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Biological Control-Parasitoids and Predators

Introduced and Native Parasitoid Wasps Associated With Larch Casebearer (Lepidoptera: Coleophoridae) in Western Larch

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ABSTRACT The larch casebearer [*Coleophora laricella* (Hubner)], a non-native insect, continues to impact western larch (*Larix occidentalis* Nutt.) through defoliation events in the Pacific Northwest. Biological control programs starting in the 1960s released seven species of parasitoid wasps to control *C. laricella* outbreaks. However, information about current population dynamics of *C. laricella* and associated parasitoids remains lacking. Therefore, the goal of this study was to document the presence, current distributions, densities, and parasitism rates of introduced and native parasitoid wasps occurring on *C. laricella* throughout the Northwestern U.S. range of *L. occidentalis*. We sampled *L. occidentalis* trees at multiple sites in Oregon, Washington, Idaho, and Montana. *C. laricella* was present at all sites with average state densities ranging from 6.2 to 13.1 moths/100 buds. We recovered two introduced hymenopteran biological control agents; *Agathis pumila* (Ratzeburg: Braconidae) at 79% of the sites, and *Chrysocharis laricinellae* (Ratzeburg: Eulophidae) at 63% of the sites. Fourteen species of native parasitic wasps were also recovered. The most common species were: *Bracon* sp., *Spilochalcis albifrons*, and *Mesopolobus* sp. The average native species parasitism rate across the four states was 9.0%, which was higher than the introduced species *Ch. laricinellae* (2.9%), but not as high as *A. pumila* (19.3%). While survey results suggest that native species may be more important for the control of *C. laricella* than previously thought, *A. pumila* remains the major source of regional control. However, further research is needed to better understand how introduced and native parasitoids interact to control invasive pest populations.

KEY WORDS *Agathis pumila, Coleophora laricella, Larix occidentalis*, biological control, parasitoid

Introduction

The larch casebearer [*Coleophora laricella* (Hubner) Lepidoptera: Coleophoridae] was inadvertently introduced from Europe into eastern North America in the 1800s, where it became a serious pest of tamarack [*Larix laricina* (Du Roi) K. Koch]. There it was successfully controlled following the purposeful release of two imported European Hymenopteran parasitoids, *Agathis pumila* (Ratzeburg: Braconidae) and *Chrysocharis laricinellae* (Ratzeburg: Eulophidae) (Quednau 1970). In the 1950s, *C. laricella* extended its range to western larch (*Larix occidentalis* Nutt.) in the Pacific Northwest (PNW) and regained its pest status, limited there only by high elevations and northern latitudes (Denton 1979, Tunnock and Ryan 1985, Long 1988). As a result, *L. occidentalis* experienced significant defoliation and growth impacts across Idaho, Montana, northeastern Washington, and northeastern Oregon (Ryan et al. 1987).

Seven non-native species of parasitoid wasps have been released into the range of *C. laricella* in *L. occidentalis* (Table 1; Bousfield et al. 1974, Ryan et al. 1974, Ryan 1990). Introduction of *A. pumila* began in Idaho in 1960 (Bousfield et al. 1974, Denton 1979) and continued at various intensities throughout the range of *L. occidentalis* until 1981 (Ryan 1981, Ebel et al. 1982, Ryan et al. 1987). *Ch. laricinellae* and four other Eulophids, *Dicladocerus japonicas* (Yshm.), *Dicladocerus westwoodii* (Westw.), *Elachertus argissa* (Walk.), and *Necremnus metalarus* (Walk.), and *Diadegma laricinellum* (Strobl) (Hymenoptera: Ichneumonidae) were also released in limited numbers (Ryan and Denton 1973; Bousfield et al. 1974; Ryan et al. 1974, 1975, 1977; Ryan 1981). Releases were conducted by industry and agency foresters, as well as forest entomologists using the "branch" method (Ebel et al. 1982), i.e., moving larch branches with *C. laricella* pupae from areas where established populations of *A. pumila* and *Ch. laricinellae* were known to be abundant to areas where the parasitoids were absent.

By the mid-1980s, *A. pumila* had become well-established throughout the range of *L. occidentalis* and contributed to the highest overall rates of parasitism of all the introduced wasps (Ryan et al. 1987, Long 1988, Ryan 1990). *Ch. laricinellae* was successfully established by 1977 in eastern Washington, northern Idaho, northeastern Oregon, and western Montana (Ryan and Theroux 1981) due to the intensive release programs

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during 1972–1976, with very high rates of parasitism in some areas (Long 1988, Ryan 1997). As a result, *C. laricella* population densities were reduced throughout the region and the biological control programs were considered a success largely due to *A. pumila*, and *Ch. laricinellae*, while the other five introduced parasitoid wasps did not become widely established (Tunnock and Ryan 1985, Ryan 1997).

