzeella* groups. Within each species, there is variation in the mating frequencies, though it is difficult to extract from my data why this variation exists. It could simply be the acquisition of matings as time after eclosion increases (Calcote *et al.*, 1984) or result from intraspecific variation in mating frequency (Van Dongen, 1999; Wedell and Cook, 1999; Jiménez-Pérez *et al.*, 2003; Torres-Vila *et al.*, 2005). Future research should assess the benefits that polyandrous females accrue through multiple matings and the factors that affect mating frequency like temperature and photoperiod.

Many aspects of the reproductive behaviour displayed by *D. abietivorella* suggest that this species is more aligned with the income breeding mating strategy (Jönsson, 1997). As seen in other synovigenic Lepidoptera (Lawrence and Bartell, 1972; Howlander and Gerber, 1986), female age affects calling behaviour and, in *D. abietivorella*, coincides with the degree of egg maturity. Females *D. abietivorella* are synovigenic, and eclose with no or few mature eggs in their ovaries and require time post-eclosion for egg maturation. Females are delayed in their expression of sexual receptivity post-eclosion and the propensity to call coincides with egg maturation in *D. abietivorella*. Calling activity increases with age and females in older age groups were more likely to call and initiated calling earlier in the evening than younger females. Though based on few males captures, older females attracted males earlier in the scotophase than younger females, earlier calling may indicate that they have optimized calling with the beginning of diurnal male flight. Future research should assess age-specific pheromone titres and signal quality. Temperature and photoperiod effects on calling behaviour should be considered. Moths with a long flight period like *D. abietivorella* experience different conditions throughout the season that can affect reproductive behaviours like calling (*e.g*. Webster and Cardé, 1982; Delisle and Royer, 1994; Zhou *et al.*, 2000).

My data indicate that female calling behaviour is not affected by the presence of cones or foliage. *Dioryctria abietivorella* is polyphagous and may not use a specific cue for calling as there are plenty of opportunities for mates in different habitats. Females do sense monoterpenes and oviposition is stimulated in the presence of some eastern white pine, *Pinus strobus* Linnaeus (Pinaceae) monoterpenes (Shu *et al.*, 1997). Future research should address the role of host volatiles in close-range host selection for oviposition by females. Research should also be directed towards the perception of host volatiles by males and potential synergistisc effects of host volatiles in male pheromone reponse.

The assessment of life history trade-offs indicates that female *D. abietivorella* (*abietella* species group) suffer from reductions in longevity as a result of reproduction.

This is particularly interesting given that mating frequencies as high as eight in *D. abietivorella* were observed in the wild, though most of females in the laboratory study mated just once. In some Lepidoptera, females experience increased longevity and fecundity through polyandry and this is typical of income breeding species like *Bicyclus anynana* Butler (Lepidoptera: Nymphalidae) (Fischer, 2007) and *P. napi* (Wiklund *et al.,* 1993) that receive nutrients from the male. Mating reduced the longevity of adult moths but increased the realized and potential fecundity of female *D. abietivorella*. Mating-stimulated increases in fecundity are common in Lepidoptera that are synovigenic (Ramaswamy *et al.*, 1997) and have been linked to changes in hormone titres associated with choriogenesis (Webb et al., 1999; Corbitt, 2009) or male accessory gland compounds (McNamara *et al.*, 2008). Decreases in female longevity suggest that males do not provide females with nutrients that mitigate lifespan costs. In fact, *D. abietivorella* is polyandrous and as a result of sperm competition, male ejaculate could contain elements that negatively impact female lifespan (Chapman *et al.*, 1995; Fisher, 2007). Conversely, mating status did not affect male *D. abietivorella* longevity, which was predicted only by male body weight and is typically a capital-breeding trait (Jervis *et al.,* 2005). This result may be an experimental artifact as males generally mated once, which may not reflect what happens in the wild. Future research should investigate energetic costs like mating finding and address the potential for male contributions towards female fecundity.

