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Identification, biology, and management of conifer sawflies (Hymenoptera: Diprioninae) in eastern North America

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Pine sawflies (Hymenoptera: Diprionidae) are eruptive herbivores found throughout eastern North America. The Diprionidae family, which contains at least 140 species, constitutes the most persistent threat to conifers as population outbreaks can cause widespread defoliation. Because some species are more prone to large, destructive outbreaks than others, species identification is critical to effective management. Although existing taxonomic keys are primarily based on internal adult morphology, substantial variation among species in larval color traits, geographic location, overwintering strategy, host plant, and egg patterns can be diagnostic at the species level. Here, we focus on the Pinaceae-feeding subfamily Diprioninae, of which there are 25 species in eastern North America. We describe the general biology, life cycle, and host-use ecology of Diprioninae, with an emphasis on the variation among these traits within this subfamily. In addition, we provide tools for species identification, including a taxonomic key that utilizes external diagnostic characteristics. Finally, we discuss available management strategies.

Key words: Hymenoptera, conifer, pine, sawfly, key

Pine sawflies (Hymenoptera: Diprionidae) are pests of natural, ornamental, and commercial pine trees and other conifers, which are grown for timber, turpentine, and other byproducts, and for ornamental sale and Christmas trees (Welch 1991, Darr et al. 2022). Despite the name, sawflies are not flies—rather, they are relatives of ants, bees, and wasps that use saw-like ovipositors to lay their eggs in pine needles. Although the eggs themselves are rarely noticeable, sawfly activity becomes evident when the eggs hatch and larvae consume the host foliage. Damage can range from nearly unnoticeable to significant, covering a single branch or tree up to widescale landscape defoliation events. Several pine sawfly species are eruptive herbivores, and population outbreaks can cause widespread defoliation covering thousands of hectares (Haack and Mattson 1993, Larsson et al. 1993, Lyytikäinen-Saarenmaa and Tomppo 2002). Damage from these outbreaks can be both direct, including defoliation, tree mortality, and stunted tree growth, or indirect, increased susceptibility to other pests, including bark beetles (Dewey et al. 1974, Annila et al. 1999, Ciesla and Smith 2011). Here we discuss 25 pine sawfly species in eastern North America (bounded to the west by the Great Plains), provide tools for identification, and discuss management strategies.

Taxonomy and Identification

The family Diprionidae, the conifer sawflies, consists of at least 140 species in 13 genera (11 extant and 2 extinct) found almost everywhere across the Northern Hemisphere (Taeger et al. 2018). Distinguishing morphological characteristics for this family include front wings with only 1 marginal cell, 2 apical spurs on the tibia of the front leg, and distinctive antennae with at least 13 segments that are pectinate (comb-like) in males and serrate (saw-like) in females (Goulet and Huber 1993) (Supplementary Fig. S1). Diprionid larvae feed either on the leaves (needles) or developing cones of conifer trees in the families Pinaceae or Cupressaceae. While some sawfly species from other families also feed on conifers, the Diprionidae represent the largest and most persistent threat to conifers, with several species prone to large, destructive outbreaks (Taeger et al. 2018). This family consists of 2 subfamilies: Cupressaceae-feeding Monocteninae (3 extant genera) and Pinaceae-feeding Diprioninae (8 extant genera). We focus here on the Diprioninae, of which there are 25 species in eastern North America: 1 *Diprion* species, 2 *Gilpinia* species, and 22 *Neodiprion* species (Table 1). Among these are 4

Table 1. Characteristics of eastern North American Diprioninae species
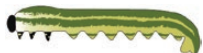
Species	Hosts **Primary,** *nonnative,* *rare	Distribution*	Generations, overwintering and timing**
Introduced pine sawfly *Diprion similis* (Hartig) 	**Eastern white pine,** Jack pine, Pitch pine, Red pine, Loblolly pine, Virginia pine, *Scots pine, Mugo pine,* *Pond pine	USA: ME, VT, NH, MA, CT, RI, NY, PA, MD, DC, DE, NJ, WV, VA, OH, KY, TN, IN, MI, WI, MN, IA, IL, MO, NC, SC, WA, OR. Canada: ON, MB, QC, NL, NB, PE, NS, BC.	1–5 generations per year. Larvae early June to late October, peaking in late August and September. Cocoon overwinterer.
Gilpinia frutetorum (Fabricius) 	**Red pine,** *Scots pine, Austrian pine, Mugo pine*	USA: CT, RI, MA, NH, NJ, NY, MN, WI, IL, IN, MI, OH Canada: ON, QC.	1–2 generations per year. Larvae from June to early October. Peaking in August. Cocoon overwinterer.
European spruce sawfly *Gilpinia hercyniae* (Hartig) 	**White spruce,** *Norway spruce,* Black spruce, Colorado spruce, Engelmann spruce, Red spruce, *Balsam fir, *Silver fir	USA: ME, NH, VT, MA, NY, PA, OH, IL, IN, MI, MN, IA, WI, TN. Canada: ON, MB, QC, NL, NB, PE, AB	1–2 generations per year. Larvae May to October, peaking in August. Cocoon overwinterer.
Redheaded pine sawfly *Neodiprion lecontei* (Fitch) 	**Jack pine, Red pine, Shortleaf pine, Virginia pine, Slash pine, Loblolly pine,** Pond pine, Sand pine, Pitch pine, *Eastern white pine, *Scots pine, *Norway spruce, *Larches	USA: ME, VT, NH, MA, CT, RI, NY, PA, MD, DC, DE, NJ, WV, VA, OH, KY, TN, IN, MI, WI, MN, IL, MO, AR, NC, SC, GA, FL, AL, MS, LA, TX. Canada: ON, MB, QC, NL, NB, PE, NS.	1-5 generations per year. Larvae late May to late October, peaking from late July to September. Cocoon overwinterer.
White pine sawfly *Neodiprion pinetum* (Norton) 	**Eastern white pine,** *Pitch pine, *Shortleaf pine, *Red pine, *Mugo pine*	USA: ME, VT, NH, MA, CT, RI, NY, PA, MD, DC, DE, NJ, WV, VA, OH, KY, TN, IN, MI, WI, MN, IL, MO, AR, NC. Canada: ON, QC, NB, PE, NS, NL.	1–3 generations per year. Larvae late May to late October, peaking from late July to September. Cocoon overwinterer.
Blackheaded pine sawfly *Neodiprion excitans* (Rohwer) 	**Loblolly pine, Shortleaf pine, Longleaf pine,** Table-mountain pine, Slash pine, Pitch pine, Pond pine, Spruce pine, Sand pine, Caribbean pine	USA: OK, TX, AR, LA, MS, AL, GA, FL, NC, SC, VA, TN.	4-5 generations per year. Larvae from mid-October to April, with peaks in April and November. Cocoon overwinterer.
Neodiprion hetricki (Ross) 	**Loblolly pine, Pond pine**	USA: GA, TN, NC, SC, VA.	1 generation per year. Larvae from late March to early June. Egg overwinterer.
Neodiprion pinusrigidae (Norton) 	**Pitch pine, Shortleaf pine**	USA: NJ, PA, NY, MA, CT, RI, VT, NH, ME Canada: NB, QC, NS	1–3 generations per year. Larvae from late May to October. Cocoon overwinterer.
Swaine jack pine sawfly *Neodiprion swainei* (Middleton) 	**Jack pine,** Red pine, White pine, *Scots pine*	USA: MI, WI, MN, Canada: ON, QC,	1 generation per year. Larvae July to September. Cocoon overwinterer
Neodiprion maurus (Rohwer) 	**Jack pine**	USA: WI, MN, MI Canada: ON, QC	1 generation per year Larvae from early May to mid-June. Adult overwinterer in cocoon.
Virginia pine sawfly *Neodiprion pratti* (Dyar) 	**Jack pine,** Pitch pine, Red pine **Loblolly pine, Shortleaf pine, Virginia pine,** Sand pine, Slash pine, *Scots pine*	USA: MD, DC, NC, VA, KY, PA, MA, NY, NJ CT, RI, NH, SC, GA, FL, IL, IN, WI, MI Canada: ON, NS, QC, NB, PE	1 generation per year Larvae from March to October, peaks in late April, June. Egg overwinterer