Table 1. Introduced parasitoid wasps released in the Northwest during the 1960s–1980s and genera and species of native parasitoid wasps commonly recovered from larch casebearer and found by our survey in 2010/2011

Genus/Species/Family	Introduced/Native	Present
Agathis pumila (Ratz.) Braconidae	Introduced	Yes
Diadegma laricinellum (Strobl) Ichneumonidae	Introduced	No
Chrysocharis laricinellae (Ratz.) Eulophidae	Introduced	Yes
Dicladocerus japonicas (Yshm.) Eulophidae	Introduced	No
D. westwoodii (Westw.) Eulophidae	Introduced	No
Elachertus argissa (Walk.) Eulophidae	Introduced	No
Necremnus metalarus (Walk.) Eulophidae	Introduced	No
Bracon Braconidae	Native	Yes
Gelis Ichneumonidae	Native	Yes
Scambus Ichneumonidae	Native	Yes
Itoplectis Ichneumonidae	Native	Yes
Pristomerus Ichneumonidae	Native	Yes
Campoplex Ichneumonidae	Native	Yes
Spilochalcis albifrons Chalcididae	Native	Yes
S. leptis Chalcididae	Native	Yes
Mesopolobus Pteromalidae (Chalcididae)	Native	Yes
Habrocytus Pteromalidae	Native	Yes
Tetrastichus Eulophidae	Native	Yes
Euderus Eulophidae	Native	Yes

From Bousfield et al. 1974, Ryan et al. 1977, Ryan 1979, Denton 1979, Ryan 1981.

Previous research has found up to 39 species of native parasitoid wasps associated with *C. laricella* in the western United States (Bousfield and Lood 1971, 1973, Ismail and Long 1982, Niwa et al 1986, Long 1988; Table 2). However, native parasitoids vary widely in their abundance, and their presence may largely depend on other factors such as vegetation composition and abundance (Nathanson 1983, Long 1988). The most common native hymenopteran parasitoid wasps documented in the PNW are *Spilochalcis albifrons* (Walsh) (Chalcididae), *Mesopolobus* sp. (Pteromalidae), *Bracon* sp. (Braconidae), *Dicladocerus* sp. (Westwood), *Pristomerus* sp. (Ichneumonidae), and *Tetrasticus coerulescens* Ashm. (Eulophidae) (Bousfield and Lood 1973, Miller and Finlayson 1974, 1977; Niwa and Hard 1981; Ismail and Long 1982; Table 2).

The last published survey of parasitoid wasps associated with *C. laricella* ended in the 1990s (Ryan 1997) and since then regional flare-ups have been documented by forest entomologists across the range of *L. occidentalis*. A 35,000 ha defoliation event in Northeastern Oregon (United States Forest Service [USFS] 2008) created concern that parasitoid wasps were not controlling *C. laricella* populations. There have been no recent published studies assessing densities or parasitism rates of introduced biological control agents or native parasitoid species and a thorough understanding of the ecology of *C. laricella* population control is lacking. Therefore, the goal of our regional survey was to document the presence, current distribution, densities, and parasitism rates of introduced and native parasitoid wasps occurring on *C. laricella* throughout the US range of *L. occidentalis*.

Materials and Methods

Western larch is a component of the mixed conifer montane forest zone and grows in moderately moist sites and north slopes from 1,000 to 2,200 m in Oregon, and 500 to 1,800 m in Washington and British Columbia and east into Idaho and Montana (Arno and Hammerly 1977). The tree is winter deciduous,

Table 2. Number of native parasitoid wasps, location, and major species found in surveys and studies of parasitoid wasps of *Coleophora laricella*

Source	Number of native parasitoids	Locations	Major species
Current Study	14	OR, WA, ID, MT	SPAL, MESO,CAMP, BRAC, SCAM
Niwa and Hard 1981	7 + others	ID, MT	SPAL, MESO, DICL, GETE
Nathanson 1983	10	ID	SPAL, MESO
Long 1988	35	Northwest	SPAL, MESO
Denton 1972	16	Area of original *C. laricella* infestation	SPAL
Denton 1979	39	West	SPAL
Bousfield and Lood 1971, 1973	19	MT, ID, WA	SPAL, DICL, Others
Miller and Finlayson 1974, 1977	32	Kootenay, B.C.	DICL, SPAL, BRAC, MESO, TETR
Ismail and Long 1982	14	Northern ID	MESO, SPAL, TETR
Flavel 1979	5 + others	MT, ID	SPAL, BRAC, MESO, PRIS

KEY: *Spilochalcis albifrons* (SPAL), *Mesopolobus* sp. (MESO), *Bracon pygmaeus* or sp. (BRAC), *Pristomerus* spp. (PRIS), *Dicladocerus* sp. (DICL), *Tetrastichus* sp. (TETR), *Scambus* sp. (SCAM), *Gelis* sp. (GETE), *Campoplex* sp. (CAMP).

requires full light for best growth, and is an early-successional species that follows fire and other disturbances. *Larix occidentalis* rarely dominates entire stands exclusively, and is mostly found in mixed stands with lodgepole pine (*Pinus contorta* Dougl. ex Loud.), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), western white pine (*Pinus monticola* Dougl. ex D. Don), grand fir (*Abies grandis* (Dougl) Lindl.) and ponderosa pine (*Pinus ponderosa* Dougl. ex Laws) (Johnson and Clausnitzer 1992). For this study, 52 sites were located across the range of *L. occidentalis* in Oregon (13 sites), Washington (13), Idaho (11), and Montana (15) (Fig. 1). The 13 Oregon sites were original release and monitoring sites in previous studies (Ryan 1983, 1997).

