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Insects and Related Arthropods Associated with Greenleaf Manzanita in Montane Chaparral Communities of Northeastern California

Michael A. Valenti **George T. Ferrell** **Alan A. Berryman**

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Abstract

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Specimens representing 19 orders and 169 arthropod families (mostly insects) were collected from greenleaf manzanita brushfields in northeastern California and identified to species whenever possible. More than 500 taxa below the family level were inventoried, and each listing includes relative frequency of encounter, life stages collected, and dominant role in the greenleaf manzanita community. Specific host relationships are included for some predators and parasitoids. Herbivores, predators, and parasitoids comprised the majority (80 percent) of identified insects and related taxa.

Retrieval Terms: *Arctostaphylos patula*, arthropods, California, insects, manzanita

The Authors

Michael A. Valenti is Forest Health Specialist, Delaware Department of Agriculture, 2320 S. DuPont Hwy, Dover, DE 19901-5515. **George T. Ferrell** is a retired Research Entomologist, Pacific Southwest Research Station, 2400 Washington Ave., Redding, CA 96001. **Alan A. Berryman** is Professor of Entomology, Washington State University, Pullman, WA 99164-6382.

All photographs were taken by Michael A. Valenti, except for Figure 2, which was taken by Amy H. Valenti.

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Figure 1–Greenleaf manzanita in Shasta County, California, several days after budbreak.

Introduction

Greenleaf manzanita (*Arctostaphylos patula* E. Greene) is a broadleaf evergreen shrub that commonly grows in the Sierra Nevada of California (Hickman 1993) (*fig. 1*). This species grows in mesic habitats associated with montane forests generally above 1,000 m in elevation (Ball and others 1983). After a natural or human-caused disturbance, such as a fire or clearcutting, greenleaf manzanita shrubs often become established and quickly dominate a site preventing or prolonging the successional sequence or inhibiting growth of planted conifer seedlings (McDonald and Fiddler 1990, Oliver 1990). This type of domination, in which shrubs prevent the establishment of important conifers (e.g., ponderosa pine [*Pinus ponderosa* Dougl. ex Laws. var. *ponderosa*]), inhibit conifer growth, and reduce conifer survival (Conard and Radosevich 1982, Lanini and Radosevich 1986, Radosevich 1984), has been termed "inhibition succession" (Connell and Slatyer 1977).

Current shrub control methods (e.g., mechanical removal, prescribed burning, and herbicide treatments [Bentley and Graham 1976, Paley and Radosevich 1984]) can have drawbacks such as high costs, poor efficacy (Lanini and Radosevich 1982), damage to conifer seedlings (Newton 1963), and environmental risks such as adverse effects on non-target organisms. Past restrictions on controlling undesirable vegetation have significantly increased the total area of competing vegetation on Federal lands (Walstad and others 1987). The controversy over current direct control techniques and the increase in demand for more environmentally sound control methods has increased the need for alternatives such as using native herbivorous insects to control greenleaf manzanita in northeastern California (Valenti 1994).

In this study, we compiled a list of insects known to be associated with greenleaf manzanita. An extensive literature search yielded only a few general books (e.g., Furniss and Carolin 1977, Johnson and Lyon 1988, Keen 1952) and several research publications (e.g., Duckworth 1964, Furniss and Barr 1975, Heinrich 1923) that mention insects, mostly lepidopteran larvae known to feed on manzanita species. A more intensive study by Focarile (1975) reported 111 insect taxa from the cosmopolitan manzanita species *A. uva-ursi* (L.) Spr. in Italy's Aosta Valley. In addition, the North American Hymenoptera catalog (Krombein and others 1979) listed 27 pollinating hymenopteran species that visit greenleaf manzanita flowers. However, these species accounts were inadequate for our investigation because information concerning

herbivorous insects feeding specifically on greenleaf manzanita or surveys of insects occurring in brushfield ecosystems (e.g., montane chaparral communities) are scant in the literature (Force 1990, Haws and others 1988). Therefore, we conducted an intensive survey to identify the insects associated with greenleaf manzanita and to determine their respective roles in the manzanita community.

This paper summarizes the results of a detailed entomofaunal survey of arthropods that use greenleaf manzanita for food and shelter. The inventory can be used in an effort to accelerate succession of greenleaf manzanita-dominated sites to conifers on sites historically dominated by the latter. This paper also includes information on the characterisitc damage caused by major groups of insect herbivores. As the problems of manipulating native competing species become more pressing, these lists may contain critical information about insect communities (e.g., faunal associations) that can be a valuable asset to biologists and ecologists in the future.

Study Area

The four study areas in northern California were Logan Lake, Tamarack Swale, Bear Wallow, and Hat Creek; plant identifications were based on descriptions given by Munz (1973).

Logan Lake

The Logan Lake site (elevation 1,512 m [4,960 ft]) was located 3.2 km northwest of California Route 89 near Old Station and 1.6 km west of Logan Lake, about 24 km south of Hat Creek (T32N R4E S2&3). The 50+ ha site was on an east-facing slope and was mechanically cleared of all standing vegetation in 1976 and planted to ponderosa pine the following year. Dominant vegetation (measured as percent canopy coverage) consisted of greenleaf manzanita (74 percent), tobacco brush (*Ceanothus velutinus* Dougl. ex Hook.) (11 percent), and planted ponderosa pine (9 percent). Greenleaf manzanita shrubs averaged 1.5 to 2.0 m in height.

Tamarack Swale

The site was located in a valley 6.4 km southwest of California Route 89 about 5 km south of Hat Creek (T33N R4E S4&9) (elevation 1,646 m [5,400 ft]). In 1974 this 25+ ha site was mechanically cleared and ponderosa pine seedlings were planted in 1975. Greenleaf manzanita shrubs were removed again in 1984 during a second mechanical clearing treatment; however, shrubs have subsequently become reestablished and average about 0.75 m high. Tobacco brush (16 percent) and planted ponderosa pine (8 percent) were mixed in with the most abundant plant species, greenleaf manzanita (61 percent).

Bear Wallow

This 20+ ha old-growth greenleaf manzanita brushfield (elevation 1,524 m [5,000 ft]) was located 3 km (by dirt road) from California Route 89 in Old Station (about 6.6 km south- southwest of the Logan Lake site) (T32N R4E S10). Greenleaf manzanita comprised about 85 percent of the total canopy closure and averaged about 1.5 to 2.0 m high.

Hat Creek

Located adjacent to the USDA Forest Service work center at Hat Creek (T34N R4E S16) (elevation 1,018 m [3,340 ft]), this site consisted of a variety of woody plant species. Greenleaf manzanita accounted for less than 30 percent of the total canopy closure. Other apparent plant species included sagebrush (*Artemisia tridentata* Nutt.), curl-leaf mountain-mahogany (*Cercocarpus ledifolius* Nutt.), birch-leaf mountain-mahogany (*C. betuloides* Torr.), antelope bitterbrush (*Purshia tridentata* [Pursh] de Cand.), California black oak (*Quercus kelloggii* Newb.), and a mixture of conifers (30+ years old) including ponderosa pine, sugar pine (*Pinus lambertiana* Doug.), California white fir (*Abies concolor* [Gord.] var. *lowiana* Lemm.), Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), incense-cedar *Calocedrus decurrens* Torr.), and western juniper (*Juniperus occidentalis* Hook.). This site was also characterized by extensive areas of exposed lava.

Materials and Methods

Arthropods (mostly insects) were sampled from all four study sites by using a variety of collecting techniques. In descending order of relative importance, or frequency of use, these techniques included beating branches and foliage over a muslin cloth or bag (*fig. 2*), hand-picking individuals from plants, sweeping foliage with a canvas net, using an aerial net for flying insects, pitfall-trapping, attracting adults to black light, using a Berlese funnel, and Malaise-trapping (*fig. 3*). Collecting occurred at a minimum of 1-week intervals (and often more frequently) and generally began in May and ended in August from 1989 to 1994. Specimens were collected in the field and transported to the USDA Forest Service's Forest Insect Laboratory, Hat Creek, California, for preparation. All adult specimens were

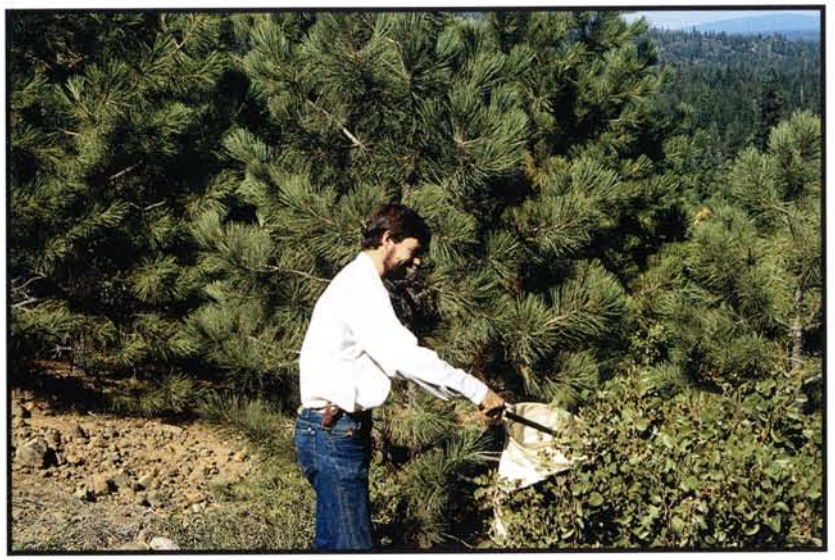

Figure 2–Insects were collected at the Logan Lake site in 1989 by beating greenleaf manzanita branches over a muslin bag.