Table 1. Continued

Species	Hosts **Primary**, *nonnative*, *rare	Distribution[*]	Generations, overwintering and timing[**]
Loblolly pine sawfly *Neodiprion taedae* (Ross) 	**Loblolly pine**, shortleaf pine, *Virginia pine	USA: AR, LA, TX, MS, SC, MO, OH, IL, VA, MD, DE, PA, NJ, NY, CT, RI, MA, VT, NH, ME	1 generation per year Larvae from March to early June Egg overwinterer.
Neodiprion abbotii (Leach) 	**Loblolly pine, Slash pine, Longleaf pine, Shortleaf pine**, *Red pine, *Caribbean pine	USA: WI, VA, NC, SC, GA, AL, FL. Canada: ON, QC.	3 generations per year. Larvae from May to December, with peaks in July and August Cocoon overwinterer.
Neodiprion fabricii (Leach) 	**Loblolly pine, Shortleaf pine**	USA: GA, FL, NC, TN, VA	1-3 generations per year. Larvae from April to September. Cocoon overwinterer
Neodiprion nigroscutum (Middleton) 	**Jack pine**	USA: WI, MN, MI Canada: ON	1-2 generations per year Larvae from May-June, then again from August-September. Cocoon overwinterer
Brownheaded jack pine sawfly *Neodiprion dubiosus* (Schedl) 	**Jack pine**	USA: WI, MN, MI Canada: ON, MB	1-2 generations per year Larvae in May-June and again in August-September. Cocoon overwinterer
Neodiprion knereri (Linnen and Smith) 	**Sand pine**	USA: FL	1-3 Generations per year Larvae from February to September. Cocoon overwinterer
Slash pine sawfly *Neodiprion merkeli* (Ross) 	**Slash pine, Cuban pine, Caribbean pine**	USA: FL Cuba, Bahamas	Many generations per year Larvae from October to July. Cocoon overwinterer.
Redheaded jack pine sawfly *Neodiprion rugifrons* (Middleton) 	**Jack pine**	USA: WI, MN, MI Canada: ON	1-2 generations per year Larvae in July to August and again in September–October Cocoon overwinterer
Neodiprion virginiana (Rohwer) 	**Virginia pine**, Loblolly pine	USA: KY, TN, NC, WV, VA, MD, PA, DC, GA.	1-3 generations per year. Larvae from June to October, peaking in September. Cocoon overwinterer
Neodiprion warreni (Ross) 	**Spruce pine, Shortleaf pine, Sand pine**, Loblolly pine	USA: FL, GA, MS, AL, AR, LA	1-2 generations per year. Larvae from May to October. Cocoon overwinterer
European pine sawfly *Neodiprion sertifer* (Geoffroy) 	**Jack pine, Red pine**, White pine, Shortleaf pine, Pitch pine, Table-mountain pine, *Scots pine, Mugo pine*, Austrian pine, Japanese red pine	USA: ME, VT, NH, MA, CT, RI, NY, PA, MD, DC, DE, NJ, WV, VA, OH, KY, IN, MI, WI, MN, IA, IL, WA, OR, CA. Canada: ON, MB, QC, NB, PE, NS, BC.	1 generation per year Larvae from early April to early July, peak in late May. Egg overwinterer.

Table 1. Continued

Species	Hosts Primary, *nonnative*, *rare	Distribution[*]	Generations, overwintering and timing[**]
Red pine sawfly *Neodiprion nanulus nanulus* (Schedl)	**Red pine, Jack pine,** white pine, *Japanese red pine, Mugo pine*	USA: ME, VT, NH, NY, MI, WI, MN Canada: NB, QC, ON, MB, SK	1 generation per year Larvae June to August Egg overwinterer.
Balsam fir sawfly *Neodiprion abietis* (Harris)	**Balsam fir,** Black spruce, White spruce, White fir, *Jack pine, *Red pine, *Norwegian spruce*	USA: ME, Canada: NL, PE, NS, NB, QC, ON, MB, SK, BC	1 generation per year Larvae from May to June Egg overwinterer
Neodiprion compar (Leach)	**Red Pine, Jack Pine**	USA: ME, VT, NH, MA, CT, RI, NY, PA, MD, DC, DE, NJ, WV, VA, OH, KY, TN, IN, MI, WI, MN, IL, MO, AR, NC, SC, GA, FL, AL, MS, LA, TX. Canada: ON, MB, QC, NL, NB, PE, NS.	1 generation per year Larvae from July to August. Cocoon overwinterer.

*iNaturalist research grade data was used for all species in addition references from main text.

**Dates are approximate based on best available data from references, collections, and iNaturalist.

nonnative species that were each introduced from Europe approximately a century ago: *Diprion similis* Hartig, *Gilpinia frutetorum* F., *Gilpinia hercyniae* Hartig, and *Neodiprion sertifer* Geoffroy (Baker 1972). The remaining 21 *Neodiprion* species are native to eastern North America.

Existing taxonomic keys for Diprionidae are primarily based on adult morphology, with special emphasis on the female 'saw' (ovipositor) for distinguishing between species (Ross 1955, Smith 1974). However, evaluating saw characteristics requires carefully dissecting ovipositors and examining them under a microscope. Here, we focus instead on diagnostic characteristics that can be evaluated from external morphology. Compared to adult *Gilpinia* and *Diprion*, adult *Neodiprion* males and females tend to have slimmer bodies (Supplementary Fig. S2). *Diprion* adults, on the other hand, tend to have smaller cenchri (small lobes on the insect's back) and larger mesoscutella (plate on back of insect) than the other 2 genera. Adult male coloration is very similar across the 3 genera: males tend to be dark black or all brown, sometimes with lighter undersides. By contrast, adult female coloration is more variable and useful for diagnosing genera. *Neodiprion* female color ranges from tan to reddish brown, with some black or brown dorsal patterning, although this patterning tends to be less pronounced than in *Gilpinia* and *Diprion* females. *Gilpinia* and *Diprion* females also tend to have more darkly pigmented heads than *Neodiprion* females. Additionally, compared to *Diprion* and *Neodiprion*, *Gilpinia* females are more yellow in coloration. Among *Neodiprion*, *N. compar* Leach females are unique in their dark pigmentation, uniformly black/dark with a light stripe along the abdomen (Wilson 1977).

Although external adult morphology can be used to identify pine sawflies to genera and sometimes species, larval morphology and coloration is far more variable between species and therefore often diagnostic at the species level (Table 1, see 'Key to eastern North American Diprioninae species based on their larval morphology'). Larvae are also encountered more frequently because they are present on the trees for several weeks, whereas adults usually do not live for more than a few days. Larvae also cause conspicuous feeding damage (Fig. 1), while adults do not feed at all. All 3 non-*Neodiprion* species have very distinctive larval coloration patterns not found in any eastern North American *Neodiprion* species: *Diprion similis* larvae have an unusual mottled pattern consisting of black, white, and yellow pigmentation (Supplementary Fig. S3); *Gilpinia frutetorum* larvae have a distinctive triangle on the front of the head; and *G. hercyniae* larvae have thin white stripes along the body.

Among the 22 eastern North American *Neodiprion* species there is variation in several larval color traits: head color (jet black, brown, red, or multicolored), body color (from bright white to pale yellow, green, or bright yellow), and striping or spotting patterns (see Figs. 2 and 3). One note of caution is that these traits change dramatically over the course of larval development. Both the earliest instars (first 1–2 molts posthatching) and the last instar (a wandering, nonfeeding larval stage) tend to look very different from mid-late instars and are not as easy to identify. For this reason, our comparison table (Table 1) and identification key (see 'Key to eastern North American Diprioninae...', below) focus on coloration in mid-late instar feeding larvae. Specifically, color becomes informative once feeding larvae reach approximately 10–20 mm in length and have well-defined markings along the body (vs. smaller, minimally marked early instars). Feeding larvae can be distinguished from nonfeeding larvae because the latter have a pronounced reduction in head pigmentation. There can also be considerable color variation within species, especially for widespread species such as *N. lecontei* Fitch (Linnen et al. 2018, Lindstedt et al. 2022) and *N. pratti* Dyar (Knerer 1984).