Sampling was done during pupation of *C. laricella*. The original release and monitoring sites from Ryan (1997) in Oregon were visited in June 2010 as part of a pilot study. The following year, new sites were established in Washington, Idaho, and Montana in late May to early June 2011. Field sampling methods followed Ryan (1990). At each site we randomly selected 10 western larch trees, within the range of 6–25 m in height; trees were selected based on height, so a branch could be sampled from the upper crown. From each tree, four 45-cm branches were cut, one from the lower, two from the mid, and one from the upper crown, using a pole pruner. The four branches were placed into a single rearing box in the field and brought back to the laboratory to rear out. The four branches together were considered one sample.

C. laricella and associated parasitoid wasps were reared out in the laboratory or under cover of an out-building under moderate light. The rearing box had a hole cut in the side; a funnel and cup covered in netting were placed over the hole, to provide a single light source to attract the moths and wasps into the cup. Material was sorted approximately 6 wk after the last moth emergence because parasitoid emergence can occur several weeks after moth emergence. The numbers of buds, moths, cases, and wasp species were recorded. Up to 100 *C. laricella* cases per box were dissected to determine the number of un-emerged adult wasps and moths. Parasitoids were identified to the lowest possible taxonomic level using the key by

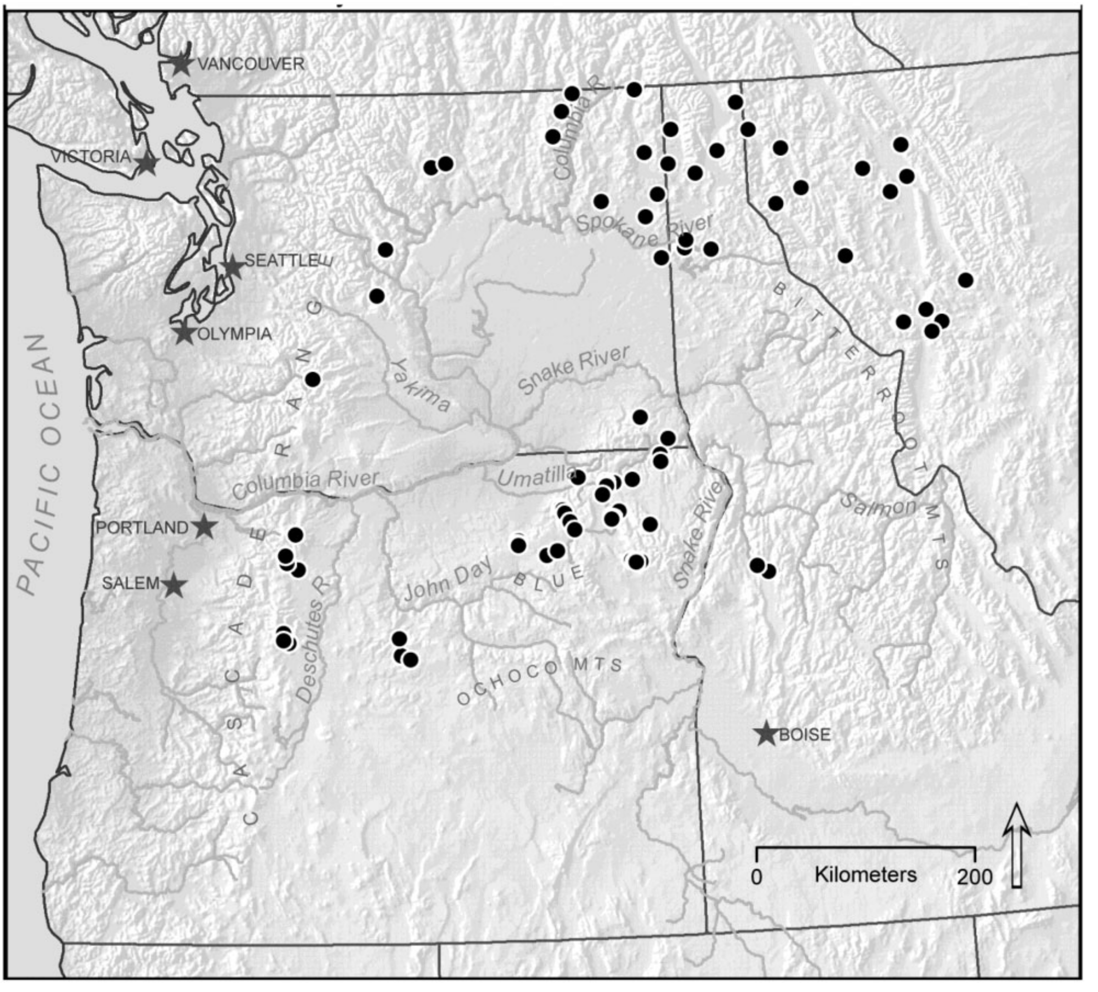

Fig. 1. Location of study sites across Oregon, Washington, Idaho, and Montana in the range of western larch.

