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Arthropod diversity in peas with normal or reduced waxy bloom

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Abstract

Crop traits can alter economically important interactions between plants, pests, and biological control agents**.** For example, a reduced waxy bloom on the surface of pea plants alters interactions between pea aphids and their natural enemies. In this study, we assess whether the effect of wax reduction extends beyond the 2 or 3 arthropod species closely associated with the plants and into the structure of the broader arthropod community of over 200 taxa at our site. We sampled arthropods on lines of peas with normal and reduced wax in Latah Co., Idaho using pitfall traps within randomly assigned pairs of 5 x 5 meter plots. During the 1998 and 1999 growing seasons, we collected 12,113 individual arthropods from 221 unambiguously identified morphospecies. The number of individuals collected from each morphospecies responded idiosyncratically to the reduced wax peas. To test whether arthropod community structure differed between the collections from plots having peas with normal or reduced wax, we performed a randomization test. The collection from peas with reduced wax had higher species evenness and thus higher community diversity despite having lower species richness. Our results demonstrate the potential of a single plant trait, epicuticular wax, to affect a community of arthropods. Two pests of peas had opposite responses to peas with reduced wax. The number of pea aphids collected was greater from peas with normal wax peas than those with reduced wax. In contrast, the number of pea leaf weevils collected was greater from peas with reduced wax.

Keywords: Acyrthosiphon pisum, *Sitona lineatus*, multitrophic interactions, pitfall sampling

Introduction

Plant traits such as leaf shape, trichomes, leaf surface waxbloom, and chemical compounds can affect the animals associated with the plant (Hare 2002; Whitham et al. 2003). Plant traits may affect both herbivores and predators, and interactions between predators and their prey may be altered to produce indirect ecological effects (Hare 2002). Studies of hybrid plants and their parent species indicate that traits affecting community structure can have a genetic basis (Whitham et al. 2003). Species associated with hybrid plants can have idiosyncratic responses and may increase or decrease in abundance (Fritz et al. 1994; Messina et al. 1996). The responses of each associated species to hybrid genotypes can change the species richness and evenness of the associated community. For example, leaf-galling aphid survival on individual poplar trees within a hybrid zone varies 75-fold (Whitham 1989). The subsequent decrease in aphid density reduces associated arthropod species richness by 31% (Dickson and Whitham 1996). The pattern of community structures of associated arthropods on two *Eucalyptus* species and their F1 and F2 hybrids is comparable to patterns expected from inherited quantitative traits (Dungey et al. 2000). However, many traits differed between the hybrids and their parents (Dungey et al. 2000). Studies of isoline or near-isoline plants that vary in only one trait may help pinpoint genetic mechanisms that affect community structure.

Knowledge of genetic mechanisms that affect community structure in a crop-based system may improve pest management (Bottrell et al. 1998). All else being equal, a crop variety with a trait that reduced pest density would be clearly preferable to a variety without that trait. However, even recognizing traits that increase one pest but decrease another may aid in developing integrated pest management strategies (Smith and Van den Bosch 1967; Pedigo 2002). In peas, *Pisum sativum* L., single gene mutations can change the amount and composition of waxy bloom that the plant produces (Marx 1969; Holloway et al. 1977). The peas in our study differ at one locus, *Wel/wel*. One line possesses the dominant allele *Wel*, which produces wax normally. The other line is homozygous for the allele *wel* and has reduced wax crystals over its stems, leaves, stipules, and pods (Eigenbrode et al. 1998b).

Certain ecological interactions between insects differ between peas with reduced wax and normal peas. Foraging predators can walk more effectively on peas with reduced wax, thereby increasing predation on the pea aphid (*Acyrthosiphon pisum* Harris) (Eigenbrode et al. 1998a; White and Eigenbrode 2000). The

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convergent lady beetle (*Hippodamia convergens* Guerin-Meneville), a green lacewing (*Chrysoperla plorabunda* Fitch), and a parasitoid wasp (*Aphidius ervi* Haliday) all cause greater pea aphid mortality on peas with reduced wax than on normal wax peas (Eigenbrode et al. 1998a; White and Eigenbrode 2000, Chang et al. 2004). Such enhanced predation is partly responsible for consistently lower field densities of the pea aphid on peas with reduced wax than on normal peas (White 1998; White and Eigenbrode 2000; Rutledge et al. 2003; Chang et al. 2004). However, some interactions remain the same on peas with reduced wax. For example, interactions between a carabid (*Poecilus scitulus* LeConte) and the pea aphid and convergent lady beetle do not appear to be altered on peas with reduced wax (Chang and Eigenbrode 2004).

