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Coccinellid predators of *Pineus strobi* (Hartig) (Hemiptera: Adelgidae) on western white pine *Pinus monticola* Douglas ex D. Don

Alexander C. Rose*,#, Stephen P. Cook and Frank W. Merickel

Department of Plant, Soil and Entomological Sciences, 606 Rayburn Street, University of Idaho, Moscow, ID 83844-2339, USA.

ABSTRACT

Adelgids (Hempitera: Adelgidae) are minute insects that include some invasive species detrimental to North American forests. Adelgids feed on various species of conifers. Two of the most significant pest adelgids in North America are the hemlock woolly adelgid (*Adelges tsugae*) and the balsam woolly adelgid (*A. piceae*). These adelgids cause severe, often mortal damage to native North American host species (hemlock woolly adelgid on eastern hemlocks *Tsuga caroliniana*, and balsam woolly adelgid on true firs). Biological control is one potential tactic for managing these pests. We investigated native predators as potential biocontrol agents of adelgids. Predators were associated with populations of *A. piceae* infesting subalpine fir, *A. cooleyi* infesting spruces, *A. abietis* infesting Norway spruce, *A. lariciatus* infesting cones of western larch, and *Pineus strobi* infesting western white pine (*Pinus monticola*). Most of the predators were found on western white pine. Two coccinellid beetles (*Coccidophilus atronitens* and *Scymnus coniferarum*) previously presumed to be specialists on pine needle scale, were also found to prey upon *P. strobi* and other adelgids. A third coccinellid and presumed scale specialist, *S. humboldti* consumed *A. cooleyi*. The research was both observational and experimental, and involved opportunistically surveying for potential predators in the field, followed by presenting predators with adelgids in the laboratory (both in no-choice and then choice trials). The successful predation on adelgids by diverse predators and the elucidation of predation preferences increase the understanding of ecosystem dynamics and provide information on potential steps for biocontrol.

KEYWORDS: *Coccidophilus atronitens* Casey, *Scymnus coniferarum* Crotch, *Scymnus humboldti* Casey, predation, Coccinellidae, Adelgidae

INTRODUCTION

Adelgids (Hemiptera: Adelgidae) have complex, polymorphic lifecycles, broadly categorized as either holocyclic or anholocyclic [1]. Holocyclic adelgids exhibit ancestral host alternation and have sexual generations. Typically, the two-year long holocycle involves three sexual generations on the primary host species (always spruce, *Picea* spp.), followed by two asexual generations on the secondary or alternate host of a different genus, namely *Abies* (true firs), *Larix* (larch), *Pinus* (pine), *Pseudotsuga* (Douglas-fir), or *Tsuga* (hemlock). All sexual adelgids alternate hosts. In contrast, anholocyclic adelgids only reproduce asexually and host alternation is the exception. Most adelgids exhibiting the anholocycle live exclusively on spruce,

*Corresponding author: roseal@onid.oregonstate.edu
#Current address: Department of Forest Ecosystems and Society, Oregon State University, 321 Richardson Hall, Corvallis, OR, 97331, USA.

but some species occur only on the alternate host species. The anholocycle usually takes a year to complete. Only adults that disperse between hosts have wings.

Including both native and non-native species, there are two genera (*Adelges* and *Pineus*) and at least 13 species of adelgids that occur in North America [1]. Worldwide, with one known exception, all adelgids induce gall formation on spruce and develop within these structures during at least part of their life cycles (e.g., in North America, *Adelges cooleyi* (Gillette)) [2]; none form galls on their alternate hosts, instead they feed externally, such as on the bole of the tree, on the surface of host needles, or on branches (e.g., in North America, *Pineus strobi* (Hartig)) [1]. Infestations of *P. strobi* can be unsightly and damaging to white pines, sometimes warranting chemical control [3]. The adelgid species in North America have both holocyclic or anholocyclic lifecycles and are significant both ecologically and as potential pests of several species of native North American conifers.

