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Jeffrey C. Miller

The known biology of *Bareogonalos canadensis* (Harrington) is based on literature records of six collections from three areas in the Pacific Northwest. The objective of this study was to obtain fundamental knowledge on the biology of *B. canadensis*, especially its distribution, abundance, and host species, as well as its potential for biological control of yellowjackets. This was accomplished by analyzing yellowjacket colonies from the Willamette Valley and the adjacent Coast Range forest.

In 1986 and 1987 *B. canadensis* was found in 50 of 89 yellowjacket colonies collected from the Coast Range foothills of Oregon bordering the Willamette Valley. No *B. canadensis* were found in 103 colonies collected in the Willamette Valley. The parasitoid was reared from colonies of *Vespula vulgaris* (L.), *V. pensylvanica* (Saussure), *V. atropilosa* (Sladen) (new host record), *V. consobrina* (Saussure) (new host record), and *Dolichovespula arenaria* (F.), but was absent in nests of *D. maculata* (L.). Significant control of nests or worker populations was not shown. Females were found to oviposit primarily in Douglas-fir needles [*Pseudotsuga menziesii* (Mirb.) Franco] but also in other foliage including western hemlock [*Tsuga heterophylla* (Raf.) Sarg.], huckleberry (*Vaccinium parvifolium* Smith), and snowberry [*Symphoricarpos albus* (L.) Blake]. They did not oviposit in leaves of grass (*Poa* sp.), cultivated bean (*Phaseolus vulgaris* L.), or pitch pine (*Pinus resinosa* Ait). All collections of this parasitoid came from areas with Douglas-fir.

The taxonomic history of the Trigonalyidae is presented. It was shown that the holotype of *B. canadensis* had its labels switched with an autotype, and another autotype is mislabeled as the holotype. A note on the yellowjacket parasitoid *Sphecophaga vesparum burra* (Cresson), and a list of trigonalyid species, hosts, and distribution are given as appendices.

Biology of the Yellowjacket Parasitoid *Bareogonalos canadensis* (Harrington) (Hymenoptera: Trigonalyidae)

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David Carmean

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Associate Professor of Entomology, Dr. J. C. Miller
in Charge of Major

Redacted for Privacy

Chairman of Department of Entomology, Dr. R. Berry

Redacted for Privacy

Dean of Graduate School

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INTRODUCTION

Trigonalyidae occur in most tropical and temperate regions but are seldom collected. Their complex life cycle results in mass mortality of their eggs and young larvae. All known members of the family oviposit in or on foliage, and with the possible exception of some members of an Australian genus, _Taeniogonalos_ Schulz, require an intermediate host to gain access to the final host. The leaves bearing the eggs are ingested by an intermediate host caterpillar or sawfly. The eggs then hatch inside the gut of the intermediate host. If the intermediate host is parasitized by an ichneumonid wasp or a tachinid fly, or fed to the larva of a vespid wasp, the parasitoid or the vespid larva then becomes the ultimate host of the trigonalyid. Otherwise the trigonalyid larvae die in the intermediate host (Clausen 1940).

Before 1950, the yellowjacket parasitoid _Bareogonalos_ _canadensis_ (Harrington) was known only from three locations near southern Vancouver Island, British Columbia, all from around the turn of the century (Harrington 1896, Taylor 1898, Townes 1956). In 1951, a specimen was found in northwestern Washington less than 35 km from Vancouver Island (M.C. Day, pers. comm., 1988). Then, in northern California in 1961, a single female was reared from a nest collected from Sonoma County (Stage and Slobodchikoff 1962), and in northern Idaho in 1979, 27 females and 29 males were reared from three adjacent nests collected in the forest at about

1000 m (Carmean et al. 1981).

Host yellowjackets are found throughout temperate regions of the Northern Hemisphere while *B. canadensis* has only been found in western North America. Therefore, yellowjacket distribution does not limit *B. canadensis* distribution. The small number of collections is probably an artifact due to limited collecting of yellowjackets and not representative of the actual distribution. One objective of this study was to determine some of the factors that may limit *B. canadensis* distribution.

The ability of *B. canadensis* to disperse is limited by their weak flight and their short life. Yellowjackets rarely forage more than 1000 m from their nests (see Akre et al. 1975, 1981). While being passively dispersed by the wind, intermediate host caterpillars may carry *B. canadensis* larvae. It is unlikely that humans would cause much dispersal, as most nests that are attached to any transported item are normally destroyed and foliage containing eggs is not likely to be transported where it would be available to intermediate hosts.

I looked at two aspects of the distribution of *B. canadensis*: the known distribution of the species from previous collections and the localized distribution of the species in western Oregon. I also observed oviposition behavior, different plants used for oviposition, and differing rates of parasitism for several host species of yellowjackets. Nests of other possible hosts were also examined for *B. canadensis*.

Literature Review

The most important works on the systematics of Trigonalyidae are by Schulz (1906, 1907b) and Bischoff (1938). Schulz split the family into five subfamilies with 17 genera (Table 1); only four genera were described previous to the turn of the century. His monograph (1907b) included keys to subfamily and genera and three color plates. Bischoff (1938) reviewed the family and recognized three additional genera described since Schulz (1907b) and synonymized one subfamily. Bischoff included a bibliography, host and distribution, but no descriptions, keys, or figures. The classification by Bischoff with additions of recent authors is presented in Table 2.

For North America the most important recent work is by Townes (1956). Townes (1956) included a key and biological information for the four species found north of Mexico, made *Lycogaster nevadensis* (Cresson) a subspecies of *L. pullata* Shuckard, and transferred *L. costalis* (Cresson) to the genus *Poecilogonalos* Schulz.

The biology of Trigonalyidae is covered by Clausen (1929, 1931, 1940) and Riek (1970).

Table 1. Schulz's 1907 classification of Trigonalyidae.

Subfamily	Genus Author	No. Species
Trigonaloinae	Pseudogonalos Schulz 1907	2
	Discenea Enderlein 1905	1
	Trigonalys Westwood 1835	1
	Orthogonalys Schulz 1905	1
	Mimelogonalos Schulz 1907	1
	Poecilogonalos Schulz 1906	1
	Nanogonalos Schulz 1906	1
Lycogastrinae	Lycogaster Shuckard 1841	7
	Stygnogonalos Schulz 1907	1
	Ischnogonalos Schulz 1907	1
	Labidogonalos Schulz 1906	2
	Tapinogonalos Schulz 1907	2
	Taeniogonalos Schulz 1906	4
Seminotinae	Seminota Spinola 1840	6
	Xanthogonalos Schulz 1907	2
Bareogonaloinae	Bareogonalos Schulz 1907	2
Nomadininae	Nomadina Westwood 1868	4

Source: Schulz, W.A. 1907. Hymenoptera, Fam. Trigonaloidae. Genera Insectorum fasc. 61: 24pp.

Table 2. Trigonalyidae classification from Bischoff with revisions from recent authors.

Subfamily	Genus (No. Species)	Distribution[1]	Hosts[2]
Trigonaloinae	*Pseudogonalos* (2)	Eurasia	I
	Discenea (3)	Africa	
	Trigonalys (1)	S America	
	Orthogonalys (8)	N, S Am, As, Af	T
	Mimelogonalos (6)	Australia	
	Satogonalos (4)	Asia	
	Poecilogonalos (15)	N Am, As	T,I
	Nanogonalos (5)	S Am, As	
	Lycogaster (10)	N, C Am, As	I,E
	Lycogastroides (3)	Africa	
	Lycogonalos (1)	Asia	
	Stygnogonalos (1)	C America	
	Ischnogonalos (1)	Asia	
	Labidogonalos (4)	C America	P
	Tapinogonalos (4)	Africa	
	Taeniogonalos (11)	C, S Am, As, Au	S,I
Seminotinae	*Seminota* (6)	Central, S Am	P,Pb
	Xanthogonalos (3)	Central, S Am	
Bareogonaloinae	*Bareogonalos* (4)	N Am, Asia	V
Nomadininae	*Nomadina* (5)	S America	Pb
	Bakeronymus (1)	Asia	Pb
	Pseudonomadina (1)	Asia	R

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[1] Af, Africa; Am, America; As, Asia; Au, Australia. C, Central.

[2] E, Eumeninae; I, Ichneumonidae; P, *Polistes*; Pb, Polybiini; R, Ropalidini; S, *Perga* Sawfly; T, Tachinidae; V, Vespinae.

Major source: Bischoff, H. 1938. Trigonaloidae. Hymenopterorum Catalogus pars 5: 1-18.

Taxonomic Position of the Trigonalyidae

The taxonomic position of this group has been controversial since the genus *Trigonalys* was described by Westwood in 1835. Townes (1956) said they are "aberrant wherever placed." This is because some of their characteristics (e.g. antennae usually with 16 or more segments, trochanters two segmented) are similar to the Parasitica while others (e.g. complete wing venation, supposedly reduced ovipositor) are closer to the Aculeata. Westwood (1835), in the description of the type genus, said they looked like a male velvet ant (*Mutilla*) with the antennae of a *Pamphilius* sawfly and the wings of an ant (*Myrmosa*). He further wrote "Genus anomalum familiae dubiae," and in 1840 gave further comments about them under the Mutillidae.

Shuckard (1841) said the affinities of the genus "seem to have perplexed, without any reason, an English entomologist of some repute" and went on to say "Mr. Westwood should not have been long in doubt" about their correct placement and gave his reasons, based on the antennae and trochanters, why the genus was not in the Aculeata. He then formed the family Aulacidae from *Aulacus*, *Trigonalys*, and his new genus *Lycogaster*. Westwood (1841a) answered in defense that he had long known that they were Parasitica, and others had made the same mistake. Westwood (1841b) then placed the genus in the Evaniidae with *Aulacus*, *Stephanus*, and *Megalyra*.

Disagreement continued into the twentieth century. Cresson (1887) created the family Trigonalidae (his spelling) and placed it between the Evaniidae and the Ichneumonidae. Ashmead (1902) put the family in the Vespoidea in the Aculeata but about the same time Viereck (1914) placed them with the Ichneumonoidea in the Parasitica. Townes (1956) felt the family was best placed in the Chrysidoidea (including Bethyloidea) (Aculeata). Oeser (1962) showed the ovipositor of Pseudogonalos (Trigonalis) hahni (Spinola) is not reduced, and that this and the socii (cercus-like appendages on the 10th segment), are not features of aculeates. However, though keeping them with the Parasitica, Yamane (1973) found the head of the final larval instar of Bareogonalos jezoensis (Uchida) closer to the Aculeata than the Parasitica. A standard text placed them in the Bethyloidea (Aculeata) (Borror, Delong, and Triplehorn 1976). Koenigsmann (1976) showed flaws in assigning certain relationships but did not go beyond placing Trigonalyidae into the Parasitica. Masner (1979) said they were "early stock of primitive aculeate Hymenoptera." Rasnitsyn (1980) placed them in the Ceraphronoidea (Parasitica). Gibson (1985) found "no derived states to support classifying trigonalids... with ceraphronids and megaspilids." He did say that, in excluding trigonalyids, that megalyrids, ceraphronids, and megaspilids could constitute a superfamily. The least controversial treatment seems to place the Trigonalyidae in their own superfamily in the Parasitica as Krombein et al. (1979) and Riek (1970) have done. No sister group is currently proposed for them.

Etymology of Trigonalyidae

Eight years after describing the genus Trigonalys, Westwood (1843) said that "the genus is named in allusion to the triangular form of the second submarginal cell."