In conclusion, my research has documented the occurrence, seasonal flight and voltinism of *abietella, auranticella, ponderosae* and *schuetzeella* group females in Douglas-fir, lodgepole pine and interior spruce stands in north Okanagan seed orchards. Information on seasonal phenology will assist in the refinement of integrated pest management strategies (Whitehouse *et al*., 2011). Additionally, this work has demonstrated that moths in various *Dioryctria* species groups differ in their mating strategies. This research has established that age and mating status affect reproductive behaviour and fecundity of *D. abietivorella*, which provides direction for future research addressing reproductive biology and alternative pest management tactics. These results provide a basis for future research on the factors that impact population dynamics and fecundity of *Dioryctria* species, and in particular *D. abietivorella.*

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Appendix 1

ANCOVA tables of comparison contrasts have been conducted by treatment, therefore the factor level that comes first alphabetically is used as the estimate ('intercept') and all other levels are expressed as the difference from this estimate.

Table A1.1. The influence of age on female *Dioryctria abietivorella* 2008 calling behaviour. A backwards-stepwise generalized linear regression procedure was used to select the most parsimonious model. Automatic sequential removal of insignificant variables based on analysis of deviance tests. Initial model terms: trial date * age (AIC = 65.577). N: young (0-1 days) = 39, middle (5 – 7 days) = 31, old (10-12 days) = 12.

	Estimate	Standard Error	*z* value	*P*
(Intercept)	-1.2859	1.0095	-1.274	0.2027
28 August	-1.4967	1.0411	-1.438	0.1505
31 August	-2.4070	0.9901	-2.431	0.0151
Middle	2.3734	0.8749	2.713	0.0067
Old	1.7676	1.1126	1.589	0.1121

Null deviance: 80.95 on 81 degrees of freedom
Residual deviance: 63.05 on 77 degrees of freedom
AIC: 73.045
pseudo R^2 = 22.11

Table A1.2. The influence of age on female *Dioryctria abietivorella* 2009 calling behaviour. A backwards-stepwise generalized linear regression procedure was used to select the most parsimonious model. Automatic sequential removal of insignificant variables based on analysis of deviance tests. Initial model terms: trial date * age (AIC = 151.93). N: young-0 (0 days) = 18, young-1 (1 day) = 32, middle (5 – 7 days) = 30, old (10-12 days) = 34.

	Estimate	Standard Error	*z* value	*P*
(Intercept)	-0.9555	0.5262	-1.816	0.0694
Young-1	0.5760	0.6376	0.903	0.3663
Middle	2.1451	0.6806	3.152	0.0016
Old	2.1342	0.6636	3.216	0.0013

Null deviance: 154.51 on 113 degrees of freedom
Residual deviance: 134.20 on 110 degrees of freedom
AIC: 142.20
pseudo R^2 = 13.14

Table A1.3. Influence of host material on female *Dioryctria abietivorella* calling behaviour. Middle-aged (5 – 7 day old) females were exposed to host material. A backwards-stepwise generalized linear regression procedure was used to select the most parsimonious model. Automatic sequential removal of insignificant variables based on analysis of deviance tests. Initial model terms: trial treatment + date (AIC = 108.68). N: control = 30, cones = 30 and foliage = 26.

	Estimate	Standard Error	*z* value	*P*
(Intercept)	1.9680	0.6234	3.157	0.0016
Cones	-0.8210	0.5825	-1.410	0.1587
Foliage	-0.3856	0.5968	-0.646	0.5183
23 August	-1.5648	0.6308	-2.481	0.0131
31 August	-2.2778	0.6396	-3.562	0.0004

Null deviance: 181.48 on 85 degrees of freedom
Residual deviance: 101.25 on 81 degrees of freedom
AIC: 111.25
pseudo R^2 = 44.21

Table A1.4. The influence of reproduction on the longevity of adult *Dioryctria abietivorella*. A backwards-stepwise generalized linear regression procedure was used to select the most parsimonious model. Automatic sequential removal of insignificant variables based on analysis of deviance tests. Initial model terms: wing area + weight + mating status + sex + all two-way interactions (AIC = 615.58).

