ABUNDANCE OF SPIDERS AND INSECT PREDATORS ON GRAPES IN CENTRAL CALIFORNIA

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ABSTRACT   We compared the abundance of spiders and predaceous insects in five central California vineyards. Spiders constituted 98.1% of all predators collected. More than 90% of all spiders collected were from eight species of spiders, representing six families. Two theridiids (*Theridion dilutum* and *T. melanurum*) were the most abundant, followed by a miturgid (*Cheiracanthium inclusum*) and an agelinid (*Hololena nedra*). Predaceous insects comprised 1.6% of all predators collected, and were represented by six genera in five families. *Nabis americoferis* (Heteroptera, Nabidae) was the most common predaceous insect, with its densities highest late in the growing season. *Chrysoperla carnea, Chrysoperla comanche* and *Chrysopa oculata* (Neuroptera, Chrysopidae) and *Hippodamia convergens* (Coleoptera, Coccinellidae) were most abundant early in the season. The dominance of spiders may be due to their more stable position in the vineyard predator community compared to predaceous insects. We also suggest that the low percentage of predaceous insects (e.g., lacewings) may reflect the lack of preferred prey (e.g., aphids) on grapevines.

Spiders are important predators in agroecosystems (reviews in Nyfeller & Benz 1987; Nyfeller et al. 1994). Many researchers have provided descriptions of spider species abundance or composition in a variety of agroecosystems (e.g., Bishop 1980; Dean et al. 1982; Agnew & Smith 1989; Bardwell & Averill 1997; Wisniewska & Prokopy 1997). Other researchers have provided qualitative observations on the abundance of spiders (Carroll & Hoyt 1984) or recorded spider predation events (Reichert & Bishop 1990; Nyfeller et al. 1992). However, it is less common for researchers to compare spider abundance to that of predaceous insects. Those studies that have analyzed the relative abundance of all predaceous arthropods vary considerably in the presentation of the data. For example, MacLellan (1973) reported on predaceous arthropods collected on apples in southeastern Australia, presenting numbers of spiders collected by size and numbers of predaceous insects collected by family. Plagens (1983) reported population densities of the most abundant spiders (*Misumenops* spp.) found on Arizona cotton, presenting predaceous insects as overall percentages but not itemizing for different taxonomic groups. In these publications, the amount of detail presented reflects the focus of the research, depending in part upon the breadth of the predator taxon being studied. More commonly, researchers present more detailed descriptions of the predaceous insect fauna, while spiders are grouped together and data presented as an overall mean, numerical rank or percentage of the number collected (e.g., Roach 1980; Knutson & Gilstrap 1989; Royer & Walgenbach 1991; Braman & Pendley 1993). Few studies have provided equivalent comparisons of spiders and predaceous insects at the genus or species level (but see Breene et al. 1989).

In vineyards, several researchers have cataloged the abundance of predaceous arthropods on grapevines. In southern Germany, Buchholz & Schruft (1994) presented numbers of predaceous insects by family, identifying salticids to species and thomisids to genus, but leaving most spiders unidentified. In California vineyards, spider species composi-

tion, relative abundance and seasonal occurrence were described by Costello & Daane (1995) and Roltsch et al. (1998), but neither study included data on predaceous insects. Here, we present data that compare the relative abundance of spiders to predaceous insects on grapevines in California's central valley.

METHODS

Study sites.—The data presented are from five central valley vineyards that were sampled from 1995–1997. Grapevine cultivar and cultural practices varied among the sites. In 1995, three vineyards in Fresno County were sampled: a raisin vineyard (*cultivar* ''Thompson Seedless'' near Del Rey, California) a table grape vineyard (*cultivar* ''Ruby Seedless'' near Reedley, California) and a juice vineyard (*cv* ''Thompson Seedless'' near Parlier, California). In 1995 and 1996, a winegrape vineyard in San Joaquin County (*cv* ''Cabernet Sauvignon'' near Woodbridge, California) and, in 1996 and 1997, a juice vineyard in Madera County were sampled (*cv* ''Thompson Seedless'' near Ripperdan, California). These sites were part of studies designed to determine the impact of cover crops on vineyard insect pests and their natural enemies (see Costello & Daane 1998b; Daane & Costello 1998). All of the study sites were bordered by cultivated vineyards or orchards.