Figure 3–Malaise trap used to collect flying insects at the Logan Lake site. Insects fly into and land on the sides of the trap and crawl upwards becoming trapped in a container at the top.

either pinned or preserved in alcohol and labelled with complete collecting information. Specimens were sent to various taxonomic experts for positive identification. The ecological role of each taxon (i.e., how it functions in the manzanita community) was determined by direct observations and rearings, or inferred from related species by consulting general entomological references (e.g., Borror and others 1989, Essig 1958, Powell and Hogue 1979). Unless otherwise indicated, voucher specimens are now stored in the Maurice T. James Entomological Museum, Department of Entomology, Washington State University, Pullman.

We attempted to rear herbivorous immature insects (mainly Lepidoptera) collected from greenleaf manzanita plants to adulthood because larval forms usually cannot be identified to species. Individual larvae were placed in small plastic containers or screen cages with host material and allowed to develop and pupate. Many pupae required a cold treatment (e.g., 90 days at 4 °C) for adults to emerge. From these larval rearings, parasitic flies (Diptera) and wasps (Hymenoptera) were also collected.

Arthropods collected in greenleaf manzanita brushfields were grouped by their dominant role in the community. Sampling was biased towards these groups because the primary goal of this study was to identify important greenleaf manzanita herbivores and their associated predators and parasitoids. Other groups of arthropods, such as fungivores and pollinators, were generally not actively sought, and their presence should be considered mostly a random encounter during the collection of herbivores and their natural enemies.

Results and Discussion

Specimens representing 19 orders and 169 arthropod families (mostly insects) were collected from greenleaf manzanita brushfields and identified to species whenever possible (*table 1*). More than 500 taxa below the family level were inventoried and each listing includes relative frequency of encounter, life stages collected, and dominant role in the greenleaf manzanita community. Specific host relationships are included for some predators and parasitoids. Herbivores, predators, and parasitoids comprised the majority (80 percent) of identified insects and related taxa (*fig 4*).

Fungivores

Eleven arthropod taxa that feed on fungi were collected in this survey including a mite (Acari: Eupodidae), a true bug (Hemiptera: Aradidae), a beetle (Coleoptera: Erotylidae), four fungus gnats (Diptera: Mycetophilidae), three dark-winged fungus gnats (Diptera: Sciaridae), and an ant (Hymenoptera: Formicidae).

Pollinators

To Krombein's (1979) list we added 10 more pollinator taxa (all in the order Hymenoptera) associated with greenleaf manzanita flowers: three solitary bees (Halictidae [2] and Andrenidae [1]), two long-tongued bees (Anthophoridae), and one honey bee and four bumble bees (Apidae). One additional solitary bee (*Andrena cerasifolii* Cockerell [Andrenidae]) was also encountered and is included in the list by Krombein and others (1979).

Herbivores

A total of 184 herbivorous insect species representing 7 orders and 55 families were collected. This group includes insects that feed on any part of a living greenleaf manzanita plant (i.e., wood, roots, and leaves).

Xylophagous forms (wood-feeders)

Adult beetles (Coleoptera) of species suspected of using greenleaf manzanita as a host (in the larval form) were collected from foliage. These species include six metallic wood-boring beetles (Buprestidae), five long-horned beetles (Cerambycidae), and three powderpost beetles (Anobiidae). Small (3 mm) D-shaped holes were frequently observed in dead and dying stems of greenleaf manzanita. Such adult exit holes are typical of beetles belonging to the genus *Agrilus* (Buprestidae).

Rhizophagous forms (root-feeders)

Cicada nymphs (Homoptera: Cicadidae) and larvae of certain scarab beetles (Coleoptera: Scarabaeidae), elater beetles (Coleoptera: Elateridae), weevils (Coleoptera: Curculionidae), and moths (Lepidoptera: Hepialidae) are all known to feed on plant roots. Representatives of all groups were collected, as adults, in association with greenleaf manzanita and we suspect the immature forms feed on the roots. However, because we focused on foliovores and detailed studies were not made on root-feeders, we cannot be absolutely sure of direct association with greenleaf manzanita plants.

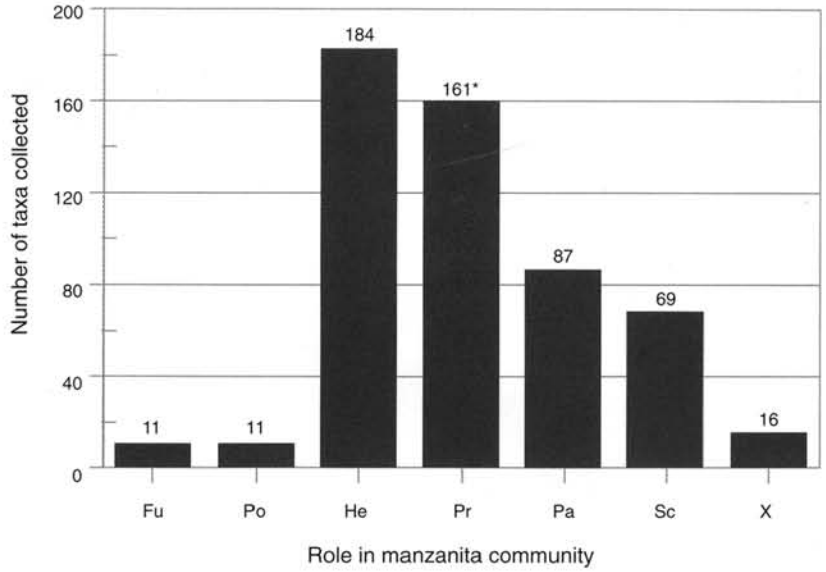

Figure 4–Number of arthropod taxa (below family level) grouped by their dominant role in a greenleaf manzanita brushfield community. All specimens were collected in Shasta County, California from 1989 to 1994. Fu, fungivore; Po, pollinator; He, herbivore (including wood boring forms); Pr, predator; Pa, parasitoid (including hematophagous forms); Sc, scavenger (including detritivores and coprophagous forms); X, no apparent direct association with manzanita. *Does not include 50+ species of unidentified spiders.

Table 1—Arthropods associated with greenleaf manzanita brushfields in Shasta County, California

Taxon	Relative frequency[1]	Stages encountered[2]	Role in community[3]
ARANEAE			
Thomisidae			
Misumenops celer (Hentz)	R	A	Pr
host: *Synaxis cervinaria* (Packard) (Lepidoptera: Geometridae)			
Xysticus sp.	R	J	Pr
host: *Synaxis cervinaria* (Packard) (Lepidoptera: Geometridae)			
Salticidae			
Metaphidippus sp.	R	J	Pr
host: *Synaxis cervinaria* (Packard) (Lepidoptera: Geometridae)			
families and species (50+) undet.	C	J,A	Pr
ACARI			
Ascidae			
Proctolaelaps sp.	O	A	Pr*
Ixodidae			
species undet.	R	A	Hm
Bdellidae			
Spinibdella sp.	O	A	Pr†
Eupodidae			
Eupodes sp.	R	N	Fu‡
found in leaf galls formed by *Tamalia coweni* (Cockerell) (Homoptera: Aphididae)			
Erythraeidae			
Balaustium sp.	O	A	Pr‡
Erythraeus sp.	R	L	Pr‡
associated with *Tamalia coweni* (Cockerell) (Homoptera: Aphididae)			
Phytoseiidae			
Typhalodromia sp.	R	A	Pr‡
associated with *Tamalia coweni* (Cockerell) (Homoptera: Aphididae)			
Johnstonianidae			
Lassenia sp., prob. n. sp.	R	L	Pr‡
associated with *Tamalia coweni* (Cockerell) (Homoptera: Aphididae)			
PSEUDOSCORPIONES			
family and species undet.	O	I,A	Pr
DIPLOPODA			
family and species undet.	C	I,A	Sc
CHILOPODA			
family and species undet.	C	I,A	Pr