Cresson (1887) was the first worker to recognize a family based on the genus Trigonalys, and named it the Trigonalidae. Since Cresson (1887) several variations of spelling have been proposed. Krieger (1894) used the spelling Trigonalyidae. Schulz (1907b) unjustifiably emended Westwood's spelling of "Trigonalys" to "Trigonalos" and changed the family name to "Trigonaloidae." Since then most American workers have continued to use Cresson's spelling while other nationalities have been divided between Trigonalidae and Trigonaloidae. Oehlke (1983) showed that the stem of the type genus is Trigonaly- and not Trigonal- so the family name should be Trigonalyidae.

The genus Bareogonalos was described by Schulz (1907b) from two North American species, Trigonalys canadensis Harrington and Trigonalys scutellaris Cameron (=T. flavonotata Cameron). The morphological characters Schulz used to divide the family included the thickness and number of antennal segments and the shape of the mouth parts. This latter character, which in Bareogonalos Schulz called 'schnabelfoermig' or beak-shaped, is not apparent, even when compared with other members of the family.

Schulz's 1907 description of the genus Bareogonalos gives no derivation of the name, however, two specimens at the Humboldt Museum (Berlin) bear his determination labels with the spelling "Barygonalos." Thus, I suggest that "bareo" is derived from "bary." "Bary" is a common root for many genera and is Greek for heavy. Other trigonalyid genera described in the same monograph have similar Greek roots: Ischnogonalos (ischno- lean), Mimelogonalos (mime- mimic), Nanogonalos (nano- dwarf), Poecilogonalos (poecilo- variegated or many colored), Pseudogonalos (pseudo- false), Stygnogonalos (stygno- hatred), Taeniogonalos (taenio- band), Tapinogonalos (tapino- low), Xanthogonalos (xantho- yellow). Schulz (1908), when re-describing several of these genera, gives these as prefixes and states -gonalos is the usual ending for names of trigonalyid genera.

Taxonomic History of Bareogonalos

Since Schulz (1907b) revised the family there have been two Asian species described in the genus. Uchida (1929) described the genus and species *Nippogonalos jezoensis* from northern Japan, and Bischoff (1938) sunk *Nippogonalos*, placing the species in *Bareogonalos*. Vecht (1934) found *B. jezoensis* in large numbers in Java, Indonesia. I know of no collection localities between these areas. Yamane and Yamane (1975) expected to find *B. jezoensis* in Taiwan and instead found a species they described as *Bareogonalos huisuni* (Table 3). Like males of *B. scutellaris*, *B. huisuni* does not have a pyramidal postscutellum. Yamane is working on the phylogeny of trigonalyids attacking social Hymenoptera and is describing a new genus for *Bareogonalos huisuni* (Sk. Yamane, pers. comm., 1986).

Table 3. Collections of *Bareogonalos*.

B. canadensis

Year	No., Sex	Host	Location	Reference
1893	1M	*D. arenaria*[1]	SW B.C.	Harrington 1896
1897	23F, 4M	*V. pensylvanica*	SW B.C.	Taylor 1898
1908	1M	?	SW B.C.	Townes 1956
1951	1M	?	NW Wash.	British Museum
1961	1F	*D. arenaria*	N Calif.	Stage & Slobodchikoff 1962
1979	29M, 27F	*V. vulgaris* *V. acadica*	N Idaho	Carmean et al. 1981

B. scutellaris[2]

Year	No., Sex	Location	Reference
?	2M	Omilteme (8000ft), Guerrero, Mexico	Cameron 1897
?	1F	Xucumanatlan (7000ft), Guerrero, Mexico	Cameron 1897

B. jezoensis

Year	No., Sex	Location	Reference
1904	F (Holotype)	Hokkaido, Japan	Uchida 1929
1928	M (Allotopotype)	Hokkaido, Japan	Uchida 1929
1932	"multitude"	Puntjak-Pass, (1200-1500 m) West-Java	Vecht 1934
1930-1972	23M,9F +immatures	Hokkaido	Yamane 1973
1983	6F +immatures	Honshu, Japan	Ono 1987

B. huisuni

Year	No., Sex	Location	Reference
1973	3M, 2F	Kwantau-Shih (720-1100 m), Nantou, Taiwan	Sk. and S. Yamane 1975

[1] Originally given as *Vespa occidentalis* (=*Vespula pensylvanica*). See text.

[2] One male at Humboldt, and two syntypes of *T. scutellaris* (one minus abdomen) and a type of *T. flavonotata* at British Museum.

Bareogonalos scutellaris (Cameron) was collected in Mexico in the nineteenth century at 2100 m and 2450 m (7000 and 8000 ft) above sea level (Table 3). Schulz (1907a, b) placed *scutellaris* in *Bareogonalos* and synonymized *Trigonalys flavonotata* Cameron with *B. scutellaris*.

Bareogonalos canadensis was first collected from a yellowjacket nest located on a veranda in Victoria, B.C., Canada (Harrington 1896) (Table 3). According to Harrington, Fletcher, who was President of the Entomological Society of Ontario and a regular visitor to British Columbia, received the specimen (a male) in September, 1893, and gave it to Harrington, who described the species from the one specimen in 1896. Harrington (1896) said the holotype "was taken from the cell of a wasp (probably *Vespa occidentalis* [=*Vespula pensylvanica*]) which had built on his [Mr. Wilkinson of Victoria] verandah." His information was third hand and written three years after Fletcher received the holotype. Taylor (1898) said the host of the holotype "had built a suspended nest on the underside of a veranda roof" and Harrington (1898) responded that "Mr. Taylor suggests that the wasp from whose nest the Victoria female[sic] was taken was *V. fernaldi*, Lewis [=*Dolichovespula arenaria*], but I have not seen any examples of that species from Victoria." If Taylor was correct in saying the nest was suspended it was very likely *D. arenaria*, which is common in Victoria (Buckell and Spencer 1950). Harrington (1896) also mentions the presence "of a smaller species of hymenopteron," which would most likely be *Sphecophaga vesparum burra* (Cresson), and which is occasionally found with *D. arenaria* but rare with *Vespula pensylvanica* (Saussure) (MacDonald et al. 1975, Greene et al. 1976, Carmean et al. 1981).

In October 1897 the Reverend George Taylor, a serious amateur naturalist living about 120 km north of Victoria, collected a series of B. canadensis emerging from two V. pensylvanica nests (Taylor 1898). He discussed adult behavior outside the nests and published records of the date, time, and gender of specimens emerging. However, he misidentified their gender and stated that "Harrington's type was a female" (Taylor 1898). In an addendum, Harrington (1898) unfortunately agreed with the mistaken identification of gender by Taylor.

Additional collections of B. canadensis consist only of four sites involving 59 individuals (Table 3). Two males were collected in 1908 and 1951, the first at Departure Bay, Vancouver Island, (probably by Taylor, as he worked at Departure Bay from 1907 until his death in 1912) and the other at Crescent Lake, Washington State (35 km south of Vancouver Island) (M.C. Day, pers. comm., 1988,). In 1961 a female was reared from a nest of D. arenaria collected in Sonoma County, California (Stage and Slobodchikoff 1962). In 1979, 56 B. canadensis were reared from three parasitized yellowjacket nests within 3 m of each other in the woods of northern Idaho (Carmean et al. 1981). They reported on observations of behavioral interactions between yellowjacket workers and emerging B. canadensis in the nest, differences between individuals from reproductive cells and worker cells, and the protective pupal cap.

The Sex and Deposition of the Holotype

Attempts to correct presumed mistakes have led to a quandary with the holotype of B. canadensis. Evidence suggests that the holotype and autotype at the Zoologisches Museum der Humboldt-Universitaet (Humboldt), Berlin, have had their locality labels switched, and also suggests that two specimens at the Canadian National Collection (CNC), Ottawa, labeled holotype and paratype are both autotypes. These mistakes apparently occurred because later workers tried to make the specimens and labels fit Harrington's (1898) mistaken identification of sex.

Harrington (1896) described B. canadensis from the only specimen known at the time (thus the holotype by monotypy), a male collected in 1893 in Victoria, British Columbia, Canada. Taylor (1898) detailed the collection of 23 males and 4 females from Gabriola Island, British Columbia, in October 1897. Comparison of specimens from this series with the description (Taylor 1898), showed he actually collected 23 females and 4 males (Table 4). As mentioned, Harrington (1898) agreed with Taylor's mistaken determination of gender. He wrote that the male "differs in general appearance from the female, chiefly in the larger and broader abdomen, which makes it look more robust." This is the opposite of what is correct. Harrington also incorrectly stated that the holotype was a female and described the "male" sex using three females (autotypes) from the series collected by Taylor. Except for Schulz (1907b), subsequent workers (Bischoff 1938, Townes 1956, Carlson 1979, Sarazin 1986) have described the holotype as a female.

Schulz (1907a) received "the typical pair" from Harrington. This pair with type labels, plus an additional pair, are now at Humboldt. The male type has labels that read: "Gabriola Isd. B.C., Taylor, 24-10-97 [Taylor's handwriting]/Trigonalys canadensis Harrington, Type ♂ [Harrington's handwriting]/Zool. Mus., Berlin. [printed label]." The type female labels read: "Victoria V.I. [no date, Harrington's handwriting]/ Trigonalys canadensis Harrington, Type ♀ [Harrington's handwriting]/ Zool. Mus., Berlin. [printed label].

The labels of these two type specimens are inconsistent. The current deposition of all four males from Taylor's series is known; the type male at Humboldt is in addition to these four (see Table 4). Taylor listed four "males" (actually four females) collected on 24-10-97, and the current location of three of these is known (Table 4). The simplest explanation is that at some point the two type specimens at Humboldt had their labels switched and if the locality labels of these two type specimens were switched back, all four females collected on 24-10-97 would be accounted for, and the male would match the description of the holotype in Harrington (1896).

Table 4. Specimens of *Bareogonalos canadensis* from Gabriola Island, B.C., Canada, collected in October, 1897.

Date[1]	Number, Sex[1]	Deposition
21 Oct	9 females	3 at CNC (1 with yellow paratype label[2])
		1 Townes (1956)
22 Oct	3 females	
	3 males	2 at CNC
		1 at Humboldt
23 Oct	2 females	1 at CNC
24 Oct	4 females	2 at CNC
		1 at Humboldt
		female at Humboldt with Victoria label (no date) believed to be autotype from this date[3]
		(male at Humboldt with this date believed to be holotype[3])
25 Oct	2 females	2 at CNC
	1 male	Townes (1956)
26 Oct	2 females	1 at CNC
		1 at Washington State University
27 Oct	1 female	CNC (With a red holotype label[2])

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[1] This information from Taylor (1898) but corrected for gender.

[2] Type labels at CNC appear to be added after 1950 to autotypes.

[3] Labels of these two specimens switched (see text).

The problems with labels and the holotype were not limited to Germany. Sarazin (1986) reported that the holotype of B. canadensis is deposited in the CNC. This was based on a female specimen labeled: "Gabriola Isd., B.C. Taylor, 27-10-97 [in Taylor's handwriting; reported by Sarazin as 27-IX-93]/Trigonalys canadensis, Harr. Type ♂, [Harrington's handwriting]/ HOLOTYPE [printed, red paper], Trigonalys canadensis Harr. No. 2367 [handwritten]." This specimen, and another female with a yellow paratype label, are the remaining two of the three autotypes (Harrington 1898). The origin of the holotype and paratype labels is unclear. Townes (1956) mentioned he saw the B. canadensis specimens at the CNC but did not mention any erroneous labels. He stated that the holotype of B. canadensis was lost. Harrington (1896) and Taylor (1898) clearly stated that the holotype came from Victoria, and Harrington (1896) said that the holotype was received in September 1893. He did not say it was collected at that time. It is therefore consistent that the holotype did not have a date associated with it.