In each year, all vineyards received multiple applications of sulfur for control of powdery mildew, *Uncinula necator* Burrill, and one or two applications of cryolite (sodium aluminofluoride) for control of omnivorous leafroller, *Platynota stultana* Walshingham 1884 (Lepidoptera, Tortricidae), and grapeleaf folder, *Desmia funeralis* (Hübner 1796) (Lepidoptera, Pyralidae).

Sampling.—Costello & Daane (1997) provide a detailed description of sampling methods. In brief, the Del Rey, Ripperdan, Parlier and Woodbridge vineyards were sampled by shaking a 0.89 m^2 section of vine foliage into a funnel shaped collector, and the Reedley vineyard was sampled by shaking the foliage of two grapevines onto a drop cloth and collecting all predators with small battery-powered vacuums. Samples were taken monthly, from May to September, except for the Ripperdan vineyard in 1996, which was sampled from July to September. On each sampling date, samples were taken between 0700–1200 h PDT. Samples from the replicated cover crop studies were pooled across treatments and sample dates. A total of 100 samples was taken from the Reedley vineyard, 180 from the Del Rey vineyard and 120 from the Parlier vineyard (one season each). A total of 243 samples was taken from the Ripperdan vineyard and 360 from the Woodbridge vineyard (two seasons each). Voucher specimens were deposited at the Essig Museum at the University of California at Berkeley.

For each vineyard and sampling method, means were transformed to numbers of predators per vine. Seasonal abundance of spiders and predaceous insects were plotted against cumulative degree days above 10 °C (the lower developmental threshold for grapevines) from 1 January, for each sample year.

RESULTS

We collected a total of 13,348 spiders (2781 at Del Rey, 6468 at Woodbridge, 1273 at Ripperdan, 679 at Parlier and 2147 at Reedley) and 219 predaceous insects (36 at Del Rey, 122 at Woodbridge, 6 at Ripperdan, 43 at Parlier and 12 at Reedley). Over all sites, spiders constituted 98.1% of all predators collected, whereas the insect predators comprised just 1.6% of total predators. At individual sites, spiders comprised at least 94% of predators collected, with the highest percentage at Ripperdan (99.5%) and the lowest at Parlier (94.0%) (Table 1). Predaceous insects comprised 6.0% or less of all predators at each site, the highest percentage found at Parlier (5.9%) and the lowest at Ripperdan and Reedley (0.5%) (Table 1). The only other arthropod predator collected was *Anystis agilis* (Banks 1915) (Acari, Anystidae), a predaceous mite that feeds on insects as opposed to spider mites. Only 17 *Anystis agilis* were collected, all at the Reedley site, comprising 1.5% of the predators collected there.

Spiders.—Eight species from six families constituted >90% of all spiders collected. By family, these were: (1) Miturgidae: *Cheiracanthium inclusum* (Hentz 1847); (2) Corinnidae: *Trachelas pacificus* (Chamberlin & Ivie 1935); (3) Theridiidae: *Theridion dilutum* Levi 1957 and *Theridion melanurum* Hahn 1831; (4) Oxyopidae: *Oxyopes scalaris* Hentz 1845 and *Oxyopes salticus* Hentz 1845; (5) Agelinidae: *Hololena nedra* Chamberlin &

Table 1.—Mean season-wide density and population percentage of predatory arthropods in five central valley vineyards, 1995–97, data pooled across years for each site. Superscript "1" indicates *Theridion dilutum* and *Theridion melanurum*. Superscript "2" indicates *Oxyopes scalaris* and *Oxyopes salticus*.