Table 1, continued

Taxon	Relative frequency[1]	Stages encountered[2]	Role in community[3]
COLLEMBOLA			
Isotomidae			
species undet.	C	I,A	De
Entomobryidae			
species undet.	C	I,A	De
Sminthuridae			
species undet.	C	I,A	De
MICROCORYPHIA			
Machilidae			
species undet.	C	I,A	De
ODONATA			
Aeshnidae			
Aeschna palmata Hagen	O	A	Pr
Anax junius (Drury)	O	A	Pr
Cordulegasteridae			
Cordulegaster dorsalis Hagen	R	A	Pr
Libellulidae			
Libellula sp.	R	A	Pr
Pantala hymenea (Say)	O	A	Pr
Tarnetrum corruptum (Hagen)	R	A	Pr
Lestidae			
species undet.	O	A	Pr
Coenagrionidae			
species undet.	O	A	Pr
ORTHOPTERA			
Acrididae			
Camnula pellucida (Scudder)	R	A	He
Melanoplus aridus (Scudder)	O	N,A	He
M. sanguinipes (F.)	R	N,A	He
Tettigoniidae			
Capnobotes attenuatus Rentz & Birchum	R	A	He
Scudderia furcata Brunner von Wattenwyl	C	N,A	He
Gryllacrididae			
Ceuthophilus sp.	C	N,A	Sc
Stenopelmatus sp.	O	N,A	Sc
Gryllidae			
Oecanthus sp.	R	N,A	He
BLATTARIA			
Blattellidae			
Parcoblatta americana (Scudder)	O	N,A	Sc

continued

Table 1, continued

Taxon	Relative frequency[1]	Stages encountered[2]	Role in community[3]
PSOCOPTERA			
Psocidae			
species undet.	C	N,A	Sc
THYSANOPTERA			
Aeolothripidae			
Aeolothrips sp., nr. *oregonus* Hood	R	A	Pr*
A. sp.	R	A	Pr
Thripidae			
Chirothrips aculeatus Bagnall	R	A	He
Frankliniella occidentalis (Pergande)	C	N,A	He
Thrips tabaci Lindeman	R	A	He
Phlaeothripidae			
Leptothrips mcconelli (Crawford)	R	A	Pr
HEMIPTERA (HETEROPTERA)			
Pentatomidae			
Banasa dimiata (Say)	O	A	He
B. sp.	R	A	He*
Chlorochroa ligata (Say)	C	E,N,A	He
parasitoid reared from eggs: *Telenomus* sp. (Hymenoptera: Scelionidae)			
Euschistus sp.	R	A	He
Holcostethus abbreviatus Uhler	R	A	He
Thyanta pallidovirens (Stål)	C	E,N,A	He
Scutelleridae			
Homaemus bijugis Uhler	R	A	He
Vanduzeeina californicus Van Duzee	R	A	He
Cydnidae			
Macroporus repetitus Uhler	R	A	He
Coreidae			
Leptoglossus clypealis Heidemann	I	A	X
Alydidae			
Alydus eurinus (Say)	O	A	He
Tollius quadratus Van Duzee	O	A	He
Rhopalidae			
Arhyssus sp.	R	A	He
Lygaeidae			
Ashlockaria sobria (Uhler)	C	A	He
Eremocoris sp., prob. *semicinctus* Van Duzee	R	A	He
Geocoris pallens Stål	O	A	Pr
Lygaeus kalmii Stål	R	A	Pr
Malezonotus grossul Van Duzee	C	A	He
Thylochromus nitidulus Barber	R	A	He
Berytidae			
Jalysus wickhami Van Duzee	R	A	He
Neides muticus (Say)	R	A	He

Table 1, continued

Taxon	Relative frequency[1]	Stages encountered[2]	Role in community[3]
HEMIPTERA (HETEROPTERA), *continued*			
Aradidae			
Mezira sp.	O	A	Fu
Tingidae			
Garaphia iridescens Champion	R	A	He
Phymatidae			
Phymata sp.	R	A	Pr
Reduviidae			
Apiomerus sp.	O	A	Pr
Pselliopus spinicollis Champion	O	A	Pr
Sinea sp.	R	A	Pr
Zelus tetracanthus Stål	C	A	Pr
Nabidae			
Nabis alternatus Parshley	C	A	Pr
Anthocoridae			
Anthocoris whitei Reuter	C	E,N,A	Pr
host: *Tamalia coweni* (Cockerell) (Homoptera: Aphididae)			
Orius tristicolor (White)	R	A	Pr
Miridae			
Chlamydatus manzanitae Knight	C	A	He
Deraeocoris brevis (Uhler)	C	A	He
D. fulgidus (Van Duzee)	R	A	He
D. vanduzeei Knight	C	A	He
Ectopiocerus anthracinus Uhler	R	A	He
Irbisia sp.	R	A	He
Lygus hesperus Van Duzee	R	A	He
Macrotyloides sp.	C	N,A	He
Parthenicus sp.	R	A	He
Phymatopsallus sp.	C	A	He
Phytocoris hettenshawi Bliven	C	A	He
Pilophorus sp.	R	A	He
HEMIPTERA (HOMOPTERA)			
Cicadidae			
Okanagana ferrugomaculata Davis	R	A	He
Platypedia putnami (Uhler)	C	A	He
Membracidae			
Telamona woodruffi Ball	O	A	He
Tortistilus wickhami (Van Duzee)	C	A	He
Cercopidae			
species undet.	O	N	He
Clastopteridae			
Clastoptera sp.	R	A	He
Cicadellidae			
Aceratagallia californica (Baker)	O	A	He
A. longula (Van Duzee)	C	A	He

Table 1, continued

Taxon	Relative frequency[1]	Stages encountered[2]	Role in community[3]
HEMIPTERA (HOMOPTERA),			
Cicadellidae, *continued*			
A. lyrata (Baker)	O	A	He
Aligia sp.	C	A	He
Balclutha incisa (Matsumura)	R	A	He
B. neglecta (DeLong & Davidson)	O	A	He
Ballana aperta DeLong	O	A	He
B. dira DeLong	C	A	He
B. latula DeLong	C	A	He
B. titusi (Ball)	O	A	He
Colladonus geminatus (Van Duzee)	C	A	He
Dikraneura variata Hardy	O	A	He
Empoasca filamenta DeLong	O	A	He
E. pallida Gillette	C	A	He
Exitianus exitiosus (Uhler)	O	A	He
Gyponana sp.	R	A	He
Liburnia sp.	O	A	He
Momoria turgida (Beamer & Lawson)	C	A	He
Neocoelidia lineata Baker	C	N,A	He
Osbornellus borealis DeLong & Mohr	R	A	He
O. curvatus (Beamer)	R	A	He
Paraphlepsius apertinus (Osborn & Lathrop)	R	A	He
Delphacidae			
Delphacodes sp.	O	A	He
Cixiidae			
Oeclidius sp.	R	A	He
Dictyopharidae			
Scolops abnormis Ball	R	A	He
Achilidae			
Epiptera henshawi (Van Duzee)	R	A	He
Synecdoche albicosta (Van Duzee)	O	A	He
S. rubella (Van Duzee)	C	N,A	He
Nogodinidae			
Dictyssa clathrata Melicher	O	A	He
D. marginepunctata Melicher	O	A	He
Psyllidae			
Euglyptoneura robusta (Crawford)	R	A	He
Euphalerus vermiculosus Crawford	O	A	He
Neophyllura arctostaphyli (Schwarz)	C	A	He
N. arctostaphyli var. *bifasciata* (Crawford)	C	A	He
N. bicolor (Martin)	C	A	He
N. separata (Tuthill)	C	A	He
Aleyrodidae			
Trialeurodes vaporariorum? (Westwood)	C	N,A	He
Aphididae			
Cinara sp.	O	N,A	He
Dactynotus sp.	O	N,A	He

Table 1, continued

Taxon	Relative frequency[1]	Stages encountered[2]	Role in community[3]
HEMIPTERA (HOMOPTERA),			
Aphididae, *continued*			
Tamalia coweni (Cockerell)	C	N,A	He
Wahlgreniella nervata (Gillette)	O	N,A	He
Diaspididae			
Lepidosaphes sp.	O	A	He
Pseudococcidae			
Puto arctostaphyli Ferris	O	N,A	He
NEUROPTERA			
Raphidiidae			
Raphidia assimilis Albarda	R	A	Pr
R. bicolor (Albarda)	C	L,A	Pr
R. sp., prob. *bifurca* Banks	R	A	Pr
R. herbsti Esben-Peterson	R	L	Pr
R. sp., prob. *neglecta* Carpenter	R	A	Pr
R. unicolor (Carpenter)	C	L,A	Pr
Inocelliidae			
Inocellia inflata Hagen	R	A	Pr
Coniopterygidae			
Coniopteryx sp.	R	A	Pr
Conwentzia sp.	R	A	Pr
Hemerobiidae			
Hemerobius sp., prob. *ovalis* Carpenter	R	A	Pr
H. sp., prob. *pacificus* Banks	O	A	Pr
Micromus posticus Hagen	R	A	Pr
M. variolosus Hagen	R	A	Pr
Sympherobius sp.	R	A	Pr
Chrysopidae			
Chrysopa sp.	C	L,P,A	Pr
Chrysoperla carnea (Stephens)	C	L,P,A	Pr
C. oculata Say	O	A	Pr
Eremochrysa fraterna Banks	O	A	Pr
Berothidae			
Lomamyia sp., prob. *latipennis* Carpenter or nr.	R	A	Pr
Myrmeleontidae			
Brachynemurus sp.	O	A	Pr
Mantispidae			
Climaciella brunnea (Say)	R	A	Pr
COLEOPTERA			
Cicindelidae			
Cicindela purpurea lauta Casey	O	L,A	Pr
Carabidae			
Calosoma luxatum Say	C	A	Pr