Fig. 1. Diprioninae feeding damage is characterized by skeletonization of the needles (A–B) by newly hatched larvae, followed by consumption of the entire needle tissue down to the fascicle (C–D) as larvae grow. Some Diprioninae species can completely defoliate trees (D), potentially leading to tree death. Photos by Ashleigh Glover (A and C) and Robin Bagley (B and D).

Therefore, it is often useful to use color in conjunction with other information to identify species (see Table 1 and 'Key to eastern North American Diprioninae…').

Two useful pieces of information that can be used to distinguish between at least some similarly colored larvae are geographic location and host plant (Table 1). The 2 *Gilpinia* species are uncommon in North America and are generally restricted to locations north of the 40th parallel. *Diprion similis* has a much broader range, extending further south to the southern limits of the range of eastern white pine (*Pinus strobus* L.). *Neodiprion* species vary considerably in geographic range, with assemblages of southern species (*N. excitans* Rohwer, *N. fabricii* Leach, *N. merkeli* Ross, *N. knereri* Linnen and Smith, and *N. warreni* Ross), central/mid-Atlantic species (*N. virginiana* Rohwer and *N. hetricki* Ross), northern species (*N. abietis* Harris, *N. maurus* Rohwer, *N. rugifrons* Middleton, *N. dubiosus* Schedl, *N nigroscutum* Middleton, *N. swainei* Middleton, *N. pinusrigidae* Norton, and *N. nanulus nanulus* Schedl), and more wide-ranging species that span 2 or more of these regions (*N. compar* Leach, *N. abbotii* Leach, *N. pratti* Dyar, *N. lecontei* Fitch). In terms of host use, *Gilpinia hercyniae* and *Neodiprion abietis* are the only species to use nonpines (firs and spruces), *Gilpinia frutetorum* prefers naturalized Scots pine, and *Diprion similis* and *Neodiprion pinetum* Norton are the only species that regularly use white pine as a host (Linnen and Farrell 2010). Many *Neodiprion* species specialize on 1 or 2 host species, such as *N. dubiosus, N. rugifrons,* and *N. maurus* on jack pine; *N. knereri* on sand pine; and *N. merkeli* on slash pine. Other species feed on many species of pines, most notably *N. lecontei*, which uses many different native and introduced pines across a range that spans from Florida to southern Canada. Species also differ in their preferences for different size or age classes of their hosts. For example, *N. swainei* feeds almost exclusively on older trees (Atwood 1960, Lyons 1964) of its preferred hosts, while *N. lecontei*—which often defoliates entire trees regardless of foliage age—is notable for preferring and more severely defoliating younger trees (0.3–5 m tall, Atwood and Peck 1943, Atwood 1960, Baker 1972). Finally, as described below, time of year and other behavioral traits can be useful for describing species due to differences in overwintering strategies.

General Biology, Life Cycle, and Host-Use Ecology

All eastern North American diprionid species share the same basic life cycle (Fig. 4). This cycle begins when adult males and females meet and mate on one of their preferred host plants. The mated female then uses a specialized saw-like ovipositor to cut narrow slits in the host's needles, into which she lays her eggs. These eggs develop within the needles, and the neonates crawl out of the egg pockets and migrate to a feeding site on the host foliage. Larvae undergo several molts before entering a final, wandering stage that searches for a suitable location to spin a fibrous cocoon, usually on the host, on vegetation near the host, or in the litter beneath the host. Pupation occurs in the cocoon and eventually an adult chews its way out to start the life cycle again. Although the basic sequence of events is the same for the species we consider here, there is also substantial variation in many details, some of which have diagnostic value or implications for pest status or biocontrol strategies. Here, we describe each diprionid life stage in more detail, with an emphasis on characteristics that vary across species.

Fig. 2. Variation in Diprioninae larval color traits. (A) Redheaded, pale-bodied and brown-headed, yellow-bodied *Neodiprion lecontei* larvae. (B) *N. compar* larvae. (C) A *N. maurus* larva. (D) A *N. pinetum* larva. (E) A *N. fabricii* larva. Head coloring varies among and within species, from red to brown (A) to black (C and D) to multicolored (B and E). Body color also varies among and within species, from bright white (D) to pale (either yellowish or greenish; A, C, and E) to green (B) to bright yellow (A). Finally, body patterning also varies among and within species, from larvae having only spots (A and D), only stripes (B and E), or a combination of stripes and spots (C). Photos by Ryan Ridenbaugh (A, D, and E) and Robin Bagley (B and C).

Overwintering Strategy and Voltinism

Perhaps the most striking difference among the life cycles of different diprionid species is how they spend the winter months (overwintering strategy) and how many generations they can have in 1 growing season (voltinism). Eastern North American Diprioninae overwinter at 1 of 3 life stages (Table 1): (i) as eggs within host needles, (ii) as prepupae in cocoons, or (iii) as fully formed adults within cocoons (only a single species, *N. maurus*). These overwintering strategies also dictate voltinism and seasonal phenology in this group. The egg-overwintering species are univoltine and are the first species to hatch and begin feeding on trees in the spring or early summer. After spinning their cocoons, they enter a dormant state that lasts throughout the hot summer months. Adults emerge in the fall to mate and lay eggs that will spend the winter in the needles.

Prepupal overwinterers can be univoltine or multivoltine, depending on the length of the growing season. Adults emerge from cocoons any time between late spring and late summer, depending on the species. Once laid, eggs immediately begin developing, generally hatching within 1–3 weeks. Feeding larvae are present between early summer and fall and there can be anywhere from 1 to 5 generations per year, depending on the species and the climate. Diapause in prepupal overwinterers is usually triggered by short days and cool temperatures, although day length appears to be the primary cue (Knerer 1984, Dunbar and Wagner 1992). As such, voltinism varies

by latitude. Species—and populations within widespread species—in cold, northern latitudes have fewer generations per year than species and populations in more southern latitudes. For example, Canadian populations of *N. lecontei* have 1 generation per year (with larvae gone by mid-September) whereas far southern populations in Florida do not overwinter at all (Wilson et al. 1992). Finally, 1 northern species—*N. maurus*—has evolved a somewhat unusual overwintering strategy (Knerer 1990). Like egg-overwintering species (and unlike prepupal overwinters), adult development in *N. maurus* occurs before the onset of winter. However, instead of emerging to lay eggs in the fall, *N. maurus* adults remain in the cocoon until spring. Thus, their larvae tend to be present in the field later than egg overwinterers, but earlier than prepupal overwinterers.

Because species tend to stick to a single overwintering strategy (with some possible exceptions, e.g., *N. excitans*; Baker 1972), the time of year that larvae are found can be very useful for identifying species: spring feeders are almost always egg-overwinterers; summer and fall feeders tend to be prepupal overwinterers. These different strategies also result in different propensities for host damage. Because they feed once per year and on old foliage only, univoltine egg-overwintering species cause less damage to the host plant than species that tend to have multiple generations per year and feed on both the new growth in addition to the old (Lyytikäinen-Saarenmaa and Tomppo 2002, Kulman 1971).

Fig. 3. Visual guide to larvae of Diprionid pine sawflies of Eastern North America, showcasing variation in larval coloration and markings. More diagnostic characteristics can be found in Table 1 and the key within text.

