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Spider predation on *Platynota stultana* (Lepidoptera: Tortricidae) in California vineyards

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Abstract. We developed a monoclonal antibody (MAb) to *Platynota stultana* (Tortricidae, common name omnivorous leafroller), a key pest of grape in California, and used it to detect predation by spiders in San Joaquin Valley vineyards. Using an enzyme-lined immunosorbant assay, we found a MAb with high specificity to *P. stultana*, with no cross reaction to several non-lepidopteran insects, and minor reaction to other lepidopteran species. We tested the MAb on four spiders: *Cheiracanthium inclusum* (Hentz, 1847) (Cheiracanthiidae), *Trachelas pacificus* Chamberlin & Ivie, 1935 (Trachelidae), *Oxyopes* spp. (Oxyopidae) and *Hololena nedra* Chamberlin & Ivie, 1942 (Agelenidae), and found for all but *C. inclusum*, there was reactivity to spiders which had eaten *P. stultana* larvae in the laboratory. We sampled spiders from two Fresno County vineyards, assaying by species and weight at antigen dilutions of 1:100 and 1:1000. None of the small-sized *Oxyopes* spp. or *H. nedra* specimens was positive, but 8.8% of the medium-sized *Oxyopes* spp. and 33.3% of the medium- and large-sized *H. nedra* specimens were. 28.5% of the small-, 57.1% of the medium- and 66.6% of the large-sized *T. pacificus* specimens tested positive. Our interpretation is that the *H. nedra* positives resulted from *P. stultana* moth capture, and that *Oxyopes* spp. prey upon *P. stultana* larvae, but have a limited ability to capture them. *Trachelas pacificus* appears to be an effective predator of immature *P. stultana*, capable of finding and consuming those hidden in their nests, and may play a positive role in lowering its population density.

Keywords: Gut analysis, monoclonal antibody, grape, omnivorous leafroller, biological control

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Spiders are a significant component of the predator community in many agroecosystems, as shown by recent studies which have focused on species diversity and density (Bao et al. 2018; Yang et al. 2018; Salman et al. 2019; Saranya et al. 2019) as well as several earlier reviews (Nyffeler & Benz 1987; Bogya & Mols 1996; Nyffeler & Sunderland 2003). In commercial grape vineyards, spider diversity and density has been documented in many countries, including Portugal (Nobre & Meierrose 2000; Gonçalves et al. 2017), Italy (Isaia et al. 2006), Australia (D'Alberto et al. 2012), South Africa (Gaigher & Samways 2014), Spain (Rosas-Ramos et al. 2018), Germany (Kolb et al. 2020) and Argentina (Pompozzi et al. 2021).

Important to the understanding of spiders in agroecosystems is the question of what prey they feed on and if they have a significant impact on insect pest density. Studies have either quantified spider predation on insects, or attempted to correlate spider and insect pest populations, drawing inferences with regard to the potential pest suppression impact of spiders (reviews by Michalko et al. 2019a, b). Others have focused on identifying spider prey items and estimating the frequency with which these prey are fed upon, and there are several non-molecular methods to accomplish these objectives. The most basic is direct observation, which is most straightforward when counting prey in webs (Nyffeler et al. 1988) but is, usually, limited to web-spinning spiders. This method has also been used for hunting spiders (Nyffeler et al. 1987; Bardwell & Averill 1997), and a variation has used sentinel prey items, which can be placed on cards or tethered, and observations are then made on the cards/tethers (Pfannenstiel 2008). Direct observations provide clear evidence of predation, but those involving hunting spiders come with a higher risk of disturbing them. An alternative which avoids disturbance is the use of video cameras to monitor the sentinel prey (Frank et al. 2007; Reiff et al. 2021). Exclusion methods involve either confining spiders and their prey (Costello & Daane 2003; Hogg & Daane 2011, 2014) or preventing spider access to prey items (Rusch et al. 2015), and then comparing the density of prey between exclusion and non-exclusion zones. This can provide statistical evidence for predation, but does not include physical evidence, and the manipulation (confinement) may not fully reflect real conditions.

Molecular or elemental detection methods enable detection of prey remains in the alimentary canal of spiders. This can be done by rearing, marking with radioactive or rare elements (such as rubidium), or antigens which can be detected with immunochemical (serological) methods such as enzyme-linked immunosorbent assay (ELISA). The prey items are then released, and after a time, spiders in the vicinity are collected and assayed for the marker (Yu et al. 2002; Rendon et al. 2018). These methods can estimate the proportion of the spider population that has fed on a prey item, although a disadvantage is that the prey items need to be reared in high quantity, then released in such a fashion that they are readily available to the spider population.