Predator Group	Ripperdan Mean (±SE)	%	Woodbridge Mean (±SE)	%	Del Rey Mean (±SE)	%	Reedley Mean (±SE)	%	Parlier Mean (±SE)	%
Araneae										
Theridion spp.[1]	7.85 (1.06)	36.20	28.76 (2.24)	57.20	22.40 (2.37)	41.28	0.32 (0.67)	2.96	3.26 (0.74)	14.66
Cheiracanthium inclusum	4.79 (0.34)	22.04	11.27 (0.75)	22.41	4.06 (0.40)	7.49	0.45 (0.06)	4.05	4.92 (0.69)	22.13
Trachelas pacificus	1.54 (0.28)	7.11	0.20 (0.06)	0.40	4.00 (0.45)	7.38	4.53 (0.47)	41.35	4.27 (0.62)	19.22
Hololena nedra	5.75 (0.41)	26.50	0.55 (0.09)	1.09	16.95 (1.24)	31.23	1.85 (0.19)	16.87	1.04 (0.19)	4.70
Oxyopes spp.[2]	0.92 (0.18)	4.22	1.84 (0.24)	3.65	1.59 (0.27)	2.94	1.33 (0.20)	12.17	0.21 (0.09)	0.97
Metaphidippus vitis	0	0	0	0	0.67 (0.13)	1.24	0.84 (0.09)	7.61	4.89 (0.59)	21.87
Erigone dentosa	0.12 (0.04)	0.55	4.66 (0.61)	9.28	3.23 (0.56)	5.95	0.25 (0.05)	2.27	1.26 (0.24)	5.63
Other spiders	0.39 (0.09)	2.34	1.84 (0.15)	3.65	0.67 (0.12)	1.24	1.24 (0.10)	10.66	1.17 (0.20)	5.22
Spider total	21.62 (1.48)	99.53	49.14 (2.74)	97.72	53.57 (3.54)	98.72	10.73	97.90	20.90 (1.92)	94.08
Acari										
Anystis agilis	0	0	0	0	0	0	0.17 (0.08)	1.54	0	0
Insecta										
Hippodamia convergens	0.017 (0.016)	0.08	0.19 (0.04)	0.38	0.23 (0.06)	0.42	0.03 (0.02)	0.32	0.12 (0.06)	0.55
Chrysopidae	0.017 (0.016)	0.08	0.55 (0.08)	1.09	0.21 (0.06)	0.39	0.01 (0.01)	0.09	0.12 (0.06)	0.55
Nabis americoferus	0.017 (0.016)	0.08	0.22 (0.59)	0.44	0.23 (0.09)	0.42	0.01 (0.01)	0.09	0.83 (0.29)	3.73
Orius spp.	0.034 (0.023)	0.16	0.06 (0.02)	0.13	0.02 (0.02)	0.03	0	0	0.09 (0.05)	0.41
Geocoris spp.	0.017 (0.016)	0.08	0.01 (0.01)	0.02	0	0	0	0	0.09 (0.07)	0.41
Zelus renardii	0	0	0.04 (0.02)	0.09	0	0	0	0	0	0
Tenodera aridifolea sinensis	0	0	0.04 (0.02)	0.09	0	0	0.005 (0.005)	0.05	0.06 (0.06)	0.27
Insect predator total	0.101 (0.040)	0.47	1.14 (0.12)	2.27	0.69 (0.13)	1.28	0.06 (0.02)	0.56	1.32 (0.33)	5.92

Ivie 1942; and (6) Salticidae: *Metaphidippus vitis* (Cockerell 1895).

Overall spider abundance varied among sites, ranging from a high of 49.1 spiders per vine (Woodbridge site) to a low of 10.7 spiders per vine (Reedley site) (Table 1). Species composition also varied among sites and may have contributed to differences in spider abundance. For example, overall spider abundance was highest at the Del Rey and Woodbridge sites, where the dominant spiders were the small, web-building theridiids, *T. dilutum* and *T. melanurum*. In contrast, overall spider abundance was more than 50% lower at the other sites, where larger spiders, such as the nocturnal hunters *C. inclusum* and *T. pacificus*, dominated the spider community (Table 1).