continued

Table 1, continued

Taxon	Relative frequency[1]	Stages encountered[2]	Role in community[3]
COLEOPTERA,			
Carabidae, *continued*			
Lebia perita Casey	R	A	Pr
Pterostichus inanis? Horn	R	A	Pr
P. lama Ménétries	R	A	Pr
P. melanarius Illiger	R	A	Pr
P. planctus? LeConte	R	A	Pr
P. protractus? LeConte	C	A	Pr
Staphylinidae			
Staphylininae	R	A	Pr
Bolitobius sp.	O	A	Pr
Eusphalerum sp.	R	A	Pr
Medon sp.	O	A	Pr
Quedius sp.	R	A	Pr
Sepedophilus sp.	O	A	Pr
Stictolinus sp.	R	A	Pr
Tachyporus sp.	R	A	Pr
Histeridae			
Xerosaprinus sp.	R	A	Sc
Scydmaenidae			
Lophioderus sp.	R	A	Sc
Stenichnus (*Brachycepis*) *fuchsi?* Brendel	R	A	Sc
Lucanidae			
Platyceroides latus (Fall)	R	A	De
Scarabaeidae			
Aphodius opacus LeConte	C	A	Co
Canthon simplex LeConte	R	A	Co
Cremastocheilus armatus Walker	R	A	Sc
Dichelonyx backi (Kirby)	C	A	He
D. valida (LeConte)	R	A	He
Serica anthracina LeConte	C	A	He
S. curvata LeConte	O	A	He
Buprestidae			
Acmeodera mariposa mariposa Horn	R	A	Wb(L)
A. plagiaticauda plagiaticauda Horn	R	A	Wb(L)
A. vandykei Fall	R	A	Wb(L)
Agrilus arbuti Fisher	O	A	Wb(L)
Anambodera gemina (Horn)	R	A	Wb(L)
Anthaxia deleta deleta LeConte	C	A	Wb(L)
Chrysobothris dentipes (Germar)	I	A	X
Chrysophana placida (LeConte)	I	A	X
Elateridae			
Athous imitans Fall	R	A	Pr
A. nigropilis (Motschulsky)	R	A	Pr
Cardiophorus edwardsi Horn	R	A	Pr
C. sp., nr. *tenebrosus* LeConte	R	A	Pr
C. tumidicollis LeConte	R	A	Pr

Table 1, continued

Taxon	Relative frequency[1]	Stages encountered[2]	Role in community[3]
COLEOPTERA,			
Elateridae, *continued*			
Ctenicera pallidipes (Brown)	O	A	Pr
C. tigrina (Fall)	O	A	Pr
Dalopius sp.	O	A	Pr
Hemicrepidius dilaticollis (Motschulsky)	O	A	Pr
Limonius bicolor Van Dyke	R	A	Pr
L. ornatulus LeConte	C	A	Pr
Megapenthes aterrimus (Motschulsky)	R	A	Pr
Neopristilophus maurus (LeConte)	O	A	Pr
Selatosomus edwardsi (Horn)	R	A	Pr
Phengodidae			
Zarhipis sp.	O	L,A	Pr
Cantharidae			
Cantharis sp.	R	A	Pr
Silis sp.	R	A	Pr
Anobiidae			
Oligomerus sp., prob. undesc. sp.	R	A	Wb(L)
Xylentinus fucatus LeConte	R	A	Wb(L)
X. sp., nr. *rotundicollis* White	R	A	Wb(L)
Ptinidae			
Ptinus fallax Fall	R	A	Sc
Bostrichidae			
Scobicia declivis (LeConte)	I	A	X
Cleridae			
Phyllobaenus funebris (Chevrolat)	R	A	Pr
P. scaber (LeConte)	C	A	Pr
Melyridae			
Amecocerus sp.	R	A	Pr
Hapalorhinus sp.	R	A	Pr
Nitidulidae			
Thalycra sp.	R	A	Sc
Erotylidae			
Dacne californica Horn	C	A	Fu
Coccinellidae			
Adalia bipunctata (L.)	R	A	Pr
Anatis rathvoni LeConte	O	A	Pr
Cycloneda polita Casey	O	A	Pr
Exochomus californicus Casey	C	A	Pr
Hippodamia apicalis LeConte	R	A	Pr
H. convergens Guerin	C	A	Pr
Hyperaspis sp.	R	A	Pr
Mulsantina picta (Randell)	R	A	Pr
Psyllobora borealis Casey	R	A	Pr
Scymnus (*Pullus*) *mendocino* Casey	O	A	Pr
host: *Tamalia coweni* (Cockerell) (Homoptera: Aphididae)			

Table 1, continued

Taxon	Relative frequency[1]	Stages encountered[2]	Role in community[3]
COLEOPTERA, *continued*			
Lathridiidae			
Corticarina fuscul (Gyllenhal)	R	A	Sc
Tenebrionidae			
Coelocnemis californica Mannerheim	C	A	Sc
C. rugulosa Doyen	O	A	Sc
Coniontis subpubescens? LeConte	O	A	Sc
Eleodes hybridus? Blaisdell	C	A	Sc
E. scabricula LeConte	R	A	Sc
Helops simulator Blaisdell	R	A	Sc
Scotobaenus sp., prob. *parallelus* LeConte	R	A	Sc
Alleculidae			
Isomira variabilis Horn	C	A	Sc
Mycetochara pubipennis (LeConte)	R	A	Sc
Pseudocistela or *Telacis* sp.	R	A	Sc
Stenochidus cyanescens LeConte	C	A	Sc
Melandryidae			
Anaspis? sp.	O	A	Sc
Mordellidae			
Mordella albosuturalis Liljeblad	R	A	Sc
Meloidae			
Lytta sp.	I	A	X
Anthicidae			
Anthicus punctulatus LeConte	R	A	Sc
Ischyropalpus nitidulus (LeConte)	C	A	Sc
Cerambycidae			
Centrodera spurca (LeConte)	R	A	Wb(L)
Leptura obliterata (Haldeman)	I	A	X
Necydalis sp., prob. *laevicollis* LeConte	O	A	Wb(L)
Neoclytus baltaetus (LeConte)	R	A	Wb(L)
N. resplendens Linsley	R	A	Wb(L)
Ulochaetes leoninus LeConte	I	A	X
Xylosteus ornatus (LeConte)	R	A	Wb(L)
Xylotrechus longitarsis Casey	I	A	X
Bruchidae			
Acanthoscelides aureolus (Horn)	R	A	He
Chrysomelidae			
Altica bimarginata Say	R	A	He
Colaspidea sp., prob. *grata* Fall	C	A	He
Cryptocephalus sanguinicollis sanguinicollis Suffrian	O	A	He
Glyptoscelis juniperi Blake or nr.	O	A	He
Pachybrachis sp., nr. *m-nigrum* (Melsheimer)	C	A	He
P. relictus Fall	R	A	He
Saxinis saucia LeConte	C	A	He
Typophorus nigritus (F.)	R	A	He

Table 1, continued

Taxon	Relative frequency[1]	Stages encountered[2]	Role in community[3]
COLEOPTERA, *continued*			
Curculionidae			
Anthonomus sp., prob. *signatus* Say spp. complex	I	A	X
Gymnetron tetrum (F.)	R	A	He
Leposoma segnis (LeConte)	O	A	He
L. sp., nr. but not *tanneri* Van Dyke	R	A	He
Lepidophorus sp.	C	A	He
Nemocestes montanus Van Dyke	R	A	He
Pachyrhinus cinereus (Casey)	I	A	X
Panscopus (*Dolichontus*) sp.	C	A	He
P. (*Nomidus*) sp.	R	A	He
Peritelinus oregonus Van Dyke	C	A	He
Pselaphorhynchites aureus (LeConte)	C	A	He
Scolytidae			
Hylastes nigrinus (Mannerheim)	I	A	X
DIPTERA			
Tipulidae			
species undet.	C	A	De(L)
Mycetophilidae			
Acomoptera sp.	R	A	Fu(L)
Allodia sp.	R	A	Fu(L)
Megophthalmidea occidentalis Johannsen	R	A	Fu(L)
Mycetophila sp.	R	A	Fu(L)
Sciaridae			
Bradysia spp. (3)	O	A	Fu(L)
Cecidomyiidae			
Asphondylia sp.	R	A	He(L)
Lestodiplosis sp.	R	A	He(L)
Porricondyla sp.	R	A	He(L)
Winnertzia sp.	R	A	He(L)
Simuliidae			
Simulium (*Psilozia*) *vittatum* Zetterstedt	R	A	Hm
S. (*Simulium*) *decorum* Walker	R	A	Hm
Chironomidae			
species undet.	C	A	Hm
Tabanidae			
Chrysops coloradensis Bigot	O	A	Hm
C. excitans Walker	O	A	Hm
Tabanus aegrotus Osten Sacken	O	A	Hm
T. similis Macquart	O	A	Hm
Rhagionidae			
Symphoromyia sp.	O	A	Pr
Therevidae			
species undet.	O	A	?