One of the more damaging adelgids that is invasive within various geographic regions of North America is *A. piceae*, balsam woolly adelgid, a pest of native firs in both eastern and western North America. The introduced population of *A. piceae* is anholocyclic, consisting entirely of parthenogenically-reproducing females [4]. In western North America, *A. piceae* is a serious threat to grand fir (*Abies grandis* Douglas) at lower elevations in western Oregon and Washington and to subalpine fir (*A. lasiocarpa* Nuttall) at higher elevations [5]. Similarly, by killing dominant and foundational tree species, *A. tsugae* can drastically alter ecosystem composition, function, and structure [6, 7].

Biological invasions can threaten native biodiversity [8] and cause major economic harm [9]. Adelgids include some of the most detrimental invasive species currently affecting North American forests. Further, climate change will likely facilitate the spread and range expansion of many invasive species [9, 10]. One tool being used in an attempt to slow the spread of invasive species and to aid in their management is the use of natural enemies such as predators and parasitoids to consume the pest species (biological control). The implementation and utilization of biological control against invasive pests usually include the introduction of natural enemies from the area of origin of the pest species. However, native populations of natural enemies may also prey upon and therefore, have some impact on populations of invasive pests. Specialist predators that develop entirely on the identified pest species are desirable for use as biocontrol agents because they can provide targeted control of the prey with minimal impacts on non-target organisms [11]. However, predators with relatively general feeding habits may also contribute as potential biocontrol agents against pest species.

Two common families of predaceous beetles (Coleoptera) that have been captured in association with multiple species of adelgids in the Northwestern United States are the Coccinellidae and Derodontidae [12]. Multiple species of adelgids are found in close proximity to one another feeding on their various host conifers in the University of Idaho’s Arboretum and Botanical Garden located in Moscow, ID, USA (Cook and Rose, personal observation). We hypothesized that predators that were utilizing adelgids as prey items would be associated with the observed adelgid populations. The objective of the research was to identify species of coccinellids associated with one of the native adelgid species, *P. strobi*, and determine the acceptability of alternative prey items, including other adelgids, to the beetles.

MATERIALS AND METHODS

Adelgids examined

Adelgids were collected for the experiments during June and July of 2014. Populations of *A. piceae* infesting subalpine fir (*A. lasiocarpa*), *A. cooleyi* infesting Douglas-fir (*Pseudotsuga menziesii* Franco) and Engelmann spruce (*P. engelmannii* Engelmann), *A. abietis* infesting Norway spruce (*Picea abies*) and Engelmann spruce, *A. lariciatus* infesting cones of western larch (*Larix occidentalis* Nuttall), and *P. strobi* infesting western white pine (*Pinus monticola*) were collected from multiple locations on the campus of the University of Idaho, Moscow, Idaho, USA. For the purposes of clarity, hereafter, all adelgids collected from trees other than western white pine will have an abbreviation for the tree species from which they were collected (subalpine fir: SF; Douglas-fir: DF; Engelmann spruce: ES; Norway spruce: NS; western larch: WS). *A. piceae* were also collected from SF on the St. Joe National Forest, Idaho near Fishhook Creek (47.13143 N, 115.86647 W) and Webfoot Creek (47.13498 N, 115.76623 W) on 15 July and 16 July, respectively. *P. strobi* is anholocylic, not living on spruce and only living freely on pine [1]. Thus, *P. strobi*, as the sole adelgids in the study found on pine, was distinguishable from the other adelgid species. *A. lariciatus* is holocyclic, forming galls on spruce as well as living on larch cones [13]. However, *A. lariciatus* galls can be distinguished morphologically from *A. abietis* and *A. cooleyi* galls, both of which can also be distinguished morphologically from one another [1, 14, 15, 16].

Potential predators

Collection of potential predatory species was opportunistic, but all tree species other than NS were sampled. For each tree that was sampled, branches below approximately 2 m were hit a minimum of five times. Insects deemed to be potential predators were collected as they fell onto a 1.0 m^2 white beating sheet (Ripstop Beating Sheet, BioQuip®). All potential predators were brought to the laboratory where choice tests with various prey species were conducted. Following the experiments, insects that actually preyed upon the various species of adelgids that were presented to them were identified. Voucher specimens of the predators were placed at the William Barr Entomological Museum at the University of Idaho.