The direct and indirect effects of peas with reduced wax may change community structure. Visual canopy sampling of arthropods found 12 unambiguous morphospecies that responded differently to peas with reduced wax (Rutledge et al. 2003). For example, predatory syrphids are more abundant on normal peas, while coccinellids are more abundant on peas with reduced wax (Rutledge et al. 2003). However, information on the effects of wax on the broader community of arthropods is lacking. We used pitfall sampling to complement and extend the information on community effects of peas with reduced wax. Pitfall sampling has advantages and disadvantages (New 1998). In our case, one advantage is that many more morphospecies, over 200 taxa at our site, could be counted and identified from pitfalls than from visual canopy sampling. However, a limitation of pitfalls is that they will only capture individuals that walk or fall into them. Thus, mostly ground-dwelling species are collected, although some foliage-dwelling and flying insects may fall into the traps. We used pitfall trap data to address two related questions: 1) does wax expression of peas alter the structure of the arthropod community, and 2) which taxa show the greatest disparity in abundance between normal and peas with reduced wax?

Materials and Methods

The arthropods associated with peas were assessed at the University of Idaho (U.S.A.) Plant Science Research Farm (46°43' N, 116°57' W) in 1998 and 1999. The peas are near isolines differing in expression of the mutation *wel* (Marx 1969), which reduces wax crystals over the stems, leaves, stipules and pods (Eigenbrode et al. 1998b). Four pairs in 1998, and five pairs in 1999, of 5 x 5 m plots were located on the farm. One plot in each pair was planted with normal peas, while the other was planted with peas with reduced wax. The assignment of normal and reduced-wax pea plots within a pair was random. With the exception of the line of peas planted, identical cultivation practices were used on all of the plots.

One pitfall trap (8-cm diameter plastic cups) was placed in the center of each plot buried flush with the soil surface. Each cup contained approximately 30 ml of automobile antifreeze (containing propylene glycol). Pitfall contents were collected daily from 24-June through 12-August-1998 and from 15-June through 3-August-1999. Collected arthropods were identified in the laboratory to order, and when possible, to family, genus, or species. Therefore, a "morphospecies" in this study refers to the finest taxonomic level at which individuals could be classified and is our best estimate of a single species. The number of individuals collected in the pitfall traps is our best estimate of the abundance of a morphospecies, although pitfall trap captures are influenced by density and activity level (Thomas et al. 1998). Voucher specimens were deposited at the W.F. Barr Entomological Museum at the University of Idaho.

The individuals collected in pitfalls from each of the two types of peas were the effective arthropod communities for our analyses of the diversity of community structure. The number of individuals was plotted versus abundance rank for the total samples ranked within plots with normal peas and plots with reduced-wax peas. A randomization test for difference in community structure was performed according to Solow (1993). For the randomization test, the Shannon and Simpson diversity indices were calculated for both normal and reduced-wax peas. The Shannon index is more sensitive to species richness, while the Simpson index is more sensitive to species evenness (Magurran 1988). Simulated datasets were generated by randomly partitioning the total number of observed individuals into two sets equal in size to the observed numbers of individuals in normal and reduced-wax plots. For each simulation, Shannon and Simpson diversity indices were calculated for both types of peas, and the difference between the diversity indices from normal peas and peas with reduced wax were calculated. The number of simulations producing a difference in the diversity indices greater than or equal to that observed from the pitfall traps estimates the probability that any observed difference was due to chance. The advantage of using a randomization test on the pooled data is that it retains information from species that occurred only once in our samples.

The number of morphospecies collected per plot over each sampling period was tallied as the measure of species richness. A 2-way ANOVA was performed with species richness as the dependant variable and wax level and year as factors and plots as replicates.

Wardle's (1995) index V was modified to calculate the disparity between captures in normal and reduced-wax pea plots for each taxon:

$$V = \frac{2M_n}{M_r + M_n} - 1$$

M_r being captures in peas with reduced wax, M_n being captures in normal pea plots. As we have defined it, the value of V increases when relatively more individuals of a morphospecies were collected from normal peas, and decreases when relatively more individuals were collected from peas with reduced wax. Disparity was used to identify taxa with an apparent preference for either pea variety. The observed values of V were tested for whether morphospecies with 20 or more individuals in our total collection differed from what would be expected from chance. An expected distribution of V was generated based on chance by calculating V for each morphospecies with 20 or more individuals in each of 10 simulated datasets (the random partitions of the observed individuals, as described above). The fit of the observed distribution of V to the simulated distribution of V was then assessed. The observed absolute values of V were grouped into categories of 0.05 increments, with $V > 0.2$ lumped into a single category to eliminate sparse cells for a G-test (Sokal and Rohlf 1981).

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The number of captures of the selected morphospecies from 1998 and 1999 was tested using MANOVAs with wax level as a factor. MANOVA can detect a difference in situations where species have traded places in terms of relative abundance, without changing the species richness or evenness of the community. Such a change in community structure cannot be detected by a randomization test based on a diversity index (Solow and Costello 2001). Furthermore, inspection of univariate ANOVAs within a MANOVA can reveal which species changed in response to the difference in wax. However, our application of MANOVA is restricted for two reasons. First, the statistical power of MANOVA decreases with the inclusion of more dependant variables (Scheiner 2001). Second, the number captured of many of the morphospecies in our data set deviate too much from the normal distribution to meet the assumptions of MANOVA. Deviation from normality is particularly problematic in our data because several morphospecies occur in one year but not the other (or were extremely abundant in one year and not the other). Therefore, two separate MANOVAs were applied, one to data from 1998, and one to data from 1999. The 3 most abundant morphospecies in both 1998 and 1999 were analyzed (Appendix 1).