This accounts for the holotype (Harrington 1896) and three female autotypes (Harrington 1898) of B. canadensis. The holotype has been damaged since the description; only the pedicel and scape of the antennae remain attached, 13 segments of the right antenna (missing the final three segments) are glued to the right eye and scape. The middle left leg is broken between the two trochanters, and the middle right leg and hind legs are missing the last tarsomeres and tarsal claws. The right front wing is torn around the subcostal vein, and the left front wing is torn in the anal region. The lack of pubescence on the frons (normally very pubescent) matches the holotype description.

Hosts of Trigonalyidae

Only 19 of 99 species of trigonalyids have known hosts (see Appendix). Two species are known as hyperparasites of tachinids and five of ichneumonids. Ten are known from various types of wasps including one that has been collected from ichneumonids parasitic on Lepidoptera and solitary wasps. *Taeniogonalos maculata* (Smith) of Australia, a parasite of the sawflies *Perga nemoralis* Wilson and *P. dorsalis* Leach, and possibly other species of the genus, are the only trigonalyids believed not to have an intermediate host. The first trigonalyid shown to be parasitic was *Seminota depressa* (DeGeer) which was found in a nest of *Polistes lanio* F. (Smith 1851). This fueled speculation about hosts of other species and made Dours (1874) speculate that yellowjackets were the host of the European trigonalyid *Pseudogonalos hahni*. This suggestion has, as Reichert (1911) put it, been dragged though the literature. *Pseudogonalos hahni* has been reared only from Lepidoptera pupae parasitized by ichneumonids. Still, yellowjackets have been called hosts of *P. hahni* by Clausen (1940) and Thompson (1958).

Ten different genera of vespoid wasps are known to be hosts of 10 species (6 genera) of trigonalyids (Table 5). *Lycogaster p. pullata* and *L. p. nevadensis* are known from a caterpillar provisioning-wasp and from ichneumonid parasites of caterpillars (Carlson 1979).

Table 5. Wasp hosts of Trigonalyidae.

Wasp	Trigonalyid Genus
Eumeninae	
Euodynerus	*Lycogaster*
Polisitinae	
Ropalidini	
Ropalidia	*Pseudonomadina*
Polybiini	
Stelopolybia	*Nomadina*
Polybia	*Nomadina*
Parachartergus	*Seminota*
Parapolybia	*Bakeronymus*
Polistini	
Polistes	*Seminota*
Vespinae	
Vespa	*Bareogonalos*
Vespula	*Bareogonalos*
Dolichovespula	*Bareogonalos*

Yellowjacket Biology

Yellowjacket colonies are normally annual. A solitary inseminated queen initiates a nest in the spring. She forages for food (mostly live insects) and paper until her workers take over these functions. The colony rapidly increases in size and eventually starts producing reproductives. Only mated queens overwinter, the workers and original queen usually die. The biology of yellowjackets and other vespoid wasps was covered by Spradbery (1973) and Edwards (1980). Keys and information on North American species are found in Akre et al. (1981). A bibliography of yellowjackets was given by Akre et al. (1974). The classification and names used here follow Akre et al. (1981) and Carpenter (1987).

Yellowjackets (*Vespula* Thomson, including *Paravespula* Bluethgen, and *Dolichovespula* Rohwer) are endemic to the Holarctic region of the world (with the exception of extremely cold or dry areas) and hornets (*Vespa* L.) are endemic to Asia, Europe, and North Africa, while trigonalyids parasitic on them have only been found in western North America and eastern Asia. These three genera have all served as hosts for *Bareogonalos* (Yamane 1973). The host of *B. scutellaris* is not known. Of the social Vespidae, Polybiini [*Mischocyttarus* spp., *Brachygastra mellifera* (Say), and *Polybia* spp.], Polistini (*Polistes* spp.), and Vespinae [*Vespula squamosa* (Drury)] are found in the same region of Mexico that *B. scutellaris* was collected.

Prey of Yellowjackets and the Intermediate Host of B. canadensis

No intermediate host of Bareogonalos has been identified. Based on what is known about other members of the family, it is assumed that yellowjacket larvae are infected with B. canadensis by being fed an intermediate host that has fed on leaves containing B. canadensis eggs. This intermediate host is brought into the yellowjacket nest by workers and must be a chewing insect that ingests the trigonalyid egg with the foliage. It is most likely a caterpillar or sawfly larva, but may be a beetle, a grasshopper, or a detritivore. Other species of trigonalyids are known to have Lepidoptera from several families as intermediate hosts, and one of these has also been reared from a tachinid parasitic on a tipulid detritivore (Gelhaus 1987).

Douglas-fir [Pseudotsuga menziesii (Mirb.) Franco] was shown in this study to be an important plant for B. canadensis oviposition, and it would follow that the intermediate host of B. canadensis would be a foliage feeder of Douglas-fir. Furniss and Carolin (1977) list caterpillars, sawflies, and a few adult beetles as the only chewing insects feeding on mature Douglas-fir foliage and a grasshopper as feeding on young trees.

Vespula pensylvanica and Vespula vulgaris (L.) feed on Homoptera and Hemiptera, as well as on flies, phalangids, spiders, grasshoppers, and slugs. They also scavenge for protein from carrion and meat. None of these are likely intermediate hosts. Dolichovespula *arenaria* have similar foraging habits as *V. pensylvanica* except they only rarely accept dead material. Their prey includes grasshoppers, spittlebug adults, leafhoppers, lygus bugs, caterpillars, flies, and spiders (Akre et al. 1981). To a lesser extent, yellowjackets feed on caterpillars and beetle larvae. *Hyphantria cunea* (Drury) (the fall webworm) is recorded as an intermediate host of *Lycogaster p. nevadensis* (Townes 1956) and also is preyed upon by *V. vulgaris* and *D. arenaria* (Morris 1972).

The baldfaced hornet, *Dolichovespula maculata* (L.), is the only common species of yellowjacket present within the range but not recorded as a host of *B. canadensis*. *Dolichovespula maculata* preys mainly on flying insects, including flies, bees, and other yellowjackets. None of these are suitable intermediate hosts.

Other Parasitoids of Yellowjackets

General information on parasitoids of yellowjackets was given in Spradbery (1973). More specific information is found in MacDonald et al. (1975) and Akre (1982). The role of natural enemies in controlling yellowjackets is usually not considered as important as abiotic factors (Akre and Reed 1981). The discussion here is limited to the two parasitoids other than *B. canadensis* found in this study.

Sphecophaga vesparum (Ichneumonidae)- This is a holarctic pupal ectoparasitoid which enters yellowjacket nests as an adult and lays eggs into the pupae through the pupal cap (Donovan and Read 1987, pers. obs.). It is most common in *D. arenaria*, *V. vulgaris*, and *V. atropilosa* (MacDonald et al. 1975). In this study it was found in nests of these species and also heavily parasitizing one large and two small *V. pensylvanica* nests. Originally considered separate species, *S. v. vesparum* (Curtis) from Europe and *S. v. burra* (Cresson) from North America were reduced to subspecies (Townes and Townes 1962). Further discussion is in Donovan and Read (1987) and in an appendix to this thesis.

Dibrachys cavus (Walker)(Pteromalidae)- This gregarious pupal-parasitoid has been collected from several orders of insects (Burks 1979) as well as pupae of yellowjackets (R.D. Akre, pers. comm., 1981). I reared it from *V. vulgaris* combs in 1986. Since the colony was collected 16 September and the *D. cavus* emerged in the second week of October it is very possible that they were parasitized in the laboratory.

MATERIALS AND METHODS

Previous Collections

A literature search and correspondence with curators and visits to museum collections were conducted to determine the existence of previously collected specimens of B. canadensis.

Field

Parasitism of Yellowjacket Nests

During the summer and fall of 1986 and 1987, 192 yellowjacket colonies were collected for observations on the parasitoid B. canadensis. All colonies were located in or adjacent to Benton County, Oregon. Each nest was recorded as being from the Willamette Valley or the Coast Range coniferous forest based on the flora and terrain (fig. 1). Nests collected within about 400 m of the contiguous Coast Range coniferous forest, which were areas usually distinctly more hilly and above the elevation of the valley, were classified as being from the Coast Range forest. This closely follows the forested area on the U. S. Geological Survey 15 minute maps for Corvallis and Monroe (revised 1956 and 1957, respectively). Other nests were recorded from the Willamette Valley, which has very little coniferous forest and is relatively flat except for some outcrops. One site, Witham Hill, was categorized within the Willamette Valley because it is separated from the foothills by 1 km or more of valley suburban development.

Colonies were collected during daylight. A vacuum-powered aspirator (modified from Akre et al. 1973) captured workers near the nest entrance hole, and after most workers were captured (15-120 min), the nest was removed and put into a plastic bag. The nests were transported to the laboratory in an ice chest and placed in a walk-in refrigerator at 3°C. Nests were refrigerated 1-14 days.

Adults remaining in the nests were removed in the laboratory, and nest associates were recorded. In 1986, outlines of the combs were traced on paper so their total area could be measured and the locations of B. canadensis pupal caps noted. Combs were then placed in clear plastic bags or in plastic freezer containers that had screened ventilation holes. Daily records were kept on parasitoid emergence. In 1987, combs were photocopied, and the location and type of visible parasitoid cells recorded on the copy. Combs were placed in wood-framed boxes with screen sides and glass bottoms and tops for rearing. Most combs were inverted so that the openings of the cells and the pupal caps were visible from above. Emerging yellowjackets and parasitoids were removed, and combs were sprayed with water daily to keep the pupae from drying out. Voucher specimens of B. canadensis and each yellowjacket species collected were placed in the Systematic Entomology Laboratory at Oregon State University and at the United States National Museum.

The number of B. canadensis present in nests was compared with the size of nests, species of host, date, and location of collection. Parasitism by B. canadensis was quantified for each nest by comparing the number of parasitoid pupal caps with the total number of pupal caps. This was the same method used by Yamane (1973) and has the advantage of being nondestructive. Determination of absolute percent parasitism by dissection of all yellowjacket immatures sacrifices biological information dependent on live material and rearing out parasitoids is dependent on the quality of the rearing methods. The number of parasitoid pupal caps per comb area, and number of B. canadensis emerged per comb area were also tabulated. Two-way linear regression analyses were conducted to determine relationships between colony size and parasitism. Nest area and number of host pupal caps were used as independent variables and the number of B. canadensis pupal caps and the number of B. canadensis reared from each nest as dependent variables.

Nests of paper wasps [Polistes aurifer Saussure and Mischocyttarus flavitarsis (Saussure)] were also examined for evidence of B. canadensis.

B. canadensis in the Field

A Malaise trap was set up from 11 September to 8 November 1987 to collect adult B. canadensis. The site chosen was at the edge of a forest clearing where five yellowjacket colonies with B. canadensis had been collected. In addition, visual searches and sweep net samples were conducted in 1986 and 1987 in areas where nests with B. canadensis were collected. Search time in the field varied from 5 min to 3 h and totaled about 14 h. In 1986, 1987, and 1988 branches of Douglas-fir and western hemlock [Tsuga heterophylla (Raf.) Sarg.] were returned to the laboratory and checked for eggs or oviposition marks. Foliage of other potential host plants, including Acer circinatum Pursh, Symphoricarpos albus (L.) Blake, Vaccinium spp., and Gaultheria shallon Pursh was also searched.

Laboratory

Oviposition

Observations on the oviposition behavior of B. canadensis were conducted using reared females that had not been previously exposed to any foliage. The females were placed on plants or paper, and their response was observed. Females were left on the foliage until they laid eggs, flew or dropped off the plant, or were quiescent for at least 20 seconds. Then they were placed on a standard (Douglas-fir), their response was recorded, and then they were replaced on the test surface. A series of choices were given to each female. Douglas-fir was chosen as a standard because of the readiness with which it was accepted. With two exceptions, only unmated females were available for these experiments. The number of times a female grasped the leaf with her gaster in a given amount of time was also used to measure preference.