Laboratory rearing and prey testing

Potential predators that were captured in the field were transported to the laboratory where they were maintained in arenas (plastic petri dishes with a diameter of 3.5 cm) in a light:dark regimen of 12:12 hours and at a temperature of 25 ^{o}C. Approximately equal pieces of moistened paper towel were placed in each arena to prevent desiccation of the insects. H_2O was applied to the paper towel as needed.

The first set of experiments that occurred throughout the experimental period were no-choice feeding trials that were conducted in arenas (plastic petri dishes with a diameter of 9 cm). Arenas contained pieces of moistened paper towel to prevent desiccation, and individual predators were presented with individual species of prey. Individual prey items that were not consumed were counted and replaced as needed on a daily or 2-day interval.

After establishing which prey species were acceptable and consumed by the predators, these prey species were presented to individual predators in choice trials. For each paired-choice trial, equal numbers of two prey species were placed equidistant from the center of the arena and on opposites sides of a large petri dish (diameter = 9.0 cm). A minimum of four individual predators of the same species that were collected on the same day were placed in individual arenas for each set. Arenas were checked daily, the number and species of prey that remained in each arena were counted, prey of the appropriate species were replaced if they were desiccated or eaten and the petri dishes were rotated 360 degrees. Each set of arenas was run for one week or until all the predators had died or, in the case of immature predators, the measurements were separated into two sets. One set was terminated when larvae pupated, but for the predators that pupated, observations of the individuals continued for the adults following eclosion.

Statistical analyses

In the no-choice trials in which potential predators were only presented with a single prey species, the percentage of each prey species consumed was determined but no statistical comparisons were conducted. The percentage of the total number of individuals consumed by the predators of the various prey species was calculated for each of the potential predators in the choice trials. Paired Student's *t*-tests conducted using STATISTIX® software [17] were used to determine if there were significantly different percentages of individuals selected for one of the prey species presented versus the other.

RESULTS

A total of 139 potential predators from multiple taxa (Table 1) were collected. Predators were collected on all of the targeted tree species, but the majority (n = 126) were found on western white pine

Table 1. Predators, the adelgid prey presented to them, and the tree species from which both were collected are shown. Abbreviations are as follows: for trees, WWP: western white pine (*Pinus monticola*), ES: Engelmann spruce (*Picea engelmannii*), NS: Norway spruce (*Picea abies*), SAF: subalpine fir (*Abies lasiocarpa*), WL: western larch (*Larix occidentalis*), DF: Douglas-fir (*Pseudotsuga menziesii*); for prey, *P.*: *Pineus*, *A.*: *Adelges*; for the rightmost column, +: consumed by the predators, -: not consumed by the predator, NA: not tested on that predator. Note that none of listed predators failed to consume any of the listed adelgids when presented with them. This bears some significance in terms of the generalist nature of these predators. Also note that most predators were collected from WWP.

Predator species	Life stage (adult or immature)	Tree species collected from	Potential prey on the tree	Prey presented in lab (tree collected from)	Consumed (+/-, NA)
Coccidophilus atronitens	adult	WWP	*P. strobi*	*A. abietis* (ES)	+
		WWP	*P. strobi*	*A. abietis* (NS)	+
		WWP	*P. strobi*	*A. cooleyi* (ES)	+
				A. cooleyi (DF)	NA
		WWP	*P. strobi*	*A. lariciatus* (WL)	+
				A. piceae (ES)	NA
		WWP	*P. strobi*	*P. strobi* (WWP)	+
Anthocoridae	adult	WWP	*P. strobi*	*A. abieitis* (ES)	+
		WWP	*P. strobi*	*A. abietis* (NS)	+
		ES	*A. cooleyi*, *A. abietis*	*A. cooleyi* (ES)	+
				A. cooleyi (DF)	NA
				A. lariciatus (WL)	NA
				A. piceae (ES)	NA
		WWP	*P. strobi*	*P. strobi* (WWP)	+
Coccinellidae	larvae			*A. abietis* (ES)	NA
				A. abietis (NS)	NA
		ES	*A. cooleyi*, *A. abietis*	*A. cooleyi* (ES)	+
		WWP	*P. strobi*	*A. cooleyi* (ES)	+
				A. cooleyi (DF)	NA
		WWP	*P. strobi*	*A. lariciatus* (WL)	+
		SAF	*A. piceae*	*A. piceae* (ES)	+
		WWP	*P. strobi*	*P. strobi* (WWP)	+
Mulsantina picta	larvae			*A. abietis* (ES)	NA
		WWP	*P. strobi*	*A. abietis* (NS)	+
				A. cooleyi (ES)	NA
				A. cooleyi (DF)	NA
				A. lariciatus (WL)	NA

Table 1 continued..