Results

A total of 12,737 individual arthropods were recovered in the pitfall traps, 6,657 in the reduced-wax and 6,080 in the normal peas. Of those individuals, 12,113 were identified to one of 229 morphospecies, with 171 taxa in reduced wax and 186 in normal plots. Eleven taxa were identified to species and 21 others were identified to genus (Appendix 1). Of the remaining morphospecies, most were identified to family. The randomization test suggested an effect of wax reduction on the overall community structure (Table 1). In particular, the Simpson Index was lower in normal pea plots than in peas with reduced wax. Inspection of the rank abundance curves revealed greater species evenness in the reduced-wax plots than in the normal pea plots, particularly among the eight most abundant taxa (Figure 1). The most captured taxon on both normal and reduced-wax peas was the pea aphid, which constituted 27% of all individuals collected in normal peas and 19% in peas with reduced wax. The next 7 highest ranked taxa collectively constituted 35% of all individuals in normal peas but made up 46% in peas with reduced wax. The difference between the Shannon Index obtained from plots of the two pea varieties was not significantly greater than what was expected from chance.

The distribution of Wardle's index V for morphospecies represented by ≥ 20 individuals in the total sample indicated that arthropod taxa in peas responded idiosyncratically to the peas with reduced wax. Several taxa illustrate apparent preference for normal or reduced-wax peas, as well as species that were about evenly divided between the two lines (Appendix 1). The observed and simulated distributions of V (Figure 2) were significantly different ($\chi^2 = 43.556$, df = 16, $P < 0.001$, n = 53). In particular, the observed distribution of V had a higher frequency of morphospecies with large disparities in captures in one pea variety versus the other (a higher absolute value of V; note the "flatter" distribution of observed frequencies of V compared to the simulated frequencies). The mean (± SE) number of morphospecies per plot in 1998 was 74.3 ± 3.8 and 73.8 ± 3.6 in reduced-wax and normal peas, respectively; in

Table 1. Results of randomization test using 1,000 random partitions.

Shannon index	
Observed, normal plots	4.576
Observed, reduced wax plots	4.685
Difference, δ	-0.109
Number simulated $\|\delta\|$ > observed $\|\delta\|$	18
Number simulated δ < observed δ	11
Simpson index	
Observed, normal plots	0.892
Observed, reduced wax plots	0.924
Difference, δ	-0.032
Number simulated $\|\delta\|$ > observed $\|\delta\|$	0
Number simulated δ < observed δ	0

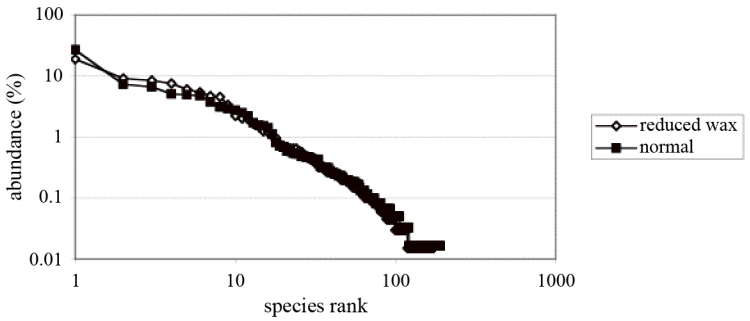


Figure 1. Rank abundance curves for arthropod morphospecies found in pitfall traps within plots of normal and reduced wax peas. Species rank is determined within a variety; in other words, the rank order of a morphospecies in reduced wax peas is different from that in normal peas.

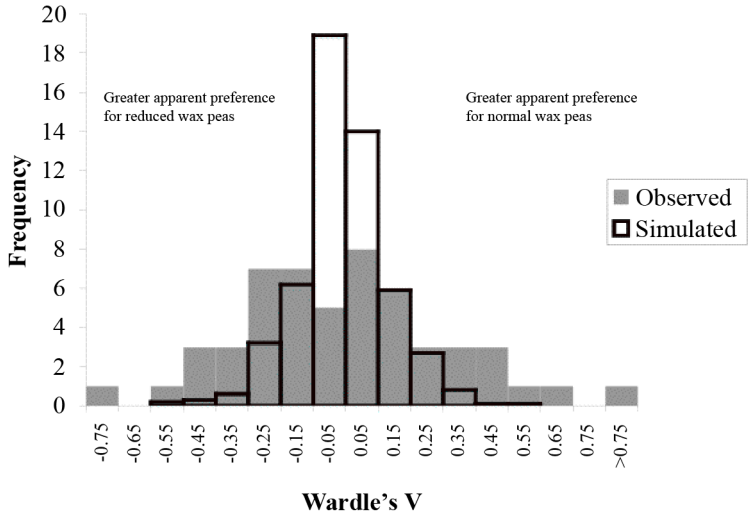


Figure 2. Histogram of observed and simulated values of Wardle's (1995) index V. Observed V's were calculated for 53 morphospecies that were represented by 20 or more individuals in our total sample. Simulated V's were generated randomly from 10 simulations as described in the text. V = 0 for morphospecies with equal numbers of individuals collected from reduced wax and normal pea plots. Positive values of V indicate that more individuals were collected from normal wax peas, while negative values indicate that more individuals were collected from reduced wax peas. Greater absolute values indicate a greater disparity in collections from the two types of peas.