There were also differences in spider seasonal abundance (Fig. 1). *Theridion* spp. was the most abundant spider group, with the highest overall spider density in both the early-season (~17 per vine) and late-season (~34 per vine) samples, but equivalent with *C. inclusum* in mid-season samples (~7.5 per vine). *Cheiracanthium inclusum* was the next most abundant spider, with densities relatively low early in the season (~2 per vine) and peaking late in the season (~18 per vine). The agelinid, *Hololena nedra*, maintained a relatively steady population density of ~4.7 spiders per vine throughout the season. The seasonal abundance patterns reported here are consistent with those reported in Costello & Daane (1995).

Insects.—Predaceous insects collected include *Hippodamia convergens* Guérin-Méneville 1842 (Coleoptera, Coccinellidae); *Chrysoperla comanche* Banks 1938, *Chrysoperla carnea* (Stephens 1836), and *Chrysopa oculata* Say 1839 (Neuroptera, Chrysopidae); *Nabis americoferus* Carayon 1961 (Heteroptera, Nabidae); *Orius* spp. (Heteroptera, Anthocoridae); *Geocoris* spp. (Heteroptera, Lygaeidae); *Zelus renardii* Kolenati 1856 (Heteroptera, Reduviidae); and *Tenodera aridifolia sinensis* Saussure 1871 (Mantodea, Mantidae).

Overall, predaceous insect density was lowest at the Reedley and Ripperdan sites, with seasonal means of 0.06 and 0.10 predators per vine, respectively, and most abundant at the Woodbridge and Parlier sites, averaging 1.1 and 1.3 predators per vine, respectively (Table 1). There were also differences among sites in
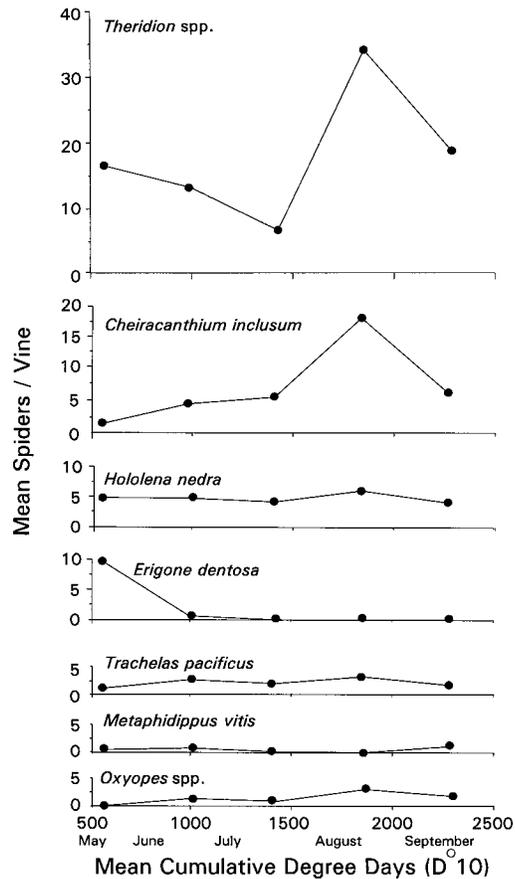

Figure 1.—Mean seasonal abundance of the most abundant spider species on grapevines, plotted against cumulative seasonal degree days above 10 °C (since January 1), all vineyards and years combined.

species composition. At the Woodbridge site, the most abundant insect predators were the chrysopids (0.5 per vine), whereas at the Parlier site, *N. americoferus* was most frequently collected (0.8 per vine) (Table 1).

