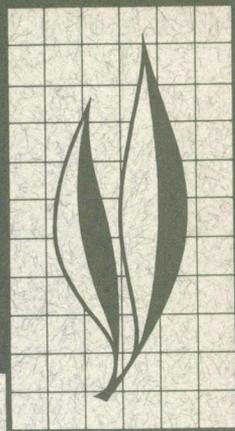


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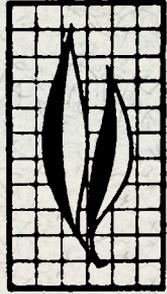


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Bionomics of *Neodiprion* Species on White Fir in Northeastern California

Katharine A. Sheehan and Donald L. Dahlsten

End of Volume



ABSTRACT

Two sawfly species that feed on white fir were studied in Modoc County, California: *Neodiprion* near *deleoni* Ross and *N. abietis* complex. *Neodiprion* near *deleoni* comprised 91 percent of the field *Neodiprion* populations and spun opaque brown cocoons in the litter or soil. *Neodiprion abietis* accounted for 9 percent of the field population and spun translucent cocoons that appear green and are attached to foliage. Full-grown larvae, pupae, and adults of the two strains were morphologically distinct, though eggs and young larvae were not. Differences in morphology, phenology, physiology, and behavior are described for the two species.

Mortality factors are identified, primarily for *N. near deleoni*. Parasitoids emerged from eggs and cocoons; many parasitoids that emerge from cocoons attack larvae. Larval predation was observed only rarely, except for predation by theridiid spiders. Sampled cocoons showed: 16 to 21 percent parasitized, 21 to 22 percent attacked by predators, 24 to 37 percent unknown mortality, and 25 to 34 percent sawfly emerged. Encapsulated ichneumonid eggs were found in 10 to 41 percent of emerging sawflies.

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Bionomics of *Neodiprion* Species on White Fir in Northeastern California¹

INTRODUCTION

SAWFLIES IN THE GENUS *Neodiprion* (Hymenoptera: Diprionidae) feed exclusively on the Pinaceae. Outbreaks occur occasionally, often causing growth loss and sometimes tree mortality (Coppel and Benjamin 1965; O'Neil 1962). Larvae of *Neodiprion abietis* (Harris) complex feed on spruce (*Picea* spp.), Douglas fir (*Pseudotsuga* spp.), and hemlock (*Tsuga* spp.) (Furniss and Carolin 1977; Ross 1955). It is a transcontinental species complex; the common name for this species is the balsam fir sawfly (ESA 1982), although western populations are often referred to as the white fir sawfly (Anonymous 1949-1979; Struble 1957).

Very little information about western populations of *N. abietis* complex is available beyond the initial biological investigations of Struble (1957). Certain aspects of polymorphism in the *N. abietis* were described by Knerer and Atwood (1972, 1973), who identified three strains: an early balsam fir strain, a late balsam fir plus spruce strain, and a white fir strain. These strains or morphs differed with respect to coloration, phenology, host specificity, larval feeding pattern, and other characteristics. In their laboratory, all crosses yielded viable offspring.

Variation has also been noted within the California populations of this complex. Struble (1957) recorded that most sawfly cocoons were found in the soil, but "infrequently" some were found attached to foliage. According to his rearing notes, those attached to the foliage were green, in contrast to the more common brown cocoons found in the soil.

Most previous reports regarding *Neodiprion* on true firs in California have classified these sawflies as *N. abietis* or *N. abietis* complex (Furniss and Carolin 1977; Knerer and Atwood 1973; Ross 1955; Struble 1957). However, recent determination of sawflies reared from white fir (*Abies concolor* [Gordon and Glendinning] Lindley) in California identified those emerging from brown cocoons as *N. near deleoni* and those from green cocoons as *N. abietis* complex. *Neodiprion near deleoni* was described by Ross (1955); the holotype and paratypes were found on grand fir (*Abies grandis* [Douglas ex D. Don] Lindley) in North Port, Washington.

Observations on the biology and behavior of *N. near deleoni* and *N. abietis* found on white fir in northeastern California will be documented in this paper. Attention will be drawn to differences between the two species. Voucher specimens for both species have been deposited in the U.S. National Collection of Insects at the Smithsonian Institution, Washington, D.C.

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METHODS

Field work was conducted in Modoc County, California from 1978 to 1980. The areas chosen have historically supported high sawfly populations (Anonymous 1949-1979). Field studies in 1978 were carried out near Yellowjacket Springs ("Yellowjacket:" T39N, R11E, S13, Mt. Diablo Meridian), while in 1979 and 1980 both Yellowjacket and an area on the neighboring ridge near Hilton Spike Camp ("Hilton Spike:" T39N, R11E, S7) were used. The elevation at both sites was approximately 1600 m (5500 ft). Overstory vegetation consisted primarily of white fir and ponderosa pine (*Pinus ponderosa* Lawson), with some incense cedar (*Libocedrus decurrens* Torrey) and western juniper (*Juniperus occidentalis* Hook). Understory vegetation was generally sparse, and included grasses, wildflowers, basin sagebrush (*Artemisia tridentata* Nuttall), and regeneration of the overstory species.

Naturally occurring sawfly colonies were marked and regularly checked in the field during 1978-1980 to study sawfly phenology, behavior, and certain mortality agents. A sawfly colony was defined for this study as a cluster of two or more *Neodiprion* eggs, separated by at least 10 cm from any other *Neodiprion* eggs. Details about colony selection and observations are provided by Sheehan (1982).

Colonies of eggs and larvae were collected and reared on fresh foliage bouquets at ambient temperatures for laboratory studies on phenology, feeding, behavior, and natural enemies; some larvae were reared individually, and others were reared together as colonies. Cocoons were collected from samples of litter and soil and were reared individually in gelatin capsules. Sheehan (1982) describes the collection methods, rearing conditions, and measurements taken during these laboratory studies.

RESULTS AND DISCUSSION

General Biology and Behavior

Eggs

It was not possible to distinguish between eggs of the two strains. The results in this section, therefore, combine observations of the more abundant *N. near deleoni* and the less common *N. abietis*.

Niches. In the fall, females used their ovipositors to saw pockets or egg niches in the sides of needles; one egg was laid per niche. The egg was completely enclosed within the pocket. By the following spring, the egg niches were usually discolored (yellow-green to yellow, or brown). The discoloration extended from the edge of the needle in to the central vascular bundle or, less commonly, across the entire width of the needle.

Color. Most eggs were turquoise in color. However, in 1979, 7.8 percent of 77 females reared from field-collected larvae or prepupae and picked at random for dissection yielded yellowish brown eggs; egg color was visible through the abdomens of adult females. In 1980, 3.8 percent of 80 females collected as large larvae and 4.3 percent of 94 females collected as eggs produced yellow-brown eggs. The latter females were from two colonies and were the only females reared from those colonies. All 13 females that bore yellow-brown eggs were *N. near deleoni* (though in 1979 very few *N. abietis* females were observed).

Struble (1957) reported only turquoise eggs, while Bird (1929) described the eggs of *N. abietis* in Manitoba as "whitish in color." Lyons (1977a) noted interfemale variation in egg color for *N. nanulus nanulus* Schedl and *N. swaini* Middleton, but its significance was not determined. Dahlsten (1966) found three distinct *N. fulviceps* complex egg colors accompanied by differences in numbers of eggs per female. In the present study, females bearing turquoise eggs did not carry significantly different numbers of eggs compared to females bearing yellow-brown eggs (40.85 ± 11.68 eggs/female for 13 females bearing yellow-brown eggs vs 40.39 ± 12.55 for 141 females bearing turquoise eggs).

Egg colonies. The mean number of eggs per colony and number of shoots occupied per colony are shown in table 1. For this study, all the foliage that developed from one bud during a single year was defined as a "shoot." The number of eggs per colony closely matches the number of eggs dissected per female (table 2). Struble (1957) reported higher numbers of eggs per colony ("often...more than 60 eggs"), as well as higher numbers of eggs dissected from adult females (mean = 67, range = 53-83). These results provide circumstantial evidence that females usually lay their entire egg complement in one colony.

Age of foliage. Most eggs were oviposited in needles formed during the current year; that is, eggs laid in 1980 were generally found on foliage produced in 1980. The numbers of eggs found by foliage age (in years) for 1978 to 1980 are shown in table 3. Causes of the steady decline in percentage of eggs laid on current foliage are not clear.

TABLE 1. MEAN AND STANDARD DEVIATION FOR NUMBERS OF EGGS PER COLONY AND SHOOTS OCCUPIED PER COLONY FOR *NEODIPRION* SPP. FOUND ON WHITE FIR IN MODOC COUNTY, CALIFORNIA (1978-1980)

<i>Neodiprion</i>	1978	1979	1980	Overall
Eggs/colony				
Mean number	30.4	33.8	42.0	40.7
Standard deviation	19.1	20.0	18.6	19.0
Shoots/colony				
Mean number	—*	4.4	5.6	5.4
Standard deviation	—*	2.5	2.7	2.7
Number of colonies observed	8	29	220	257

*Dash indicates no data available.