Observations were made on the effect eggs had on Douglas-fir foliage as well as the longevity of eggs in foliage of potted and wild Douglas-fir.

RESULTS

Previous Collections

Only one unreported specimen was found through correspondence with curators of collections. It was a male from NW Washington state at the British Museum, Natural History (M.C. Day, pers. comm., 1988) (Table 3).

Field

Only nests collected in or near the coast forest contained *B. canadensis*. The parasitoid was most abundant in colonies of *V. pensylvanica* and *V. vulgaris*, scarce in *D. arenaria*, and absent from *D. maculata* (baldfaced hornet) (Table 6). It was also absent from 19 nests of *Polistes aurifer* and three *Mischocyttarus flavitarsis* nests that were collected in an area with five yellowjacket nests parasitized by *B. canadensis*.

Of nests collected from the Coast Range forest in 1986, *B. canadensis* was present in all six *V. vulgaris* nests, in six of seven *V. pensylvanica* nests, in one of three *D. arenaria* nests, and in none of five *D. maculata* nests. The parasitoid was found in greater numbers (measured by number of pupal caps) in *V. vulgaris* nests ($n=6$, $\bar{x}=51$, range 8-169, 17 cm^2 of comb per parasitoid) than in *V. pensylvanica* ($n=6$, $\bar{x}=22$, range 2-83, 32 cm^2 of comb per parasitoid). The *D. arenaria* nest had only one cell with *B. canadensis*.

Of the nests collected in the Coast Range in 1987, *B. canadensis* was present in 20 of 23 *V. vulgaris* nests, in 11 of 13 *V. pensylvanica* nests, in one *V. consobrina* nest, in two of four *V. atropilosa* nests, in three of 17 *D. arenaria* nests, and in none of eight *D. maculata* nests. In 1987 the parasitoid was not found in greater numbers in *V. vulgaris* nests (n=19, $\bar{x}$=22, range 1-118, 250 cm^2 of comb per parasitoid pupal cap) compared to *V. pensylvanica* (n=10, $\bar{x}$=26, range 1-106, 152 cm^2 of comb per parasitoid)(Table 7). The number of parasitoids was also less for the other species: *D. arenaria* one, three, and five pupal caps from the three nests, *V. atropilosa* one and four from the two nests, and *V. consobrina*, seven from one nest.

Table 6. _Bareogonalos_ _canadensis_ in yellowjacket nests from western Oregon, 1986-87.

	Coast Range Forest		Valley		All Areas
Yellowjacket species	total no. nests	with _Bareo-gonalos_	total no. nests	with _Bareo-gonalos_	total no. nests
Dolichovespula					
arenaria	20	4	43	0	63
maculata	13	0	26	0	39
Vespula					
atropilosa	6	2	2	0	8
consobrina	1	1	0	0	1
pensylvanica	20	17	21	0	41
vulgaris	29	26	11	0	40
Total	89	50	103	0	192

Table 7. Abundance of *Bareogonalos canadensis* compared with size of different species of yellowjacket nests from the Coast Range of Oregon in 1987.

Yellowjacket species	Indicators of nest size		Numbers of *B. canadensis*	
	Area of nest (cm^2)	Number pupal caps	pupal caps	total reared
Dolichovespula arenaria	426	31	1	0
	801	537	3	0
	1075	525	5	4
Vespula atropilosa	11	52	4	0
	269	385	1	0
consobrina	161	288	1	7
pensylvanica	141	236	0	1
	445	932	7	6
	461	895	12	10
	561	992	4	5
	952	1321	10	6
	1214	2420	2	1
	2260	4327	18	20
	2281	1559	8	3
	2507	3415	106	89
	2732	1882	28	20
	3029	2477	61	38
vulgaris	154	274	1	0
	215	367	7	8
	226	579	1	0
	255	378	38	46
	468	877	5	3
	555	1250	5	0
	617	1280	1	1
	673	1265	16	21
	737	1904	1	3
	808	941	22	0
	867	1694	68	66
	871	1772	1	0
	1013	1586	75	65
	1097	1969	1	1
	1145	2078	4	2
	1395	1274	22	26
	1680	3402	17	9
	1722	2156	118	122

Although fewer *B. canadensis* were found in *D. arenaria* nests, these nests were also smaller and had fewer pupae than *V. vulgaris* and *V. pensylvanica*. In 1987, in those nests that contained *B. canadensis*, this parasitoid was found in fewer numbers per comb area but in a larger proportion of the pupae. This is because the nests had so few pupae compared to *V. vulgaris* and *V. pensylvanica*. If all the *D. arenaria* nests in the area with *B. canadensis* are looked at as an aggregate, *D. arenaria* had fewer pupae parasitized.

No correlation ($r^2 = 0.2-0.3$) was found when the number of *B. canadensis* in nests was compared with the area of nests, the number of capped cells, or the date of collection [the number of pupal caps of *B. canadensis* and the comb area of *D. arenaria* were highly correlated ($r^2 = 0.99$) but with only a sample of three nests]. Date of nest collection compared with the area of nests had a higher correlation, $r^2 = 0.64$ for all nests with trigonalyids.

Regressions comparing the presence or absence of *B. canadensis* from nests collected in the Coast Range forest with the date, area, and species of the nests collected found no correlation between area of nests and the presence of *B. canadensis* ($r^2 = 0.14$, 54 nests) or between the date of collection and presence of *B. canadensis* ($r^2 = 0.14$, 58 nests), regardless of species.

Observations of *B. canadensis* in the field were limited. The parasitoid was found in the entrance tunnels of one *V. vulgaris* nest and one *V. pensylvanica* nest and was collected in loose leaf litter while excavating a nest of *V. pensylvanica*. Attempts to collect adults apart from nests were unsuccessful. Attempts to find eggs in field-collected foliage were unsuccessful in 1986 and 1987 but they were found in Douglas-fir foliage collected in the spring of 1988.

Laboratory

Adult Interactions

Social insects, especially yellowjackets, are known for their ability to defend their colonies from intruders. Less is known about their defense against foreigners reared within the colony, but it appears to vary with host species. In 1986 a *V. vulgaris* worker bit (but apparently did not damage) a *B. canadensis*'s wings and the posterior end of the gaster. In 1987 a male parasitoid remained still while a *V. vulgaris* worker mouthed or grabbed whatever part it contacted. When the yellowjacket stopped the parasitoid moved away. In another interaction a worker pulled the hind leg of a male trigonalyid, while another worker mouthed the wings and legs. A newly emerged worker was observed chewing on a trigonalyid wing, and bent it ninety degrees. Most importantly, no damage resulted from these mild interactions. However, some trigonalyids that remained in emergence cages with many yellowjackets had their wings or tarsi damaged.

Mating was observed in the fall of 1986 when pairs were placed in 30 ml clear plastic cups. One of the pairs (emerged 28 Oct.) mated 29 Oct, 30 Oct, and 1 Nov. The male was above the female with his gaster reaching down below the female's gaster (fig. 2). On two occasions I observed males mounting males despite the presence of females in the same cup. On another occasion one of two males in a cup was observed for two days with its genitalia out attempting to mate with a yellowjacket larva.

When a Douglas-fir sprig was placed in a sleeve cage with male and female B. canadensis the males appeared to ignore the sprig while most of the females were soon on the needles. Males placed on Douglas-fir branches did not change their behavior in any obvious way, and did not show any apparent recognition or interest in females on the branch.

Longevity

Females placed in 30 ml plastic cups lived 5.0±1.2 days at 22±2°C (n=8) and males lived 5.5±1.5 days at 22±2°C (n=9). Individuals were given water only. Individuals lived much longer when kept at cooler temperatures. At 15±2°C males lived an average of 12.0 ±3.6 days (n=6) and females 10.2±2.4 days (n=5). At 12±2°C females lived 11.5±2.1 days (n=6).

Oviposition

The female abdomen is highly modified for curving around and grasping a leaf and injecting an egg into it (fig. 3). The mid-dorsal intersegmental membranes between the abdominal terga were exposed each time the female placed an egg into a leaf. Leg position was variable, the middle pair of legs might be on the leaf being oviposited in, or on another leaf near it. Antennae were placed forward, curving down. Eggs were placed into the spongy mesophyll 0.2-0.5 mm from the edge of leaves (fig. 4). Sometimes a few eggs were left outside of the leaf, but eggs outside a leaf desiccated within minutes to hours depending on temperature and humidity. Eggs appeared healthy and viable after one winter in leaves of potted and wild Douglas-fir.

Figure 1. The Willamette Valley with the Coast Range forest in background.

Figure 2. Mating.

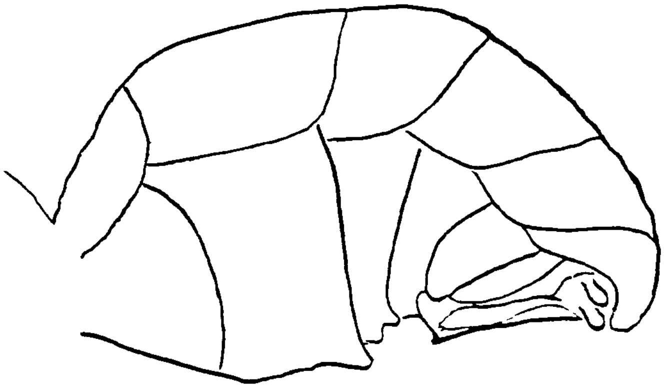

Figure 3a. Side view of a female <u>Bareogonalos canadensis</u> gaster.

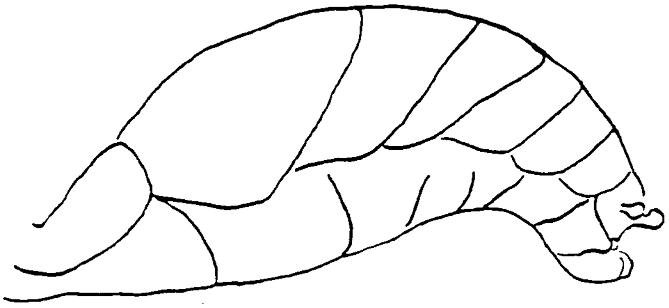

Figure 3b. Side view of a male <u>Bareogonalos canadensis</u> gaster.

Figure 4. Oviposition in a Douglas-fir leaf.

While ovipositing, females normally made a fine slit in the underside of the leaf, and later a small heel-shaped bruise (brown area) would become visible on the opposite side. When eggs were laid in such large numbers that they crowded against one another in the leaf, which happened in the laboratory when I enclosed females on branch tips, a portion of the leaf was killed and sometimes dropped off. A small number of eggs had no apparent affect on the leaf.

Bareogonalos canadensis have tremendous numbers of eggs to disseminate and do so rapidly on Douglas-fir. One female B. canadensis from a worker cell of a V. vulgaris nest had ca. 11,000 eggs in her ovaries. The rate of oviposition varied with the type of plant. Egg laying rates on Douglas-fir were measured for a newly emerged female at 71 thrusts per 203 sec (or a thrust every 2.9 sec). A two day old female thrust a total of 133 times in 202 sec (thrust every 1.5 sec). Total measurements on Douglas-fir were 330 thrusts in 607 sec (thrust every 1.8 sec).