Table 3. Total number of individuals, average number of individuals/100 larch buds, and frequency of species (based on occurrence at 52 sites)

Species	Total	Number per 100 buds	Frequency (% of sites)
C. laricella	28,161	8.77	100
A. pumila	4733	1.57	79
Ch. laricinellae	1068	0.367	63
S. albifrons	717	0.244	41
Mesopolobus	444	0.143	39
Bracon	107	<0.1	51
Scambus	64	<0.1	37
Campoplex	188	<0.1	35
Gelis	30	<0.1	24
Dicladocerus	16	<0.1	22
S. leptis	18	<0.1	20
Pristomerus	87	<0.1	20
Itoplectis	16	<0.1	12
Ichneumonid	8	<0.1	9.8
Habrocytus	22	<0.1	7.8
Tetrastichus	4	<0.1	3.9
Unknown 1	4	<0.1	5.8

Total number of trees = 476 at 52 sites across four states. n = negligible average/tree (<0.1). *Agathis pumila* = *A. pumila*, *Chrysocharis laricinellae* = *Ch. laricinellae*, *S.* = *Spilochalcis*.

Ryan (1979). Identifications were confirmed using voucher specimens from the Oregon State University Arthropod Collection (http://osac.science.oregonstate.edu/). Voucher specimens from this current collection have also been deposited there.

Moth density is reported as number of moths/100 larch buds. This value was determined by dividing the number of total moths per site by the standardized value of larch buds (total number of larch buds at each site divided by 100). The total number of parasitoid wasps is presented, as well as the frequency at sample sites ($N = 52$). The density of parasitoid wasps is also presented as number/100 larch buds. Percent parasitism of *C. laricella* by parasitoid wasps was determined by dividing the total number of moths per site by the total number of moths plus parasitoids per site.

Results

C. laricella was found at all 52 of our sites ranging in density from 73.80 ± 12.94 moths/100 buds to 0.014 ± 0.013/100 buds. The four-state average for *C. laricella* was 8.8 ± 0.73 moths/100 buds (Table 3 and Fig. 2). Average densities varied by state from 13.1 moths ± 2.3/100 buds in Washington to 6.2 ± 0.9 in Montana (Fig. 2). Site location data is provided in Table 4.

Only two of the seven parasitoids originally released in the 1960s-1980s were found: *A. pumila* and *Ch. laricinellae* (Table 1). Both introduced parasitoids varied in frequency by state; *A. pumila* was found at 100% of the sites in Oregon, 62% in Washington, 91% in Idaho, and 67% in Montana. In contrast, *Ch. laricinellae* was found at 62% of the sites in Oregon, 62% in Washington, 82% in Idaho, and 53% in Montana. *A. pumila* occurred at 79% of the sites with an average site density of 1.57 ± 0.15/100 buds (Table 3). In contrast, *Ch. laricinellae* was found at 63% of the sites at an average density of 0.367 ± 0.05/100 buds. While average parasitism rates varied by state (Fig. 3), the four-state average for *A. pumila* was 19.32% compared to 2.85% for *Ch. laricinellae.*

Fourteen native species or species groups of parasitoids were recovered from *C. laricella* (Table 1); all were present in both 2010 and 2011. While the two most common native species of parasitoids varied by state, those with the highest overall densities were *S. albifrons* and *Mesopolobus* sp. (Table 3).

The four-state average native species parasitism rate was 9.0%. Interestingly, native parasitoids accounted for nearly half the total parasitism documented in Idaho, 15.2% (Fig. 4). The other states had native species parasitism rates of: Montana, 9.0%; Washington, 7.6%; and Oregon, 4.1%. *Ch. laricinellae* parasitism rates were consistently lower than for all native species combined (Fig. 4).

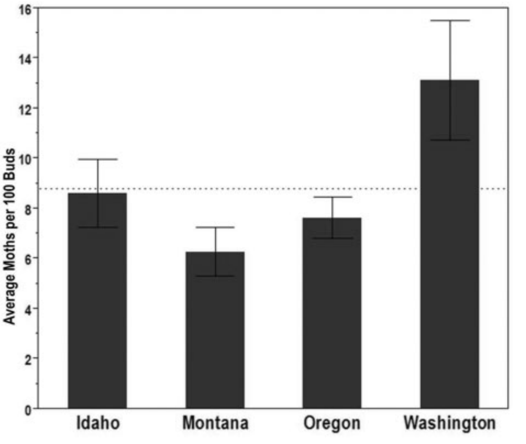

Fig. 2. Average number of larch casebearer moths/100 larch buds by state. Dotted line indicates the combined average across states. Error bars are standard error.