Mating and Reproduction

Like all Hymenoptera, Diprionidae are haplodiploid, meaning that males are haploid (1 set of chromosomes) and females are diploid (2 sets of chromosomes). Most diprionid species have a form of haplodiploidy called arrhenotoky in which unfertilized eggs develop into haploid males and fertilized eggs develop into diploid females (Normark 2003, but see Cook and Crozier 1995, Harpur et al. 2013, Harper et al. 2016). However, one introduced North American diprionid—*Gilpinia hercyniae*—reproduces mostly via thelytoky, a form of parthenogenesis in which virgin females produce diploid females (Smith 1941, Morris 1958, Pschorn-Walcher 1982, Normark 2003). For this reason, male *G. hercyniae* are rarely produced (<1% of all adults; Raizenne 1957) while most other diprionid sex ratios tend to be female-biased (Craig and Mopper 1993).

Upon emerging from cocoons, egg-laden females locate a suitable host for oviposition, typically not far from the cocoon site (Coppel and Benjamin 1965, Baker 1972). Factors that determine host suitability vary among sawfly species. In addition to having variable preferences by host species and age (see above), sawfly females also vary in their preferred site characteristics. Whereas some species preferentially lay their eggs in open-grown hosts (e.g., *N. abietis*, *N. merkeli*), others such as *N. excitans* and *N. warreni* prefer moderately to densely packed stands (Atwood 1960, Baker 1972; Wilkinson 1971; ANG and CRL personal observations). Still other species, such as *N. lecontei* and *N. pinetum*, are either indifferent to tree density or have variable preferences among populations. Within a location and host species, females may also show preferences for specific trees. For example, *N. sertifer* preferentially oviposit in *Pinus sylvestris* trees with
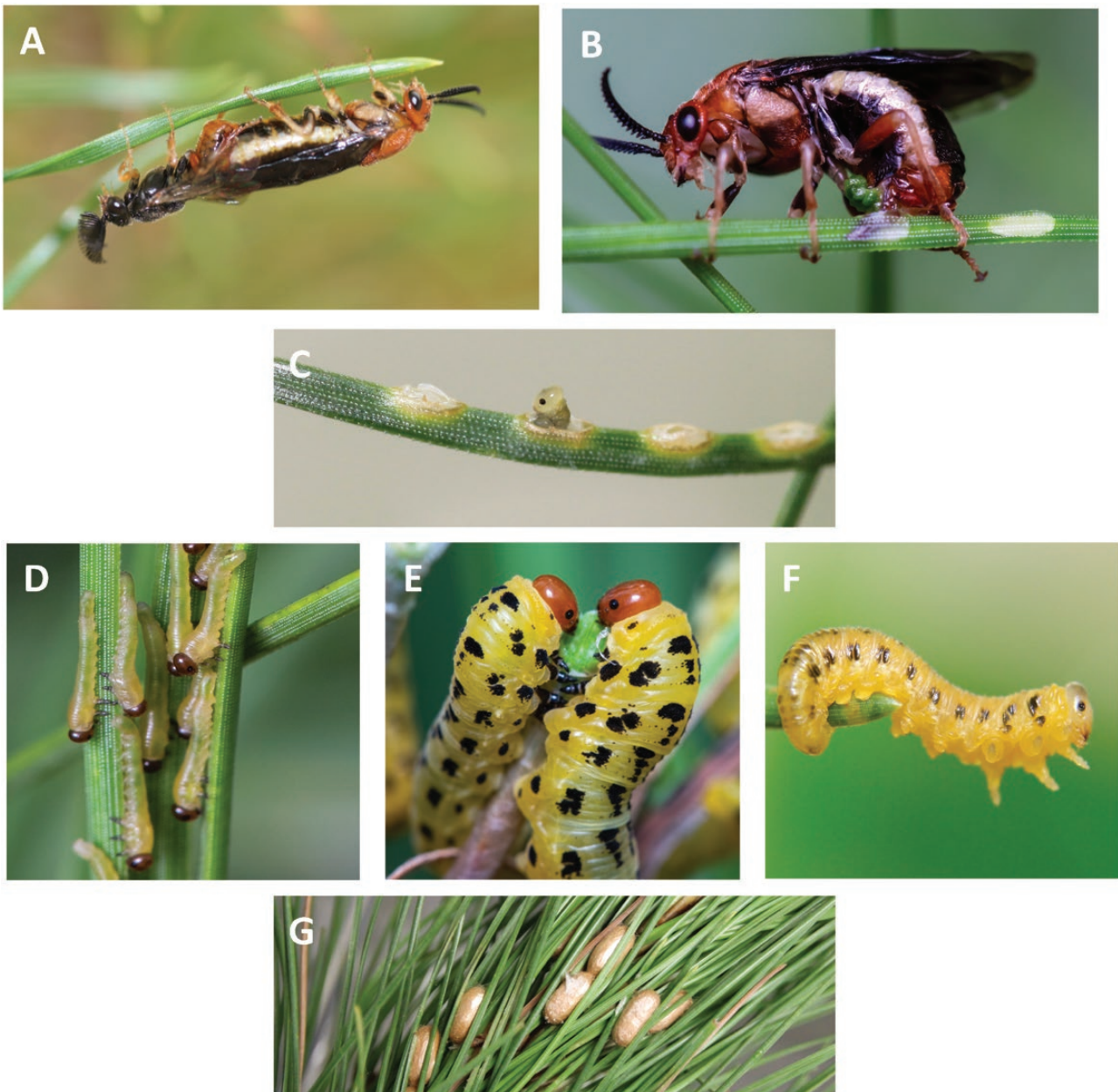
Fig. 4. *Neodiprion lecontei* life cycle. (A) An adult male and female mate on their host. (B) The mated female uses her saw-like ovipositor to cut egg pockets into the host needle, where she deposits her eggs. The eggs develop within the needles. (C) Larvae hatch from the eggs and migrate to a feeding site on the host. Larvae undergo several molts (D–F), from early instars (D) to mid-late, feeding instars (E) to final, wandering instars (F). (G) Final, wandering instars spin fibrous cocoons on the host or in the soil beneath the host. Adults emerge from the cocoons to repeat the life cycle. Photos by Robin Bagley (A, C, F, and G) and Ryan Ridenbaugh (B, D, and E).

longer needles and high resin acid (diterpenoid) content, the latter of which reduced larval susceptibility to parasitoids (Björkman et al. 1997). Female oviposition may also be affected by the presence of other females. There is evidence of an oviposition deterrent factor produced by females of at least 1 western North American species, *N. fulviceps* (Tisdale and Wagner 1991). However, there is no evidence of an oviposition deterrent factor in *N. sertifer* and field studies suggest that females may actually preferentially group their eggs with those of other females (Bluemke and Anderbrant 1997).

Once a suitable host has been located, females orient themselves so that they are facing the base of the needle until they are approached by a male (Benjamin 1955). Male attraction occurs via a strong sex pheromone, the existence of which was first confirmed

almost 50 years ago (Jewett et al. 1976). Since then, female sex pheromone composition and male behavioral response to these compounds have been studied in several diprionid species (reviewed Anderbrant 1993). All sex pheromones identified to date consist of acetate or propionate esters of saturated alcohols called diprionols. These compounds have either 8 or 16 stereoisomers, but it is generally only one of the stereoisomers that is attractive to males, although synergistic effects of other stereoisomers are possible (Jewett et al. 1976, Anderbrant 1993, Anderbrant et al. 2021).

Shortly after emergence, adult males take flight in search of females. Their heavily branched antennae are specialized for capturing odor molecules in the air. Males are also far better flyers than females, capable of dispersing at least a kilometer within a day (Östrand et

al. 2001), with favorable wind conditions. Male responses to female pheromone blends have been demonstrated via a combination of electrophysiology (i.e., recording of antennal responses to specific odors) and field trapping studies (i.e., baiting traps with different pheromone blends). Although there are some species-specific differences in female pheromone composition and male attraction, similarities in these traits also appear to be common (Anderbrant 1993).