Predator species	**Life stage (adult or immature)**	**Tree species collected from**	**Potential prey on the tree**	**Prey presented in lab (tree collected from)**	**Consumed (+/-, NA)**
Mulsantina picta	larvae			*A. piceae* (ES)	NA
		WWP	*P. strobi*	*P. strobi* (WWP)	+
	adult	WWP	*P. strobi*	*A. abietis* (ES)	+
				A. abietis (NS)	NA
		WWP	*P. strobi*	*A. cooleyi* (ES)	+
				A. cooleyi (DF)	NA
		WWP	*P. strobi*	*A. lariciatus* (WL)	+
				A. piceae (ES)	NA
		WWP	*P. strobi*	*P. strobi* (WWP)	+
Neuroptera	larvae	WWP	*P. strobi*	*A. abietis* (ES)	+
		WWP	*P. strobi*	*A. abietis* (NS)	+
		WWP	*P. strobi*	*A. cooleyi* (ES)	+
		WWP	*P. strobi*	*A. cooleyi* (DF)	+
		WWP	*P. strobi*	*A. lariciatus* (WL)	+
		SAF	*A. piceae*	*A. piceae* (ES)	+
		WWP	*P. strobi*	*P. strobi* (WWP)	+
	adult	WWP	*P. strobi*	*A. abietis* (ES)	+
				A. abietis (NS)	NA
				A. cooleyi (ES)	NA
		WWP	*P. strobi*	*A. cooleyi* (DF)	+
				A. lariciatus (WL)	NA
				A. piceae (ES)	NA
		WWP	*P. strobi*	*P. strobi* (WWP)	+

and were associated with *P. strobi*. Given our initial results, more emphasis was placed on collecting predators from western white pine than from the other tree species (Figure 1). The most abundant species of predators that were collected as adults was *Coccidophilus atronitens* and the predators that most readily accepted adelgids as prey items were coccinellid and neuropteran (Chrysopidae and Hemerobiidae) larvae.

There were a total of 33 adult and 14 larval coccinellids collected and tested in no-choice trials. The coccinellids represented five species, namely *Mulsantina picta* (adults and larvae), *C. atronitens* (adults), *C. marginata* (adults), *Scymnus humboldti* (adults), *S. coniferarum* (adults) and *Scymnus* spp. (larvae) (Tables 1, 2, and 3). All five species of coccinellids captured and tested in the no-choice trials accepted adelgids as prey.

Overall, in the no-choice trials, *C. atronitens* adults consumed some of every species of adelgid presented to them, but approximately 37% (7 of the 19 of the individuals tested) did not consume any adelgids (Table 3). Most (n = 14) of the