continued

Table 1, continued

Taxon	Relative frequency[1]	Stages encountered[2]	Role in community[3]
DIPTERA, *continued*			
Vermileonidae			
Vermileo sp.	O	A	Pr
Asilidae			
Dioctria sp.	R	A	Pr
Asilus sp.	R	A	Pr
Bombyliidae			
species (6) undet.	C	A	Pa(L)
Empididae			
Apalocnemis sp., nr. *hirsuta* Melander	R	A	Pr
Rhamphomyia sp.	R	A	Pr
Dolichopodidae			
Medetera sp.	R	A	Pr
Phoridae			
species undet.	R	A	?
Syrphidae			
Blera humeralis (Williston)	R	A	Pr(L)
B. scitula (Williston)	R	A	Pr(L)
Chrysotoxum fasciatum Müller	R	A	Pr(L)
C. flavifrons Macquart	O	A	Pr(L)
Eupodes fumipennis (Thompson)	R	A	Pr(L)
E. lapponicus (Zetterstedt)	O	A	Pr(L)
E. volucris Osten Sacken	R	A	Pr(L)
Helophilus latifrons Loew	R	A	Pr(L)
Heringia sp.	C	L	Pr(L)
host: *Tamalia coweni* (Cockerell) (Homoptera: Aphididae)			
Ocyptamus diversifasciatus (Knab)	R	A	Pr(L)
O. lemur (Osten Sacken)	R	A	Pr(L)
Paragus haemorrhous Meigen	R	A	Pr(L)
P. variabilis Vockeroth	R	A	Pr(L)
Scaeva pyrastri (L.)	R	A	Pr(L)
Toxomerus marginatus (Say)	R	A	Pr(L)
Tephritidae			
Paracantha gentilis Hering	I	A	X
Tephritis sp.	I	A	X
Trupanea californica Malloch	I	A	X
T. femoralis (Thomson)	I	A	X
Sepsidae			
Sepsis sp.	O	A	Sc(L)
Lauxaniidae			
Lauxania sp.	R	A	De(L)
Chamaemyiidae			
Leucopis (*Leucopis*) sp.	C	E,L,P,rA	Pr(L)
host: *Tamalia coweni* (Cockerell) (Homoptera: Aphididae) parasitoids reared from puparia:			

Table 1, continued

Taxon	Relative frequency[1]	Stages encountered[2]	Role in community[3]
DIPTERA,			
Chamaemyiidae, *continued*			
Pachyneuron sp., either *P. eros* Girault or *P. mucronatum* Girault (Hymenoptera: Pteromalidae)			
Melanips sp. (Hymenoptera: Figitidae)			
undet. sp. (Hymenoptera: Eulophidae)			
Agromyzidae			
species (2) undet.	O	L,A	He(L)
Heleomyzidae			
Pseudolaria sp.	R	A	Sc(L)
Suillia barberi (Darlington)	C	A	Sc(L)
S. hemorum (Meigen)	C	A	Sc(L)
S. limbata (Thomson)	C	A	Sc(L)
Trixoscelididae			
Trixoscelis frontalis Fallén	R	A	Sc(L)
T. tumida (Melander)	R	A	Sc(L)
Chloropidae			
Liohippelates robertsoni (Sabrosky)	R	A	Sc(L)
Thaumatomyia bistriata (Walker)	R	A	Sc(L)
T. rubida (Coquillett)	R	A	Sc(L)
Anthomyiidae			
Delia platura (Meigen)	R	A	He(L)
Muscidae			
Caricia sp.	R	A	Sc(L)
Coenosia sp.	O	A	Sc(L)
Fannia sp.	C	A	Sc(L)
Helina troene (Walker)	C	A	Sc(L)
Limnophora sp.	R	A	Sc(L)
Lispe neouliginosa Snyder	R	A	Sc(L)
Neomyia cornicina (F.)	R	A	Sc(L)
Pentacricia aldrichi Stein	R	A	Sc(L)
Phaonia spp. (5)	O	A	Sc(L)
Schoenomyza dorsalis Loew	O	A	Sc(L)
Calliphoridae			
Eucalliphora latifrons (Hough)	C	A	Sc(L)
Phaenicia sericata (Meigen)	R	A	Sc(L)
Phormia regina (Meigen)	R	A	Sc(L)
Sarcophagidae			
Amobia aurifrons (Townsend)	R	A	Sc(L)
Blaesoxipha sp.	R	A	Sc(L)
Hilarella hilarella (Zetterstedt)	O	A	Sc(L)
Metopia argyrocephala (Meigen)	O	A	Sc(L)
Phrosinella pilosifrons Allen	R	A	Sc(L)
Ravinia lherminieri (Robineau-Desvoidy)	O	A	Sc(L)
R. planifrons (Aldrich)	R	A	Sc(L)
Senotainia trilineata (Wulp)	C	A	Sc(L)

Table 1, continued

Taxon	Relative frequency[1]	Stages encountered[2]	Role in community[3]
DIPTERA,			
Sarcophagidae, *continued*			
Sphenometopa tergata (Coquillett)	R	A	Sc(L)
Taxigramma heteroneura (Meigen)	R	A	Sc(L)
Tachinidae			
Allophorocera sp., nr. *occidentalis* (Coquillett)	O	A	Pa(L)
Aplomya theclarum (Scudder)	R	A	Pa(L)
Campylochaeta sp.	O	L,P,rA	Pa(L)
host: *Synaxis cervinaria* (Packard) (Lepidoptera: Geometridae)			
Cryptomeigenia sp.	R	A	Pa(L)
Cylindromyia fumipennis (Bigot)	R	A	Pa(L)
Cyzenis sp.	R	A	Pa(L)
Deopalpus sp., nr. *contiguus* (Reinhard)	R	A	Pa(L)
host: *Hesperumia fumosaria impensa* Rindge (Lepidoptera: Geometridae)			
Enrogalia morigera? Reinhard	R	A	Pa(L)
Erynnia tortricis (Coquillett)	O	L,P,rA	Pa(L)
hosts: *Choristoneura rosaceana* complex (Lepidoptera: Tortricidae)			
Pseudochelaria manzanitae (Keifer) (Lepidoptera: Gelechiidae)			
Euclytia flava (Townsend)	R	A	Pa(L)
Eumea caesar (Aldrich)	O	L,P,rA	Pa(L)
host: *Choristoneura rosaceana* complex (Lepidoptera: Tortricidae)			
Eutrixa sp.	O	A	Pa(L)
Lespesia sp.	R	L,P,rA	Pa(L)
host: *Saturnia mendocino* Behrens (Lepidoptera: Saturniidae)			
Leucostoma simplex (Fallén)	R	A	Pa(L)
Madremyia saundersii (Williston)	R	A	Pa(L)
host: *Hesperumia fumosaria impensa* Rindge (Lepidoptera: Geometridae)			
Microchaetina sp.	R	A	Pa(L)
Myatelemus? sp.	R	A	Pa(L)
Nilea or *Lespesia* sp.	R	L,P,rA	Pa(L)
host: *Choristoneura rosaceana* complex (Lepidoptera: Tortricidae)			
Periscepsia helymus (Walker)	O	L,P,rA	Pa(L)
hosts: *Apharetra californiae* McDunnough (Lepidoptera: Noctuidae)			
Aseptis ethnica Smith (Lepidoptera: Noctuidae)			
Phantasiomyia sp., prob. n. sp.	R	A	Pa(L)
Phryxe pecosensis (Townsend)	R	A	Pa(L)
host: *Hesperumia fumosaria impensa* Rindge (Lepidoptera: Geometridae)			
Siphona sp., nr. *pacifica* O'Hara	R	A	Pa(L)
Strongygaster robustus (Townsend)	O	A	Pa(L)
Tachina sp.	R	A	Pa(L)
Voria sp., nr. *ruralis* (Fallén)	R	A	Pa(L)
LEPIDOPTERA			
Hepialidae			
Hepialis hectoides (Boisduval)	O	A	He(L)
Tineidae			
species (2) undet.	R	A	He(L)
Psychidae			
Hyaloscotes fumosa Butler	O	L,P,rA	He(L)
Gracillariidae			
species undet. (serpentine mine)	C	L	He(L)
species undet. (blotch mine)	C	L	He(L)
Coleophoridae			
Coleophora glaucella Walsingham	O	L,P,rA	He(L)
parasitoids reared from larvae:			
Agathis sp. (Hymenoptera: Braconidae)			
Chelonus sp. (Hymenoptera: Braconidae)			
Gelechiidae			
Gelechia sp., nr. *panella* Busck	O	L,P,rA	He(L)
Pseudochelaria manzanitae (Keifer)	O	L,P,rA	He(L)
parasitoid reared from larvae:			
Erynnia tortricis (Coquillett) (Diptera: Tachinidae)			
Tortricidae			
Amorbia cuneana (Walsingham)	R	L,P,rA	He(L)
Choristoneura sp., *rosaceana* (Harris)			
spp. complex	C	L,P,rA	He(L)
parasitoids reared from larvae:			
Erynnia tortricis (Coquillett) (Diptera: Tachinidae)			
Eumea caesar (Aldrich) (Diptera: Tachinidae)			
Nilea or *Lespesia* sp. (Diptera: Tachinidae)			
Epinotia arctostaphylana (Kearfott)	C	L,P,rA	He(L)
E. miscana (Kearfott)	C	L,P,rA	He(L)
E. subplicana (Walsingham)	C	L,P,rA	He(L)
E. terracoctana (Walsingham)	C	L,P,rA	He(L)
Pyralidae			
Tulsa oregonella? (Barnes & McDunnough)	R	A	He(L)
Hesperiidae			
Hesperia sp.	I	A	X
Lycaenidae			
Celastrina ladon (Cramer)	R	A	He(L)