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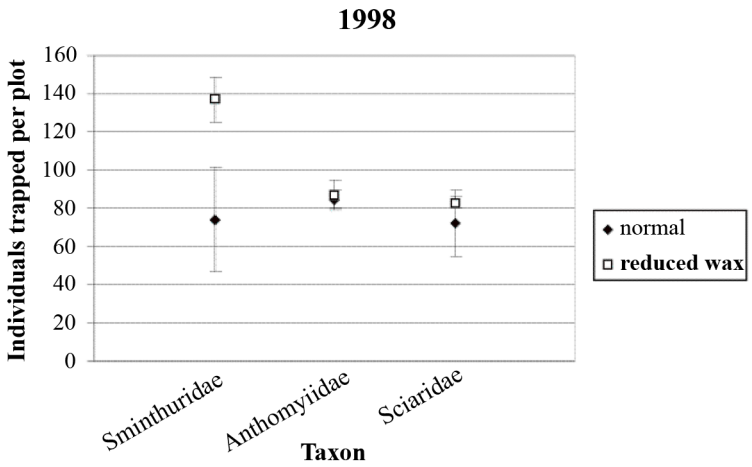


Figure 3. Mean abundances of the 3 most abundant morphospecies in pitfall collections from peas, 1998. The taxa on the x-axis are listed in descending order of abundance in all plots. Bars represent the standard error of the mean abundance of each morphospecies per plot (n = 4).

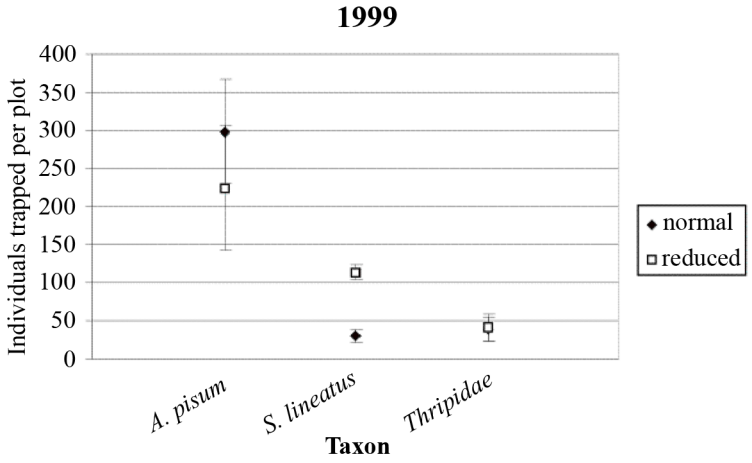


Figure 4. Mean abundances of the 3 most abundant morphospecies in pitfall collections from peas, 1999. The taxa on the x-axis are listed in descending order of abundance in all plots. Bars represent the standard error of the mean abundance of each morphospecies per plot (n = 5).

1999, 55.8 ± 2.3 and 54.4 ± 3.2 morphospecies were captured in reduced-wax and normal peas. The number of morphospecies captured in 1998 was significantly greater than in 1999 ($F_{1, 14} = 34.76$, $P < 0.0001$), but wax type and its interaction with year were not significant ($P > 0.05$).

MANOVA of each year's 3 most abundant taxa did not find a significant overall effect of pea variety in 1998 (Hotelling-Lawley trace = 3.083, $F_{3,1} = 1.03$, $P = 0.6033$; Figure 3). Pea variety did have a significant effect on the 3 most abundant taxa in 1999 (Hotelling-Lawley trace = 38.871, $F_{3,2} = 25.91$, $P = 0.0374$; Figure 4). Univariate F-tests within the 1999 MANOVA revealed that pea leaf weevil (*Sitona lineatus*) were strongly influenced by wax reduction. The pea leaf weevil was three times more abundant in peas with reduced wax than in normal peas in 1999 (Figure 4).

Discussion

Community ecologists are broadly interested in what factors determine levels of biodiversity. Communities of arthropods often differ depending on the plant species they are associated with (Ehrlich and Raven 1964; Price 1984). Differences in arthropod communities are likely to be related to differences in plant traits. For example, changes in pubescence among species in the genus *Arctostaphylos* correspond to changes in their associated arthropod communities (Andres and Connor 2003). Other similar plants such as hybrids, their parental species, and backcrosses between those hybrids and parental species, can also harbor different communities of arthropods (Whitham et al. 1999; Whitham et al. 2003). Differences were found in the arthropod communities associated with two near isolines of peas. Peas with the *wel* homozygous genotype have a reduced-wax phenotype, which increased the evenness of the associated arthropod community. Species richness, another component of diversity, was not significantly different between normal and peas with reduced wax. The change in evenness was driven by changes in the capture frequency of particular species, and responses of insects to peas with reduced wax were idiosyncratic (Appendix 1). For example, two herbivores of agronomic importance had contrasting responses to peas with reduced wax. Pea aphid capture frequency was greater from normal peas whereas the pea leaf weevil was much more frequently captured from peas with reduced wax.