TABLE 2. SUMMARY OF MEAN NUMBER OF EGGS DISSECTED FROM *NEODIPRION* SPP. FEMALES COLLECTED IN MODOC COUNTY, CALIFORNIA (1979-1980)

<i>Neodiprion</i> females	Year(s)	Mean	Standard deviation	Number observations
Collected as larvae and/or pupae	(1979)	43.10	9.92	77
	(1980)	38.65	13.27	108
Collected as larvae	(1979 + 1980)	40.39	12.55	141
Collected as pupae	(1979 + 1980)	41.09	10.95	44
Collected as eggs, reared individually	(1980)	48.50	9.57	94
Females bearing yellow-brown eggs	(1979 + 1980)	40.85	11.68	13
<i>N. near deleoni</i> females collected as larvae	(1980)	38.4	16.5	22
<i>N. abietis</i> females collected as larvae	(1980)	38.9	10.45	58

TABLE 3. DISTRIBUTION OF *NEODIPRION* SPP. EGGS ON WHITE FIR FOLIAGE IN MODOC COUNTY, CALIFORNIA, ACCORDING TO FOLIAGE AGE

Foliage	1978		1979		1980		Total	
	No. eggs	%						
Current year	214	88.1	772	78.7	6391	69.1	7377	70.5
Previous year	23	9.5	197	20.1	2486	26.9	2706	25.9
Older	6	2.5	12	1.2	367	4.0	385	3.7
Number colonies observed	8		29		220		257	

Age of needles bearing eggs was nearly identical for this project and Struble's studies (1957). A preference for current growth has also been noted for *N. fulviceps* complex (Stark and Dahlsten 1965; Dahlsten 1966), *N. n. nanulus* (Kapler and Benjamin 1960), and *N. tsugae* Middleton (Furniss and Dowden 1941).

Number per needle. Most eggs were laid singly on needles: only 2 percent of the needles bore more than one egg. The mean number of eggs per needle found during 1978 to 1980 is shown in table 4. The maximum number of viable eggs found per needle was four (seen only once). Struble (1957) noted 5 percent of the needles with two or more eggs—probably a minor difference due to smaller sample size and/or between-year differences in needle physiology or anatomy.

TABLE 4. NUMBER OF *NEODIPRION* SPP. EGGS FOUND PER NEEDLE ON WHITE FIR FOLIAGE IN MODOC COUNTY, CALIFORNIA (1978-1980)

Needles	1978		1979		1980		Overall	
	No.	%	No.	%	No.	%	No.	%
With one egg	235	96.7	938	95.6	9095	98.4	10268	98.1
With two eggs	8	3.3	43	4.4	147	1.6	198	1.9
With three eggs	0	0	0	0	2	(.1)	2	(.1)

Development. From oviposition in the fall until the following spring, the eggs remained approximately the same size; there was no noticeable swelling of the needle, and egg niche discoloration or shavings left behind by the female were the only external clues that an egg was present. When the egg began to swell in the spring, the sides of the niche were first forced apart, so that the turquoise-green egg inside was visible. Soon after the egg was visible, swelling of the needle itself (when viewed laterally) was noticeable, and the egg color paled. Later, two distinct regions were visible in the egg: one-third was milky white, and the other two-thirds were pale turquoise. When 10 eggs from each of 20 colonies were examined, egg orientation was such that the milky white portion was towards the needle base for 198 out of 200 eggs. Finally, just before eclosion, the egg darkened, becoming dark grey (in previously turquoise areas) or light grey (in previously white areas). When the eggs were fully swollen, the slit openings averaged 2.0 mm (standard deviation = 0.1) in length, and the portion of the egg visible through the slit averaged 1.5 mm (standard deviation = 0.1) in "length" (based on 10 eggs from each of 7 colonies). This pattern of egg development is similar to that reported for other *Neodiprion* spp. (Dahlsten 1966).

Phenology. The timing of egg eclosion for field colonies (1979-1980) is shown in figure 1. While there were no significant differences between Yellowjacket and Hilton Spike for a given year, the differences between years (both sites combined) were highly significant ($p < .01$). In 1980, when eclosion occurred later, several weeks of cool temperatures occurred from May to early June (before any sawfly eggs had hatched). Differences in egg hatch date between the two species were not measured; however, six late-hatching colonies (still unhatched while nearby colonies on the same tree had mostly third instars) that were collected as eggs all yielded only *N. abietis*. Knerer and Atwood (1973) also found differences in eclosion phenology between sympatric eastern *N. abietis* strains, and Dahlsten (1966) reported over a month's difference in emergence dates for eggs from two *N. fulviceps* strains on the same branch tip. Within-colony synchronization of egg hatch was studied for 18 colonies. By interpolation, the number of days required for 50, 75, 90, and 100 percent of the viable eggs to hatch was calculated (table 5). Within a colony, egg eclosion usually occurred over a 2.5- to 3-day period.

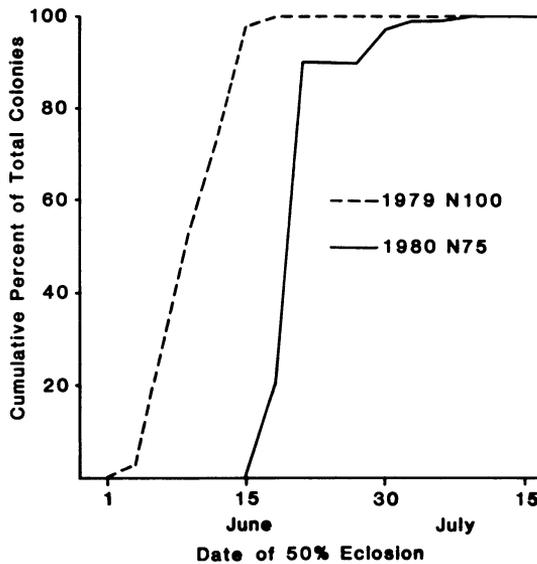


Fig. 1. Phenology of *Neodiprion* species egg hatch in Modoc County, California (1979-1980): cumulative percent of colonies with at least 50 percent egg hatch

TABLE 5. WITHIN-COLONY SYNCHRONY OF EGG HATCH* FOR *NEODIPRION* SPP. ON WHITE FIR IN MODOC COUNTY, CALIFORNIA (1980)

Percent eggs hatched	Mean number days after first egg hatched	Number colonies observed	Standard deviation
50	1.39	18	.758
75	1.92	18	.827
90	2.50	18	.970
100	3.29	17	.920

*Mean number of days to 50%, 75%, 90%, and 100% egg hatch (based on observation of 18 colonies in 1980).

The mean length of white fir buds at the time of egg hatch (ca. 50+% of larvae emerged) was 9.2 mm (standard deviation = 5.2, 141 observations) while the mean length of unswollen vegetative buds was 2.1 mm (standard deviation = 0.3, 119 observations). White fir buds that were 8 to 10 mm long usually still had a cap of bud scales, though the cap was separated from the basal bud scales and the new needles were visible. This study confirmed the observations of Struble (1957), who noted that eclosion occurred just prior to or during bud burst.

The flowering times of certain wildflowers relative to egg hatch was fairly consistent in 1979 and 1980. The estimated peak blooming period of dwarf waterleaf (*Hydrophyllum capitatum* Douglas) and mountain violet (*Viola purpurea* Kellogg) came before any sawfly eggs hatched. Dwarf waterleaf had a shorter flowering period, and few flowers remained at the end of the egg hatch period, while some mountain violet blossoms were present at least 2 weeks after most sawflies had hatched. Both Eaton's daisy (*Erigeron eatoni* Gray) and low phacelia (*Phacelia humilis* Torrey and Gray) reached their peak blooming time during the sawfly's egg hatch period; daisies were starting to fade by the end of egg hatching, while many low phacelia flowers still remained. Lupine (*Lupinus* sp.) and mule's ears (*Wyethia* sp.) began blooming during the egg hatch period, but the peak flowering period for both of these species came after most sawfly eggs had hatched.

The timing of both white fir bud swelling and the blooming of certain wildflowers (particularly Eaton's daisy and low phacelia) may be useful as a guide or indicator for eclosion dates.

Feeding larvae

Species composition of colonies. Sawfly colonies found in the field were generally pure with respect to species; they were usually either *N. abietis* or entirely *N. near deleoni*. Of the 159 colonies collected as eggs in 1980 and reared separately, 90.6 percent were *N. near deleoni*, and the remaining 9.4 percent were *N. abietis*. Three of those colonies had one individual of the other species present—these may have been accidentally introduced with the foliage used for rearing. Of the 95 colonies that were collected in 1979 and 1980 as third to fifth instars, 92 percent were nearly all *N. near deleoni* (less than two individuals of the opposite form), 6 percent were nearly all *N. abietis*, and 2 percent were mixed.

Number of instars. Table 6 shows number of instars according to both sex and species as determined from individually reared sawflies. Females of both species had six instars; among males, however, nearly all *N. abietis* males had five instars, while *N. near deleoni* males were divided between having five (41 percent) and six (59 percent) instars.

Head capsule width measurements of 685 field-collected larvae (both species combined) show five distinct peaks (fig. 2). Head capsule widths of 10 larvae positively identified as last instars were virtually identical to the widths of penultimate instar larvae. Frons widths from the same 685 larvae also showed five peaks, though not as clearly (fig. 3).