	Estimate	Standard Error	*z* value	*P*
(Intercept)	3.2762	0.1956	16.749	< 0.0001
Weight	-0.0025	0.0044	-0.571	0.5682
Mating status-virgin	-0.5929	0.2768	-2.142	0.0322
Sex-male	-0.1278	0.0537	-2.379	0.0174
Weight * mating status-virgin	0.0181	0.0067	2.718	0.0066

Null deviance: 116.05 on 91 degrees of freedom
Residual deviance: 95.03 on 87 degrees of freedom
AIC: 606.39
pseudo R^2 = 18.11

Table A1.5. The influence of reproduction, based on realized fecundity, on the longevity of adult female *Dioryctria abietivorella*. A backwards-stepwise generalized linear regression procedure was used to select the most parsimonious model. Automatic sequential removal of insignificant variables based on analysis of deviance tests. Initial model terms: wing area + weight + mating status + realized fecundity + all two-way interactions (AIC = 294.33).

	Estimate	Standard Error	*z* value	*P*
(Intercept)	3.007e-00	6.451e01	4.661	< 0.0001
Wing	2.455e-01	1.522e-01	-1.613	0.1067
Weight	1.559e-02	1.522e-01	2.035	0.0419
Mating status-virgin	-6.955e-01	6.149e-01	-1.131	0.2580
Realized fecundity	6.558e-03	2.446e-03	2.681	0.0073
Wing area * mating status-virgin	3.591e-01	1.830e-01	1.963	0.0500
Weight * realized fecundity	-1.164e-04	5.468e-05	-2.128	0.0333
Mating status –virgin * realized fecundity	-2.103e-03	6.682e-04	-3.147	0.0017

Null deviance: 69.29 on 44 degrees of freedom
Residual deviance: 44.65 on 37 degrees of freedom
AIC: 293.44
pseudo R^2 = 35.56

Table A1.6. The influence of reproduction, based on potential fecundity, on the longevity of adult female *Dioryctria abietivorella*. A backwards-stepwise generalized linear regression procedure was used to select the most parsimonious model. Automatic sequential removal of insignificant variables based on analysis of deviance tests. Initial model terms: wing area + weight + mating status + potential fecundity + all two-way interactions (AIC = 295.98).

	Estimate	Standard Error	*z* value	*P*
(Intercept)	3.007e-00	6.451e01	4.661	< 0.0001
Wing	2.455e-01	1.522e-01	-1.613	0.1067
Weight	1.559e-02	1.522e-01	2.035	0.0419
Mating status-virgin	-6.955e-01	6.149e-01	-1.131	0.2580
Potential fecundity	6.558e-03	2.446e-03	2.681	0.0073
Wing area * mating status-virgin	3.591e-01	1.830e-01	1.963	0.0500
Weight * potential fecundity	-1.164e-04	5.468e-05	-2.128	0.0333
Mating status–virgin * potential fecundity	-2.103e-03	6.682e-04	-3.147	0.0017

Null deviance: 69.29 on 44 degrees of freedom
Residual deviance: 44.65 on 37 degrees of freedom
AIC: 293.44
pseudo R^2 = 35.56

Table A1.7. The influence of reproduction on the longevity of adult male *Dioryctria abietivorella*. A backwards-stepwise generalized linear regression procedure was used to select the most parsimonious model. Automatic sequential removal of insignificant variables based on analysis of deviance tests. Initial model terms: wing area + weight + mating status + all two-way interactions (AIC = 319.55).

	Estimate	Standard Error	*z* value	*P*
(Intercept)	2.5990	0.2140	12.146	< 0.0001
Weight	0.0135	0.0053	2.553	0.0107

Null deviance: 55.36 on 46 degrees of freedom
Residual deviance: 49.04 on 45 degrees of freedom
AIC: 313.59
pseudo $R^2 = 11.42$