Predaceous insect seasonal patterns show that *N. americoferus* was the most abundant insect predator overall (Fig. 2). Its population rose from near zero in early-season samples to ~0.6 per vine in late-season samples. Chrysopids were the most abundant predaceous insects in early-season samples, with densities of ~0.6 per vine, but thereafter were quite rare (Fig. 2). Coccinellidae were also relatively abundant in early-season samples (0.35 per vine at the first sampling period) and their density also steadily dropped in later samples.
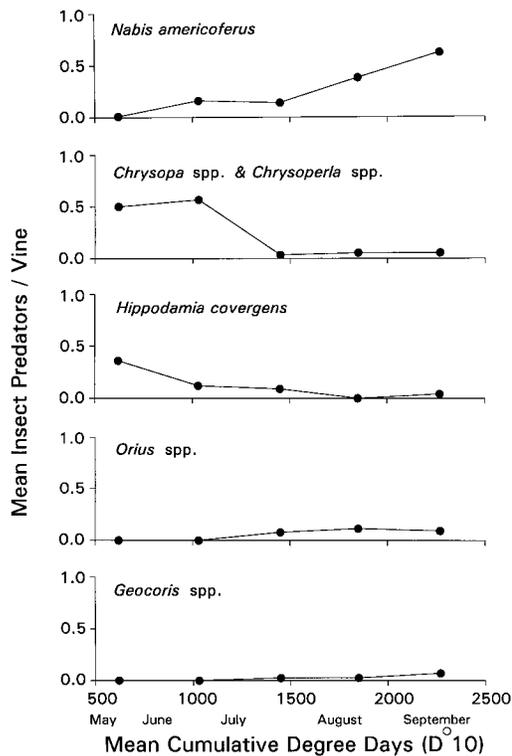
Figure 2.—Mean seasonal abundance of the most abundant predaceous insect groups on grapevines, plotted against cumulative seasonal degree days above 10 °C (since January 1), all vineyards and years combined.

Orius spp. and *Geocoris* spp. were not collected until the third sampling period (midsummer), and peaked in late-season samples at 0.11 and 0.06 per vine, respectively.

DISCUSSION

These results show that spiders overwhelmingly outnumber predaceous insects on grapevines in California's central valley. The explanation for this may partly lie in the type and abundance of prey species: the low number of predaceous insects may reflect the lack of preferred prey on grapevines. At all of our study sites, the most abundant insects on grape foliage are various Diptera, which are most abundant in the spring and early summer, and the leafhoppers *Erythroneura elegantula* Osborn 1928 and *E. variabilis* Beamer 1929 (Homoptera, Cicadellidae). *Erythroneura* spp. have three generations in the central valley, with nymphal peaks occuring in late May,

mid-July and early September. Leafhopper densities which reach 10–15 nymphs per leaf may require insecticide treatment to prevent economic damage. In comparison, there were low densities of other potential arthropod prey, such as lepidopteran larvae (*Platynota stultana* and *Desmia funeralis*), mealybugs (*Pseudococcus maritimus* Ehrhorn 1900) and spider mites (*Tetranychus pacificus* McGregor 1919 and *Eotetranychus willametti* [McGregor 1917]). Prey such as aphids and whiteflies are only occasionally found on grapevines, and at relatively low densities.

Insect predators such as coccinellids and chrysopids will feed on a variety of soft bodied insects, including *Erythroneura* spp.; however, they are better known as predators of aphids and mealybugs (Daane et al. 1998). The lack of preferred prey likely affects the dispersal habits of adult coccinellids and chrysopids, and their density on grapevines. For example, migration of *Hippodamia convergens* from overwintering sites in the Sierra Nevada foothills to the San Joaquin Valley is arrested when adult beetles find aphids and their honeydew (Hagen 1962). Similarly, *Chrysopa carnea* responds to aphid honeydew (Hagen 1950). It is well known that cover crops such as vetches and cereals support high populations of aphids (Bugg et al. 1991), and we suspect that the relatively high early season populations of *H. convergens* and chrysopids we found on the grapevines were due to the presence of aphids on cover crops and weeds in and around the study vineyards at that time. The decline of these predators, during the season, followed the decline of their preferred prey on the cover crops.