continued

Table 1, continued

Taxon	Relative frequency[1]	Stages encountered[2]	Role in community[3]
LEPIDOPTERA,			
Lycaenidae, *continued*			
Incisalia augustus iroides Boisduval	O	L,P,rA	He(L)
Nymphalidae			
Nymphalis californica (Boisduval)	C	P,rA	He(L)
Geometridae			
Aethaloida packardaria (Hulst)	R	E,L,P,rA	He(L)
Anacamptodes clivinaria clivinaria (Guenée)	O	L,P,rA	He(L)
Apodrepanulatrix litaria (Hulst)	R	A	He(L)
Chlorosea nevadaria Packard	R	A	He(L)
Cyclophora dataria (Hulst)	R	A	He(L)
Drepanulatrix rectifascia (Hulst)	R	A	He(L)
D. unicalcararia (Guenée)	R	A	He(L)
Eupithecia sp.	R	L,P,rA	He(L)
Hesperumia fumosaria impensa Rindge	O	E,L,P,rA	He(L)
parasitoids reared from larvae:			
Deopalpus sp., nr. *contiguus* (Reinhard) (Diptera: Tachinidae)			
Madremyia saundersii (Williston) (Diptera: Tachinidae)			
Phryxe pecosensis (Townsend) (Diptera: Tachinidae)			
Aleiodes nolophanae (Ashmead) (Hymenoptera: Braconidae)			
Itame guenearia (Packard)	R	A	He(L)
I. quadrilinearia (Packard)	O	A	He(L)
Nemoria darwiniata (Dyar)	O	A	He(L)
N. glaucomarginaria (Barnes & McDunnough)	O	E,L,P,rA	He(L)
Sabulodes edwardsata (Hulst)	R	A	He(L)
Semiothisa signaria dispuncta (Walker)	R	A	He(L)
Sericosema juturnaria (Guenée)	R	A	He(L)
S. wilsonensis (Cassino & Swett)	R	A	He(L)
Synaxis cervinaria (Packard)	O	E,L,P,rA	He(L)
parasitoids reared from eggs:			
Trichogramma sp. (Hymenoptera: Trichogrammatidae)			
Telenomus alsophilae Viereck (Hymenoptera: Scelionidae)			
parasitoids reared from larvae:			
Campylochaeta sp. (Diptera: Tachinidae)			
Aleiodes n. sp. (Hymenoptera: Braconidae)			
Meteorus rubens (Nees) (Hymenoptera: Braconidae)			
Dusona nigritibialis (Viereck) (Hymenoptera: Ichneumonidae)			
Euplectrus sp., poss. *plathypenae* Howard (Hymenoptera: Eulophidae)			
parasitoid observed attacking larval instar III:			
Goniozus gracilicornis (Kieffer) (Hymenoptera: Bethylidae)			
predators observed attacking larvae:			
Misumenops celer (Hentz) (Araneae: Thomisidae)			
Xysticus sp. (Araneae: Thomisidae)			
Metaphidippus sp. (Araneae: Salticidae)			
Lasiocampidae			
Malacosoma californicum (Packard)	O	L,P,rA	He(L)

Table 1, continued

Taxon	Relative frequency[1]	Stages encountered[2]	Role in community[3]
LEPIDOPTERA,			
Lasiocampidae, *continued*			
M. constrictum (Henry Edwards)	O	L,rA	He(L)
M. disstria Hübner	O	L,P,rA	He(L)
Pyllodesma americana (Harris)	R	L,P,rA	He(L)
Lymantriidae			
Orgyia cana Henry Edwards	R	L,P,rA	He(L)
Saturniidae			
Hemileuca eglanterina shastaensis (Grote)	O	L,P,rA	He(L)
Hyalophora euryalus (Boisduval)	C	E,L,P,rA	He(L)
Saturnia mendocino Behrens	O	E,L,P,rA	He(L)
parasitoid reared from pupae:			
Lespesia sp. (Diptera: Tachinidae)			
Sphingidae			
Hyles lineata (F.)	O	A	He(L)
Paonias myops (J. E. Smith)	O	L,P,rA	He(L)
Sphinx vashti Strecker	O	L,P,rA	He(L)
Arctiidae			
Spilosoma vestalis Packard	O	A	He(L)
Noctuidae			
Acronicta perdita Grote	R	L,P,rA	He(L)
Apharetra californiae McDunnough	O	L,P,rA	He(L)
parasitoid reared from larvae:			
Periscepsia helymus (Walker) (Diptera: Tachinidae)			
Aseptis ethnica Smith	C	L,P,rA	He(L)
parasitoid reared from larvae:			
Periscepsia helymus (Walker) (Diptera: Tachinidae)			
HYMENOPTERA			
Stephanidae			
Schlettererius cinctipes (Cresson)	R	A	Pa(L)
Aulacidae			
Pristaulacus montanus (Cresson)	R	A	Pa(L)
Braconidae			
Aleiodes nolophanae (Ashmead)	R	L,P,rA	Pa(L)
host: *Hesperumia fumosaria impensa* Rindge (Lepidoptera: Geometridae)			
A. n. sp.	R	A	Pa(L)*
host: *Synaxis cervinaria* (Packard) (Lepidoptera: Geometridae)			
Agathis sp.	R	A	Pa(L)†
host: *Coleophora glaucella* Walsingham (Lepidoptera: Coleophoridae)			
Apanteles sp.	R	A	Pa(L)
Bassus sp.	R	A	Pa(L)
Chelonus sp.	R	A	Pa(L)†
host: *Coleophora glaucella* Walsingham			

Table 1, continued

Taxon	Relative frequency[1]	Stages encountered[2]	Role in community[3]
HYMENOPTERA,			
Braconidae, *continued*			
(Lepidoptera: Coleophoridae)			
Cotesia sp.	R	A	Pa(L)
Dolichogenidea cacoeciae (Riley)	R	A	Pa(L)
Macrocentrus gravitarsis Muesebeck	R	A	Pa(L)
host: genus and species undet. (Lepidoptera: Lymantriidae)			
Meteorus rubens (Nees)	C	L,P,rA	Pa(L)
host: *Synaxis cervinaria* (Packard) (Lepidoptera: Geometridae)			
Trioxys sp.	R	A	Pa(L)
Urosigalphus sp.	R	A	Pa(L)
Ichneumonidae			
Dusona nigritibialis (Viereck)	O	A	Pa(L)
host: *Synaxis cervinaria* (Packard) (Lepidoptera: Geometridae)			
species (7) undet.	O	A	Pa(L)
Trichogrammatidae			
Trichogramma sp.	O	E,L,P,rA	Pa(L)
host: eggs of *Synaxis cervinaria* (Packard) (Lepidoptera: Geometridae)			
Eulophidae			
Aprostocetus sp., nr. *hibus* Burks	O	L,P,rA	Pa(L)
host: *Tamalia coweni* (Cockerell) (Homoptera: Aphididae)			
Euplectrus sp., poss. *plathypenae* Howard	O	L,P,rA	Pa(L)
host: *Synaxis cervinaria* (Packard) (Lepidoptera: Geometridae)			
Tetrastichus chrysopae (Crawford)	R	A	Pa(L)
Zagrammosoma sp.	R	A	Pa(L)
genus and species undet.	O	A	Pa(L)
host: *Leucopis* sp. (Diptera: Chamaemyiidae)			
Eupelmidae			
species undet.	O	A	Pa(L)
Torymidae			
Pseudotorymus sp.	R	A	Pa(L)
Torymus tubicola (Osten Sacken)	O	A	Pa(L)
Pteromalidae			
Catolaccus aineoviridis (Girault)	R	A	Pa(L)
Gastrancistrus sp.	R	A	Pa(L)
Pachyneuron sp., either *P. eros* Girault or *P. mucronatum* Girault	R	L,P,rA	Pa(L)†
host: *Leucopis* sp. (Diptera: Chamaemyiidae)			
Pteromalus sp.	R	A	Pa(L)