The pitfall data are consistent with data on pea aphid densities and pea leaf weevil damage obtained from visual surveys of the canopy of peas (White 1998; White and Eigenbrode 2000; Rutledge et al. 2003; Chang et al. 2004). For example, in 1996 and 1997, normal wax peas were associated with higher populations of pea aphids, but peas with reduced wax suffered greater damage from adult pea leaf weevils (White and Eigenbrode 2000). Different mechanisms may explain the contrasting response of pea leaf weevils and pea aphids. Predators decrease pea aphid densities on peas with reduced wax relative to normal peas because they are able to walk and thus forage more effectively when less wax is on the plant surface (White and Eigenbrode 2000). However, surface waxes generally defend plants against herbivorous beetles (Eigenbrode 1996). All of the pea leaf weevils captured were adults, which are highly mobile and probably able to choose to forage upon peas with reduced wax.

Apparent preferences of predatory arthropods for either normal or reduced-wax peas may be a function of both prey abundance and prey accessibility in each habitat (Stephens and Krebs 1986). Although pea aphids are more abundant on normal peas than on peas with reduced wax, greenhouse experiments in which pea aphids were presented in equal densities on the two types of peas have found that aphids on peas with reduced wax are more accessible to certain predators (Eigenbrode et al. 1998a; White and Eigenbrode 2000). Therefore, all else being equal, it can be predicted that the ratio of predators to pea aphids will be higher on peas with reduced wax than on peas with normal wax, although no clear prediction

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can be made regarding the absolute densities of predators. Indeed, several predators had higher ratios to pea aphids on peas with reduced wax. This group includes *H. convergens*, coccinellid larvae which were probably mostly *H. convergens*, *Geocoris* sp., spiders (as a group), and green lacewings (two morphospecies combined; Appendix 1). Other predators had higher ratios to pea aphids in peas with normal wax; namely, adult *Coccinella* (two species combined), Nabidae (two morphospecies combined), and Syrphidae (six morphospecies combined). Some of the apparent preferences of predators for peas with normal wax may be an artifact of low capture rates of the taxa involved, but ecological factors may also explain some of the apparent paradoxes. For example, some syrphids prefer to oviposit on normal brassicas to those with reduced wax (Chandler 1968). The syrphids in our study may have had a similar preference for peas with normal wax. Finally, the greater slipperiness of peas with normal wax may have increased the number of active insects such as coccinellids captured in the pitfall traps located in those plots.

The relative abundances of arthropods might be affected by changes in the environment that extend beyond the foliar surfaces of the plant but are ultimately due to differences in plant wax. For example, peas with normal wax typically grow faster than peas with reduced wax (Chang and Eigenbrode 2004), probably because greater amounts of cuticular wax improve the ability of plants to cope with water shortages (Fitter and Hay 2002). The amount of vegetative cover can affect abiotic conditions such as soil temperature and soil moisture (Daubenmire 1974). Certain taxa may be responding to habitat differences that are an indirect consequence of the difference in wax, while predators or competitors may mediate the responses of other species. Experiments with taxa that had contrasting responses may be revealing. For example, the two most abundant carabids captured were *Po. scitulus* and *Pterostichus melenarius*. *Po. scitulus* was over three times more frequently captured on peas with reduced wax (V = -0.52), while *Pt. melenarius* was nearly three times more frequently captured on normal peas (V = 0.44). The biology and ecology of most species in our study is poorly known. Future work might determine whether their contrasting responses are caused by different preferences in abiotic conditions or some degree of competitive exclusion. We also suggest that differences in the arthropod communities captured in 1998 versus 1999 are also largely due to differences in abiotic conditions. During the 1998 sampling period, mean monthly temperatures were higher and more rain fell than in 1999 (Idaho State Climate Services 2004).

The comparison between normal peas and peas with reduced wax illustrates considerations for rational crop design. One advantage of peas with reduced wax is that they supported fewer pea aphids. The greater evenness of the arthropod community in peas with reduced wax may also be desirable if a crop is being managed for biodiversity in addition to yield (Hails 2002). However, peas with normal wax supported fewer pea leaf weevils. Furthermore, the greater growth rate of peas with normal wax under water-limited conditions (Chang and Eigenbrode 2004) will be an important practical consideration in many environments. Knowledge of the relative advantages and disadvantages of different crop varieties may improve the match between specific cultivars and particular geographic regions.

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Appendix 1. Arthropods captured in pitfall traps by pea line, 1998 and 1999, Latah Co., ID, USA.