Although spiders are polyphagous, we found differences among vineyard species in prey preference. For example, *Metaphidippus vitis* does not feed on leafhoppers in the laboratory; and, in this study, its numbers were relatively low compared with other spider species. In contrast, field observations suggest that *Theridion* spp. feed primarily on leafhoppers, with high populations of *Theridion* positively correlated with high leafhopper densities (Costello & Daane 1995). In this study, *Theridion* spp. reached the highest density of any spider group. *Theridion* spp. numbers were highest at the Woodbridge and Del Rey sites, where there were also high population levels of leafhoppers (Daane & Costello

1998). *Theridion dilutum* and *T. melanurum* are small (adults are ~0.5 cm), have low food requirements, occupy very little territory compared to larger spiders such as *Cheiracanthium inclusum* and *Hololena nedra*, and *Theridion* spp. populations increase considerably from mid- to late-summer. Therefore, *Theridion* spp. densities may be highest because they readily feed on leafhopper nymphs and because grapevines can support more of these spiders per given area compared with other spider species.

That nabids increased over the course of the season may reflect their ability to use leafhoppers as food. Nabids are good predators of leafhoppers (Martinez & Pienkowski 1982; Flinn et al. 1985). Other insect predators, such as *Orius* spp., prefer thrips and spider mites. *Geocoris* spp. feed on lepidopteran and hemipteran eggs and nymphs, spider mites, aphids and whiteflies (Hagler & Cohen 1991). The low densities of these prey items on vines may explain the low density of *Orius* and *Geocoris* species we found.

Spiders may also comprise the majority of the predator community because most species overwinter in the vineyard and are therefore permanent residents. They are a more stable part of the predator community than insect predators because of their broader diet breadth and their ability to subsist for long periods of time without food. Insect predators such as *Hippodamia convergens* and chrysopids are more migratory, and often follow migratory pest populations. All but one of the spiders mentioned in this study have been found overwintering in cardboard bands placed around the vine trunks, the exception being *Erigone dentosa* (M.J. Costello & K.M. Daane unpubl. data). None of the predaceous insects has been found overwintering on the vines. That *E. dentosa* was not found overwintering in vineyards and was only found in the early part of the growing season, suggests that it is more migratory than the other spider species, probably ballooning into vineyards in the spring and leaving for other habitats during the summer.

Finally, the sampling methods used will affect the kinds and numbers of predators collected. Costello & Daane (1997) compared the D-vac to foliage beating in vineyards, and found that spider density was underestimated by 87% with the D-vac, and overestimated by 35% with the funnel shake method. The D-vac also biased samples toward smaller and more mobile spiders compared to beating or shaking methods. In addition, foliage shaking methods do not collect flying predators. This is most important for the tiger fly, *Coenosia humilis* Meigen 1826 (Diptera, Muscidae), which can be quite common in San Joaquin Valley vineyards. The adult captures its prey on the wing and has been observed feeding on leafhopper adults (immature *Coenosia* feed on earthworms in the soil and, therefore, are not collected). We have collected this fly with the D-vac and have usually found the mean density to be less than 5 per vine (unpubl. data). In addition, very small predators such as *A. agilis* may never be sampled with the D-vac, and are probably more efficiently sampled with the drop cloth method than the funnel method. This may partly explain why an additional small insect predator, *Leptothrips mali*, was observed at the Woodbridge site but was never found in the samples.

This is the first report that spiders comprise such a high percentage of a predator community in vineyards. The great number of spiders in comparison to other predators reveal, empirically, why so much research has focused on spiders as vineyard predators (Zalom et al. 1993; Costello & Daane 1998; Roltsch et al. 1998). These results suggest that predaceous insects play a minor role in suppressing insect pest populations in California vineyards. We note that leafhoppers were the primary prey species in our study sites. In vineyards with high mealybug or lepidopteran populations, the natural densities of predaceous insects may be higher. More work is needed in determining the role of spiders on economically important vineyard insects such as leafhoppers and the lepidopteran complex. We are currently working on the development of immunochemical assays to estimate prey consumption by vineyard spiders.

ACKNOWLEDGMENTS

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