TABLE 6. NUMBERS OF INSTARS BY SEX AND SPECIES FOR *NEODIPRION* SPP. ON WHITE FIR IN MODOC COUNTY, CALIFORNIA (1980)

Sex	Instars	<i>N. near deleoni</i>		<i>N. abietis</i>	
	No.	No.	%	No.	%
Females	6	84	100	17	100
Males	5	20	41	23	96
	6	29	59	1	4

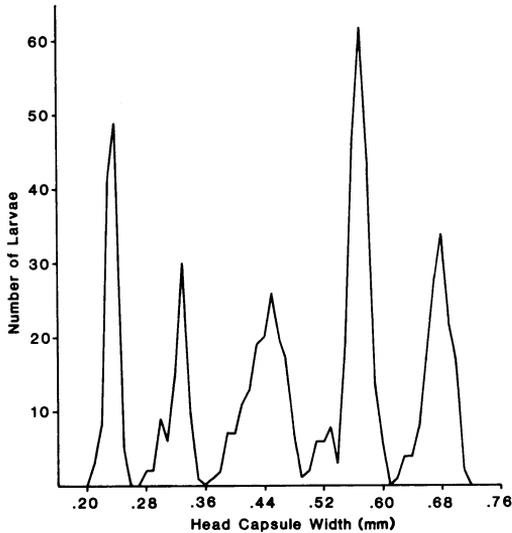


Fig. 2. Field-collected *Neodiprion* species larvae from Modoc County, California (1978, n = 685)

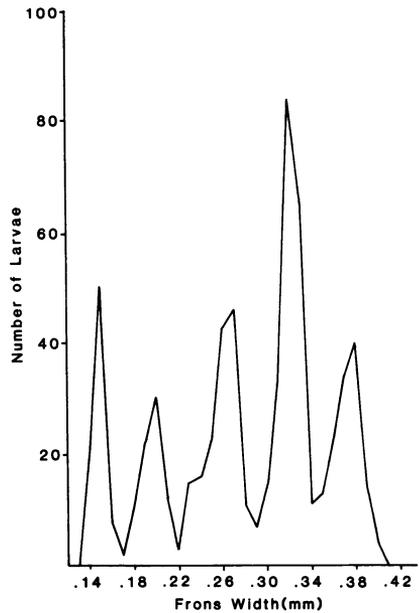


Fig. 3. Field-collected *Neodiprion* species larvae from Modoc County, California (1978, n = 685)

Struble (1957) reported that both sexes had six instars; however, he was dealing almost entirely with the *N. near deleoni*, and a low percentage of males with only five larval stadia may have gone unnoticed. Bird (1929) noted six instars for both male and female *N. abietis* in Manitoba.

Head capsule width measurements may mask the number of instars for certain males. For example, when periodic larval collections were made in this study, head capsule width measurements showed five distinct peaks (fig. 2) even though individual rearing demonstrated variations in numbers of larval stadia (table 6). Five peaks were found rather than six because the last, nonfeeding instar apparently has the same head capsule size as the penultimate instar, as has been shown for other *Neodiprion* species (Furniss and Dowden 1941; Dahlsten 1961, 1966).

Frons width measurements may be a useful substitute for head capsule measurements in some situations. Frons widths may be measured on exuviae, allowing observations on an individual larva at each instar, while accurate head capsule width measurements are difficult to make without injuring the larva. On the other hand, for these populations the overlap among instars was greater for frons widths than for head capsule widths. A cleaner separation in frons widths among instars has been reported for *N. fulviceps* complex by Dahlsten (1966).

Coloration. Larvae that had just hatched or moulted had dark gray-green bodies and pearly white head capsules. The head of seven larvae (observed beginning minutes after eclosion or moulting) darkened to a jet black color in 3 hours on the average (standard deviation = 1.0; range = 1 h. 10 min. to 4 h. 50 min.). Larvae were dark olive green colored just after moulting and gradually became more yellowish green as they fed.

First and second instars of *N. near deleoni* were solid colored. Third instars usually bore two broad dark olive stripes running lengthwise dorso-laterally, framing a lighter green dorsal stripe. Fourth instars sometimes had the same color pattern as thirds, but more

often had two additional dark lateral stripes. The stripes of fifth instars were usually more distinct, showing greater contrast than those of earlier instars.

Larvae of the *N. abietis* had the same coloration as did *N. near deleoni* for the first three instars, but during the fourth instar tended to retain the same stripe pattern as for third instars. Fifth instar *N. abietis* females had the color pattern of either third or fourth instar *N. near deleoni* sawflies. During the last feeding instar of *N. abietis*, bright green patches usually began to appear in the midabdominal region—in definite contrast to the olive green to yellow-green color of *N. near deleoni*. Except for late instars of *N. abietis*, the larval coloration and pattern of stripes were similar to that reported by Struble (1957) and Knerer and Atwood (1972, 1973).

Feeding habit. Feeding position in both laboratory and field were the same: when undisturbed, larvae were oriented parallel to the needle, with their heads facing the needle apex. When disturbed, larvae immediately stopped feeding or moving. If the disturbance persisted, the larvae usually threw their heads back, rearing up on their thoracic legs and exuding a drop of liquid from their mouths. Eisner et al. (1974) described the chemical composition, source, and defensive properties of the liquid droplets produced by *N. sertifer* (Geoffroy). Larvae may remain in the reared-back position for several seconds, or flick back and forth rapidly from the normal feeding position to the reared-back position. Struble (1957) reported that only younger larvae displayed this rearing-back reaction when disturbed, while during this study larvae of all ages exhibited this reaction.

If the disturbance continued, larvae usually then turned and crawled down the needle to the twig, where they remained clumped together. Older larvae (fourth and fifth instars) sometimes dropped from the needle instead of crawling to the needle base. During and after a heavy rain, when needles were covered with water droplets, larvae congregated on the undersides of needles or twigs.

The pattern of feeding of individually reared larvae usually changed as the larvae grew older, as shown in figure 4. Young larvae (first and second instars) generally fed only on the top side of a needle. By the third instar, larvae generally fed either on the topside only or from the needle edge to the midrib (consuming needle tissue on one side excluding the midrib). Fourth and fifth instars usually fed on one or both sides of the needle leaving the midrib. Sheehan (1982) provides additional information about variation in feeding habits among sexes and species.

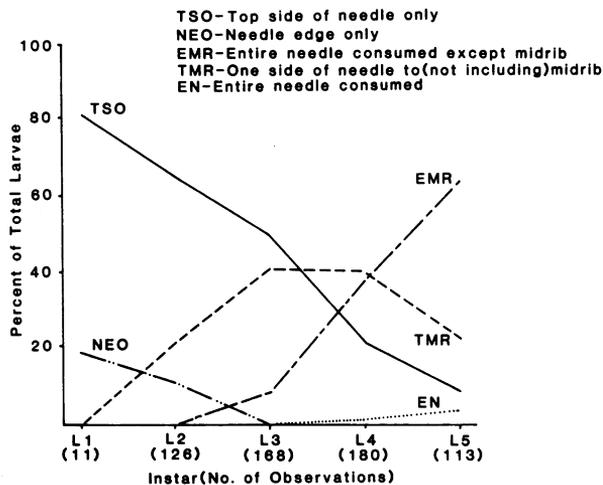


Fig. 4. Pattern of feeding on white fir needles for individually reared *Neodiprion* species larvae from Modoc County, California (1980)

Knerer and Atwood (1973) found that some *N. abietis* strains (those collected from balsam fir) generally avoided the needle midrib while other strains (those collected on spruce or white fir) consumed the entire needle; complete mortality was observed when larvae from strains that consumed entire needles fed on balsam fir. Hybrid sawflies avoided the midribs of balsam fir but consumed the entire needle for other host species. The authors hypothesized that the midrib-avoidance behavior may reduce larval consumption of allelochemicals that are concentrated in the midribs of balsam fir foliage. Knerer and Atwood (1972, 1973) reported that their white fir strain larvae usually fed on the entire needle of balsam fir whereas feeding observations reported here (for individually reared larvae) plus Struble's work (1957) found that most larvae of this strain do not consume white fir needle midribs. Larvae collected from white fir may recognize (and respond with a specific feeding behavior) their usual host but not another closely related species.

Larval colonies. Table 7 summarizes (by instar) the mean number of larvae per colony, mean number of shoots occupied per colony, and the age of foliage eaten for colonies observed in the field (1979 and 1980 combined). The number of larvae per needle decreased as the larvae grew older, and the number of shoots of foliage occupied by the larvae increased. There was no clear trend with respect to foliage age, though most fed on 1- or 2-year-old foliage. The number of sawflies per colony varied tremendously and showed a slight decrease for the oldest larvae.

TABLE 7. *NEODIPRION* SPP. LARVAL COLONY CHARACTERISTICS*
OBSERVED IN THE FIELD ON WHITE FIR IN MODOC COUNTY, CALIFORNIA

Instar†	Larvae	Shoots	Larvae	Foliage age‡
	per colony	per colony	per needle	
	No.	No.	No.	
First				
Mean	22.8	2.3	3.5	2.0
No. obs.	468	221	468	340
Stand. dev.	17.3	1.4	1.7	.8
Second				
Mean	26.3	2.6	2.9	2.0
No. obs.	344	281	344	273
Stand. dev.	17.6	1.6	1.2	.9
Third				
Mean	24.0	3.1	2.1	1.8
No. obs.	273	262	273	168
Stand. dev.	15.3	1.9	.8	.9
Fourth				
Mean	19.8	3.3	1.6	2.2
No. obs.	356	350	354	162
Stand. dev.	14.4	2.3	.5	1.3

*Based on 100 colonies collected in 1979 and 75 colonies collected in 1980.

†Instar = age of majority of larvae in a colony; fifth instars never formed the majority of a colony.

‡Current year = 0, previous year = 1, and soon.

Decreases in both colony size and number of larvae per needle as larvae grow older have been previously reported for *N. abietis* (Bird 1929; Struble 1957) and other *Neodiprion* species (Dahlsten 1966; Rauf and Benjamin 1980). Reasons for the relatively stable colony size found in this study are not clear, though the standard deviations observed were large. The purity of field-collected colonies with respect to species composition (only 2 percent were mixed) is an indirect indication that surviving larvae tend to stay in their original

colony. The slight decrease in mean colony size is probably primarily due to larval mortality rather than larval dispersal to other colonies. A preference for 1- or 2-year-old foliage (if available) has also been reported for many other *Neodiprion* species (Kapler and Benjamin 1960; Lyons 1964; Hard 1976).