Discussion

Prior to the introduction of biological control agents in the 1960s, Oregon state site densities of *C. laricella* averaged 50.03 moths/100 buds during outbreak years (Ryan 1983, 1997). During the 10 years following introduction and control by *A. pumila*, average annual moth densities were reduced to 1.63 moths/100 buds (Ryan 1997). Our study recovered *C. laricella* from all 52 sites in the four states, with average state densities ranging from 6.2 to 13.1 moths/100 buds (Table 3 and Fig. 2). Therefore, while *C. laricella* continues to be widely distributed in the PNW, average state densities from this survey are much lower than outbreak levels reported by Ryan (1997).

Our study recovered only the two most promising biological control agents, *A. pumila* and *Ch. laricinellae*, of the seven parasitoids introduced during the 1960s to 1980s (Table 1). Ryan (1997) concluded that *A. pumila* was the most important parasitoid wasp

Table 4. List of western larch survey sites by state where larch casebearer was collected in 2010 and 2011 for rearing moths and parasitoid wasps: latitude/longitude location, elevation (m), and number of trees sampled

Site	Location		Elevation (m)	Number of trees sampled
Oregon sites (13)				
BCC5	N45 43 58.2	W117 50 31.2	1176	10
BCC6	N45 44 27.1	W 117 55 8.9	1051	10
BCC8	N45 27 53	W117 51 33.8	1132	10
BCC10	N45 29 58	W117 46 56.4	1167	10
TOLL	N45 47 22.6	W118 14 38.5	1151	10
CHAR	N46 15 52.2	W 117 29 10.2	1408	10
EMIG	N45 32 36.9	W 118 27 52.2	1164	10
CATH	N45 05 35.9	W117 39 45.8	1342	10
BATT	N45 16 59	W 118 58 15.9	1254	10
FIELD	N46 04 46.8	W117 10 8.4	1210	10
FLORA	N45 53 27	W 117 15 46.6	1345	5
LOST	N45 22 49.6	W117 25 23.9	1311	10
SRIM	N45 56 43.8	W117 16 20.2	1223	10
Washington sites (13)				
LOUP1	N48 23.481	W119 53.284	1246	10
LOUP2	N48 25.097	W119 42.804	1034	10
ENT	N47 43.058	W120 28.102	1089	4
HAV	N48 03.566	W117 49.738	666	10
MEAD	N48 45.332	W117 36.464	920	10
BOYD	N48 49.228	W118 16.385	784	10
KETT	N48 37.005	W118 23.415	1053	10
ORIENT	N48 58.090	W118 08.116	762	10
MET	N48 58.834	W117 21.677	771	5
GARY	N48 06.091	W117 08.777	767	10
USK	N48 26.982	W117 16.984	636	10
MIC	N47 34.429	W117 08.264	821	4
SPO	N47 55.222	W117 18.167	598	10
Montana sites (15)				
BONNER	N46 53.333	W113 49.652	1015	10
BUTTE	N47 00.044	W113 59.998	1497	6
PAT	N46 48.968	W113 57.301	1291	10
BF	N48 06.603	W114 05.833	928	10
DEEP	N46 54.500	W114 16.835	1083	10
SL	N47 12.432	W113 29.956	1329	5
SWEDE	N48 20.662	W115 29.348	798	10
MCKAY	N47 57.920	W115 42.565	737	10
PLAINS	N47 29.562	W114 54.836	751	10
MILLER	N48 04.978	W115 23.836	918	10
CEDAR	N48 25.476	W115 36.820	637	10
ASH	N48 12.358	W114 37.815	1212	10
STONE	N47 59.764	W114 18.709	1209	10
YAAK	N48 35.699	W115 59.577	698	10
HORSE	N48 22.413	W114 02.091	1072	10
Idaho sites (11)				
COEUR	N47 38.792	W116 51.065	735	10
CEDAR	N48 25.476	W115 36.820	637	10
CNURSE	N47 42.727	W116 49.676	685	10
NORD	N48 37.926	W116 56.617	800	10
PRIEST	N48 20.939	W116 59.871	772	10
JULY	N47 37.348	W116 31.690	930	10
DOVER	N48 15.526	W116 40.130	640	10
MOYIE	N48 49.602	W116 07.357	927	10
SANDYN	N48 26.147	W116 23.482	809	10
PSP	N44 56.465	W116 04.476	1557	10
MEADOWS	N44 59.733	W116 12.203	1665	10