Table 1, continued

Taxon	Relative frequency[1]	Stages encountered[2]	Role in community[3]
HYMENOPTERA,			
Pteromalidae, *continued*			
Zatropis sp.	R	L,P,rA	Pa(L)
host: *Tamalia coweni* (Cockerell) (Homoptera: Aphididae)			
Perilampidae			
Perilampus sp.	R	A	Pa(L)
Eurytomidae			
Sycophila sp.	R	A	Pa(L)
Figitidae			
Melanips sp.	R	L,P,rA	Pa(L)
host: *Leucopis* sp. (Diptera: Chamaemyiidae)			
Scelionidae			
Telenomus alsophilae Viereck	O	A	Pa(L)
host: eggs of *Synaxis cervinaria* (Packard) (Lepidoptera: Geometridae)			
T. sp.	O	A	Pa(L)
host: eggs of *Chlorochroa ligata* (Say) (Heteroptera: Pentatomidae)			
Chrysididae			
Chrysis sp.	R	A	Pa(L)
Omalus glomeratus (Buysson)	O	A	Pa(L)
Encyrtidae			
Encyrtus sp.	R	A	Pa(L)
Bethylidae			
Goniozus columbianus Ashmead	R	A	Pa(L)
G. gracilicornis (Kieffer)	R	A	Pa(L)
host: *Synaxis cervinaria* (Packard) (Lepidoptera: Geometridae)			
Epyris clarimontensis Kieffer	R	A	Pa(L)
Dryinidae			
Gonatopus sp.	R	A	Pa(L)
Sphecidae			
Ammophila azteca Cameron	R	A	Pr
A. regina Menke	R	A	Pr
Ancistromma capax (Fox)	C	A	Pr
Aphilanthops subfrigidus Dunning	R	A	Pr
Astata sp.	O	A	Pr
Eucerceris similis Cresson	O	A	Pr
Gorytes sp.	O	A	Pr
Harpactus rugulosus (Bohart)	R	A	Pr
Isodontia elegans (Smith)	R	A	Pr
Mimesa serrana Finnamore	R	A	Pr
Sceliphron caementarium (Drury)	R	A	Pr
Steniolia tibialis Handlirsch	R	A	Pr
Trypoxylon tridentatum Packard	R	A	Pr

continued

Table 1, continued

Taxon	Relative frequency[1]	Stages encountered[2]	Role in community[3]
HYMENOPTERA, *continued*			
Halictidae			
Dialictus sp.	C	A	Po
Evylaeus sp.	R	A	Po*
Andrenidae			
Andrena cerasifolii Cockerell	R	A	Po
Nomadopsis sp.	R	A	Po*
Anthophoridae			
Anthophora urbana (Cresson)	R	A	Po
Epeolus sp.	R	A	Po*
Apidae			
Apis mellifera L.	C	A	Po
Bombus edwardsii Cresson	R	A	Po
B. vandykei (Frison)	R	A	Po
B. vosnesenskii Radowszkowski	C	A	Po
Psithyrus insularis (Smith)	R	A	Po
Mutillidae			
Dasymutilla aureola Cresson	O	A	Pr
D. sackenii (Cresson)	O	A	Pr
Sphaerophthalma sp.	R	A	Pr
Pompilidae			
Ageniella coronata Banks	R	A	Pr
A. euphorbiae (Viereck)	R	A	Pr
Anoplius insolens (Banks)	R	A	Pr
Aporinellus completus Banks	R	A	Pr
Aporus luxus Banks	R	A	Pr
Pompilus angularis Banks	R	A	Pr
P. fumipennis eureka (Banks)	C	A	Pr
P. solonis (Banks)	R	A	Pr
Priocnemis notha navajo Banks	R	A	Pr

Table 1, continued

Taxon	Relative frequency[1]	Stages encountered[2]	Role in community[3]
HYMENOPTERA, *continued*			
Vespidae			
Ancistrocerus sp.	R	A	Pr
Euodynerus sp.	R	A	Pr
Stenodynerus sp.	O	A	Pr
Vespula pensylvanica (Saussure)	C	A	Pr
Formicidae			
Aphaenogaster occidentalis (Emery)	O	A	Fu
Camponotus essigi M. R. Smith	C	A	Pr
C. laevigatus (F. Smith)	C	A	Pr
C. vicinus Mayr	C	A	Pr
Crematogaster coarctata Mayr	R	A	Pr
Formica haemorrhoidalis Emery	C	A	Pr
F. podzolica Francoeur	C	A	Pr
F. subpolita Mayr	C	A	Pr
Leptothorax rugatulus Emery	O	A	Pr
Myrmica sp.	C	A	Pr
Solenopsis molesta (Say)	C	A	Pr
Tapinoma sessile (Say)	C	A	Pr

[1]Relative frequency: I, incidental (transient species); R, rare (only a few individuals encountered during five field seasons); O, occasional (individuals encountered fairly frequently); C, common (individuals locally abundant and encountered very frequently).

[2]Stages encountered: E, egg; I, immature; J, juvenile; N, nymph; L, larva; P, pupa or puparium; A, adult; rA, adult reared from immature form.

[3]Dominant role in community (stage performing role if other than stage encountered): Fu, fungivore; Po, pollinator; Wb, wood borer; He, herbivore; Pr, predator; Pa, parasitoid; Hm, hematophage; Sc, scavenger; De, detritivore; Co, coprophage; X, no apparent direct association with manzanita.

*Voucher specimens retained by the USDA Agricultural Research Center, Beltsville, Maryland.

†Voucher specimens retained by Crop Protection Division, Agriculture Canada, Ottawa, Ontario.

‡Voucher specimens retained by the Florida State Arthropod Collection, Gainesville, Florida.

Figure 5–Greenleaf manzanita leaves tied together with silk from an unidentified caterpillar in the family Gelechiidae or Tortricidae (Lepidoptera).

Figure 6–*Choristoneura sp., rosaceana* (Harris) complex (Lepidoptera: Tortricidae) larva in an unraveled leaf bundle. This species generally completes its larval development before new leaves expand in the late spring and pupation occurs within a loose silken cocoon inside the tied leaf bundle. Damage can be locally severe.

Foliovores (foliage-feeders)

Leaf rollers/tiers

As soon as leaf buds break in the late spring or early summer, injury due to leaf rollers and tiers becomes evident (*figs. 5-6*). This type of damage is caused by a guild of caterpillars (Lepidoptera: Gelechiidae and Tortricidae). Numbers of tied leaf bundles fluctuate from year to year but the bundles are usually quite obvious. Larvae use silk to tie leaves together. The resulting bundle of leaves affords protection from natural enemies and provides a source of food as larvae feed on leaf tissue inside the bundle. After larvae fully mature, individuals of most species drop to the leaf litter to pupate leaving behind a loosely tied bundle of leaves containing frass or droppings. In time, the silken threads wear away, allowing leaves to expand and produce photosynthates. Although damage by leaf rollers and tiers often appears severe, greenleaf manzanita plants are usually able to withstand repeated yearly attacks by these foliage-feeders.

Leaf miners

Three types of leaf mines were frequently encountered throughout this study: serpentine, blotch, and hollow (*figs. 7-9*). Larvae causing mining damage feed between the outer two layers of a leaf and "mine" the inner layers leaving behind a characteristic damage pattern. Damage to greenleaf manzanita plants is typically minor because only a portion of the leaf is usually damaged.

Gall formers

The manzanita leaf gall aphid, *Tamalia coweni* (Cockerell) (Homoptera: Aphididae), causes the edge of a newly expanding leaf to curl, thus causing the formation of a leaf gall. Damage to greenleaf manzanita plants can be quite obvious but not usually serious (*fig. 10*). A number of arthropods were found in association with this leaf gall aphid, including predators, scavengers, and opportunistic shelter-seekers (Valenti and others 1996). One other type of gall, formed within a newly expanding stem, was occasionally found but we were not able to identify the arthropod reponsible for its formation.

Piercing/sucking insects

Insects with piercing/sucking mouthparts (e.g., thrips [Thysanoptera], true bugs [Hemiptera], and homopterans ([Homoptera]) suck plant

Figure 7–Serpentine mine caused by an undetermined species (Lepidoptera: Gracillariidae).

Figure 8—Blotch mine caused by an undetermined species (Lepidoptera: Gracillariidae).

Figure 9–Characteristic leaf mine caused by *Epinotia miscana* (Kearfott) (Lepidoptera: Tortricidae) (note adult exit hole near base of leaf).

Figure 10–Greenleaf manzanita plant infested with leaf galls caused by the manzanita leaf gall aphid, *Tamalia coweni* (Cockerell) (Homoptera: Aphididae). Emerging alate forms are sexual winged males and females which mate and produce eggs that overwinter.

Figure 11–Non–gall forming aphids (Homoptera: Aphididae) congregated on a leaf (also note two leaf galls in the photograph).