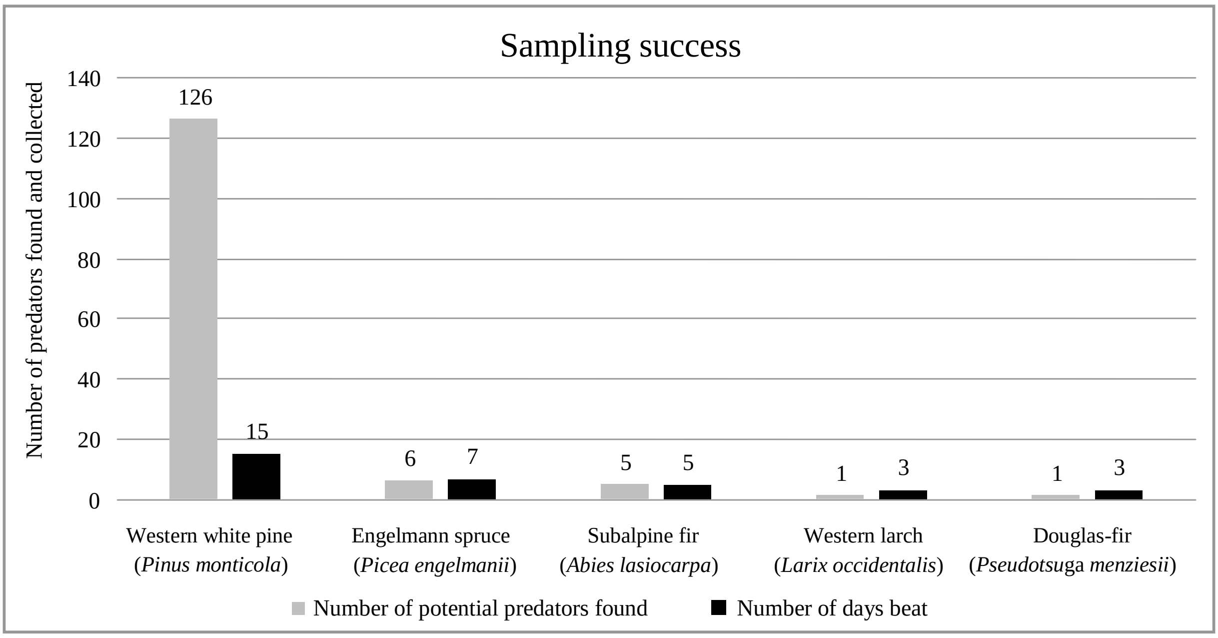

Figure 1. The number of potential predators found and collected and the number of days spent using a beating sheet (representing relative effort) are shown for the different tree species that were sampled. Note that most effort focused on western white pine (*Pinus monticola*), but that this bias was more than justified by the number of predators found on that species. Initially, an attempt was made to sample all of the tree species somewhat evenly; however, western white pine generally became increasingly targeted toward the end of the study.

Table 2. The number of adelgids consumed by individual adult *Coccidophilus atronitens*, *Scymnus coniferarum*, and *S. humboldti* (Coccinellidae) in no-choice trials, the number of days they survived on those adelgids, and the average number of adelgids eaten per day.

Species	Number of days	Total number consumed				Average per day
		Adelges cooleyi	*A. abietis*	*A. lariciatus*	*Pineus strobi*	
Coccidophilus atronitens	6	0				0
C. atronitens	5	5				1
C. atronitens	2		2			1
C. atronitens	12			29		2.42
C. atronitens	7				6	0.86
C. atronitens	8				3	0.38
C. atronitens	7				0	0
C. atronitens	4				5	1.25
C. atronitens	5				6	1.2
C. atronitens	4				4	1
C. atronitens	4				1	0.25
C. atronitens	6				1	0.17

Table 2 continued..

Species	**Number of days**	**Total number consumed**				**Average per day**
		Adelges cooleyi	***A. abietis***	***A. lariciatus***	***Pineus strobi***	
C. atronitens	4				0	0
C. atronitens	5				4	0.8
C. atronitens	5				0	0
C. atronitens	4				0	0
C. atronitens	1				0	0
C. atronitens	5				0	0
Scymnus coniferarum	13	15				1.15
S. coniferarum	2				1	0.5
S. coniferarum	10				7	0.7
S. coniferarum	10			33		3.3
S. humboldti	5	10				2

Table 3. The percentages of various presented adelgid prey consumed by individual *Coccidophilus atronitens* (Coccinellidae) are shown. *A.* stands for *Adelges* and *P.* for *Pineus*. *P. strobi* were collected from western white pine (*Pinus monticola*), *A. abietis* were collected from Engelmann spruce (*Picea engelmannii*), *A. cooleyi*, were collected from Douglas-fir (*Pseudotsuga menziessi*), and *A. lariciatus*, were collected from western larch (*Larix occidentalis*).

Prey species consumed by *Coccidophilus atronitens*	
Prey species presented	**Percent prey consumed**
A. abieitis	40
A. abieitis	40
A. cooleyi	63
A. cooleyi	0
A. lariciatus	66
P. strobi	17
P. strobi	0
P. strobi	71
P. strobi	55
P. strobi	80
P. strobi	25
P. strobi	20

Table 3 continued..