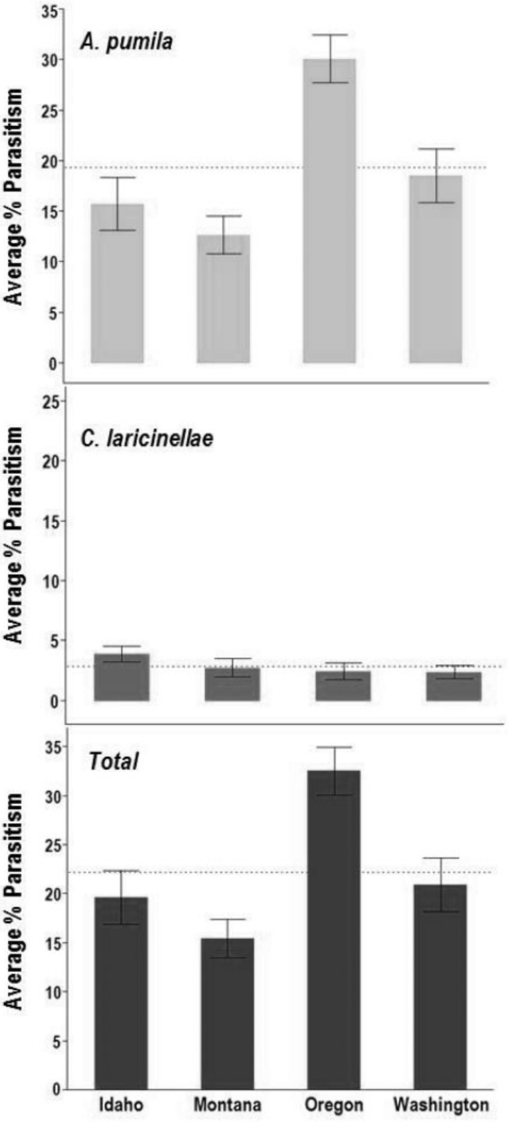

Fig. 3. Average percent parasitism in each state for *Agathis pumila* (top panel), *Chrysocharis laricinellae* (middle), and combined parasitism (bottom). Dotted lines indicate the average across states. Error bars are standard error.

regulating *C. laricella*; our study suggests this is still the case. We found *A. pumila* at 79% of our sites, with an average parasitism rate of 19.32%. This was lower than parasitism rates during outbreak years reported in a study by Ryan (1997) in northeast Oregon and southwest Washington, which found parasitism fluctuated between 40% and 60% with rates as high as 75–90% at some sites. While our study found *Ch. laricinellae* was widespread and present at 62% of all sites sampled, the average parasitism rate was only 2.9%, suggesting this species is not as important as *A. pumila* in control of *C. laricella* populations.

Interestingly, we found native parasitism rates were much higher than previously documented at the regional scale, averaging 9.0% across all four states. Ryan (1997) suggested native parasitoid wasps were not as effective as *A. pumila* in regional control of *C. laricella*. While this is the case in Oregon and Washington, the combined native parasitism rate in Idaho was 15.2%, nearly equal to *A. pumila*'s rate of 15.8% (Fig. 4), and Montana also had relatively high rates of native

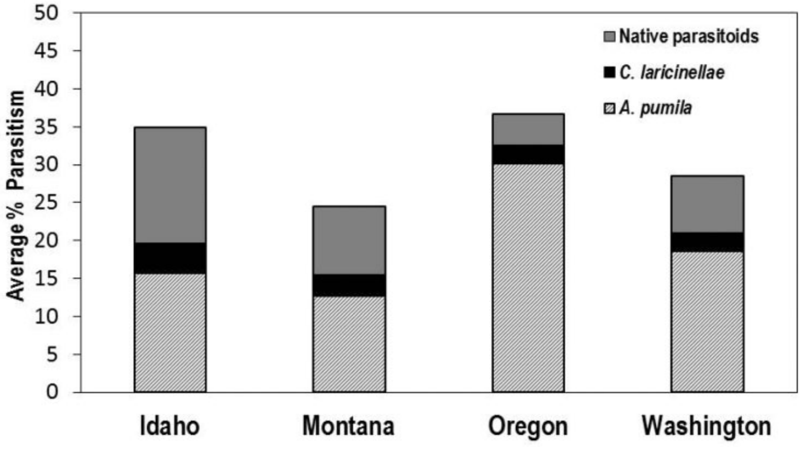

Fig. 4. Average parasitism rates in each state for native parasitoid species, *Agathis pumila*, and *Chrysocharis laricinellae*.

parasitism. This suggests that native parasitoids may be more regionally important than previously thought.

Various surveys and studies found up to 39 species or species groups of native parasitoid wasps associated with *C. laricella* in the West (Denton 1972, 1979; Bousfield and Lood 1973; Miller and Finlayson 1974, Table 2) and up to 50 native species in eastern North America (Webb 1952, Sloan and Coppel 1965). Our survey found 14 species or species groups of native parasitoid wasps associated with *C. laricella*. The most common species/complexes our survey found supported previous research (Table 2 and 3). Many of these groups of parasitoid wasps are known hyperparasites (Miller and Finlayson 1974).