Females often started to oviposit within 5-15 sec of being placed on Douglas-fir foliage. They worked up and down the limb, laying a series of individual eggs in each leaf. When transferred to another plant species or paper, they generally stopped laying or laid very few eggs, and remained motionless or dropped off the foliage. When replaced on the Douglas-fir, they normally resumed egg-laying. Oviposition even took place in three hand-held Douglas-fir needles. A female placed on western hemlock wandered over the foliage for about a minute until she came to some intermixed Douglas-fir foliage, whereupon she started laying in the Douglas-fir. At the same time another female on the hemlock appeared to oviposit, thrusting with her gaster but not with enough vigor to expose the intersegmental membranes. No eggs were found in the leaves. Similar behavior was seen on Deodar cedar [Cedrus deodara (Roxb.) Loud.]. On fir (Abies sp.) a female thrust once immediately upon being placed on the foliage but then stopped. This female then laid a series of eggs when placed on Douglas-fir. Females placed on broadleaf plants rotated their body with the head facing the center until the ventral part of the gaster contacted the leaf margin and then might start laying eggs, but at a slower rate and for a shorter time than on Douglas-fir. On vine maple (A. circinatum) a female oviposited about nine times in about 5 min. One newly emerged female laid two to three eggs in an apple leaf, then rejected the apple leaf after laying a series of eggs in Douglas-fir. A female that accepted Vaccinium parvifolium Smith thrusted 40 times in 2 min 52 sec (1 thrust/ 4.3 sec), another female thrust 3 times in 30 sec on azalea.

Observations on the oviposition behavior of mated females (n=2) coincided with what was seen in unmated females. Acceptance of foliage usually was independent of the order of exposure. At least some eggs were laid in most test plants and paper at some time (Table 8). No eggs were laid in grass (Poa sp.), even when it was placed among the Douglas-fir needles. The tarsi of the female tangled in the pubescence on bean (Phaseolus vulgaris L.) and no eggs were laid. Females attempted to oviposit in needles of Pinus resinosa Ait. and Picea sitchensis (Bong.) Carr. but could not, apparently because the needles were the wrong shape and too thick to fit into their sternum. Douglas-fir needles are flat and 0.4-0.5 mm thick while P. resinosa needles are crescent shaped in cross section, and P. sitchensis needles are almost 1 mm thick. Only two eggs were laid in a chinkapin leaf.

Table 8. Oviposition response of *Bareogonalos canadensis* to plants.

Plant	No. exposures	No. positive responses[1]
Abies sp. (fir)	2	1
Acer circinatum (vine maple)	1	1
Acer macrophylum (big-leaf maple)	5	1
Arctostaphylos (strawberry A.)	5	2
Castanopsis chrysophylla (chinkapin)	1	1
Cedrus deodara (Deodar cedar)	4	0
Corylus cornuta (filbert)	2	0
Cytisus scoparius (Scotch broom)	1	0
Daucus carota (wild carrot)	1	1
Gaultheria shallon (salal)	8	3
Lens culinaris (lentil)	2	1
Malus domestica (apple)	3	1
Phaseolus (bean, 2 varieties)	4	0
Picea sitchensis (spruce)	2	0
Pinus resinosa (pitch pine)	2	0
Poa sp. (grass)	4	0
Pseudotsuga menziesii (Douglas-fir)	41+	38+
Pseudotsuga menziesii (dead foliage)	2	2
Quercus garryana (Oregon white oak)	5	0
Rhododendron occidentale (azalea)	4	1
Sequoia sempervirens (redwood)	2	1
Spirea sp. (spirea)	3	0
Symphoricarpos albus (snowberry)	6	4
Thuja plicata (western red cedar)	4	0
Trifolium sp. (clover)	3	0
Tsuga heterophylla (hemlock)	5	3
Vaccinium parvifolium (huckleberry)	2	1
Paper (dollar bill)	2	1
(index card)	2	1
(Paper towel)	3	1

[1] A positive response means at some time the female grasped the leaf in the sternal notch and thrust with her abdomen. Exposures may have used the same female more than once on the same plant.

DISCUSSION

Differences in the presence of B. canadensis in nests from the Coast Range forest and the Willamette Valley were significant (chi-square, $p<0.005$). More than half of the nests collected in the Coast Range forest contained B. canadensis, whereas no nests from the valley contained the parasitoid.

Trigonalyidae find their ultimate hosts passively. Bareogonalos canadensis depend on the host to bring them back to the nest. Because of this, females develop in an environment removed from where they oviposit. Hopkin's Host Selection Principle[1] oviposition only act indirectly. The choice of host is made by the host such as occurs when the host yellowjacket chooses foliage-eating prey. The parasitoid's preference of a plant to oviposit in may have been selected over evolutionary time but probably is not measurably affected by the specific plant that her mother laid in. Another logical consequence of passive host finding is that a yellowjacket colony with more foragers is more likely to be parasitized by B. canadensis. This contrasts with Sphecophaga vesparum burra, which depends on weakness in the colony defense to enter the nest as an adult and lay eggs onto the yellowjacket pupae (Donovan and Read 1987, pers. obs.).

The different levels in parasitism between yellowjacket species could be explained in part by phenology. Bareogonalos canadensis may build up its numbers as the season progresses and D. arenaria might be parasitized less because it is an earlier species or because there are fewer intermediate hosts present in

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[1] the idea that a polyphagous parasitoid will tend to oviposit in the species of host that she emerged from if given the choice.

midsummer, the peak of D. arenaria activity. It also seems logical that larger and later nests would have more workers gathering prey and thus would be more likely to have parasitoids. However, I did not find a correlation between date or area and percent parasitism, nor was there a correlation between date or area and whether or not the nest was parasitized. This lack of correlation may be an indication of a patchy distribution in time and space even in areas where it is found.

Since there was a positive correlation with the date of collection and the size of nests with trigonalyids this shows that nests were bigger as the season progressed even though they were parasitized. With many more collections it may be possible to compare growth between parasitized and unparasitized nests from the same areas to see if unparasitized nests grew less. However, of the 20 V. pensylvanica and 29 V. vulgaris nests collected in the Coast Range forest only three nests of each species were not parasitized. Thus, it was impossible to separate the unknown factors that caused one nest to be parasitized and another not to be, and decide if parasitism by B. canadensis affected the production of reproductives.

Attempts to find B. canadensis adults by Malaise trap, sweep net, and visual observation may have been unsuccessful because of the adult's short life, its poor flying ability, or its general inactivity. In the past, only two specimens have been collected that are not known to have been in association with yellowjacket nests. However, most other trigonalyid species are taken on the wing more often than they are reared, so few have known hosts.

The parasitoid's immediate and vigorous oviposition response to Douglas-fir foliage may explain the limited range of B. canadensis. The range of Douglas-fir in North America (Little 1971) overlaps the known range of B. canadensis. However, Douglas-fir is found in many areas where B. canadensis is not. Other factors may also be important, such as sufficient moisture for adult survival and reproduction, or temperature extremes during the egg and adult stages.

Because males appear not to be affected by Douglas-fir, and both males and females spend time around the entrances of yellowjacket nests (Taylor 1898), it is probable that mating takes place before dispersal from the area of the host nest.

The fact that B. canadensis oviposited in such a wide variety of plants (and even paper) can be explained two ways. They have several thousand eggs to disperse in their relatively short life. Laying excess eggs on other plants while searching for the plants normally used may be an optimization strategy if time is a limiting factor and some of the eggs laid in alternate plants are eaten by intermediate hosts. The other possibility is that the females oviposit on a wider range of plants in artificial conditions than they do in nature (Simmonds 1944). However, females that accepted broadleafed plants appeared to have a distinct turning behavior to find the edge of the leaf.

All plants used for oviposition by other species of the family are angiosperms (Carlson 1979). Trigonalyids are often considered an archaic group (Masner 1979), but the use of a gymnosperm by B. canadensis for oviposition is not evidence that this species is older than other trigonalyids considering the ultimate host.

Yamane (1973), by analyzing label data on specimens of B. jezoensis, found males were collected before yellowjacket colonies normally would have pupae, and concluded that this species may overwinter as adults. Carmean et al. (1981) suggested that inseminated females of *B. canadensis* overwinter. In the current study, numerous eggs were laid in Douglas-fir during the summer and overwintered eggs were found in laboratory and field collected Douglas-fir foliage, while adults were short-lived. From the current data I concluded the major (and perhaps only) overwintering stage is the egg. The short life span of adults in the laboratory may have been due to the artificial conditions but was also noted for Australian species (Reik 1970). Clausen (1931) reported that eggs of *Poecilogonalos* remain viable on leaves for months. However, in Australia *Taeniogonalos* Schulz overwinters in the cocoons of anthelid/ichneumonid hosts (Riek 1962), and *Poecilogonalos thwaitesi* (Westwood) appears to overwinter as a first larval instar in its host caterpillar (Clausen 1929). I know of no caterpillar in Oregon that overwinters and remains a caterpillar until yellowjackets are actively foraging (at least May). Another possibility is that the parasitoid is transtadial, i.e., the larva remains in the intermediate host until the host becomes an adult and then this adult is captured by the yellowjacket worker and fed with the trigonalyid to the yellowjacket larvae. Since yellowjackets often prefer flying prey this is possible but it would be a departure from known life histories.

The identity of the intermediate hosts for *B. canadensis* and other trigonalyids parasitic on vespids is still unknown. They must be phytophagous chewing insects, such as caterpillars or sawfly larvae, as is known for other species of the family (Clausen 1940, Townes 1956).

Yellowjacket workers must feed the intermediate host to their larvae for *B. canadensis* to complete its life cycle. Workers of *D. arenaria* normally only forage for live prey. *Vespula pensylvanica* and *V. vulgaris* feed on live prey as well as scavenge. All three feed on flies, true bugs, and to a lesser extent, caterpillars (Akre et al. 1981).

The difference in parasitism between *Vespula* (*Paravespula* group) and *Dolichovespula* may be the result of a lack of host suitability, differences in prey preference, size of nests, or nesting phenology. Though the apparent differences (size and color) between *D. maculata* and the other yellowjackets are great, these differences should not affect the development of the parasitoid. Queens of other yellowjacket species are suitable hosts though larger than workers of *D. maculata*. *Dolichovespula maculata* feeds mainly on flying insects, few of which are chewing herbivores, thus possibly explaining why *B. canadensis* has not been reared from colonies of this species. Trigonalyids, including *B. canadensis*, have a wide host range; thus, *D. maculata* may be physiologically suitable but do not normally prey on *B. canadensis*'s intermediate host. *Bareogonalos* has been reared from *Vespa*, *Vespula* (both *vulgaris* and *rufa* species groups), and *Dolichovespula* (Yamane 1973). Cooper (1954) reared *Lycogaster pullata* from an eumenid wasp but it is more common from ichneumonid parasitoids of Lepidoptera. *Poecilogonalos costalis* has been reared from different genera of tachinids parasitic on various Lepidoptera caterpillars (Carlson 1979) and tipulid larvae (Gelhaus 1987). However, Clausen (1931) noted that in Japan large numbers of Japanese beetles (*Popillia japonica* Newman) parasitized by tachinids were reared, but none had trigonalyids.

Parasitoids of social insects use many methods to evade detection by their hosts. No other parasitic Hymenoptera enter their hosts through the gut (Iwata 1976). It may be that Bareogonalos larvae are able to parasitize some species of yellowjackets but the adults are not able to get out of the nests successfully. I found B. canadensis in the entrance tunnels of V. vulgaris and V. pensylvanica, and Taylor (1898) found them around the entrances of two V. pensylvanica nests. These collections show that these two yellowjacket species are suitable hosts for B. canadensis, not only physiologically but behaviorally as well. This contrasts with Sphecophaga, which is normally attacked and eaten by V. pensylvanica (R. D. Akre, pers. comm., 1988, but see appendix). Because B. canadensis develop inside the vespid nest they may escape detection by acquiring at least some of the host-colony odors.

Because of the low numbers of trigonalyids their impact on yellowjackets in nature is probably minimal. None of the colonies surveyed appeared to lose a significant number of reproductives to parasitoids and genes from yellowjackets in the valley would probably minimize selection pressure on yellowjackets by B. canadensis.