Once a male detects an appropriate pheromone signal, he will approach the female in a zigzag pattern until he gets close, at which point visual cues become more important (Coppel and Benjamin 1965). Courtship is minimal, but an unreceptive female may fly away, aggressively buzz her wings, or even attack a male that is attempting to mate. When mating does occur, the male approaches the female from behind, bends his abdomen under the female, and then maneuvers his body into a final position in which the male and female face opposite directions. Mating pairs usually sit quietly on the pine needle; if undisturbed, mating can last anywhere from a few minutes to more than 30 min (personal observations JSD, ANG, CRL, Coppel and Benjamin 1965). After mating, females typically begin laying eggs almost immediately, whereas males may fly off in search of another female (Benjamin 1955). Thus, while females tend to mate only once in most species, males may mate with more than 1 female.

Oviposition Behavior and Eggs

To locate a suitable needle, a female walks up and down the pine needles, palpating with her antennae. Once an acceptable needle is found, the female faces the tip of the needle and backs herself down to the base or midpoint of the needle. Some species proceed to cut a 'test-slit' to further evaluate the needle (or possibly to drain off excess resin, McCullough and Wagner 1993, Bendall et al. 2017). Next, the female uses her ovipositor to carve an egg pocket into the needle, into which she deposits an egg. Some species lay multiple eggs in the same needle (e.g., *N. lecontei* and *D. similis* can lay more than 20 eggs in a single needle), moving towards the tip of the needles as they oviposit, whereas other species (e.g., *G. frutetorum* and *N. abietis*) lay only a single egg per needle (Fig. 5, Ghent 1955, 1959, Coppel and Benjamin 1965, Baker 1972). Some species (e.g., *N. lecontei* and *N. pinetum*) lay their entire egg complement on a single branch terminus, while others (e.g., *D. similis*, *N. compar*, and *N. abbotii*) tend to distribute their eggs across multiple branch tips (Ghent 1959, Terbot 2021). Thus, although the general egg-laying procedure is similar across species, the specific pattern in which eggs are laid—location on the needle (near the tip or base), number of eggs per needle (one, a few, or many), the spacing between eggs (small or large gaps), and distribution across branch tips (1 tip or several)—varies across species and can be a useful diagnostic tool (Ghent 1959). Egg pigmentation also varies within and between species, from white to pale yellow (*N. lecontei*, *N. pratti*) to bright green (*N. abbotii*) to blue (*D. similis*) (Wallace 1964, Coppel and Benjamin 1965, Linnen and Smith 2012). The color of the eggs is often visible through the female abdomen and can be used to distinguish between species (*N. fabricii* and *N. abbotii*, Linnen and Smith 2012).

Larval Behavior

Historically, larvae have been classified as either 'gregarious' or 'solitary' based on whether or not they tend to feed in large groups (Coppel and Benjamin 1965, Knerer and Atwood 1973, Larsson et al. 1993). However, larval group size is a complex trait determined by multiple factors that all vary among species, including female fecundity, female tendency to cluster or divide eggs across branch tips, and larval behaviors that promote or reduce colony cohesion
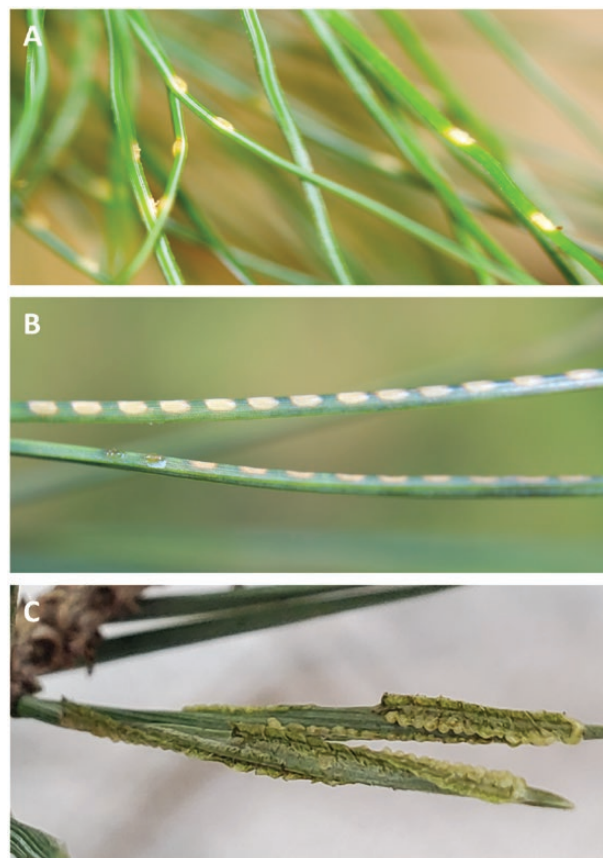
Fig. 5. Variation in Diprioninae egg patterns. (A) *Neodiprion pinetum* eggs. *N. pinetum* only lay 2–3 eggs per needle. (B) *N. lecontei* eggs. *N. lecontei* lay many eggs per needle. (C) *Diprion similis* eggs. *D. similis* lay many eggs per needle. However, unlike *Neodiprion*, the eggs are only partially embedded in the host needle and are covered with a protective layer secreted by the female during oviposition. Photos by Kim Vertacnik (A), Robin Bagley (B), and Jeremy Davis (C).

(Terbot et al. 2017, Terbot and Linnen 2019). Therefore, it is more useful to think of larval group size as a continuum from nonexistent or very small (e.g., *Diprion similis, N. compar, G. frutetorum,* and *G. hercyniae*) to very large groups (e.g., *N. lecontei, N. sertifer,* and *N. abietis*.

Regardless of group size, newly hatched larvae typically migrate away from egg-bearing needles to a feeding site. They then form small clusters that circle the tip of a needle and begin consuming its external portions, leaving the resinous core. This skeletonizing behavior produces straw-like feeding damage that can be the first visible sign on sawfly feeding activity. In most species, larvae will shift from skeletonizing to whole-needle feeding as they grow. One exception is the balsam fir sawfly (*N. abietis*) which continues to skeletonize the host needles throughout the entire feeding period, presumably to avoid defensive compounds in this highly toxic host (Knerer and Atwood 1972, 1973).

For large-group ('gregarious') species, feeding damage becomes very apparent once whole-needle feeding commences, and larvae will migrate to new branches as foliage is consumed. Large-group species also exhibit behaviors that actively maintain group cohesion, such as seeking out and staying close to other larvae (Costa and Louque 2001, Flowers and Costa 2003, Terbot et al. 2017). Chemical cues and trail-following behaviors keep the colony intact as they migrate from 1 feeding site to the next. Although these feeding sites are often on the same tree, some species can reportedly migrate several