Long (1988) suggested *S. albifrons* and *Mesopolobus* sp. were potential regulating agents of *C. laricella*, as they were found so consistently at high densities. The most common native parasitoid wasp we found was *S. albifrons*, with average densities third only to *A. pumila* and *Ch. laricinellae* (Table 3), which supports previous studies (Denton 1972, Ryan and Denton 1973). Hansen (1980) found the life history of *S. albifrons* matches very well with *C. laricella*. Adults attack pupae in a wide variety of hosts, have at least two generations per year, and may act as facultative secondary parasites or hyperparasites. However, studies show most adults that emerge from *C. laricella* are males, which may limit its ability to effectively control *C. laricella* populations (Denton 1972, Ryan and Denton 1973). These parasitoids also typically require alternative hosts or a specific food source, which limits their effectiveness (Long 1988).

In conclusion, while it appears that the introduced biological control agent *A. pumila* remains the most important regional source of *C. laricella* control, native parasitoids may be more important than previously thought, especially locally. There is very little understanding about what contributes to the success of these native parasitoids and how they interact with the introduced biological control agents to exert control. Therefore, future work should assess how best to evaluate population control considering interactions between native and non-native species. In addition, investigations should include what other factors may influence control by native species, such as vegetation structure and community composition (Jervis et al. 1993). These studies may give us a better understanding and ability to predict the critical factors necessary for control of *C. laricella* and other invasive insect populations.

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References Cited

Arno, S. F., and R. P. Hammerly. 1977. Northwest trees. The Mountaineers, Seattle, Washington, DC.

Bousfield, W. E., and R. C. Lood. 1971. Impact of parasites on the larch casebearer in the northern region 1970. USDA For. Serv. Report 71–4, Northern Region, Missoula, MT.

Bousfield, W. E., and R. C. Lood. 1973. Parasites of the larch casebearer in Montana, Idaho, and Washington. Environ. Entomol. 2: 212–213.

Bousfield, W., S. Tunnock, L. Pettinger, and D. Ross. 1974. Establishment and distribution of the larch casebearer parasite *Agathis pumila* in Idaho, Montana, Washington, Oregon, and British Columbia. USDA For. Serv. Report 74-3. Northern Region, Missoula, MT.

Denton, R. E. 1972. Establishment of *Agathis pumila* (Ratz.) for control of larch casebearer, and notes on native parasitism and predation in Idaho. USDA Forest Service Res. Note INT-164, Intermountain Forest and Range Experiment Station, Moscow, ID.

Denton, R. E. 1979. Larch casebearer in western larch forests. USDA Forest Service, General Technical Report INT-55, Intermountain Research Station, Ogden, UT.

Ebel, F., P. Joseph, L. N. Kline, L. F. Pettinger, J. Swaby, E. Tarnasky, and R. B. Ryan. 1982. Recolonizations of the larch casebearer parasites, *Agathis pumila* and *Chrychocharis laricinellae*, in Oregon using the branch method, 1977-1981. USDA For. Serv. Admin. Report, PNW Research Station, Portland, OR.

Flavel, T. H. 1979. Reevaluation of larch casebearer parasites in casebearer-infested stands of Region 1. USDA Forest Service, Report 79-3, Forest Insect and Disease Management, Northern Region, Missoula, MT.

Hansen, J. D. 1980. The life history and behavior of *Spilochalcis albifrons* (Hymenoptera: Chalcididae), a parasite of the larch casebearer, *Coleophora laricella* (Lepidoptera: Coleophoridae). J. Kans. Entomol. Soc. 53: 553–566.

Ismail, A. B., and G. E. Long. 1982. Interactions among parasites of the larch casebearer (Lepidoptera: Coleophoridae) in northern Idaho. Environ. Entomol. 11: 1242–1247.

Jervis, M. A., N.A.C. Kidd, M. G. Gitton, T. Huddleston, and H. A. Dawah. 1993. Flower-visiting by hymenopteran parasitoids. J. Nat. Hist. 27: 67–105.

Johnson, C .G, Jr., and R. R. Clausnitzer. 1992. Plant Associations of the Blue and Ochoco Mountains. USDA For. Serv., R6-ERW-TP-036-92, Pacific Northwest Region, Portland, OR.

Long, G. E. 1988. The larch casebearer in the intermountain northwest. pp. 233–242. *In* A. A. Berryman (ed.), Dynamics of Forest Insect Populations: patterns, causes, implications. Plenum, New York, NY.

Miller, G. E., and T. Finlayson. 1974. Native parasites of the larch casebearer, *Coleophora laricella* (Lepidoptera: Coleophoridae), in the west Kootenay area of British Columbia. J. Entomol. Soc. Br. Columbia 71: 14–21.