Field-observation colonies were checked regularly until the colonies disbanded. About this time at least some of the mature larvae dispersed throughout the tree, feeding alone or in groups of two or three, before spinning cocoons.

Phenology. Table 8 summarizes by sex and species the phenology of sawfly larvae that were reared individually in 1980. For both species, females of a given instar occurred earlier than males of the same instar. Because the number of instars often varied, however, males and females of a given species ended up spinning cocoons at approximately the same time.

The duration of most feeding instars was usually 6 to 7 days. The last feeding instar (or prepupa), however, generally lasted 8 to 10 days (except for *N. near deleoni* males that passed through six instars, whose last feeding instar lasted 7.1 days on the average). Last instar *N. abietis* larvae usually spun cocoons sooner after moulting than did *N. near deleoni* larvae.

TABLE 8. LARVAL PHENOLOGY FOR *NEODIPRION* SPP. REARED INDIVIDUALLY IN MODOC COUNTY, CALIFORNIA, ON WHITE FIR: MEAN AND STANDARD DEVIATION(S) FOR DATE OF MOULTING AND NUMBER OF DAYS PER INSTAR (1980)

Sex	Second (L2) instar	Third (L3) instar	Fourth (L4) instar	Fifth (L5) instar	Sixth (L6) instar	Total no. days	
Species	Mean(s)	Means(s)	Mean(s)	Mean(s)	Mean(s)	L2-6	L3-6
<i>Female, near deleoni</i>							
1st day*	4.7 (2.4)	12.3 (3.3)	19.5 (3.2)	26.8 (2.6)	35.0 (2.7)		
No. days	6.5 (1.9)	7.3 (1.6)	7.2 (1.5)	8.3 (1.5)	2.9 (1.6)	32.2	25.6
No. obs.	54	82	84	84	84		
<i>Female, abietis</i>							
1st day	11.0 (0)	16.9 (4.4)	24.0 (3.4)	30.7 (3.3)	40.0 (3.2)		
No. days	7.0 (0)	6.9 (1.5)	6.7 (1.0)	9.0 (1.8)	1.4 (0.5)	30.4	24.5
No. obs.	4	16	17	17	17		
<i>Male, near deleoni (total)</i>							
1st day	8.0 (4.6)	15.9 (4.1)	22.9 (3.5)	30.2 (3.8)	(see below)		
No. days	7.9 (1.3)	7.1 (1.8)	7.5 (2.4)	5.1 (3.0)			
No. obs.	20	48	49	49			
<i>Male, near deleoni (larvae with six instars)</i>							
1st day	8.6 (4.8)	16.1 (3.8)	22.7 (3.1)	28.5 (3.2)	35.7 (3.0)		
No. days	7.9 (0.9)	6.6 (1.5)	6.2 (1.5)	7.1 (2.1)	2.4 (1.3)	30.1	22.2
No. obs.	7	29	29	29	29		
<i>Male, near deleoni (larvae with five instars)</i>							
1st day	7.7 (4.6)	15.6 (4.6)	22.8 (5.1)	32.6 (3.4)	—†		
No. days	7.9 (1.4)	7.9 (2.0)	9.3 (2.1)	2.3 (0.8)	—†	26.9	20.0
No. obs.	13	19	20	20			
<i>Male, abietis (total)</i>							
1st day	—†	23.9 (2.5)	28.7 (6.3)	40.0 (3.6)	—†		
No. days	—†	5.9 (1.4)	10.0 (2.3)	1.5 (1.4)	—†	—†	17.6
No. obs.		19	24	24			

*1st day = day of moult for a given instar (May 20, 1980 = day 1).

†No data available.

Prepupae and pupae

Coloration. The final instar *N. near deleoni* had a tan or light brown head capsule and a striped, dull, pinkish brown body. The stripes consisted of a pair of thin dark stripes ventrally and one wider dark stripe on each side. The exarate pupa was the same tan color as the final instar.

Last instar *N. abietis* had tan head capsules and bright, lime green bodies, with the same pattern of stripes as *N. near deleoni*. Pupae of *N. abietis* were also bright green. The final instars of both species fed very little, if at all, when reared individually.

Cocoon description. Mature larvae of the *N. near deleoni* dropped or crawled to the ground to spin cocoons. These thin, papery but tough cocoons were usually bright, golden brown at first; older cocoons were often duller and darker. However, some cocoons from the previous years' generations (sifted from the soil while the current generation was still feeding) were indistinguishable in color from typical newly spun cocoons. Also, some newly formed cocoons darkened after a few days in the laboratory. Cocoon color was, therefore, not used in this study as an indicator of cocoon age.

Prepupae of *N. abietis* usually spun cocoons attached to individual needles. These cocoons were translucent yellow; the bright green prepupae or pupae inside showed through the cocoons, giving them a bright green color also. Empty cocoons made by this species were sometimes found on the ground (usually with the impression where the cocoon had been attached to the needle still visible); these were probably dislodged from the foliage by wind, rain, snow, or other physical disturbance.

Mean cocoon lengths and widths plus analyses of variance are shown in table 9. Differences between sexes were highly significant and accounted for large proportions of the total

TABLE 9. MEAN COCOON WIDTHS, LENGTHS, AND ANALYSIS OF VARIANCE TABLES FOR *NEODIPRION* SPP. COCOONS COLLECTED IN MODOC COUNTY, CALIFORNIA (1978, 1980)

N. species	Sex	No. of cocoons	Mean length(s)		Mean width(s)	
Near <i>deleoni</i>	female	86	8.12	(.642)	3.56	(.268)
	<i>abietis</i> female	86	7.44	(.566)	3.09	(.225)
Near <i>deleoni</i>	male	86	6.91	(.356)	2.91	(.178)
	<i>abietis</i> male	86	6.50	(.483)	2.59	(.172)

Cocoon lengths						
Source	df	SS	MS	F	prob.	ω^2
Sex	1	96.2	96.2	240.5	.001	.35
Species	1	16.9	16.9	42.3	.001	.07
Sex × species	1	9.2	9.2	23.0	.001	.04
Error	340	134.3	.4			
Total	343	256.6				.46

Cocoon widths						
Source	df	SS	MS	F	prob.	ω^2
Sex	1	28.2	28.2	587.5	.001	.47
Species	1	13.3	13.3	277.1	.001	.23
Sex × species	1	.7	.7	14.6	.001	.01
Error	340	16.4	.05			
Total	343	58.6				.71

variance. Much of the ω^2 values were also attributable to sex; when ω^2 is large, the differences between group means are large relative to the variability of observations within each group (Lindman 1974). Differences in cocoon lengths between species, plus interactions for sex and species (both lengths and widths), all showed significant differences, but accounted for much smaller proportions of the variance.

The cocoon dimensions reported in this study are similar to those reported by Struble (1957). Sexual dimorphism in cocoon dimensions (females' cocoons being longer and wider) has also been found by Hard (1976) for *N. tsugae* and Dahlsten (1961) for *N.* species.

Phenology. The prepupae remain inside their cocoons during the summer. Development within cocoons was visible for some individuals in the laboratory when the larvae spun cocoons attached to a glass container. In 1980, most of these observable larvae pupated in the first 3 weeks of September. Adults remained inside their cocoons for 11 to 46 days (mean = 20.5 days; standard deviation = 7.4, 39 sawflies [mostly *N. abietis*] observed). Coppel and Benjamin (1965) noted that adults of some sawfly species remained in their cocoons for a day or more. In the current study, handling the cocoon often resulted in rapid emergence of the adults—a possible escape-from-predators response.

Adults escaped from their cocoons by cutting off one end with their mandibles. Usually two smooth semicircular motions were employed, though sometimes the entire cap was cut off with one continuous motion.

Adults

Coloration and morphology. Adults were sexually dimorphic. Males had feathery, biramate antennae and slim, tan or dark brown abdomens, while females had slightly serrate antennae and somewhat swollen abdomens colored turquoise or brownish by the eggs inside.

Females of *N.* near *deleoni* had 19.2 antennal segments on the average (29 females observed; standard deviation = 0.49), 10 annuli on the lancet, and straight scopal processes that were not markedly expanded. *Neodiprion abietis* females, however, had a mean of 18.0 antennal segments (29 females observed, standard deviation = 0.33), 9 annuli on the lancet, and oblique scopal processes that were expanded. The key, developed by Ross (1955), includes illustrations of scopal process expansion and angle, which are the characteristics used to distinguish between *N. abietis* complex and *N. deleoni*.

Neodiprion near *deleoni* males had bicolored mesepisternites (tan dorsally and dark brown ventrally) and tan abdominal sternites. *Neodiprion abietis* males, however, had uniformly dark brown mesepisternites and abdominal sternites.

Emergence. Adult emergence times for sawflies collected as mature larvae and reared in the laboratory are shown for 1979 and 1980 in figure 5; emergence in 1978 was intermediate in terms of both length of emergence period and extent of differences between sexes in emergence times. In both 1978 and 1979, most emergence occurred from mid-September to early November; males emerged in greater number at first, but eventually more females emerged (sex ratios [females:males] were 1:0.74 [1978] and 1:0.50 [1979]). In 1980, however, most emergence occurred over a much shorter period (mid-September to early October), and more males than females emerged (sex ratio was 1:1.28). Struble (1957) noted that the sex ratio was about even.