Distinct black markings on dorsal side of last body segment
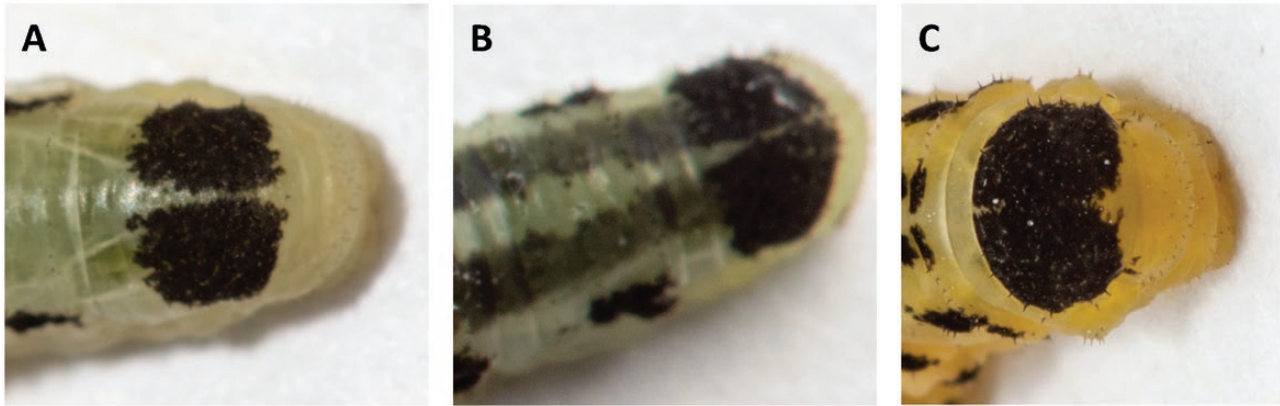
No distinct black markings on dorsal side of last body segment
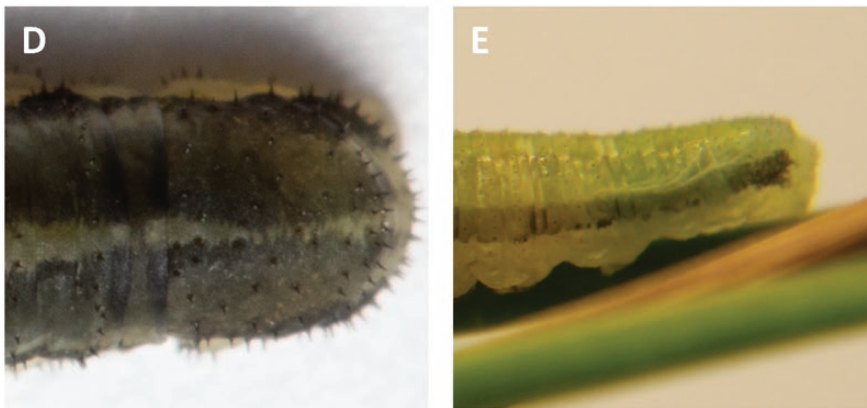
Fig. 6. Variation in Diprioninae markings on the dorsal side of the last body segment. Examples of species with (A–C) and without (D–E) distinct black markings on the dorsal side of the last body segment. The distinct black marking can be divided into two egg-shaped patches (A and B), or fused (C). *N. fabricii* larvae (D) tend to not have a distinct marking on the dorsal side of the last body segment because the pigmentation is a continuation of the dorsal stripes. Although *N. merkeli* (E) larvae exhibit a black marking on their last body segment, the marking is in the lateral zone rather than the dorsal zone. Photos by Ryan Ridenbaugh (A–D) and Robin Bagley (E).
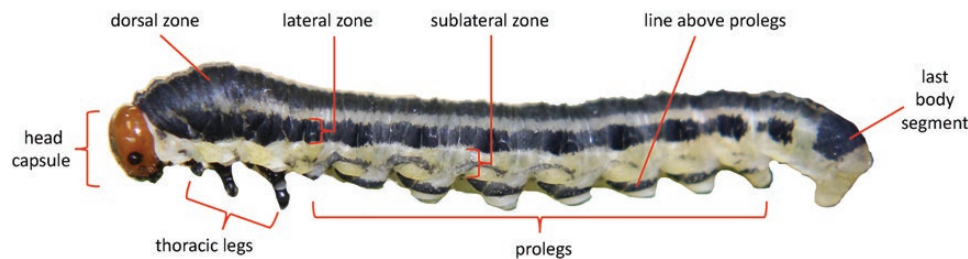
Fig. 7. Body zones of Diprioninae larvae. The dorsal zone runs along the entire backside of the larva and may contain stripes, spots, or neither. The lateral zone is directly under the dorsal zone along the side of the body and may contain stripes, spots, or both. The sublateral zone is directly under the lateral zone and above the prolegs. Pigmentation in the sublateral zone and a line above the prolegs may be absent.

yards (*N. lecontei*, Baker 1972) or 200 yards or more (*N. swainei*, Smirnoff 1960) over the soil in search of a new host tree.

In terms of other anti-predator defenses, all diprionid species are to some extent chemically defended via resins sequestered from their conifer hosts. When disturbed, early instars tend to retreat to the base of the needles, while late- to final-instar larvae may simply drop off the branch. By contrast, when mid- to late-instar larvae are disturbed, they often lift their heads and tail-ends into a characteristic U-shape and regurgitate a bubble of host resin. These extremely sticky regurgitants, which sawfly larvae can wield with surprising accuracy, are highly effective deterrents against invertebrate predators (Eisner et al. 1974). Pine terpenes also make sawfly larvae distasteful to avian predators, which quickly learn to avoid larvae so long as their color is sufficiently conspicuous (Lindstedt et al. 2022). Just as there is a more or less continuous range between small and large groups, there is also a range of apparent defensive strategies, from very cryptic species that blend in well with pine needles (e.g., *G. frutetorum*, *N. compar*) to very brightly colored species that contrast with pine needles (see Table 1). Intriguingly, brightly colored species tend to have larger larval groups, possibly indicating that larval aggregations enhance predator deterrence (Sillén-Tullberg 1990, Alatalo and Mappes 1996, Riipi et al. 2001).

Key to eastern North American Diprioninae species based on their larval morphology

1. Larva has distinct black marking(s) on the dorsal side of the last body segment (Figs. 6 and 7)...2
   Larva lacks distinct black marking(s) on the dorsal side of the last body segment 18
2. Head capsule is primarily reddish...3
   Head capsule is primarily dark (black/gray/brown) 8
3. Larva has pigmentation in the dorsal zone that is broken into spots (can be thick or reduced). Body can be yellow or pale (Fig. 2). On a variety of pines except white pine. Larvae present in summer and fall ....*Neodiprion lecontei*
   Larva has 2 stripes in the dorsal zone (can be dark or faint)...4
4. Larva has a distinct line above the prolegs...5
   Larva lacks a line above the prolegs. Body can be yellow or pale. Row of spots in the lateral zone can be incomplete. Usually found on jack pine in the Lake
   States and eastern Canada. Larvae present in summer and fall ....*Neodiprion swainei*
5. Cocoon overwinterer: larvae present in the summer to fall...6
   Egg overwinterer: larvae present in the spring. Body is pale. On loblolly, shortleaf or Virginia pine. In southern and central eastern United States. Pigmentation in lateral zone is a stripe………………………………………………………*Neodiprion taedae linearis*
   In eastern VA to ME. Pigmentation in lateral zone is a row of dark spots...*Neodiprion taedae taedae*
6. Body is pale (creamy) 7
   Body is yellow with pigmentation in lateral zone broken into spots. Usually found on jack pine. In the Lake States and Southern Ontario ....*Neodiprion dubiosus*
7. Larvae are in northern United States into southern Canada. Additional pigmentation typically present in sublateral zone .... *Neodiprion rugifrons*
   Larvae are in southern United States. Additional pigmentation can be present in sublateral zone ....*Neodiprion warreni*
8. Egg overwinterer: larvae present in the spring 9
   Cocoon overwinterer: larvae present in the summer and fall 10
9. Body is pale and has 2 distinct black spots above the thoracic legs. A pair of thick stripes are present in the dorsal zone and pigmentation in lateral zone broken into spots. Found on loblolly and pond pines in southeastern United States...........*Neodiprion hetricki*
   Body is yellowish. Pigmentation is highly variable, but all larvae lack 2 distinct black spots above the thoracic legs. Larvae generally have 2 stripes in the dorsal zone and pigmentation in the lateral zone that can be a solid stripe or broken into spots. Darker individuals tend to have a line above the prolegs with some additional pigmentation in the sublateral zone. Found on many different pines except white pine. In the Lake States into southeastern and central Canada .....*Neodiprion pratti banksianae* In MD to Nova Scotia and Ontario ……….…………*Neodiprion pratti paradoxicus*In NC to NJ and west to IL ………….…………….….......*Neodiprion pratti pratti*
10. Larva has a distinct line above the prolegs...11
    Larva lacks a line above the prolegs 15
11. Head capsule is solid black...12
    Head capsule is black with a light area around the mouth..14
12. Pigmentation in the lateral zone is broken into spots 13
    Pigmentation in the lateral zone is a solid stripe. Body is pale. Dorsal zone contains a pair of olive-green stripes. Found on a variety of pines except white pine. In FL to Canada and west to TX..*Neodiprion abbotii*
13. Larvae are in northern United States into southeastern Canada. Usually found on jack pine. Body is pale with a pair of stripes in the dorsal zone……........*Neodiprion maurus* Larvae are in southern United States. Body is pale. A pair of dark stripes are present in the dorsal zone and additional pigmentation in the sublateral zone can be present ....*Neodiprion warreni*
14. Distinct green pigmentation (sometimes a complete stripe) present in the sublateral zone. A pair of stripes are present in the dorsal zone and are fainter than the stripe in the lateral zone. Found on shortleaf and loblolly pines in the southeastern United States ....*Neodiprion fabricii*
    Little to no pigmentation present in the sublateral zone. Body is pale. Dorsal zone contains a pair of olive-green stripes. Found on a variety of pines except white pine. In FL to Canada and west to TX ....*Neodiprion abbotii*
15. Spots present in the lateral zone are overlaid on a faint stripe. Body is greenish with a pair of stripes in the dorsal zone. Found on a variety of pines except white pine. In southeastern United States and west to TX.……………………….*Neodiprion excitans* No stripe is present under the spots in the lateral zone..16
16. Pigmentation in the dorsal zone is faint or absent..
    .. 17 Pigmentation in the dorsal zone is dark and broken into 2 rows of spots. Body is pale or yellowish. Only found on white pine. In GA to Canada.
    ………………………………………………………………………..*Neodiprion pinetum*
17. Larvae are in the northeastern United States on pitch and shortleaf pines. Body is pale with a row of spots (partial or complete in the lateral zone*Neodiprion pinusrigidae*)
    Larvae are in the central eastern United States on Virginia pine. Body is pale with a row of spots in the lateral zone*Neodiprion virginiana*
    Larvae are in FL on sand pine. Body is pale with a row of spots in the lateral zone...*Neodiprion knereri*
18. Larval host is a fir or spruce 19
    Larval host is a pine 20
19. Head capsule is primarily red. Body is green with white stripes. Found on white, red, black, and Norway spruces. In northeastern United States into Canada. Larvae present in summer to fall.. *Gilpinia hercyniae*
    Head capsule is black. Body is green with olive-green stripes in the dorsal and lateral zones. Found on balsam fir, black spruce, and white spruce. In northeastern United States, Lake States, and southern Canada. Larvae present in spring ....*Neodiprion abietis*