			Number caught in pitfall traps				
			1998; by wax:		1999; by wax:		
Order	**Family**	**Species identity**	Normal	Reduced	Normal	Reduced	Authority
Coleoptera	Anthicidae	a	33	27	60	83	
Coleoptera	Bruchidae	a	0	0	3	0	
Coleoptera	Carabidae	a	1	0	0	0	
Coleoptera	Carabidae	b	3	0	2	0	
Coleoptera	Carabidae	*Pterostichus melenarius*	3	1	64	25	Illiger
Coleoptera	Carabidae	c	1	0	5	10	
Coleoptera	Carabidae	*Calosoma cancellatum*	0	0	12	17	Eschscholtz
Coleoptera	Carabidae	d	0	0	1	0	
Coleoptera	Carabidae	e	1	1	0	1	
Coleoptera	Carabidae	f	0	0	1	0	
Coleoptera	Carabidae	g	0	1	0	0	
Coleoptera	Carabidae	h	0	1	0	0	
Coleoptera	Carabidae	*Anisodactylus sanctoecrucis*	4	7	0	0	Fabricius
Coleoptera	Carabidae	*Poecilus scitulus*	7	19	19	63	LeConte
Coleoptera	Carabidae	i	0	0	0	3	
Coleoptera	Carabidae	j	1	0	0	0	
Coleoptera	Carabidae	k	1	3	2	5	
Coleoptera	Carabidae	l	0	0	0	1	
Coleoptera	Carabidae	m	4	5	5	7	
Coleoptera	Cerambycidae	a	1	0	0	0	
Coleoptera	Chrysomelidae	a	7	10	4	7	
Coleoptera	Chrysomelidae	b	0	1	0	0	
Coleoptera	Coccinellidae	*Coccinella septempunctata*	0	0	6	3	L.
Coleoptera	Coccinellidae	*Coccinella transversogutatta*	0	0	7	0	Falderman
Coleoptera	Coccinellidae	*Hippodamia convergens*	1	2	29	26	Guerin-Meneville
Coleoptera	Coccinellidae	*Scymnus 1*	0	0	16	1	
Coleoptera	Coccinellidae	*Scymnus 2*	0	0	1	0	
Coleoptera	Cryptophagidae	a	1	1	0	1	
Coleoptera	Crytophagidae	*Caenoscelis 1*	1	2	0	0	
Coleoptera	Curculionidae	a	0	0	1	6	
Coleoptera	Curculionidae	*Sitona lineatus*	40	34	149	570	L.
Coleoptera	Dermestidae	a	0	0	10	14	
Coleoptera	Elateridae	a	0	1	8	5	
Coleoptera	Hydrophilidae	a	0	0	2	0	
Coleoptera	Lathridiidae	a	0	0	6	1	
Coleoptera	Malachiidae	b	6	1	0	0	
Coleoptera	Meloidae	a	7	11	1	3	
Coleoptera	Melyridae	a	0	0	4	3	
Coleoptera	Nitidulidae	a	0	0	3	43	
Coleoptera	Nitidulidae	b	0	0	3	1	
Coleoptera	Scarabaeidae	*Euphoria 1*	1	0	0	0	
Coleoptera	Silphidae	a	0	0	4	3	
Coleoptera	Silphidae	*Nicrophorus 1*	7	2	0	0	
Coleoptera	Staphylinidae	a	160	112	17	19	
Coleoptera	Staphylinidae	b	2	4	0	2	
Coleoptera	Staphylinidae	c	0	0	6	7	
Coleoptera	Staphylinidae	d	0	0	0	1	
Coleoptera	Staphylinidae	e	2	5	0	0	
Coleoptera	Tenebrionidae	a	0	1	1	1	
Coleoptera	Throscidae	a	0	1	1	0	