Most eggs laid in the foliage will never reach the intermediate host, and most of those that successfully start their development in the intermediate host will not reach the final hosts. Some caterpillars may be dead end hosts for Bareogonalos. The trigonalyid egg may not receive the required conditions for hatching, the caterpillar may encapsulate the larva, or yellowjackets may not prey on the caterpillar. Clausen (1931) noted that eggs that did not have their chorion broken did not hatch, and that "a considerable number were voided with the excrement."

Biological control of yellowjackets can be aimed at reducing the number of nests, reducing worker populations, or reducing the number of reproductives produced by a colony. It does not appear that *B. canadensis* is able to do any of these significantly. In addition, this parasitoid was only found in or adjacent to forested areas, not in urban or agricultural areas that have the most people in contact with yellowjackets. With more knowledge about the conditions required for *B. canadensis* to successfully parasitize yellowjackets it may be possible to harness the reproductive potential of *B. canadensis* to use it in areas where it is not found naturally. However, current chemical controls are probably more effective where they are acceptable, and effective biological controls do not appear promising.

BIBLIOGRAPHY

Akre, R.D. 1982. Social wasps. pp. 1-105. In Hermann, H.R. [ed.], Social insects. vol. 4. Academic, New York. 385 p.

Akre, R.D., A. Greene, J.F. MacDonald and H.G. Davis. 1981. The yellowjackets of America north of Mexico. USDA Agric. Handbook 552. 102 p.

Akre, R.D., W.B. Hill, and J.F. MacDonald. 1973. Artificial housing for yellowjacket colonies. J. Econ. Entomol. 66: 803-805.

Akre, R.D., W.B. Hill, J.F. MacDonald, and W.B. Garnett. 1975. Foraging distance of Vespula pensylvanica workers (Hymenoptera: Vespidae). Kansas Entomol. Soc. 48: 12-16.

Akre, R.D., J.F. MacDonald, and W.B. Hill. 1974. Yellowjacket literature (Hymenoptera: Vespidae). Melanderia 18: 67-93.

Akre, R.D. and H.C. Reed. 1981. Population cycles of yellowjackets (Hymenoptera: Vespinae) in the Pacific Northwest. Environ. Entomol. 10: 267-274.

Ashmead, W.H. 1902. Classification of the fossorial, predaceous and parasitic wasps, or the superfamily Vespoidea. (Paper No. 10). Can. Entomol. 34: 287-291.

Bischoff, H. 1938. Trigonaloidae. Hymenopterorum Catalogus pars 5: 1-18.

Borror, D.J., D.M. Delong, and C.A. Triplehorn. 1976. An introduction to the study of insects, 4rth ed. Holt, Rinehart, and Winston, New York. 852 p.

Buckell, E.R. and G.J. Spencer. 1950. The social wasps (Vespidae) of British Columbia. Proc. Entomol. Soc. Brit. Columbia 46: 33-40.

Burks, B.D. 1979. Family Pteromalidae. pp. 768-835. In Krombein, K.V. et al. 1979. Catalog of Hymenoptera in America north of Mexico, vol. 1. Smithsonian, Washington D.C. 1198 p.

Cameron, P. 1897. New species of Hymenoptera from Central America. Ann. Mag. Nat. Hist. (ser. 6) 19: 261-276, 368-79.

Carlson, R.W. 1979. Superfamily Trigonaloidea. pp. 1197-1198. In Krombein, K.V. et al. 1979. Catalog of Hymenoptera in America north of Mexico, vol. 1. Smithsonian, Wash. D.C. 1198 p.

Carmean, D., R.D. Akre, R.S. Zack, and H.C. Reed. 1981. Notes on the yellowjacket parasite Bareogonalis(sic) canadensis (Hymenoptera: Trigonalidae). Entomol. News 92: 23-26.

Carpenter, J.M. 1987. Phylogenetic relationships and classification of the Vespinae (Hymenoptera: Vespidae). Syst. Entomol. 12: 413-431.

Clausen, C.P. 1929. Biological studies on Poecilogonalos thwaitesii (Westw.), parasitic in the cocoons of Henicospilus (Hymen.: Trigonalidae). Proc. Entomol. Soc. Wash. 31: 67-79.

Clausen, C.P. 1931. Biological notes on the Trigonalidae (Hymenoptera). Proc. Entomol. Soc. Wash. 33: 72-81.

Clausen, C.P. 1940. Entomophagous insects. McGraw-Hill, New York. 688 p.

Cooper, K.W. 1954. Biology of Eumenine Wasps, IV. A trigonalid wasp parasitic on Rygchium rugosum (Saussure) (Hymenoptera, Trigonalidae). Proc. Entomol. Soc. Wash. 56: 280-288.

Cresson, E.T. 1887. Synopsis of the families and genera of the Hymenoptera of America, north of Mexico, together with a catalogue of the described species and bibliography. Trans. Am. Entomol. Soc. Suppl. 14, 350 p.

Donovan, B.J. and P.E.C. Read. 1987. Attempted biological control of social wasps, Vespula spp., (Hymenoptera: Vespidae) with Sphecophaga vesparum (Curtis) (Hymenoptera: Ichneumonidae) in New Zealand. New Zealand J. Zool. 14: 329-335.

Dours, A. 1874. Catalogue synonymique des Hymenopteres de France. Amiens. 229 p.

Edwards, R. 1980. Social wasps: their biology and control. Rentokil, East Grinstead (UK). 398 p.

Furniss, R.L. and V.M. Carolin. 1977. Western forest insects. USDA Forest Service misc. publ. 1339. Washington D.C. 654 p.

Gelhaus, J.K. 1987. A detritivore Tipula (Diptera: Tipulidae) as a secondary host of Poecilogonalos costalis (Hymenoptera: Trigonalidae). Entomol. News 98: 161-162.

Gibson, G.A.P. 1985. Some pro- and mesothoracic characters important for phylogenetic analysis of Hymenoptera, with a review of terms used for the structures. Can. Entomol. 117: 1395-1443.

Greene, A., R.D. Akre, and P. Landolt. 1976. The aerial yellowjacket, Dolichovespula arenaria (Fab.): nesting biology, reproductive production, and behavior (Hymenoptera: Vespidae). Melanderia 26: 1-34.

Harrington, W.H. 1896. A Canadian Trigonalys. Can. Entomol. 28: 108.

Harrington, W.H. 1898. Addendum by W.H. Harrington, F.R.S.C., Ottawa. Can. Entomol. 30: 15-16.

Iwata, K. 1976. Evolution of instinct: a comparative ethology of Hymenoptera. Amerind, New Delhi. 535 p.

Koenigsmann, E. 1976. Das Phylogenetische System der Hymenoptera. Deutsche Entomol. Zeit. N.S. 23: 253-279.

Krieger, R. 1894. Ein Beitrag zur Kenntnis der Hymenoptern-fauna des Koenigreichs-Sachsen. Verzeichnis der bis jetzt in Sachsen aufgefundenen Grabwespen und Bienen. Beil. Jahrsber. Nicolaigymn. Leipzig: 50 p.

Krombein, K.V. et al. 1979. Catalog of Hymenoptera in America north of Mexico, vol. 1. Smithsonian, Washington D.C. 1198 p.

Little, E.L. Jr. 1971. Atlas of United States trees. USDA Forest Service misc. publ. 1146. Washington, D.C. 200 p.

MacDonald, J.F., R.D. Akre, and W.B. Hill. 1975. Nest associates of Vespula atropilosa and V. pensylvanica in southeastern Washington State (Hymenoptera: Vespidae). J. Kansas Entomol. Soc. 48: 53-63.

Masner, L. 1979. 46. Hymenoptera. pp. 500-501. In Danks, H.V., [ed.], Canada and its insect fauna. Mem. Entomol. Soc. Can. 108. 573 p.

Morris, R.F. 1972. Predation by wasps, birds, and mammals on Hyphantria cunea. Can. Entomol. 104: 1581-1591.

Oehlke, J. 1983. Zur Nomenklatur der Gattungen Trigonalis, Stephanus und Brachygaster (Hymenoptera, Trigonalyoidea, Stephanoidea et Evanioidea). Reichenbachia, Mus. Tierk. Dresden, 21: 91-93.

Oeser, R. 1962. Reduced ovipositor of Pseudogonalos hahni with observations on the systematic position of Trigonalidae (In German). Deut. Akad. Landwirt. Berlin Tagungsber. 45:153-157.

Ono, M. 1987. Note on Bareogonalos jezoensis (Hymenoptera, Trigonalidae) discovered from a nest of Vespa simillima xanthoptera (Hymenoptera, Vespidae). Kontyû 55: 162-163.

Rasnitsyn, A.P. 1980. Origin and evolution of Hymenoptera (In Russian). Trudy Paleont. Inst. 174, 190 p.

Reichert, A. 1911. Beitrag zur Lebensweise von Pseudogonalos hahni Spin. Vergl. Berlin. Entomol. Zeit. 56: 109-112.

Riek, E.F. 1962. A trigonalid wasp (Hymenoptera, Trigonalidae) from an anthelid cocoon (Lepidoptera, Anthelidae). Proc. Linn. Soc. New S. Wales 87: 148-150.

Riek, E.F. 1970. Superfamily Trigonaloidea. pp. 894-896. In C.S.I.R.O., Insects of Australia. Melbourne Univ. Press, Canberra. 1029 p.

Sarazin, M.J. 1986. Primary types of Ceraphronoidea, Evanioidea, Proctotrupoidea, and Trigonaloidea (Hymenoptera) in the Canadian National Collection. Can. Entomol. 118: 957-989.

Schulz, W.A. 1906. Die Trigonaloiden des Koeniglichen Zoologischen Museums in Berlin. Mitt. Zool. Mus. Berlin. 3: 203-212.

Schulz, W.A. 1907a. (1906.) Alte Hymenopteren. Berlin. Entomol. Z. 51: 303-333.

Schulz, W.A. 1907b. Hymenoptera, Fam. Trigonaloidae. In P. Wytsman, Genera Insectorum fasc. 61. 24 p.

Schulz, W.A. 1908. Die Trigonaloiden des Genueser Naturhistorischen Museums. Ann. Mus. Civ. Stor. Nat. Genova Ser. 3 vol. 4 (44): 23-37.

Shuckard, W.E. 1841. On the Aulacidae, a family of Hymenoptera pupivora; and that Trigonalys is one of its components: with the description of a British species of this genus, and incidental remarks upon their collateral affinities. Entomologist 1: 115-125.

Simmonds, F.J. 1944. The propagation of insect parasites on unnatural hosts. Bull. Entomol. Res. 35: 219-226.

Smith, F. 1851. On the nest of Polistes Lanio, Fab. and a parasite found therein, and on a nest of a social wasp. Trans. Entomol. Soc. Lond. 1:(N.S.) 176-178.

Spradbery, J.P. 1973. Wasps: an account of the biology and natural history of social and solitary wasps. Univ. Wash. Press, Seattle. 408 p.

Stage, G.I. and C.N. Slobodchikoff. 1962. New distribution and host record of Bareogonalos canadensis (Harrington) (Hymenoptera: Trigonalidae and Vespidae). Pan-Pac. Entomol. 38: 97-98.

Taylor, G.W. 1898. Note on Trigonalys canadensis, Hargtn. Can. Entomol. 30: 14-15.

Thompson, W.R. 1958. A catalogue of the parasites and predators of insect pests. Sect. 2, host parasite catalogue, part 5. C.I.B.C., Ottawa. 698p.

Townes, H. 1956. The nearctic species of trigonalid wasps. Proc. U.S. Natl. Mus. 106: 295-304.

Townes, H. and M. Townes. 1962. Ichneumon-flies of America north of Mexico: 3. Subfamily Gelinae, Tribe Mesostenini. U.S. Natl. Mus. Bull. 216. 602 p.

Uchida, T. 1929. Ueber die Trigonaloiden Japans (Hym.). Insecta Matsumurana 3:77-80.