Figure 12–Adult cicada, *Platypedia putnami* (Uhler) (Homoptera: Cicadidae), resting on a greenleaf manzanita branch. In 1993 adult females were commonly encountered at the Hat Creek site notching and depositing eggs in greenleaf manzanita branches.

sap, usually from leaves. This type of feeding produces a necrotic stipling effect and, if severe enough, can cause serious damage to leaf tissue. Aphids (Homoptera: Aphididae) and leafhoppers (Homoptera: Cicadellidae) were common on greenleaf manzanita foliage during the growing season (*fig. 11*). Cicada adults (Homoptera: Cicadidae) periodically were locally abundant (*fig. 12*). Females oviposited in greenleaf manzanita stems but feeding was not observed.

Defoliators

Perhaps the most important natural enemies of greenleaf manzanita are the defoliators, defined here as those insects that possess chewing mouthparts. Damage can be severe because entire leaves can potentially be removed in a relatively short time period by a single insect. Greenleaf manzanita defoliators belong to one of three insect orders; Orthoptera, Coleoptera, or Lepidoptera. Grasshoppers (*fig. 13*) and katydids (Orthoptera) were often common as were members of several beetle (Coleoptera) families including scarabs (Scarabaeidae) (*fig. 14*), leaf beetles (Chrysomelidae), and weevils (Curculionidae). Lepidoptera (moths and butterflies), however, were the most common defoliators encountered. This group of insects is represented by numerous families and species (Valenti and Zack 1995) (*figs. 15-24*).

Figure 13–Grasshoppers, such as this immature *Melanoplus* sp. (Orthoptera: Acrididae), are quite common in greenleaf manzanita brushfields.

Figure 14–Two color variants of the ubiquitous scarab *Dichelonyx backi* (Kirby) (Coleoptera: Scarabaeidae). Adults were commonly encountered feeding on greenleaf manzanita leaves making characteristic small notches on leaf edges.

Figure 15–A case bearer, probably *Coleophora glaucella* Walsingham (Lepidoptera: Coleophoridae), and its charactersitic damage to a greenleaf manzanita leaf.

Figure 16–The slug–like caterpillar of *Incisalia augustus iroides* Boisduval (Lepidoptera: Lycaenidae). This larva grazes the surfaces of leaves and fruits.

Figure 17–Early larval instar of *Aethaloida packardaria* (Hulst) (Lepidoptera: Geometridae) in a typical resting posture on the edge of a leaf.

Figure 18–Green larval color variant of *Hesperumia fumosaria impensa* Rindge (Lepidoptera: Geometridae) that mimics newly expanding manzanita shoots. A second crimson larval color variant of this species occurs concurrently and mimics mature manzanita stems. Larvae feed on previous years' leaves and complete development by late spring generally before new leaves mature. Pupation occurs in the leaf litter and adults are active during June and July. Eggs deposited in litter overwinter.

Figure 20–*Synaxis cervinaria* (Packard) (Lepidoptera: Geometridae) fourth larval instar. Larvae mimic dead and dying manzanita twigs (see Valenti and others [1997] for details on the biology and ecology of this species).

Figure 19–An unusual greenleaf manzanita inflorescence mimic, *Nemoria glaucomarginaria* (Barnes & McDunnough) (Lepidoptera: Geometridae).

Figure 21–Mature larva of the ceanothus silk moth, *Hyalophora euryalus* (Boisduval) (Lepidoptera: Saturniidae).

Figure 22–Adult male ceanothus silk moth, *Hyalophora euryalus* (Boisduval) (Lepidoptera: Saturniidae), on top of its cocoon soon after emergence.

Figure 23–A hawk moth larva, *Sphinx vashti* Strecker (Lepidoptera: Sphingidae).

Figure 24–An unusual noctuid larva, *Acronicta perdita* Grote (Lepidoptera: Noctuidae).

Predators

Predators generally consume all or part of their prey soon after capture. During the life of the predator more than one prey individual is killed and often dozens or even hundreds are consumed. A total of 161 invertebrate predator taxa was collected in greenleaf manzanita communities representing 11 orders and 51 families. Snakeflies (Neuroptera: Raphidiidae) were common during the greenleaf manzanita growing season (*fig. 25*). These insects feed on soft-bodied arthropods such as aphids and leafhoppers. One individual was observed feeding on a small lepidopteran caterpillar. Another quite common predator group related to the snakefly includes green lacewings (Neuroptera: Chrysopidae) (*fig. 26*). Green lacewing eggs, larvae, and adults can be found easily with a minimal amount of searching during the summer months. These insects, like the snakeflies, feed on soft-bodied arthropods. Dragonflies and damselflies (Odonata) capture their prey on the wing and can be abundant at certain times of the year during hatches (mass adult emergences). These "mosquito hawks" were particularly abundant at the Logan Lake site (*fig. 27*).

Figure 25–A male snakefly, *Raphidia unicolor* (Carpenter) (Neuroptera: Raphidiidae). Snakeflies feed on soft-bodied arthropods and are extremely common during the summer months.

Figure 26–Green lacewing adult (Neuroptera: Chrysopidae).

Figure 27–Damselfly (Odonata) adult resting on a greenleaf manzanita leaf.

The most important invertebrate predators were ants (Hymenoptera: Formicidae). Ants were commonly encountered at all study sites, both on the ground and on greenleaf manzanita plants. Most ant species are generalist predators and numerous studies have shown them to be very important in regulating many insect populations (Finnegan 1971, Laine and Niemelä 1980, Youngs 1983, Valenti and others 1998).

Spiders (Araneae) are probably the second most important invertebrate predators in greenleaf manzanita communities. A variety of spiders, including orb builders (*fig. 28*), crab spiders (*fig. 29*), and jumping spiders (*fig. 30*), were encountered. More than 50 species were collected but have not yet been identified.

Parasitoids

The term parasitoid is used to describe a parasite that kills its host (usually only one), in contrast to a true parasite that feeds without killing its host, such as blood-feeding insects. Eight blood-feeders

Figure 28–Unidentified orb weaver spider (Araneae).

Figure 29–Unidentified crab spider (Araneae: Thomisidae) feeding on a larva of *Synaxis cervinaria* (Packard) (Lepidoptera: Geometridae).

Figure 30–Unidentified jumping spider (Araneae: Salticidae).

were encountered in greenleaf manzanita brushfields. These included a tick (Acari: Ixodidae), two black flies (Diptera: Simuliidae), a midge (Diptera: Chironomidae), and four deer flies (Diptera: Tabanidae). Seventy-nine parasitoids were collected from two orders and 19 families, many of which we reared from known hosts (*table 1*).

Adult tachinid flies (Diptera: Tachinidae) were commonly encountered on and around greenleaf manzanita foliage (*fig. 31*). Female flies locate a suitable host and deposit eggs or larvae on the host's body. Larvae eventually work their way into the host, feed, develop, and remain there until pupariation occurs. The host is kept alive for nearly the entire time it takes for the fly to develop. This is accomplished by the fly larva first feeding on non-vital host tissues. A number of parasitic Hymenoptera were also collected by rearing them from their lepidopteran hosts (*figs. 32-33*).

Scavengers

Sixty-nine scavengers, or organisms that feed on waste material, were captured (8 orders and 29 families). Many were collected in pitfall traps. Included in this group are detritivores and

Figure 31–Adult tachinid fly (Diptera: Tachinidae) resting on manzanita leaf.

Figure 32–Parasitoid cocoons (Hymenoptera: Braconidae) on a mature ceanothus silk moth larva, *Hyalophora euryalus* (Boisduval) (Lepidoptera: Saturniidae).

Figure 33–Fifth larval instar of *Synaxis cervinaria* (Packard) (Lepidoptera: Geometridae) being parasitized by *Euplectrus* sp., possibly *plathypenae* Howard (Hymenoptera: Eulophidae).

coprophagous forms. Detritivores feed on dead organic material and were common. Representatives of three families of springtails (Colembola: Isotomidae, Entomobryidae, and Sminthuridae), one family of jumping bristletails (Microcoryphia: Machilidae), a stag beetle (Coleoptera: Lucanidae), crane flies (Diptera: Tipulidae), and a lauxaniid fly (Diptera: Lauxaniidae) were encountered. Coprophagous forms feed on dung and are also decomposers and are represented by two scarab beetles (Coleoptera: Scarabaeidae). The majority of scavengers collected, such as muscid flies (*fig. 34*), feed on a variety of waste materials and all play an important role in decomposition and mineral recycling.

Conclusions

Northeastern California montane chaparral communities dominated by greenleaf manzanita harbor a rich diversity of insect and related arthropod fauna. Because of the need for alternatives to control competing forest vegetation in the future, arthropod diversity studies will become increasingly important. This inventory provides

Figure 34–Adult muscid fly (Diptera: Muscidae) (larvae are scavengers).

basic biological information about insect fauna associated with greenleaf manzanita that can be used in future studies. For example, a portion of the herbivorous insects encountered in this study have the potential to cause serious damage to greenleaf manzanita plants after they are released from their natural regulating agents. If this release can be accomplished on a large scale, it represents an ecologically sound method of altering vegetation composition to favor more desirable plant species such as high-value conifers.

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