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Appendix 1. *Continued*

Diptera	Agromyzidae	a	4	3	2	3	
Diptera	Anthomyiidae	a	339	349	107	150	
Diptera	Anthomyiidae	b	0	0	2	0	
Diptera	Anthomyiidae	c	1	0	0	0	
Diptera	Bombyliidae	a	1	0	0	0	
Diptera	Callipohoridae	a	24	37	4	6	
Diptera	Callipohoridae	b	29	40	0	0	
Diptera	Cecidomyiidae	a	3	5	5	4	
Diptera	Ceratopogonidae	a	0	1	2	0	
Diptera	Chironomidae	a	5	3	7	2	
Diptera	Chloropidae	a	4	2	1	1	
Diptera	Chloropidae	b	0	2	0	2	
Diptera	Chloropidae	c	2	1	0	0	
Diptera	Chloropidae	d	0	1	0	0	
Diptera	Conopidae	a	1	1	0	1	
Diptera	Drosophilidae	a	1	0	1	0	
Diptera	Empididae	a	15	13	0	0	
Diptera	Heleomyzidae	a	0	0	3	3	
Diptera	Muscidae	a	1	0	0	0	
Diptera	Phoridae	a	0	0	32	64	
Diptera	Phoridae	b	16	13	0	0	
Diptera	Phoridae	c	49	69	0	0	
Diptera	Sarcophagidae	a	8	10	4	10	
Diptera	Sarcophagidae	b	0	0	0	1	
Diptera	Sarcophagidae	c	3	1	0	0	
Diptera	Scatopsidae	a	5	1	0	0	
Diptera	Scatopsidae	b	0	0	2	0	
Diptera	Sciaridae	a	289	332	113	72	
Diptera	Sphaeroceridae	a	0	1	0	0	
Diptera	Sphaeroceridae	b	2	1	1	1	
Diptera	Syrphidae	a	0	0	19	7	
Diptera	Syrphidae	b	1	0	0	0	
Diptera	Syrphidae	c	0	1	0	0	
Diptera	Syrphidae	d	1	0	0	0	
Diptera	Syrphidae	e	25	19	3	3	
Diptera	Syrphidae	f	0	1	0	0	
Diptera	Tachnidae	a	0	0	0	1	
Diptera	Tipulidae	a	0	1	0	0	
Hemiptera	Anthocoridae	a	2	4	0	0	
Hemiptera	Lygaeidae	a	41	33	0	0	
Hemiptera	Lygaeidae	b	0	1	0	0	
Hemiptera	Lygaeidae	c	0	0	0	2	
Hemiptera	Lygaeidae	d	2	4	9	18	
Hemiptera	Lygaeidae	e	0	0	1	1	
Hemiptera	Lygaeidae	*Geocoris 1*	64	74	21	74	
Hemiptera	Miridae	a	1	2	2	4	
Hemiptera	Miridae	*Lygus* sp.	5	12	0	0	
Hemiptera	Nabidae	a	1	0	25	10	
Hemiptera	Nabidae	*Nabis 1*	4	3	0	0	
Hemiptera	Nabidae	*Pagassa 1*	0	1	0	0	
Hemiptera	Rhopalidae	a	0	1	0	0	
Hemiptera	Thyreocoridae	a	1	0	0	0	
Homoptera	Aphididae	*Acrythosiphon pisum*	151	126	1493	1124	Harris

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Appendix 1. *Continued*

Homoptera	Cercopidae	a	0	0	1	0	
Homoptera	Cicadellidae	a	227	228	61	76	
Homoptera	Cicadellidae	b	6	3	5	22	
Homoptera	Cicadellidae	c	1	0	10	0	
Homoptera	Cicadellidae	d	1	0	0	0	
Homoptera	Cicadellidae	e	1	1	0	0	
Homoptera	Cicadellidae	f	1	0	2	0	
Homoptera	Cicadellidae	g	0	0	1	0	
Homoptera	Cicadellidae	h	3	3	0	2	
Homoptera	Cicadellidae	i	0	0	0	1	
Homoptera	Cicadellidae	j	0	1	0	0	
Homoptera	Cicadellidae	k	1	0	0	0	
Homoptera	Cicadellidae	l	0	1	0	0	
Homoptera	Margarodidae	a	4	4	0	0	
Homoptera	Psyllidae	a	1	0	0	0	
Hymenoptera	Andrenidae	a	0	0	1	0	
Hymenoptera	Andrenidae	b	0	0	0	3	
Hymenoptera	Andrenidae	d	0	1	0	0	
Hymenoptera	Andrenidae	e	1	0	0	0	
Hymenoptera	Andrenidae	f	0	1	0	0	
Hymenoptera	Anthophoridae	a	1	2	0	1	
Hymenoptera	Anthophoridae	c	1	4	0	0	
Hymenoptera	Anthophoridae	d	14	17	0	1	
Hymenoptera	Anthophoridae	e	0	1	0	0	
Hymenoptera	Anthophoridae	f	0	1	0	0	
Hymenoptera	Anthophoridae	g	0	1	0	0	
Hymenoptera	Aphelinidae	b	0	2	0	0	
Hymenoptera	Aphidiidae	*Aphidius ervi*	0	0	0	1	Haliday
Hymenoptera	Apidae	*Apis 1*	2	3	0	0	
Hymenoptera	Apidae	*Bombus 1*	1	0	0	0	
Hymenoptera	Apidae	*Bombus 2*	4	1	0	0	
Hymenoptera	Apidae	*Bombus 3*	1	0	0	0	
Hymenoptera	Bethylidae	a	0	0	1	0	
Hymenoptera	Braconidae	a	4	5	0	0	
Hymenoptera	Braconidae	b	3	4	1	1	
Hymenoptera	Braconidae	c	0	2	0	0	
Hymenoptera	Braconidae	d	0	1	0	0	
Hymenoptera	Ceraphronidae	a	0	0	7	2	
Hymenoptera	Ceraphronidae	b	26	7	1	0	
Hymenoptera	Ceraphronidae	c	8	0	0	0	
Hymenoptera	Ceraphronidae	d	1	1	0	0	
Hymenoptera	Ceraphronidae	e	1	0	0	0	
Hymenoptera	Ceraphronidae	f	1	0	1	2	
Hymenoptera	Chrysididae	a	4	5	0	1	
Hymenoptera	Diapriidae	a	1	0	0	0	
Hymenoptera	Dryinidae	a	1	0	0	0	
Hymenoptera	Dryinidae	*Aphelopus 1*	0	1	0	0	
Hymenoptera	Encyrtidae	a	0	0	1	0	
Hymenoptera	Eupelmidae	a	0	0	0	1	
Hymenoptera	Formicidae	a	1	3	14	40	
Hymenoptera	Formicidae	b	1	0	0	0	
Hymenoptera	Halictidae	a	212	158	15	65	
Hymenoptera	Halictidae	b	16	55	3	25	