Prey species consumed by *Coccidophilus atronitens*	
Prey species presented	**Percent prey consumed**
P. strobi	0
P. strobi	57
P. strobi	0
P. strobi	0
winged *P. strobi*	0
winged *P. strobi*	0

C. atronitens adults were presented with *P. strobi*, and of these, eight did not feed. The two adult *C. atronitens* that were given winged *P. strobi* did not consume this life stage. In the no-choice trials involving the two species of *Scymnus*, three individual *S. coniferarum* adults each respectively preyed upon *A. cooleyi* (DF), *P. strobi*, and *A. lariciatus* (WL), and the one individual *S. humboldti* adult tested in a no-choice trial preyed upon *A. cooleyi* (DF) (Table 2). The individual *S. coniferarum* that preyed upon *A. lariciatus* (WL) was collected from western larch (*Larix occidentalis*).

In a choice test, *S. coniferarum* adults were provided a choice between *P. strobi* and the scale insect *Chionaspis pinifoliae* (Hemiptera: Diaspididae). In this trial (Table 4), the individual *S. coniferarum* consumed on average 8.10 *P. strobi* compared with 37.38 scale, a nearly significant difference (t = 2.571; df = 5; p = 0.0574). The choice test of a single adult *S. humboldti* resulted in the consumption of 10% of the scale provided and none of the *P. strobi*. This adult *S. humboldti* was one of the only two members of this species collected.

In the choice trials (Table 4 and Figure 2), *C. atronitens* adults significantly preferred *A. cooleyi* to *P. strobi* (t = 3.504; df = 4; p = 0.0248). There was not a significant difference between the number of *A. abietis* consumed compared with the number of *P. strobi* consumed. There was also not a significant difference between the number of *A. cooleyi* consumed compared with the number of *A. abietis* consumed. More scale insects were consumed than *P. strobi* when they were presented together (t = 2.160; df = 13; p = 0.1933). The two *C. atronitens* adults that were tested consumed relatively equal numbers of *A. abietis* and *A. cooleyi*.

DISCUSSION

The implementation and utilization of natural enemies against invasive pests usually include the introduction of those enemies from the pest's area of origin, a tactic referred to as classical biological control. However, native populations of natural enemies may also prey upon the invasive pests and any impact they may have on population growth by those organisms should be beneficial. While predators that can develop entirely on the identified pest species are desirable for use as biocontrol agents, a native species that is capable of preying upon a non-native pest could supplement management activities by helping to lessen damage.

Table 4. Paired-choice trials were performed on three coccinellid beetle species, five trials on *Coccidophilus atronitents*, one on *Scymnus coniferarum*, and one on *S. humboldti*. *C. atronitens* significantly preferred *Adelges cooleyi* over *P. strobi* (t = 3.504; df = 4; p = 0.0248). *S. coniferarum* consumed more scale with near significance (t = 2.458; df = 5; p = 0.0574). Abbreviations for trees, WWP: western white pine (*Pinus monticola*), ES: Engelmann spruce (*Picea engelmannii*), NS: Norway spruce (*Picea abies*), SAF: subalpine fir (*Abies lasiocarpa*), WL: western larch (*Larix occidentalis*), DF: Douglas-fir (*Pseudotsuga menziesii*).

Coccinellidae choice trial stats					
Predators	**Adelgids (tree collected from)**	**mean % consumed**	**t-value**	**d.f.**	***p***
Coccidophilus atronitens	*P. strobi* (WWP)	13.41	2.776	4	0.0687
	A. abietis (ES)	31.69			
C. atronitens	*P. strobi* (WWP)	11.50	2.776	4	0.0248
	A. cooleyi (ES)	36.46			
C. atronitens	*A. cooleyi* (ES)	46.67	3.182	3	0.1834
	A. abietis (NS)	12.50			
C. atronitens	*P. strobi* (WWP)	19.88	2.160	14	0.1933
	scale (WWP)	34.32			
C. atronitens	*A. abietis* (NS)	12.50	n/a	1	n/a
	A. cooleyi (ES)	12.50			
Scymnus humboldti	*P. strobi* (WWP)	0	n/a	n/a	n/a
	scale (WWP)	10			
S. coniferarum	*P. strobi* (WWP)	8.10	2.571	6	0.0574
	scale (WWP)	37.38			