Roughly synchronous emergence of males and females was also observed by Struble (1957); further, Lyons and Griffiths (1962) noted that an inverse relationship for *N. sertifer* between date of cocoon spinning and duration of the prepupal period insured

synchronization of male and female emergence.

Figure 6 shows differences between species for the 1980 observations. Considerable overlap in adult emergence under laboratory conditions was found between the two *Neodiprion* species in 1980, indicating that crossbreeding in the field may be phenologically feasible. In contrast, the two balsam fir strains studied by Knerer and Atwood (1973) showed no overlap of adult emergence periods.

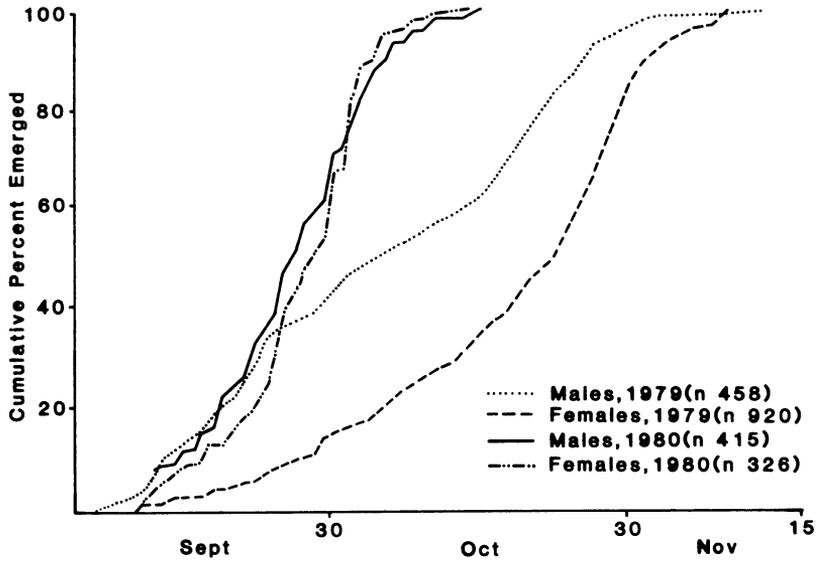


Fig. 5. Phenology of adult emergence for *Neodiprion* collected as mature larvae on white fir in Modoc County, California, (1979, 1980), by sex (both species combined)

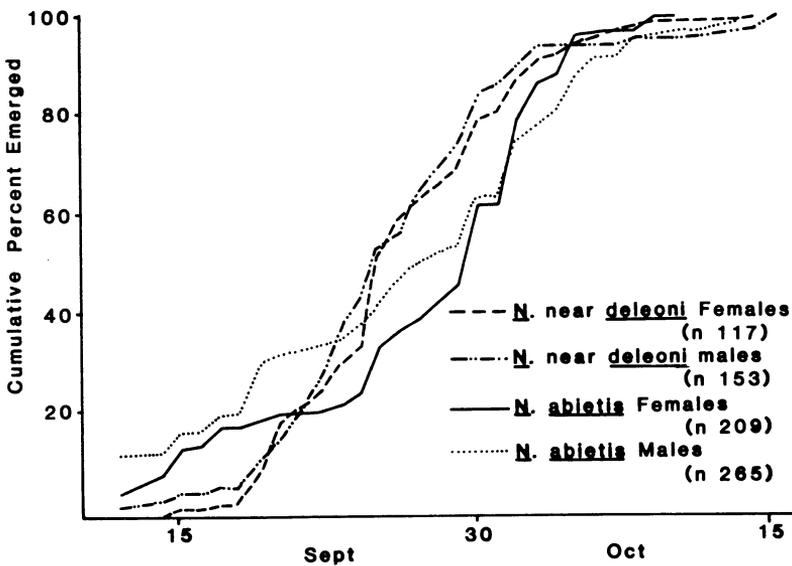


Fig. 6. Phenology of adult emergence for *Neodiprion* collected as mature larvae on white fir in Modoc County, California, by sex and species (1980)

Crossbreeding in the laboratory. In a limited number of laboratory crossbreeding experiments, *N. abietis* females mated with both *N. near deleoni* males and *N. abietis* males. *Neodiprion near deleoni* females, however, would mate with males of the same species but not with *N. abietis* males. Viability of the progeny of these crosses was not tested, nor was there any attempt to gather evidence of crossbreeding in the field. However, Knerer and Atwood (1972), working with four *N. abietis* strains (including one from white fir in Modoc County), noted that all strains readily crossbred, yielding viable offspring.

Most pairs mated only once (23 pairs observed; exceptions: one pair mated twice, and one pair mated four times). The time spent mating averaged 12.8 minutes, and ranged from 4 to 39 minutes. Coppel and Benjamin (1965) noted that sawflies may copulate for 30 minutes or more, longer than the average but within the range of times observed during this study.

The mean number of eggs per female is summarized in table 2. Significant differences were found between years for females collected as larvae or prepupae/pupae ($p < .02$) and between females collected as eggs in 1980 and reared individually and those collected as larvae in both 1979 and 1980 ($p < .001$ in both cases). The slightly higher fecundity of females reared individually may have been due to the ideal rearing conditions (i.e., ample fresh food, no disturbances by natural enemies, and so on). No significant differences were found between females collected as larvae and those collected as prepupae/pupae (both years combined; $p > .5$).

Mortality Factors

Egg mortality

One parasitoid, *Chrysonotomyia* prob. n. sp. (Hymenoptera: Eulophidae), was reared from sawfly eggs. Table 10 shows the parasitization rates of colonies collected as eggs in late spring, 1979 and 1980. Parasitized eggs swelled slightly and darkened noticeably by the time unparasitized eggs had hatched. When foliage tips bearing parasitized eggs were made into bouquets (placed in vials kept filled with water and plugged with cotton) and reared in the laboratory, the parasitoids emerged in August or September of the same year; by that time the foliage had completely dried. No parasitoids successfully overwintered in the laboratory, possibly due to the dried-out foliage. Adult parasitoids emerged by chewing round exit holes, usually through the needle top or bottom. Each spring, a small number of current-generation sawfly eggs were found with one or more similar round holes.

This parasitoid is probably the same eulophid encountered "rarely" by Struble (1957), and listed as *Derestenus* sp. *Derestenus* is most likely a misspelling of *Derostenus*, a genus whose North American species were moved to the subgenus *Achrysocharella* in the genus *Chrysonotomyia* by Yoshimoto (1978). The species reared in this study was identified as between *C. borealis* Yoshimoto and *C. ovulorum* (Ratzeburg), both in the subgenus *Achrysocharella*. Members of this subgenus are egg or larval parasitoids of Lepidoptera, Diptera, and Tenthredinoidea (Yoshimoto 1978). Fairly high rates of egg parasitism have been noted for a *Neodiprion* species that overwinters as prepupae (*N. lecontei* [Fitch], Benjamin 1955), while much lower egg parasitism rates were recorded for sawflies that overwinter as eggs (*N. sertifer* [Pschorn-Walter and Eichhorn 1973], *N. fulviceps* [Dahlsten 1966] and both *Neodiprion* species in this study).

This *Chrysonotomyia* species had at least one generation per year. Under laboratory conditions, the parasitoid adults emerged in midsummer. They may have emerged earlier than the sawfly adults due to the desiccation of their foliage bouquets (in whose needles they were developing). Alternatively, a second generation of the parasitoids may develop during the summer on an alternate host or autoparasitically, as was found by Pschorn-Walcher and Eichhorn (1973) for *Achrysocharella ruforum* Krause and *A. ovulorum* on *N. sertifer*. Alternate host genera listed by those authors and also found in California include *Acantholyda* and *Cephalcia*, both Hymenoptera: Pamphiliidae (Furniss and Carolin 1977).

The small round holes found in sawfly egg niches early in spring (long before any noticeable swelling or development of eggs) showed signs of weathering, and were probably made during the previous fall or winter. These may be punctures made by predaceous hemipterans, or exit holes made by a fall generation of egg parasitoids.

A summary of egg mortality observed in the field is shown in table 10 for 1979 and 1980. No predators were observed feeding on eggs.

Possible sources of unknown mortality include host feeding by *Chrysonotomyia* adults, nonviable eggs, and overwintering mortality due to inclement temperatures. Both winter mortality and host feeding by two *Achrysocharella* species on *N. sertifer* eggs were noted by Pschorn-Walcher and Eichhorn (1973). The higher overall egg mortality in 1980 might have resulted in part from the warm spell in early spring—during which egg development began and some swelling was noticeable—followed by several weeks of cold, snowy weather. Egg mortality due to late spring frosts had been reported for *Neodiprion* species by Benjamin (1955) and Dahlsten (1967). Lyons (1962) and Pschorn-Walcher and Eichhorn (1973) also noted that egg parasitoids may cause indirect mortality because smaller larval colonies generally suffered greater mortality.

TABLE 10. SUMMARY OF *NEODIPRION* SPP. EGG MORTALITY ON WHITE FIR IN MODOC COUNTY, CALIFORNIA (1979-1980) FOR MARKED COLONIES OBSERVED IN THE FIELD AND FOR COLONIES COLLECTED IN EARLY SPRING AND REARED IN THE LABORATORY

Observations		1979	1980
Field			
Percent total egg mortality per colony	Mean	21.0	32.1
	Standard dev.	21.5	30.3
	No. observations	100	75
Laboratory			
Percent egg mortality per colony due to unknown causes	Mean	—*	17.4
	Standard dev.	—*	16.0
	No. observations	—*	205
Percent egg mortality per colony due to parasites	Mean	14.5	7.7
	Standard dev.	21.5	17.5
	No. observations	28	215
Percent total egg mortality per colony	Mean	—*	25.1
	Standard dev.	—*	17.2
	No. observations	—*	215

*No data available.