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Appendix 1. *Continued*

Hymenoptera	Halictidae	c	0	0	1	0
Hymenoptera	Halictidae	d	4	1	0	0
Hymenoptera	Halictidae	e	0	0	1	0
Hymenoptera	Halictidae	f	40	25	3	21
Hymenoptera	Halictidae	g	1	0	0	0
Hymenoptera	Halictidae	h	4	1	0	0
Hymenoptera	Halictidae	j	0	2	0	0
Hymenoptera	Halictidae	*Specodes 1*	0	1	0	3
Hymenoptera	Halictidae	k	20	14	0	0
Hymenoptera	Ichneumonidae	a	0	0	1	0
Hymenoptera	Megachilidae	a	1	0	0	0
Hymenoptera	Megachilidae	b	3	3	0	0
Hymenoptera	Megaspilidae	c	32	38	0	0
Hymenoptera	Megaspilidae	d	17	9	0	0
Hymenoptera	Megaspilidae	*Dendoceurs 1*	1	1	0	0
Hymenoptera	Mymaridae	a	1	3	0	1
Hymenoptera	Platygasteridae	a	0	0	1	0
Hymenoptera	Pompilidae	b	1	1	0	0
Hymenoptera	Scelionidae	a	11	24	3	7
Hymenoptera	Scelionidae	b	1	0	0	0
Hymenoptera	Scelionidae	c	11	10	3	0
Hymenoptera	Scelionidae	d	1	0	0	0
Hymenoptera	Scelionidae	e	1	0	0	0
Hymenoptera	Sphecidae	a	0	0	0	1
Hymenoptera	Sphecidae	b	5	10	0	0
Hymenoptera	Sphecidae	c	0	2	0	0
Hymenoptera	Sphecidae	d	2	0	0	0
Hymenoptera	Sphecidae	e	0	0	0	1
Hymenoptera	Sphecidae	f	1	1	0	0
Hymenoptera	Sphecidae	g	4	5	0	0
Hymenoptera	Sphecidae	h	0	2	0	0
Hymenoptera	Sphecidae	i	1	1	0	7
Hymenoptera	Sphecidae	j	3	4	0	9
Hymenoptera	Sphecidae	k	1	0	0	3
Hymenoptera	Trichogrammatida	a	1	0	0	0
Hymenoptera	Trichogrammatida	b	1	0	0	0
Hymenoptera	Vespidae	a	1	1	0	0
Lepidoptera	Hesperidae	a	0	0	2	0
Lepidoptera	moth	a	0	4	0	0
Lepidoptera	Noctuidae	a	0	0	2	0
Lepidoptera	Noctuidae	*Schinia 1*	0	2	0	0
Lepidoptera	Noctuidae	b	0	1	0	0
Lepidoptera	Nymphalidae	a	1	0	0	0
Lepidoptera	Nymphalidae	*Vanessa 1*	6	1	0	0
Lepidoptera	Pieridae	*Colias 1*	10	14	1	3
Lepidoptera	Pieridae	*Pieris 1*	1	1	0	0
Lepidoptera	Pyralidae	a	0	0	1	1
Lepidoptera	Sphingidae	a	1	0	0	0
Collembola	Sminthuridae	a	297	548	14	14
Dermaptera	Forficulidae	a	3	4	7	3
harvestman	Phalangidae	a	0	1	94	50
mites	mites	a	0	0	26	11
mites	mites	b	0	0	33	16

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Appendix 1. *Continued*

mites	mites	c	151	360	0	0	
mites	mites	d	2	0	33	32	
mites	mites	e	10	18	0	0	
Neuroptera	Chyrsopidae	*Chrysopa oculata*	0	2	0	0	Say
Neuroptera	Chyrsopidae	*Chrysoperla 1*	3	7	0	0	
Orthoptera	Acrididae	a	0	1	13	8	
Orthoptera	Acrididae	b	2	1	0	0	
Orthoptera	Gryllidae	a	3	0	3	0	
Orthoptera	Tettigoniidae	a	0	0	1	0	
Thysanoptera	Phlaeothripidae	a	43	30	60	68	
Thysanoptera	Phlaeothripidae	b	15	0	4	1	
Thysanoptera	Thripidae	a	104	109	194	204	
Totals			2769	3202	2938	3204	
Ambiguous taxa							
Coleoptera	Carabidae	unidentified larvae	0	0	3	11	
Coleoptera	Coccinellidae	unidentified larvae	12	18	167	134	
Lepidoptera	Noctuidae	unidentified larvae	1	0	0	0	
millipede	Diplopoda	unsorted	121	1	12	20	
spiders	Spiders	unsorted	20	18	16	29	
centipede	Chilopoda	a	5	2	14	14	

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