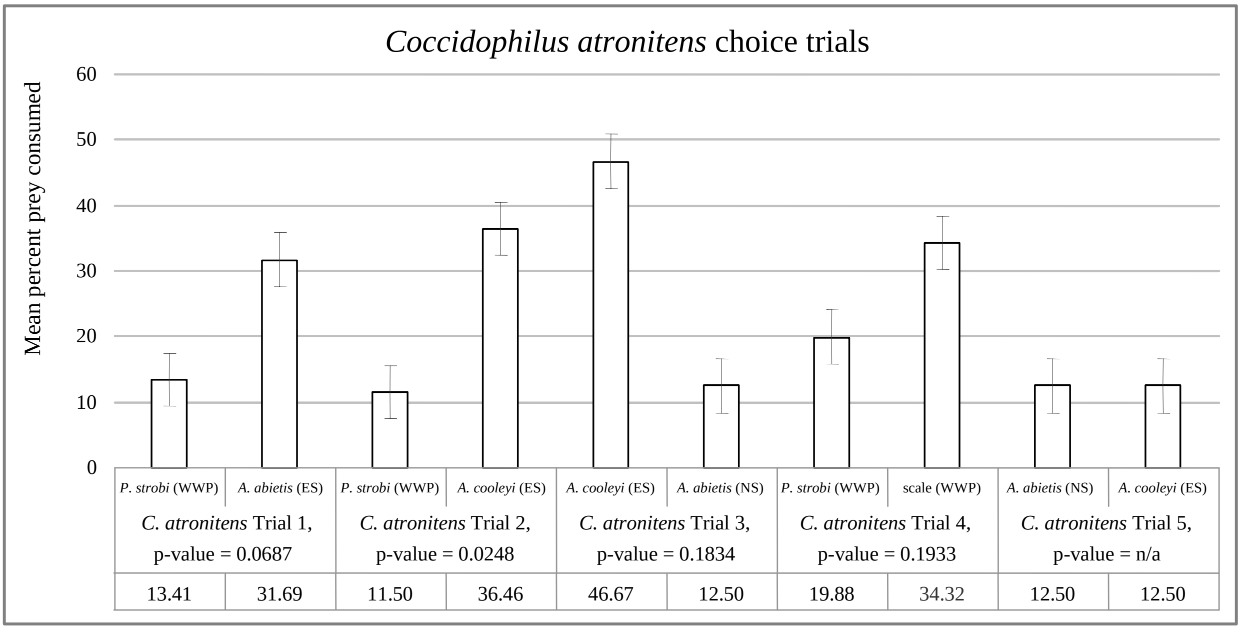

Figure 2. Mean percent prey consumed by *Coccidophilus atronitens* (Coccinellidae) in five choice trials and their respective *p*-values (except the trial represented on the right because it had a sample size of two) are shown. Error bars represent standard errors. *P.* stands for *Pineus* and *A.* for *Adelges*.

Following our initial efforts at collecting potential adelgid predators from various tree species, we subsequently focused more of our efforts on collecting from *Pinus monticola*, which probably explains the preponderance of individual predators (n = 126) associated with *Pineus strobi* (Figure 1). However, the number of predators found relative to sampling effort validates the emphasis we placed on collecting from western white pine.

Coccinellids, including some species in the genus *Scymnus*, have been used in efforts to develop an effective biocontrol program against specific species of adelgids such as *A. tsugae* [18]. In the current study, we found that one native species of *Scymnus*, *S. coniferarum*, that had been reported to be a specialist predator of scale insects (Hemiptera: Diaspididae) [19, 20] would readily accept multiple species of adelgids including *A. lariciatus*, *A. piceae*, and *P. strobi* as prey items. Another native species of *Scymnus* that had also been reported to be a scale specialist, *S. humboldtii* [19, 20], preyed on *A. cooleyi*. A third coccinellid *C. atronitens* also consumed adelgids when they were presented as potential prey items, although the species had not previously been reported to prey upon adelgids. *C. atronitens* has been found in association with *Tsuga heterophylla* and *A. tsugae* [12], but was not reported to be a predator of this adelgid. As with the *Scymnus* spp., *C. atronitens* is a predator that feeds on scale insects and has been reported to be the predator likely to suppress population densities of *Chionaspis pinifoliae* (Fitch) [19].