Larval mortality

A small percentage of first instar larvae were found trapped inside their egg niches. In these cases, the larva's head was visible, sticking out of the slit, but the rest of the body remained inside the egg niche. Of 87 colonies examined in 1980, seven (8 percent) had one or more trapped larvae. When present, the average number of trapped larvae per colony was 1.4 (standard deviation = 0.79; range = 1 to 3). Of the 3037 eggs checked, 0.3 percent contained trapped larvae.

No parasitoids emerged from sawfly larvae. Parasitoids that attacked feeding larvae and emerged from their hosts' cocoons are described in the section on prepupal and pupal mortality.

Two *Theridion* species (Araneae: Theridiidae) were the most commonly observed predators of sawfly larvae. Both *Theridion lawrencei* (Gertsch and Archer) and *T. neomexicanum* (Banks) usually spun a very loose, irregular tangle of webbing beneath a branch tip bearing a sawfly colony, and were most commonly observed hanging upside down at the base of the current year's shoot. Often one to three apparently freshly killed or paralyzed larvae were individually wrapped and stored in webbing beneath a twig. Of 37 spiders collected in 1978 while feeding on larvae or while hanging near larvae wrapped in webs, 33 (89 percent) were *T. lawrencei* (mostly females) and 4 (11 percent) were *T. neomexicanum* (three females and one male). Table 11 summarizes observations of *Theridion* spp. predation on sawfly larvae from the regularly checked field observation colonies (1978-1980).

Other predators were occasionally observed preying on sawfly larvae. On several occasions, carpenter ants (*Camponotus* sp.) were observed passing close to sawfly larvae (within 1 cm), yet completely ignoring them. Once, however, a carpenter ant was seen attacking a colony of nearly full-grown larvae. When the ant grasped a larva with its mandibles and attempted to carry it away, the larva would thrash violently, often eventually wrenching free of the ant's grasp but dropping from the branch. Eight larvae were thus displaced before the ninth was carried away by the ant. Ants have been observed removing large proportions of larval colonies of other *Neodiprion* species, as has been reviewed by Coppel and Benjamin (1965).

On separate occasions, adult hemipterans (one Nabidae, one Berytidae) and a salticid spider, were observed feeding on a sawfly larva. One *Phyllobaenus* sp. larva (Coleoptera: Cleridae) was taken from a sawfly colony containing six third and fourth instar larval carcasses and successfully reared on a diet of sawfly larvae. A few sawfly larvae were found hanging from a needle by two or three silk strands, apparently freshly killed or paralyzed.

TABLE 11. *NEODIPRION* SPP. LARVAL MORTALITY CAUSED BY *THERIDION* SPIDERS ON WHITE FIR IN MODOC COUNTY, CALIFORNIA (1978-1980)

<i>Neodiprion</i>	1978	1979	1980
No. colonies observed	15	90	58
No. colonies with spider present at least once during the season	9 (60.0%)	17 (18.9%)	11 (19.0%)
Mean percent of larvae in colony killed by spiders			
All colonies	5.4%	1.2%	1 %
Colonies with spiders (standard deviation, range)	8.1% (7.4, 0-25%)	6.2% (4.7, 0-15%)	5.3% (5.3, 0-19%)

The low mortality rates due to theridiid spiders are minimum rates, and may greatly underestimate the actual mortality caused by these predators. For example, larval carcasses may have been torn from the loose webbing by wind, rain, snow, or scavengers before they could be tallied by the observer.

During a study of arthropods occurring on white fir, Dahlsten et al. (1977) noted that spiders were the most abundant group of predaceous arthropods found, with web spinners comprising 65 percent of the spiders collected. Free-living spiders are often considered more likely predators of crawling larvae than are web spinners (Dahlsten et al. 1977; Loughton et al. 1963), yet this study indicates that the importance of *Theridion*, a web-spinning genus, merits additional study.

Prepupal and pupal mortality

Parasitoids. The following parasitoids emerged from cocoons of sawflies that had been collected as feeding larvae or in cocoons and reared in the laboratory:

Hymenoptera

Ichneumonidae

Lamachus sp.

Exenterus tsugae Cushman

Unidentified species

Pteromalidae

Trineptis klugii (Ratzeburg)

Ceraphronidae

Dendrocerus sp.

Diptera

Tachinidae

Tsugae nox Hall

Diplostichus sp., poss. *sellersi* Hall

Spathimeigenia sp., poss. n. sp.

All except the pteromalid were solitary parasitoids. The ichneumonids pupated inside the host cocoon, while the tachinids often emerged from the sawfly cocoon to pupate. Ichneumonids generally emerged during the following spring, while tachinids were equally likely to emerge in the fall as in the next spring. Table 12 shows the modest parasitization rates encountered.

TABLE 12. SUMMARY OF PARASITIZATION OF *NEODIPRION* SPP. LARVAE AND PUPAE ON WHITE FIR IN MODOC COUNTY, CALIFORNIA (1978-1980)

Family	Sawfly stage attacked	1978	1979	1980
		(n = 410)*	(n = 1813)	(n = 756)
		%	%	%
Tachinidae	Larva	7.0	1.4	0.5
Ichneumonidae	Larva	2.9	1.2	0.9
Pteromalidae	Prepupa/pupa	†	4.2	0

*n = number of cocoons examined.

†Not sampled in 1978.

Lamachus sp. was the most common ichneumonid, and the other species were found only rarely. *Tsugae nox* was the most numerous tachinid, followed by *Diplostichus* sp. and then *Spathimeigenia* sp. (comprising 70, 20, and 10 percent of the total number of tachinids, respectively). Sheehan (1982) reviewed host records noted in the literature for these parasitoids.

Rather low rates of parasitism by ichneumonids were observed in this study (0.9-2.9 percent). Parasitism rates by ichneumonids on other *Neodiprion* species recorded by other authors include 36 to 38 percent on *N. tsugae* (Furniss and Dowden 1941), 3 to 52 percent on *N. excitans* (Drooz et al. 1977), 0 to 42 percent on *N. lecontei* (Drooz et al. 1977). Lyons (1977b) reviewed parasitism rates of *Neodiprion* spp. by *Exenterus* spp., noting rates of 1 to 65 percent. *Lamachus*, the most common ichneumonid in this study, parasitized 2 to 6 percent of *N. tsugae* (Torgersen 1968). The low parasitism rates observed in this study may have been due in part to poor rearing conditions, and in part to the ability of sawfly larvae to encapsulate the parasitoid eggs.

Tritneptis klugii was reared only from sawflies collected as prepupae or pupae in cocoons. This gregarious parasitoid averaged 25.5 adults emerging per sawfly cocoon ($n = 16$; $s = 11.6$). Emergence occurred in the fall of the year when cocoons were spun.

A possible hyperparasitoid, the ceraphronid *Dendrocerus* sp., emerged from the cocoon of one sawfly that had been collected as a larva.

Rates of parasitism found for field-collected cocoons (all parasitoids combined, table 13) ranged from 13 to 24 percent. Total parasitization rates recorded for other *Neodiprion* species (reared from collected cocoons) include 39 percent for *N. tsugae* (Furniss and Dowden 1941), and 9 percent and 37.4 percent for *N. fulviceps* complex (Dahlsten 1961 and 1967, respectively). Parasitoids may further reduce sawfly reproductive capacity indirectly; Lyons (1970) noted that parasitoids may disrupt larval feeding, decrease fecundity (due to encapsulated eggs), and cause mortality when neither host nor parasitoid survives.

TABLE 13. FATE OF *N. NEAR DELEONI* COCOONS COLLECTED FROM SOIL AND LITTER SAMPLES BENEATH WHITE FIRS IN MODOC COUNTY, CALIFORNIA (1979)

Year	Sawfly sex	Cocoons examined	Sawfly emerged	Parasite emerged	Predator attacked	Miscellaneous or unknown
		No.	%	%	%	%
1979	Female	4696	28.1	13.3	22.7	35.8
	Male	4399	22.5	19.2	20.1	38.3
1980	Female	1307	36.7	18.4	20.7	24.1
	Male	1216	31.5	23.5	21.3	23.7
	Mean*		27.3	17.2	21.3	34.2

*Weighted by number of cocoons examined for each year-sex combination.

Encapsulation of ichneumonid eggs. Some sawfly larvae were able to encapsulate the eggs of one or more ichneumonid species and complete their development normally. From one to three encapsulated eggs were found per adult (fig. 7). These eggs were usually floating free in the abdomen. When reared in the laboratory from eggs, no adults of either *N. near deleoni* (77 females and 46 males) or *N. abietis* (20 females and 25 males) bore encapsulated eggs. Sometimes first instar ichneumonids were visible inside the encapsulated egg; rarely, a parasitoid larva was found encapsulated outside of its egg chorion.

Table 14 summarizes the occurrence of encapsulated eggs according to sex and species of the sawfly. Generally, encapsulated eggs were found more frequently in females and in *N. abietis*; however, when differences between sexes (for a given species) or between species (for a given sex) were tested via a chi-square test, only differences between species for females were significant ($p < .05$).