Vecht, J. van der. 1934. Zur kenntnis der Indo-Malayischen Trigonaloidea. Zool. Mededeel. (Leiden) 17: 290-296.

Viereck, H.L. 1914. Type species of the genera of ichneumon flies. U.S. Natl. Mus. Bull. 83: 186 p.

Westwood, J.O. 1835. Characters of new genera and species of Hymenopterous insects. Proc. Zool. Soc. Lond. 3: 51-54.

Westwood, J.O. 1840. An introduction to the modern classification of insects; founded on the natural habits and corresponding organization of the different families, vol. II. Longman, Orme, Brown, Green, and Longmans, London. 587 p.

Westwood, J.O. 1841a. Note on Mr. Shuckard's memoir on the Aulacidae, &c. at page 115 of the Entomologist. Entomologist 1: 139-140.

Westwood, J.O. 1841b. Communication to the Entomological Society. Ann. Mag. Nat. Hist. 7: 535-539.

Westwood, J.O. 1843. On _Evania_ and some allied genera of Hymenopterous Insects. Trans. Entomol. Soc. Lond. 3: 237-278.

Yamane, Sk. 1973. Descriptions of the second to final instar larvae of _Bareogonalos jezoensis_ with some notes on its biology (Hymenoptera, Trigonalidae). Kontyû 41: 194-202.

Yamane, Sk. and S. Yamane. 1975. A new trigonalid parasite (Hymenoptera, Trigonalidae) obtained from _Vespula_ nests in Taiwan. Kontyû 43: 456-462.

APPENDICES

APPENDIX A.

A NOTE ON SPHECOPHAGA PARASITISM OF VESPULA PENSYLVANICA

(Hymenoptera: Ichneumonidae, Vespidae)

Vespula pensylvanica (Saussure) is a scavenging ground-nesting yellowjacket of western North America that commonly attends barbecues and picnics in the late summer and fall. Sphecophaga vesparum burra (Cresson) is a parasitoid restricted to yellowjackets and is recorded from most species of yellowjackets. However it is rare to find S. v. burra attacking V. pensylvanica. From 1971-1977 Akre and associates analyzed 186 V. pensylvanica nests and only one was parasitized by S. v. burra (Akre et al. 1981). This nest had four parasitoid cocoons on the first comb (worker) and two cocoons in reproductive cells on comb 2. It was a weak colony with a slow rate of growth. MacDonald et al. (1975) found S. v. burra in over 80% of Vespula atropilosa (Sladen) nests (n=40) from 1971-1973 but none from 61 V. pensylvanica nests collected in the same period.

On 18 September 1986 I collected one very strong colony of V. pensylvanica heavily parasitized by S. v. burra. It was the only one of 17 V. pensylvanica analyzed in 1986 that was parasitized by S. v. burra. The nest was in a cut fireplace log that was partially hollow and rotten. While collecting the workers several S. v. burra were seen around an entrance at the middle of one end of the log. There were also entrances on the bottom edge and the other end of the log. The log was 51 cm long, 23 cm diam with a cavity that varied between 8 and 14 cm diam. The volume of the cavity was 7000±300 ml. The original cavity had been expanded by the workers.

The colony was larger than average as indicated by the large number of workers flying in and out. There were 142 g of workers originally aspirated and another 43 g picked out of the nest. The average for the V. pensylvanica nests collected that year was 72±61 g of workers. Hundreds of S. v. burra were reared from the combs which became moldy before a complete count could be made. Because of the high parasitism rate it is unlikely that the nest would have lasted as long as other nests, and it probably would not have produced many new queens.

In 1987 23 V. pensylvanica colonies were analyzed, and only one had S. v. burra. This was a small colony in the ground, with only a few parasitized pupae, as is typical for nests of other species of yellowjackets attacked by S. v. burra. In 1988 24 colonies were analyzed, but only one was attacked by S. v. burra. It was a small colony but similar to the 1986 colony in being more exposed than normal (on a raised platform under a vinyl covering) with a large entrance area. Several adult S. v. burra were flying around the nest. Many of the yellowjacket pupae and prepupae had six or seven eggs on them and 25% of the yellowjacket pupal caps had S. v. burra pupae under them (Table 9).

The exposed situation of the nests with large or multiple entrances would make them more vulnerable to attack. Other species of yellowjackets, even though they were attacked by S. v. burra more commonly, had much lower parasitism rates than these two colonies of V. pensylvanica. Most of the parasitism in other species was limited to a few cocoons in the first comb, suggesting the females may gain entrance to the nest from the top rather than through the entrance hole on the bottom. It is possible that V. pensylvanica can normally resist attack by S. v. burra by killing any entering the nest.

In comparison with _Bareogonalos_ _canadensis_ (Hymenoptera: Trigonalyidae), which was only found in or near the Coast Range coniferous forest, _S_. _v_. _burra_ was found in all areas studied. It was in a lower percentage of the nests of _Vespula_ spp. and a higher percentage of _Dolichovespula_ spp. (Table 11).

REFERENCES CITED

Akre, R.D., A. Greene, J.F. MacDonald and H.G. Davis. 1981. The yellowjackets of America north of Mexico. USDA Agric. Handbook 552. 102 p.

MacDonald, J.F., R.D. Akre, and W.B. Hill. 1975. Nest associates of _Vespula_ _atropilosa_ and _V_. _pensylvanica_ in southeastern Washington State (Hymenoptera: Vespidae). J. Kansas Entomol. Soc. 48: 53-63.

Table 9. *Sphecophaga vesparum burra* parasitism of *Vespula pensylvanica*, collected September 1988 in Corvallis, Oregon.

	Yellowjacket Pupae			
	Parasitized			Not Parasitized
	Sphecophaga			
comb no.	eggs	larvae	pupae	
1	46	6	33	39
2	101	3	65	100
3	16	0	16	30
Total	163	9	114	169
Percent	36%	2%	25%	37%

Table 10. *Sphecophaga vesparum burra* in yellowjacket nests from western Oregon, 1986-87.

	Coast Range Forest		Valley	
Yellowjacket species	total no. nests	with *Sphecophaga*	total no. nests	with *Sphecophaga*
Dolichovespula				
arenaria	20	9	43	7
maculata	13	2	26	0
Vespula				
atropilosa	6	1	2	0
consobrina	1	0	0	0
pensylvanica	20	1	21	1
vulgaris	29	7	11	0
Total	89	20	103	8

Table 11. _Bareogonalos_ _canadensis_ (Trigonalyidae) and _Sphecophaga_ _vesparum_ _burra_ (Ichneumonidae) in yellowjacket nests from western Oregon, 1986-87.

	Coast Range Forest				Valley	
Yellowjacket species	total no. nests	with _Bareogonalos_	with _Sphecophaga_	with both	total no. nests	with _Sphecophaga_
Dolichovespula						
arenaria	20	4	9	2	43	7
maculata	13	0	2	0	26	0
Vespula						
atropilosa	6	2	1	0	2	0
consobrina	1	1	0	0	0	0
pensylvanica	20	17	1	0	21	1
vulgaris	29	26	7	7	11	0
Total	89	50	20	9	103	8

APPENDIX B.

SPECIES, HOSTS, AND DISTRIBUTION OF TRIGONALYIDAE

This is an alphabetical list of species of the family Trigonalyidae (in capital letters), with the authors and date of description, followed by (if known), the host, the intermediate host, the areas they are known from, and the plants used for oviposition. Much of the material is from Bischoff (1938), with updates from more recent authors.

A total of 99 species and 14 subspecies are listed. Subspecies are marked with an asterisk before the authors' names.

BAKERONYMUS TYPICUS Rohwer 1922. ASIA- PHILIPPINES MINDANAO, SURIGAO.

BAKERONYMUS TYPICUS SEIDAKKA *Yamane & Terayama 1983. *Parapolybia varia*. E ASIA- TAIWAN.

BAREOGONALOS CANADENSIS (Harrington 1896). *Vespula vulgaris*, *pensylvanica*, *atropilosa*, *consobrina*, *acadica*. *Dolichovespula arenaria*. N AMERICA- W US, CANADA.

BAREOGONALOS HUISUNI Sk. and S. Yamane 1975. *Vespula*. E ASIA- TAIWAN.

BAREOGONALOS JEZOENSIS (Uchida 1929). *Vespula schrenckii*, *Vl*. *shidai*, *Vl*. *vulgaris*, *Vl*. "*lewisi=japonica*, *rufa*, *Vespa crabro*, *V*. *simillima*, *V*. *analis*, *V*. *velutina*, *Dolichovespula saxonica*. E ASIA- JAPAN JAVA.

BAREOGONALOS SCUTELLARIS (Cameron 1897). CENTRAL AMERICA- MEXICO.

DISCENEA CRASSICEPS Strand 1912. AFRICA- EQUATORIAL GUINEA.

DISCENEA MICANTICEPS Strand 1912. AFRICA- EQUATORIAL GUINEA.

DISCENEA (LYCOGASTRULA) MICANTICEPS NIGROTROCHANTERATA *Bischoff 1951. AFRICA- UGANDA.

DISCENEA NATALENSIS (Kreichbaumer 1894). S AFRICA- NATAL DELAGOA-BAY.

DISCENEA NATALENSIS LAMANI *Schulz 1910. S AFRICA- CONGO.

DISCENEA NATALENSIS MADEGASSA *Bischoff 1933. S AFRICA- CONGO.

ISCHNOGONALOS DUBIA (Magretti 1897). ASIA- BURMA.

LABIDOGONALOS FLAVESCENS Bischoff 1951. CENTRAL AMERICA- MEXICO.

LABIDOGONALOS MACULIFRONS (Cameron 1897). Bischoff 1938. CENTRAL AMERICA- MEXICO.

LABIDOGONALOS ORNATA (Smith 1860). CENTRAL AMERICA- MEXICO.

LABIDOGONALOS SANCTAECATHARINAE Schulz 1907. S AMERICA- BRAZIL.

LYCOGASTER APICIPENNIS (Cameron 1897). MEXICO.

LYCOGASTER CELEBESIENSIS (Szepligeti 1902). ASIA- CELEBES.

LYCOGASTER CELEBESIENSIS PLURIPICTA *Bischoff 1933. ASIA- CELEBES.

LYCOGASTER CELEBESIENSIS BICINCTA *Vecht 1934. ASIA- JAVA.

LYCOGASTER GUNDLACHI Cresson 1867. CENTRAL AMERICA- CUBA.

LYCOGASTER HEINRICHI Bischoff 1933. ASIA- CELEBES.

LYCOGASTER LACHRYMOSA (Westwood 1874). ASIA- MINDANAO, PHILIPPINES.

LYCOGASTER PICTIFRONS (Smith 1860). ASIA- CELEBES.

LYCOGASTER PICTIFRONS NEPHELOPTERA *Bischoff 1933. ASIA- CELEBES.

LYCOGASTER PULLATA Shuckard 1841. Ophion macrurus, Enicospilus americanus (Schulz 1911), Rygchium rugosum, Telea polyphemus. N AMERICA- E US.

LYCOGASTER PULLATA HOLLENSIS *Melander & Brues 1902. ?Ophion macrurus, Telea polyphemus. N AMERICA- E US.

LYCOGASTER PULLATA NEVADENSIS *(Cresson 1879) Townes 1956. Euodynerus foraminatus scutellaris (Parker & Bohart 1966) Hyphantria cunea N AMERICA- W US Oregon, S Dakota, Colorado, New Mexico.

LYCOGASTER RUFIVENTRIS Magretti 1897. ASIA- BURMA.

LYCOGASTER VIOLACEIPENNIS Chen 1949. E ASIA- CHINA CHEKIANG.

LYCOGASTER ZIMMERI Bischoff 1933. ASIA- CELEBES.