20. Body has a pair of stripes in the dorsal zone and 2 stripes in the lateral zones (1 on each side of the body). Stripes can be black or green 21
    Body is mottled with black, yellow, and white areas. Head capsule is black. Found on a variety of pines but most abundant on white pine. Widespread in the eastern half of the United States and into Canada ....*Diprion similis*
21. Stripe present in the lateral zone is dark green or black. Additional distinct pigmentation present in the sublateral zone 22
    Stripe present in the lateral zone is olive-green. Minimal or no additional pigmentation present in the sublateral zone 24
    Stripe present in the lateral zone is dark black and thickens at the end into a dark black blotch. Body is greenish. Head capsule is 2-toned (reddish or grayish on top, darker on the bottom). Larvae present in summer to fall. Found on slash pine in GA and FL and Caribbean pine in the Bahamas ....*Neodiprion merkeli merkeli*
    Found on Cuban pine in Cuba .... *Neodiprion merkeli maestrensis*
22. Head capsule is solid black..23
    Head capsule is black with a white area around the mouth. Distinct green coloring (sometimes a complete stripe) present in the sublateral zone. Body is greenish white. Found on shortleaf and loblolly pines. In southeastern United States. Larvae present in summer to fall...*Neodiprion fabricii*
23. Pigmentation in the sublateral zone is dark, circular, and numerous. Body is grayish green. Found on a variety of pines. In central eastern United States to Canada. Larvae present in spring...*Neodiprion sertifer*
    Pigmentation in the sublateral zone is not as numerous or distinct. Body is green to greenish white. Found on a variety of pines. In southeastern United States to Canada and west to WI. Larvae present in spring.................................... *Neodiprion nanulus nanulus*
24. Body is green 25
    Body is yellow or pale 26
25. Head capsule is red with a black blotch in the middle of the face. Found on red and Scots pines. In northeastern United States into Ontario ....*Gilpinia frutetorum*
    Head capsule is dark with a distinct masked face (white around the mouth extending to the eyes). Found on a variety of pines except white pine. In FL to Canada ....*Neodiprion compar*
26. Head capsule is red to reddish brown. Line above the prolegs is present. Usually found on jack pine but sometimes on red pine. In the Lake States to Ontario.. *Neodiprion nigroscutum*
    Head capsule is primarily dark 27
27. Larvae located south of the Lake States. Body is pale. Head capsule can be solid colored or have a light area around the mouth. Found on a variety of pines except white pine. Widespread from FL to Canada ....*Neodiprion abbotii*
    Larvae located in the Lake States or into Canada 28
28. Larva has no light area around the mouth. Colony includes 1–10 larvae. Found on jack pine ....*Neodiprion nigroscutum**
    Larva has a light area around the mouth. Colony includes more than 10 larvae. Found on red pine ....*Neodiprion abbotii**
    * *Neodiprion abbotii* and *N. nigroscutum* can be very difficult to distinguish as larvae where they co-occur: *N. nigroscutum* can occasionally be found on red pine and have a light area around the mouth; *N. abbotii* can also be found on jack pine and have a solid head. DNA sequencing is the best way to distinguish between the 2 species.

Damage

While many sawfly species exhibit preferences for particular tree species (e.g., *N. nanulus nanulus* defoliated a higher proportion of *P. rigida* than *P. echinata* in New Jersey, United States; McCormick and Andresen 1961), all pines are potential sawfly hosts. Pine sawfly outbreaks can cause high levels of defoliation (Fig. 8), and damage in both natural and managed trees and stands can lead to reduced growth and tree mortality. For instance, *N. sertifer* caused 75 and 87% defoliation in 2 different *P. sylvestris* stands in Ontario, Canada (Fogel and Slansky 1985). Tree mortality from an outbreak of *N. lecontei* on *Pinus resinosa* in Michigan, United States ranged from 1 to nearly 38% mortality with the heaviest defoliation and highest rates of mortality occurring on suppressed trees (Averill et al. 1982). Defoliation by *N. swainei* led to reduced radial growth in *P. banksiana* in Quebec, Canada (O'Neil 1963) and spring defoliation by *N. taedae linearis* led to volume increment losses ranging from 3 to 17% in *P. taeda* in Arkansas, United States (Zeide and Thompson 2005). Defoliation by *N. pratti pratti*—while typically occurring on needles—has been documented on reproductive structures of *P. echinata* in Virginia, United States (Bramlett and Hutchinson 1965). In addition to growth reductions, heavy pine sawfly defoliation can affect the appearance or aesthetics of landscape trees. As mentioned in 'overwintering strategy and voltinism' above, voltinism of each species plays an important role in amount of damage caused. Multivoltine, cocoon-overwintering species typically cause much greater damage to more trees, as second or third generations over the summer months will continue to defoliate trees until they overwinter in early Autumn. See information on species voltinism in Table 1.

Fig. 8. High levels of sawfly defoliation can completely strip host trees of needles. Here, a *Neodiprion lecontei* outbreak in northwestern Louisiana left pines completely defoliated, while the nonhost hardwoods remained green and unaffected. Photo by M. Daniels—LDAF.

Monitoring and Management Strategies

Pine sawflies are eruptive herbivores with spatiotemporal variation in both populations and subsequent damage levels (Price et al. 2005). Sawfly populations and damage are somewhat unpredictable and mediated by several extrinsic factors such as seasonal

temperature, humidity, infection, and health and age of trees attacks (Hanski 1987). Management strategies have changed very little in the last several decades. Management is seldom recommended except in cases where prolonged or extreme damage occurs, and even then, the decision to manage depends on a suite of factors (e.g., cost, local markets, stand age, level of damage, landowner or land manager tolerance for defoliation, etc.). In this section, we will discuss population monitoring using pheromone traps and different management options that are available to landowners and land managers in commercial, natural, and managed systems.