Fig. 7. Posterior view of the abdomen of a *N. near deleoni* female with genitalia removed; an encapsulated ichneumonid egg and many sawfly eggs are visible

TABLE 14. NUMBER OF *NEODIPRION* SPP. ADULTS COLLECTED FROM WHITE FIR IN MODOC COUNTY, CALIFORNIA, THAT CARRIED ENCAPSULATED ICHNEUMONID EGGS

Sex	<i>N. near deleoni</i>			<i>N. abietis</i>		
	No. adults with encapsulated eggs	Percent	Total no. adults checked	No. adults with encapsulated eggs	Percent	Total no. adults checked
Female	9	17	52	33	41	81
Males	5	10	50	10	22	45
Total	14	14	102	43	34	126

A subsample of females collected as larva in 1980 showed that females with encapsulated ichneumonid eggs carried fewer eggs (mean = 33.3 eggs per female; standard deviation = 11.96, of 28 females observed) than females without parasitoid eggs (mean = 41.3; standard deviation = 14.49, of 46 females observed; $p < .01$). The same pattern held for both species.

In addition to the encapsulated eggs, small irregularly-shaped, solid cysts were found in sawfly adults' abdomens (25 percent of 118 females). These cysts varied greatly in size and in number (from 1 to 10 per female). Cysts were most commonly found in females that also carried encapsulated eggs (72 percent of 29 females bearing cysts also bore encapsulated eggs).

Encapsulation of parasitoid eggs has been recorded for sawflies and other insects. *Neodiprion swainei* encapsulated eggs or planidia of *Olesicampe lophyri* (Riley), *Lamachus* sp. (both Hymenoptera: Ichneumonidae), *Perilampus hyalinus* Say (Hymenoptera: Perilampidae), and *Spathimeigenia spinigera* Townsend (Diptera: Tachinidae) (Tripp 1960, 1962a, 1962b, 1965). Roughly 65 percent of the hosts attacked by ichneumonids and 35 percent of those attacked by *S. spinigera* survived to the adult stage. Tripp (1962a) hypothesized that *N. swainei* was able to encapsulate the eggs only if it was attacked as an early instar. Decreased parasitization rates resulted when one of the introduced strains of the larch sawfly (*Pristiphora erichsonii* [Hartwig]) developed the ability to encapsulate the eggs of *Mesoleius tenthredinis* Morley, an introduced ichneumonid (Muldrew 1953); further, a Bavarian strain of *M. tenthredinis* is resistant to encapsulation by *P. erichsonii* (Pschorn-Walcher 1977). Salt and van den Bosch (1967) described two strains of *Bathyplectes curculionis* (Thomson) (Hymenoptera: Ichneumonidae) that attacked two geographically separated sibling species of alfalfa-feeding weevils. In contrast to Tripp's findings with sawfly larvae, van den Bosch (1964) found that first instar larvae lacked the capacity to encapsulate eggs, while older larvae had the greatest capacity. Finally, Puttler and van den Bosch (1959) noted during a laboratory study that 92 percent of *Spodoptera* (= *Laphygma*) *exigua* (Hubner) (Lepidoptera: Noctuidae) larvae containing single eggs of the ichneumonid *Hyposoter exiguae* (Viereck) encapsulated the parasitoid's egg. However, only 3.3 percent of superparasitized larvae were able to encapsulate all of the parasitoid eggs (usually only one parasitoid egg was encapsulated per larva). In the current study, one-third of the sawflies that bore encapsulated eggs carried two or three such eggs.

Tripp (1962a) noted a 20 percent reduction in the number of eggs per female for *N. swainei* bearing encapsulated eggs, as well as a 1-month delay in adult emergence. A similar egg reduction (19 percent) was found in this study, though limited observations do not suggest a parallel delay in emergence.

The dark, solid, irregular cysts that were found in high proportions in adults with encapsulated eggs have previously been reported in *Gilpinia bercyniae* (Hartwig) (Bird 1949), *N. swainei* (Smirnof 1968), and *N. sertifer* (Sullivan and Wallace 1968). Bird (1949) found these cysts associated with a virus, while Sullivan and Wallace (1968) associated them with larval-rearing temperatures.

The propensity of the ichneumonids to attack the commonly immune *N. abietis* is puzzling; possibly, the parasitoids' phenology may correspond more closely to that of this species, rather than that of the earlier-feeding *N. near deleoni*. As noted above, host strains or sibling species may have different abilities to encapsulate parasitoid eggs (Pschorn-Walcher 1977; Salt and van den Bosch 1967).

Predators. Predation of sawfly cocoons was not observed directly. Indirect observations (based on remains of cocoons found in litter and soil samples) of the percentage of total cocoons attacked by predators are shown in table 13.

Cocoon predation rates (all predation combined) ranged from 20 to 23 percent. These observed rates were low compared with previously recorded rates for other species: approximately 50 percent for *N. tsugae* (Furniss and Dowden 1941), 60.4 percent for *Gilpinia bercyniae* (Martineau 1943), 40 to 80 percent for *N. sertifer* (Holling 1958), and 33 to 45 percent for *N. fulviceps* complex (Dahlsten 1967). This may be due in part to conser-

vative estimates of predation—that is, the relatively large unknown category may include many cocoons attacked by predators.

The unknown category included no emergence and unidentifiable outcome (i.e., cocoon smashed, or for some reason outcome was uncertain), and ranged from 24 to 38 percent. Unknown outcomes were represented by 8 to 14 percent of collected *N. fulviceps* (Dahlsten 1967). Furniss and Dowden (1941) found no emergence for 33 to 48 percent of *N. tsugae* cocoons (in 2 successive years); a subsample of the latter year's unemerged cocoons yielded 65 percent with dead sawfly and dead parasitoid larvae, 34 percent with dead sawflies, and 1 percent with live parasitoids in diapause. The relatively high proportion of unknown mortality found during the current study may have been due to poor rearing conditions (in particular, exposure to high temperatures during transportation from field to laboratory).

SUMMARY

Two sawfly species have been reared from white fir in northeastern California: *Neodiprion* near *deleoni* and *N. abietis*. These univoltine species overwintered in foliage as eggs, hatching in the spring when white fir buds were 8 mm to 10 mm long. Certain wildflowers may also be used to estimate timing of egg hatch. Eggs were found in clusters averaging 40.7 eggs per colony; this mean was nearly identical to the average number of eggs per female—strong circumstantial evidence that females usually lay all their eggs in a single cluster. Ninety-eight percent of eggs were laid singly in needles, usually in the current foliage (76 percent) or previous year's foliage (26 percent). Limited evidence suggested that eggs of the *N.* near *deleoni* hatched earlier than those of *N. abietis*. Colonies collected as eggs and reared separately almost always yielded all *N.* near *deleoni* (91 percent) or all *N. abietis* (9 percent) sawflies. Table 15 summarizes differences between the two species.

TABLE 15. SUMMARY OF DIFFERENCES BETWEEN *N.* NEAR *DELEONI* (*D.*) AND *N. ABIETIS* (*A.*) FOUND ON WHITE FIR IN MODOC COUNTY, CALIFORNIA

Character	Differences between species
No. instars (males)	<i>D.</i> : 41% had 5 instars, 59% had 6 (n = 49) <i>A.</i> : 96% had 5 instars, 4% had 6 (n = 25)
Phenology	For egg hatch and larval mounting time in the lab, <i>D</i> occurs earlier than <i>A</i>
Cocoon location	Usually in litter or soil for <i>D.</i> , on foliage for <i>A.</i>
Colony purity	Colonies reared from field-collected eggs are generally entirely <i>D.</i> (91%) or <i>A.</i> (9%)
Encapsulation of ichneumonid eggs	34% of <i>A.</i> adults vs. 14% of <i>D.</i> adults bore encapsulated eggs
Larval stripe pattern	<i>A.</i> fourth instars usually have the same pattern of stripes as <i>D.</i> third instars, and so on for older larvae
Late larval coloration	<i>D.</i> : dull olive green; <i>A.</i> : bright lime green
Pupal coloration	<i>D.</i> : light brown; <i>A.</i> : bright lime green
Cocoon coloration	<i>D.</i> : golden brown to dark, dull brown (totally opaque); <i>A.</i> : translucent yellow
Adult coloration (males)	mesepisternum: <i>D.</i> : dorsal half dark brown, ventral half tan; <i>A.</i> : solid dark brown; abdominal tergites: <i>D.</i> : tan; <i>A.</i> : dark brown
Genitalia (females)	<i>D.</i> : scopal pads not enlarged; <i>A.</i> : scopal pads enlarged
No. antennal segments (females)	<i>D.</i> : usually 19; <i>A.</i> : usually 18

Certain mortality sources were described and evaluated. Eggs and larvae of the two species usually could not be distinguished at the time of sampling, so mortality estimates apply primarily to the more abundant *N. near deleoni*. Egg mortality agents included parasitoids (8.5 percent) and unknown causes (17.4 percent). No parasitoids emerged from feeding larvae, though all but one (a gregarious pteromalid) attacked that stage. Two theridiid spiders seemed to prey on sawfly colonies; though they were observed preying on up to 25 percent of the larvae in a colony, their overall predation rate was conservatively estimated at 1.5 percent. Relatively low numbers of parasitoids were reared from prepupae and pupae that had been collected as larvae (1.9 to 9.9 percent), possibly due to poor rearing conditions. However, analyses of cocoons collected in the field yielded higher estimates of parasitism (17.2 percent), as well as estimates of predation (21.3 percent) and unknown mortality (34.2 percent). From 10 to 41 percent of emerging adult sawflies carried encapsulated ichneumonid eggs, with more such eggs found in females and in *N. abietis* adults.

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LITERATURE CITED

ANONYMOUS.