LYCOGASTROIDES GRACILICORNIS Strand 1912. AFRICA- EQUATORIAL GUINEA.

LYCOGASTROIDES MAYNEI Benoit 1950. ?LIMACODIDAE: Latoia albipunctata (in vitro) AFRICA- ZAIRE.

LYCOGASTROIDES ZAIRENSIS Benoit 1950. AFRICA- ZAIRE.

LYCOGONALOS FLAVICINCTA Bischoff 1913. ASIA- SIKKIM? BURMA?.

MIMELOGONALOS BOUVIERI Schulz 1907. AUSTRALIA- TASMANIA.

MIMELOGONALOS MINUTA (Rayment 1952). AUSTRALIA- QUEENSLAND.

MIMELOGONALOS NIGRICAUDA Riek 1954. AUSTRALIA- TASMANIA HOBART.

MIMELOGONALOS NIGRITHORAX Riek 1954. AUSTRALIA- A.C.T.

MIMELOGONALOS PARTIGLABRA Riek 1954. AUSTRALIA- A.C.T., N.S.W.

MIMELOGONALOS PUNCTULATA Riek 1954. AUSTRALIA- VICTORIA, A.C.T.

NANOGONALOS FASCIATIPENNIS Schulz 1906. S AMERICA- BOGOTA.

NANOGONALOS FLAVOCINCTA Teranishi 1929. E ASIA- KOREA.

NANOGONALOS MONGOLICUS Popov 1945. ASIA- MONGOLIA CHINA.

NANOGONALOS SCHULZI Bischoff 1933. S AMERICA- BOLIVIA.

NANOGONALOS TAIHORINA Bischoff 1914. E ASIA- TAIWAN.

NOMADINA BALTEATA (Cameron 1899). S AMERICA- CHILE.

NOMADINA CISANDINA (Schulz 1905). Polybia dimidiata Ol. S AMERICA- SAO PAULO ARGENTINA.

NOMADINA NASUTA Bischoff 1933. S AMERICA- BOLIVIA.

NOMADINA PHYLOGENETICA (Schulz 1905). S AMERICA- BOLIVIA.

NOMADINA SMITHI Westwood 1868. S AMERICA- AMAZON BRAZIL.

ORTHOGONALYS ALBOMACULATA Bischoff 1951. ASIA- DARJEELING 7000 FT.

ORTHOGONALYS BOLIVIANA Schulz 1905. S AMERICA- BOLIVIA.

ORTHOGONALYS CENTRIMACULATA Bischoff 1951. ASIA- TONKIN.

ORTHOGONALYS FORMOSANA Teranishi 1931. E ASIA- TAIWAN.

ORTHOGONALYS GIGANTEA Benoit 1951. AFRICA- MADAGASCAR.

ORTHOGONALYS HOVA Bischoff 1933. AFRICA- MADAGASCAR.

ORTHOGONALYS PULCHELLA (Cresson 1867). Zenillia lobeliae (Tachinid) Archytas aterrimus (Tachinid) Acronycta lobeliae (Noctuid), N AMERICA- E US. VIBURNUM ACERIFOLIUM LIQUIDAMBER (IN LAB, NO CHOICE).

ORTHOGONALYS SEYRIGI Bischoff 1933. S AFRICA- MADAGASCAR.

POECILOGONALOS COSTALIS (Cresson 1867). Allophocera (Tachinid) Phosphila turbulenta (Noctuid), Tipula ?flavoumbrosa, Acronycta lobeliae (1891). N AMERICA- E US. Seen on Liriodendron.

POECILOGONALOS FASCIATA RUBROTHORACICA *Bischoff 1913. E ASIA- TAIWAN.

POECILOGONALOS FASCIATA Strand 1913. E ASIA- TAIWAN.

POECILOGONALOS FASCIATA KIBUNENSIS *Uchida 1929. E ASIA- JAPAN.

POECILOGONALOS FLAVOSCUTELLATA Chen 1949. E ASIA- CHINA.

POECILOGONALOS FORMOSANA Bischoff 1913. E ASIA- TAIWAN.

POECILOGONALOS FULVOSCUTELLATA Ayyar 1919. W ASIA- INDIA.

POECILOGONALOS HENICOSPILI Rohwer 1929. Henicospilus rufus Tosq. W ASIA- ASSAM.

POECILOGONALOS INTERMEDIA Chen 1949. E ASIA- CHINA.

POECILOGONALOS JAVANA Bischoff 1933. ASIA- JAVA.

POECILOGONALOS KERALA Ayyar 1919. W ASIA- INDIA (MALACCA).

POECILOGONALOS MAGA Teranishi 1929. E ASIA- JAPAN.

POECILOGONALOS MAGNIFICA Teranishi 1929. E ASIA- KOREA.

POECILOGONALOS RUFOFASCIATA Chen 1949. E ASIA- CHINA.

POECILOGONALOS THWAITESI (Westwood 1874). Henicospilus rufus Tosq. W ASIA- E ASIA- SRI LANKA TAIWAN.

POECILOGONALOS THWAITESI GESTROI *Schulz 1908. ASIA- BURMA SUMATRA JAVA.

POECILOGONALOS TRICOLOR Chen 1949. E ASIA- CHINA.

POECILOGONALOS UNIFASCIATA Chen 1949. E ASIA- CHINA.

PSEUDOGONALOS HAHNI Spinola 1840. Ophion distans, Enicospilus merdarius Grav. ?Trogus sp. (in Thompson) Agrotis latens Panolis flammea (Den. Schiff.) EURASIA- EUROPE ENGLAND JAPAN. Privit.

PSEUDOGONALOS HARMANDI Schulz 1907. INDIA- DARJEELING.

PSEUDONOMADINA BICEPS Yamane & Kojima 1982. Ropalidia flavobrunnea lapiniga Kojima. ASIA- PHILIPPINES.

SATOGONALOS DEBILIS (Teranishi 1929). E ASIA- JAPAN.

SATOGONALOS ELONGATA (Teranishi 1929). E ASIA- JAPAN.

SATOGONALOS HAGOROMONIS (Teranishi 1929). E ASIA- JAPAN.

SATOGONALOS HIRASANA (Teranishi 1929). E ASIA- JAPAN.

SEMINOTA DEPRESSA (DeGeer 1773). Polistes canadensis L., Polistes limai R.Jher.(Bertoni) S AMERICA- SURINAM.

SEMINOTA DEPRESSA BIPUSTULATA *(Smith 1851). Polistes lanio Fab. S AMERICA- BRAZIL, SAN SALVADOR.

SEMINOTA INQUIRENDA Schulz 1907. S AMERICA- VENEZUELA.

SEMINOTA LAEVICEPS (Cresson 1879). CENTRAL AMERICA- MEXICO.

SEMINOTA LEPRIEURI Spinola 1840. S AMERICA- CAYENNE.

SEMINOTA MARGINATA Westwood 1874. Polistes versicolor Ol., P. cinerasens Sauss., P. melanosoma Sauss., P. canadensis L., (? Apoica pallida Ol. in Bertoni 1911). S AMERICA- PARAGUAY VENEZUELA BRAZIL, MINAS GERAES.

SEMINOTA MEXICANA (Cresson 1879). Paracharterqus apicalis F. CENTRAL AMERICA- MEXICO.

STYGNOGONALOS CHAMPIONI (Cameron 1897). CENTRAL AMERICA- GUATEMALA.

TAENIOGONALOS CHADWICKI Riek 1954. AUSTRALIA N.S.W.

TAENIOGONALOS FASCIATIPENNIS (Cameron 1897). CENTRAL AMERICA- MEXICO.

TAENIOGONALOS JUCUNDA (Westwood 1868). S AMERICA- BRAZIL AMAZON.

TAENIOGONALOS LUGUBRIS (Westwood 1868). S AMERICA- BRAZIL AMAZON.

TAENIOGONALOS MACULATA (Smith 1851). Perga nemoralis Wilson, Perga dorsalis Leach (Raff 1934). AUSTRALIA.

TAENIOGONALOS PICTIPENNIS Strand 1914. ASIA- TAIWAN.

TAENIOGONALOS SAUTERI Bischoff 1913. Charops sp. (Ophioninae, Ichneu.) Erionatha thrax L. (Hesperiidae) Hidari irava (See Vecht 1934). ASIA- TAIWAN JAVA.

TAENIOGONALOS SEMIBRUNNEA (Bischoff 1951). AUSTRALIA QUEENSLAND.

TAENIOGONALOS TENEBROSA Riek 1954. AUSTRALIA TASMANIA.

TAENIOGONALOS TRICOLOR SIMILIS *Riek 1954. Bred from sawfly. AUSTRALIA QUEENSLAND.

TAENIOGONALOS TRICOLOR TRICOLOR Rayment 1952. AUSTRALIA QUEENSLAND.

TAENIOGONALOS VENATORIA Riek 1962. Reared from Perga affinis. AUSTRALIA- N.S.W., VICTORIA.

TAPINOGONALOS ERYTHROMELAINA Benoit 1951. AFRICA- ZAIRE.

TAPINOGONALOS MASCHUNA Schulz 1907. SOUTH AFRICA- MASHONALAND.

TAPINOGONALOS ORNATISSIMA Benoit 1950. AFRICA- ZAIRE.

TAPINOGONALOS SEMIRUBRA (Bischoff 1913). SOUTH AFRICA- TRANSVAAL.

TRIGONALYS MELANOLEUCA Westwood 1835. BRASIL PARAGUAY URUGUAY ARGENTINA BAHIA SANTOS.

XANTHOGONALOS FASCIATUS Bertoni 1911. S AMERICA- PARAGUAY.

XANTHOGONALOS ROBERTIBUYSSONI Schulz 1907. CENTRAL AMERICA- MEXICO.

XANTHOGONALOS SEVERINI Schulz 1907. S AMERICA.

APPENDIX C.

FUTURE WORK ON BAREOGONALOS CANADENSIS

Future studies of B. canadensis should be aimed at learning more about mating requirements, the egg stage, and the intermediate host. Collecting should concentrate in those areas that have already proved productive- especially forests near Corvallis. It is also necessary to study the wider distribution beyond Benton County, including the west side of the Coast Range and the Cascade Mountains. It may be possible to encourage researchers in other areas to look for the parasitoid.

Eggs should be searched for in field-collected foliage and fed to possible intermediate hosts, including Lepidoptera and Symphyta. The possibility that sawflies may serve as primary hosts should be tested. Field and laboratory studies should be conducted on how they locate plants to oviposit on, and it needs to be determined if there is any difference in oviposition behavior between the laboratory and field.

I fed eggs to geometrid caterpillars and gave these to yellowjacket workers in Corvallis near a nest. No evidence of parasitism was found when I dug up the nest. This may have been due to using unfertilized eggs, eggs that were not in the proper stage of development, using too long or short of an incubation period within the caterpillar or a caterpillar that was unsuitable as an intermediate host, or the yellowjackets that took the caterpillars were from another nest (the latter was known to be the case in at least some instances). Egg development should be studied, applying the methods of Clausen (1931) both to lab and field collected eggs. I also fed eggs to gypsy moth (Lymantria dispar L.) and fall webworm [Hyphantria cunea (Drury)] caterpillars and looked for larvae inside the hemocoele but found nothing. These were preliminary experiments and should be repeated. Studies on the development time of larvae and pupae need to reproduce temperature and humidity as found in a yellowjacket colony.

Regulation or control of yellowjacket populations (both numbers of nests and workers) needs to be looked at. It is easy to conclude that the low percentages of parasitism do not affect colonies. While this may be true for established colonies, it is not true for incipient colonies, where the death of a single worker may stop its growth.

Comparative studies on the morphology of _B. canadensis_ may help give a better understanding of the phylogeny of the Hymenoptera and suggest a sister group for the Trigonalyidae.