In the current study, *M. picta* was willing to accept free-living *A. lariciatus* and *P. strobi* from their respective alternate hosts (WL and WWP) as prey. When presented with *A. abietis* or *A. cooleyi* that had been removed from their galls, *M. picta* readily fed on these two species as well. In a prior study, *M. picta* was reported to be the second-most common predator found in association with *A. tsugae*, accounting for 83% of the coccinellid larvae captured [12]. Another report considered *M. picta* to be a predator that specializes in feeding upon conifer-infesting insects by demonstrating it to have longer residence time within patches associated with conifers when compared with a more generalist coccinellid predator [21].

CONCLUSION

The current study suggests that native predators that have been considered to specialize on small hemipterans other than adelgids may be capable of utilizing adelgids as prey. Novel predation by coccinellids was demonstrated on the invasive *A. piceae*, as well as on *P. strobi* and *A. lariciatus*, both species that, though native, can be economically harmful [3, 13, 15]. Many of these small coccinellids have not been thoroughly investigated for the breadth of prey they are willing to accept. Therefore, the overall population of predators in the environment should be evaluated to identify their potential acceptance and impact on pest species other than those they normally prey upon.

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CONFLICT OF INTEREST STATEMENT

The work reports the results of research and does not represent an endorsement of any of the products used. None of the authors have personal or financial associations with companies or their products.

REFERENCES

1. Havill, N. P. and Foottit, R. G. 2007, Annu. Rev. Entomol., 52, 325-349.
2. Furniss, R. L. and Carolin, W. M. 1977, USDA-For. Serv. Misc. Publ. No. 1339.
3. Rose, A. H. and Lindquist, O. H. 1973, Canad. For. Serv. Publ., 1313.
4. Hain, F. P. 1988, In Dynamics of Forest Insect Populations, Plenum Press, pp. 87-109.
5. Mitchell, R. G. and Buffam, P. E. 2001, West. J. Appl. For., 16, 121-126.
6. Hudak, J. and Singh, P. 1970, Plant Distrib. Surv., 50, 99-101.
7. Livingston, R. L., Dewey, J. E., Beckman, D. P. and Stipe, L. E. 2000, West. J. Appl. For., 15, 227-231.
8. Davis, M. 2003, Bioscience, 53, 481-489.
9. Ziska, L. H., Blumenthal, D. M., Runion, G. B., Hunt Jr., E. R. and Diaz-Soltero, H. 2010, Climat. Change, 105, 13-42.
10. Bertelsmeier, C., Luque, G. M. and Courchamp, F. 2013, Conserv. Biol., 27, 1458-67.
11. Obrycki, J. J. and Kring, T. J. 1998, Annu. Rev. Entomol., 69, 295-321.
12. Kohler, G. R. 2007, M. S. Thesis, Dept. For. Sci., Oregon State University.
13. Forest Genetics Council of British Columbia, Cone and Seed Insect Pest Leaflet No. 9.
14. Cook, S. P., Merickel, F., Ward, K. and Havill, N. 2012, Pan-Pac. Entomol., 88, 435-436.
15. Cummin, M. 1968, Can. Entomol., 100, 113-126.
16. Fay, P. A., Preszler, R. W. and Whitham, T. G. 1996, Oecologia, 105, 199-204.
17. Analytical Software. 2009, Tallahassee, Florida, USA.
18. McClure, M. 2001, USDA-For. Serv. For. Health Tech. Enter. Team.
19. Cooper, D. and Cranshaw, W. 1999, J. Kans. Entomol. Soc., 72, 131-133.
20. Cranshaw, W. S. 2014, Color. State Univ. Fact Sheet No. 5.514.
21. Sloggett, J. J. 2008, Proc. Neth. Entomol. Soc. Meet., 19, 95-113.