- 1949- Forest pest conditions in California. California Forest Pest Control Action Council, distributed 1979. by California Division of Forestry, 1416 Ninth Street, Sacramento, CA 95814.
- BENJAMIN, D. M.
1955. The biology and ecology of the red-headed pine sawfly. USDA Forest Service Tech. Bull. No. 1118, 57 pp.
- BIRD, R. D.
1929. Notes on the fir sawfly, *Neodiprion abietis* Harr. Ann. Rep. Entomol. Soc. Ontario 60:76-82.
1949. Tumors associated with a virus infection in an insect. Nature 163:777-78.
- COPPEL, H. C., and D. M. BENJAMIN.
1965. Bionomics of the nearctic pine-feeding diprionids. Ann. Rev. Ent. 10:69-96.
- DAHLSTEN, D. L.
1961. Life history of a pine sawfly, *Neodiprion* sp., at Willits, CA (Hymenoptera: Diprionidae). Can. Ent. 93:182-95.
1966. Some biological attributes of sawflies in the *Neodiprion fulviceps* complex in a brushfield pine plantation (Hymenoptera: Diprionidae). Can. Ent. 98:1055-83.
1967. Preliminary life tables for pine sawflies in the *Neodiprion fulviceps* complex (Hymenoptera: Diprionidae). Ecology 48:275-89.
- DAHLSTEN, D. L., R. F. LUCK, E. I. SCHLINGER, J. M. WENZ, and W. A. COPPER.
1977. Parasitoids and predators of the Douglas-fir tussock moth, *Orygia pseudotsugata* (Lepidoptera: Lyantriidae), in low to moderate populations in central California. Can. Ent. 109:727-46.
- DROOZ, A. T., R. C. WILKINSON, and V. H. FEDDE.
1977. Larval and cocoon parasites of three *Neodiprion* sawflies in Florida. Env. Ent. 6(1):60-62.
- ENTOMOLOGICAL SOCIETY OF AMERICA.
1982. Common names of insects and related organisms 1982. Entomol. Soc. of America, 132 pp.
- EISNER, T., J. S. JOHNESSEE, J. CARREL, L. B. HENDRY, and J. MEINWALD.
1974. Defensive use by an insect of a plant resin. Science 184:996-99.
- FURNISS, R. L., and V. M. CAROLIN.
1977. Western forest insects. USDA Forest Service Misc. Publ. No. 1339, 654 pp.
- FURNISS, R. L., and P. B. DOWDEN.
1941. Western hemlock sawfly, *Neodiprion tsugae* Middleton, and its parasites in Oregon. J. Econ. Ent. 34(1):46-52.
- HARD, J. S.
1976. Natural control of hemlock sawfly, *Neodiprion tsugae* (Hymenoptera: Diprionidae), populations in southeast Alaska. Can. Ent. 108:485-98.
- HOLLING, C. S.
1958. Sensory stimuli involved in the location and selection of sawfly cocoons by small mammals. Can. J. Zool. 36:633-53.
- KAPLER, J. E., and D. M. BENJAMIN.
1960. The biology and ecology of the red-pine sawfly in Wisconsin. For. Sci. 6:253-68.
- KNERER, G., and C. E. ATWOOD.
1972. Evolutionary trends in the subsocial sawflies belonging to the *Neodiprion abietis* complex (Hymenoptera: Tenthredinoidea). Am. Zool. 12:407-18.
1973. Diprionid sawflies: polymorphism and speculation. Science 179:1090-99.
- LINDMAN, H. R.
1974. Analysis of variance in complex experimental designs. W. H. Freeman and Company, San Francisco, 353 pp.
- LOUGHTON, B. G., C. DERRY, and A. S. WEST.
1963. Spiders and the spruce budworm, pp. 249-368. In: R. F. Morris (ed.), The dynamics of epidemic spruce budworm populations. Mem. Ent. Soc. Can. No. 31. 332 pp.
- LYONS, L. A.
1962. The effect of aggregation on egg larval survival in *Neodiprion swainei* Midd. (Hymenoptera: Diprionidae). Can. Ent. 94:49-58.
1964. The spatial distribution of two pine sawflies and methods of sampling for the study of population dynamics. Can. Ent. 102:68-84.
1970. Some population features of reproductive capacity in *Neodiprion swainei* (Hymenoptera: Diprionidae). Can. Ent. 102:68-84.
1977a. On the population dynamics of *Neodiprion* sawflies, pp. 48-55. In: Kulman, H. M., and H. C. Chang (eds.), Insect ecology—papers presented in the A. C. Hodson Lectures. Univ. Minn. Agr. Exp. Sta. Tech. Bull. 310, 157 pp.
1977b. Parasitism of *Neodiprion sertifer* (Hymenoptera: Diprionidae) by *Exenterus* spp. (Hymenoptera: Ichneumonidae) in Ontario, 1962-1972, with notes on the parasites. Can. Ent. 109:555-654.

LYONS, L. A., and K. J. GRIFFITHS.

1962. Observations on the development of *Neodiprion sertifer* (Geoff.) with the cocoon (Hymenoptera: Diprionidae). *Can. Ent.* 94:994-1001.

MARTINEAU, R.

1943. Population studies of the European spruce sawfly (*Gilpinia hercyniae* Htg.) in Quebec. *For. Chron.* 19:3-23.

MULDREW, J. A.

1973. The natural immunity of the larch sawfly (*Pristiphora erichsonii* [Htg.]) to the introduced parasite *Mesoleius tentbredinis* Morley in Manitoba and Saskatchewan. *Can. J. Zool.* 31:313-32.

O'NEIL, L. C.

1962. The suppression of growth rings in jack pine in relation to defoliation by the swaine jack-pine sawfly. *Can. J. Bot.* 41:227-35.

PSCHORN-WALCHER, H.

1977. Biological control of forest insects. *Ann. Rev. Ent.* 22:1-22.

PSCHORN-WALCHER, H., and O. EICHORN.

1973. Studies on the biology and ecology of the pine sawfly *Neodiprion sertifer* (Geoff.) (Hymenoptera: Diprionidae) in central Europe. *Z. angew. Entomol.* 74:286-318.

PUTTLER, B., and R. VAN DEN BOSCH.

1959. Partial immunity of *Laphygma exigua* (Hubner) to the parasite *Hyposoter exiguae* (Vierick). *J. Ecol. Ent.* 52:327-29.

RAUF, A., and D. M. BENJAMIN.

1980. The biology of the white pine sawfly, *Neodiprion pinetum* (Hymenoptera: Diprionidae) in Wisconsin. *The Great Lakes Entomologist*, 13:219-24.

ROSS, H. H.

1955. The taxonomy and evolution of the sawfly genus *Neodiprion*. *For. Sci.* 1:196-209.

SALT, G., and R. VAN DEN BOSCH.

1967. The defense reactions of three species of *Hypera* (Coleoptera: Curculionidae) to an ichneumon wasp. *J. Inv. Pathol.* 9:164-77.

SHEEHAN, KATHARINE A.

1982. Bionomics of the white fir sawfly, *Neodiprion abietis* complex (Hymenoptera: Diprionidae), in northeastern California. Ph.D. diss., University of California, Berkeley, 163 pp.

SMIRNOFF, W. A.

1968. The nature of cysts found in pupae and adults of *Neodiprion swainei*. *Can. Ent.* 100:313-18.

STARK, R. W., and D. L. DAHLSTEN.

1965. Notes on the distribution of eggs of a species in the *Neodiprion fulviceps* complex (Hymenoptera: Diprionidae). *Can. Ent.* 97:550-52.

STRUBLE, G. R.

1957. Biology and control of the white-fir sawfly. *For. Sci.* 3:306-13.

SULLIVAN, C. R., and D. R. WALLACE.

1968. Inclusions in adults of the European pine sawfly, *Neodiprion sertifer* (Geoff.). *Can. J. Zool.* 46:959-63.

TORGERSEN, T. R.

1968. Parasites of the hemlock sawfly, *Neodiprion tsugae*, in coastal Alaska. *Ann. Ent. Soc. Amer.* 61:1155-58.

TRIPP, H. A.

1960. *Spathimeigenia spinigera* Townsend (Diptera: Tachinidae), a parasite of *Neodiprion swainei* Middleton (Hymenoptera: Diprionidae). *Can. Ent.* 94:809-18.

- 1962a. The relationship of *Spathimeigenia spinigera* Townsend (Diptera: Tachinidae) to its host, *Neodiprion swainei* Midd. (Hymenoptera: Diprionidae). *Can. Ent.* 94:809-18.

- 1962b. The biology of *Perilampus hyalinus* Say (Hymenoptera: Perilampidae), a primary parasite of *Neodiprion swainei* Midd. (Hymenoptera: Diprionidae) in Quebec, with descriptions of the egg and larval stages. *Can. Ent.* 94:1250-70.

1965. The development of *Neodiprion swainei* Middleton (Hymenoptera: Diprionidae) in the Province of Quebec. *Can. Ent.* 97(1):92-107.

VAN DEN BOSCH, R.

1964. Encapsulation of the eggs of *Bathyplectes curculionis* (Thompson) (Hymenoptera: Ichneumonidae) in larvae of *Hypera brunneipennis* (Bohenian) and *Hypera postica* (Gyllenhal) (Coleoptera: Curculionidae). *J. Ins. Path.* 6:343-67.

YOSHIMOTO, C. M.

1978. Revision of the subgenus *Achrysocharella* Girault of America north of Mexico (Chalcidoidea, Eulophidae: Chrysonotomyia Ashmead). *Can. Ent.* 110:697-719.

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