Miller, G. E., and T. Finlayson. 1977. Parasites of the larch casebearer, *Coleophora laricella* (Lepidoptera: Coleophoridae), in the west Kootenay area of British Columbia. J. Entomol. Soc. Br. Columbia 74: 16–22.

Nathanson, R. A. 1983. Observations on the influence of site characteristics on parasites of larch casebearer. MS Thesis, University of Idaho. Moscow, ID.

Niwa, C. G., and J. S. Hard. 1981. Parasite complex of the larch casebearer in Idaho and Montana Progress Report. USDA Forest Service, Report No. 81-15. Northern Region, Moscow, ID.

Niwa, C. C., R. W. Stark, D. G. Burnell, and D. M. Johnson Knox. 1986. Annotated Bibliography of Larch Casebearer Parasitiods. Bulletin Number 41. Forest, Wildlife and Range Experiment Station, University of Idaho, Moscow.

Quednau, F. W. 1970. Competition and co-operation between *Chrysocharis laricinellae* and *Agathis pumila* on larch casebearer in Quebec. Can. Entomol. 102: 602–612.

Ryan, R. B. 1979. Illustrated Key to Introduced and Common Native Parasites of Larch Casebearer. USDA Forest Service, Research Paper PNW-262, PNW Forest and Range Experiment Station, Portland, OR.

Ryan, R. B. 1981. Recent (1977-1980) releases of imported larch casebearer parasites for biological control. USDA Forest Service, Research Note PNW-377. Pacific Northwest Forest and Range Experiment Station, Portland, OR.

Ryan R. B. 1983. Population density and dynamics of larch casebearer (Lepidoptera: Coleophoridae) in the Blue Mountains of Oregon and Washington before the build-up of exotic parasites. Can. Entomol. 115: 1095–1102.

Ryan, R. B. 1990. Evaluation of biological control: introduced parasites of larch casebearer (Lepidoptera: Coleophoridae) in Oregon. Environ. Entomol. 19: 1873–1881.

Ryan, R. B. 1997. Before and after evaluation of biological control of the larch casebearer (Lepidoptera: Coleophoridae) in the Blue Mountains of Oregon and Washington, 1972-1995. Environ. Entomol. 26: 703–715.

Ryan, R. B., and R. E. Denton. 1973. Initial releases of *Chrysocharis laricinellae* and *Dicladocerus westoodii* for biological control of the larch casebearer in the western United States. USDA Forest Service Research Note PNW-200, Pacific Northwest Forest and Range Experiment Station, Portland, OR.

Ryan, R. B., W. E. Bousfield, G. E. Miller, and T. Finlayson. 1974. Presence of *Chrysocharis laricinellae*, a parasite of the larch casebearer, in the Pacific Northwest. J. Econ. Entomol. 67: 805.

Ryan, R. B., W. E. Bousfield, R. E. Denton, R. L. Johnsey, L. F. Pettinger, and R. F. Schmitz. 1975. Additional releases of larch casebearer parasites for biological control in the western United States. USDA Forest Service Research Note PNW-242, Pacific Northwest Forest and Range Experiment Station, Portland, OR.

Ryan, R. B., W. E. Bousfield, C. W. Johanningmeier, G. B. Parsons, R. F. Schmitz, and L. J. Theroux. 1977. Releases of recently imported larch casebearer parasites for biological control in the western United States, including relocations of *Agathis pumila*. USDA Forest Service, Research Note PNW-290, Pacific Northwest Forest and Range Experiment Station, Portland, OR.

Ryan, R. B., and L. J. Theroux. 1981. Establishment and distribution in 1977 of *Chrysocharis laricinellae* (Hymenoptera: Eulophidae), a parasite of the larch casebearer, *Coleophora laricella* (Lepidoptera: Coleophoridae), in western forests. Can. Entomol. 113: 1129–30.

Ryan, R. B., S. Tunnock, and F. W. Ebel. 1987. The larch casebearer in North America. J. For. 85: 33–39.

Sloan, N. F., and H. C. Coppel. 1965. The insect parasites of the larch casebearer, *Coleophora laricella* Hubner (Lepidoptera: Coleophoridae), in Wisconsin with keys to the adults and mature larval remains. Wis. Acad. Sci. Arts Lett. 54: 125–146.

Tunnock, S., and R. B. Ryan. 1985. Larch Casebearer in Western Larch. Forest Insect and Disease Leaflet 96, USDA Forest Service, Washington, DC.

(USFS) United States Forest Service. 2008. Forest Health Highlights in Oregon 2007. Joint Publication of: Oregon Department of Forestry and USDA For. Serv., Pacific Northwest Region. R6-NR-FID-TP-02-2008, Portland, OR.

Webb, F. E. 1952. The larch casebearer in the Maritime provinces and Great lakes region. Can. Dep. Agric. Bi-Monthly Progress Report 8: 1.

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