Population Monitoring Via Pheromone Traps

Pine sawflies have a complex pheromone communication system (owing primarily to the many different stereoisomers present in the pheromone chemicals) that has been investigated in North America for several decades (e.g., Jewett et al. 1976, Kocienski and Ansell 1977). To date, the efficacy of several synthetic pheromone blends for trapping males and monitoring sawfly populations has been tested (Anderbrant et al. 1992, 2021, Rieske-Kinney et al. 2001), some of which are nearly as effective in attracting male sawflies as female-baited traps (Wilkinson et al. 1982). For example, using the synthetic sawfly lure (2S, 3S, and 7S)-3,7-dimethyl-2-pentadecyl acetate, Rieske et al. (2001) was able to reliably capture *N. sertifer* and determine diurnal and seasonal flight activity in Kentucky. Pheromone traps can be an effective monitoring tool (Lyytikäinen-Saarenmaa et al. 2006), though there are caveats as certain environmental conditions are known to impact trap efficacy (Jönsson and Anderbrandt 1993) and pheromones have a limited range of effectiveness (i.e., they only work on local levels; e.g., Wedding et al. 1995). These traps could be incorporated into management as a component of an 'attract and kill' method as is done for some bark beetles (Dedek et al. 1988), which would assess pest population density and provide population control in 1 step.

Population Monitoring Via Aerial Imagery

Aerial imagery to monitor and map forest defoliation events has been used for decades, first as hand sketches on a paper map, and now via fully digital methods (like seen in Fig. 8). While beyond the scope of this paper, there is a wealth of information available in archived reports that documents sawfly outbreaks at the state level (e.g., McIntyre et al. 1961). Compiling these data would likely paint a clearer picture of the true magnitude and impact of pine sawfly defoliation in the US Newer technologies, such as digital aerial imagery have been used to detect pine sawfly defoliation (e.g., Hanssen and Solberg 2007, Kantola et al. 2010, Gilichinsky et al. 2013), though this technology is limited in that it cannot differentiate which herbivore caused the defoliation.

Cultural Control

In commercial, natural, or managed landscapes, healthy trees can tolerate defoliation levels typical of sawflies. Maintaining tree vigor is essential for any tree health issue, including defoliation. There are few silvicultural management options to protect trees in forested or natural areas from sawfly damage other than maintaining healthy forest stands by using appropriate management options. Pine sawflies tend to prefer trees under moisture stress (e.g., stands with lower levels of water availability were more susceptible to *Gremmeniella abietina* damage (Nevalainen et al. 2015) and *N. lecontei* damage (Averill et al. 1982)), so silvicultural tactics that reduce plant competition will help increase tree resilience. Prescribed fire—a common silvicultural tactic used to manage pine forests in the eastern United States—can be an effective management method for pine sawflies, as fire can kill eggs on needles as well as pupae that may be close to

the ground, greatly reducing pine sawfly damage (McCormick and Andresen 1961, Land and Rieske 2006).

There is evidence that forested environments with greater heterogeneity (i.e., increased amounts and diversity of vegetation) can lead to increased predation on sawfly cocoons. For instance, predation (primarily by small mammals, but also generalist arthropods) on *N. sertifer* in Sweden was greater in areas with a higher structural and floral diversity (Kollberg et al. 2014, Bellone et al. 2017). Similar patterns were observed in Germany on *D. pini*, where small mammal predation was greatest in more species-diverse forest stands compared to primarily pine forests (Herz and Heitland 2003).

For trees in managed landscapes, several cultural control methods are available. Sawfly larvae (or eggs, if the affected needles can be identified) can be picked off the tree by hand and disposed of, either by dropping them into a pail of soapy water or crushing them. Larvae can also be knocked off the foliage by shaking or beating the tree or with a high-pressure water sprayer or hose (Wilson et al. 1992, Jorgenson 2004) or by clipping and removing the affected branch.

Biological Control

Pine sawfly populations are typically regulated by vertebrate, invertebrate, and microbial natural enemies, several of which impact sawfly populations in North America. These naturally occurring indiscriminate predators can significantly impact sawfly populations on both local and landscape scales, though their specific impacts often vary spatially, temporally, and among sawfly life stages. Vertebrate predators typically attack larger larvae or cocoons. For instance, birds are known predators of larger sawfly larvae (Dahlsten 1966) and predation by small mammals can help regulate sawfly populations (MacAloney 1936), accounting for up to 70% of cocoon mortality in some cases (Dahlsten 1966, Hanski and Parviainen 1985, Herz and Heitland 2003). Several different arthropod predators feed on sawfly eggs, larvae, pupae, and adults, including a diverse suite of arachnids, hemipterans, hymenopterans, and dipterans (Benjamin et al. 1955, Dahlsten 1961, McGugan and Coppel 1962, Drooz et al. 1977, Wilson et al. 1992). Different microorganisms can also impact sawfly populations, including various fungal species (Klein and Coppel 1973, Ciesla 1976) and nucleopolyhedrovirus (Ciesla 1976, Mohamed et al. 1982).

While many natural enemies of sawflies are endemic to North America, targeted biocontrol via the introduction of natural pests can also be an effective management tactic. For instance, the case of *G. hercyniae* in Canada is an excellent example. Around 1930, *G. hercyniae* was accidentally introduced to eastern Quebec from Europe, and quickly caused widespread damage to spruce (*Picea*) in northeastern Canada and the United States (Balch 1936). In 1932, a biological control program was initiated to introduce European hymenopteran parasitoids as natural enemies. The program was very successful, caused significant sawfly population declines by the late 1930s, and the outbreak in North America had subsided by 1945. The success of this biocontrol was largely due to the accidental introduction of the nuclear polyhedrosis virus (GhNPV), likely from parasitoid material, which was eventually intentionally disseminated. This example has been reviewed extensively (McGugan and Coppel 1962, Neilson et al. 1971, Reeks and Cameron 1971, Pschorn-Walcher 1982, Hulme and Green 1984, Magasi and Syme 1984) and represents one of the best documented and most successful examples of insect biocontrol. While targeted biocontrol strategies are not required or recommended for native species or small outbreaks, this example (and others, e.g., Mohamed et al. 1983) shows they can be effective for the management of certain invasive species.

Chemical Control

Many active ingredients are effective for sawfly management, though this strategy is seldom used as the aforementioned management tactics and factors typically keep sawfly populations below damaging levels. Systemic and contact synthetic insecticides (e.g., pyrethroids, carbamates, organophosphates) have historically been used and are effective in killing sawfly larvae (e.g., Coppel and Norris 1960, Norris 1967, Nigam 1970), as are biological insecticides such as insect growth regulators (e.g., azadirachtin, Li et al. 2003). Horticultural soaps or oils can also be effective, as these are typically labeled for many 'soft-bodied' target organisms. Effective application is critical as larvae may be difficult to access as they feed deep within host foliage. As such, aerial application may be necessary in forested or natural areas (McLeod 1968, Wallner 1968) while tree injection techniques can be effective for single tree or urban areas (Helson et al. 2001H). Chemical treatments should target young larvae as they are most susceptible, and their feeding will not yet have caused the host significant damage.

Conclusion

Pine sawflies are a diverse group of herbivorous larvae with the potential to cause considerable damage to conifers. Here we extensively review this group of insects and provide information on identifying tree damage, sawfly species, and outbreak severity. We also review a variety of management strategies for controlling outbreaks of these species, with an overall conclusion that there are many cost-effective strategies for mitigating damage given proper identification of species and outbreak size. Finally, these species have had increasing relevance as emerging model organisms for evolutionary and genetic research (Knerer 1984, Linnen and Farrell 2010, Linnen et al. 2018) and represent an important group of insects for continued study of the relationship between insects and their hosts.

Supplementary Material

Supplementary material is available at *Journal of Integrated Pest Management* online.

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