Prey taxa or specific prey can also be detected in the guts of spiders, without using the mark-release-recapture technique, but simply by capture. This removes the disadvantages of rearing, marking and releasing the prey. Two methods have been used to do this: serology (ELISA) or DNA analysis (using polymerase chain reaction or PCR). DNA extraction with PCR analysis has been used in many studies; examples include estimation of predation by spiders (primarily Thomisidae, Lycosidae and Dictynidae) on insect herbivores and omnivores in cotton (Hagler & Blackmer 2013), evaluation of predation by Lycosidae and Theridiidae on flea beetles in rapeseed (Ekbom et al. 2014) and analysis of prey detectability in different body parts of the woodlouse hunter spider (*Dysdera verneaui* [Simon, 1883] [Dysderidae]) (Macías-Hernández et al. 2018).

Serology takes advantage of the antibodies produced by vertebrate immune systems to identify molecular markers of potential prey (see reviews by Boreham & Ohiagu 1978; Sunderland 1987). Using these antibodies, prey can be detected in predators

by immunoassays such as enzyme linked immunosorbant assay (ELISA) (Hagler et al. 1994) or immunodot (Greenstone 1995). ELISA can be used with polyclonal antibodies or monoclonal antibodies (MAbs), which are quite specific and can be effective in detecting species specific or even instar specific prey items (Lenz & Greenstone 1988; Hagler et al. 1992; Zeng et al. 1998). MAbs can target broad taxa, for example, being used to detect Diptera in Linyphiidae (Harwood et al. 2007) and Lycosidae (Schmidt et al. 2012) or can be species specific, for example to estimate spider predation on the glassy-winged sharpshooter (*Homalodisca vitripennis*) (Hagler et al. 2013).

In California vineyards, spiders dominate the community of arthropod predators (Costello & Daane 1999; Hogg et al. 2010). A key lepidopteran pest in these vineyards is *Platynota stultana* (Tortricidae, common name: omnivorous leafroller), which has three generations per year in the San Joaquin Valley. Adult *P. stultana* oviposit on grape tissue soon after budbreak, and larvae feed on leaves and inflorescences. Mid- to late-season larval feeding on ripening grape berries provides an entry way for pathogens, which can lead to the loss of entire clusters. We observed that several species of spiders (*Cheiracanthium inclusum* (Hentz, 1847) [Cheiracanthiidae], *Trachelas pacificus* Chamberlin & Ivie, 1935 [Trachelidae], *Oxyopes* spp. [Oxyopidae] and *Hololena nedra* Chamberlin & Ivie, 1942 [Agelenidae]), which were frequently sampled in our earlier studies (Costello & Daane 1995), readily feed on *P. stultana* larvae in the laboratory. *Oxyopes* spp., *C. inclusum* and *T. pacificus* are hunting spiders, and *H. nedra* is a funnel web spinner. Because evidence of field predation by spiders on *P. stultana* larvae was lacking, we undertook the development of a MAb and use of ELISA to detect predation on *P. stultana* larvae by these spider species in San Joaquin Valley vineyards.

METHODS

Anti-body development and experimental methods.—Development of the monoclonal antibody took place at the North West Animal Facility at the University of California, Berkeley. We immunized three Swiss Webster mice with four injections of 100 μg *P. stultana* antigen and 50 μg Ribi adjuvant (MPL + TDM, an oil in water emulsion, Ribi Immunochem Research, Hamilton, MT) in 100 μl of physiological saline, delivered intradermally in three sites on the back. We prepared the antigen by macerating *P. stultana* larvae (instars I–V combined which had been killed by freezing at −80°C) in a minimum of phosphate-buffered saline (PBS) with a mortar and pestle. We made the second immunization seven days past initial immunization, and the third and fourth immunizations at 21 days and just prior to spleenectomy, respectively. At 28 days, we took tail bleed samples (approximately 0.5 ml of blood) and tested the blood sera for antibody titer, using enzyme immunoassay (EIA), choosing the mouse with the strongest reaction, based on serum titer in direct EIA. To create hybridomas, we took mouse splenocytes and fused them with log-phase P3X63AG8.653 myelomas (Fazekas de St. Groth & Scheidegger 1980) by electrofusion in a somatic cell hybridizer (Shimatzu Precision Instruments Inc., Kyoto Japan). Hybridomas that produced useful antibodies were expanded to 24-well culture plates, supernates collected for further study, and the cells frozen at −80°C. We selected 360 cell lines to expand in cell culture, and screen for reactivity to a variety of insect antigens, including *P. stultana* larvae, using an indirect enzyme-linked immunosorbent assay (ELISA) (Voller et al. 1976). We stored selected hybridomas in IMDM (cell culture medium) with 30% fetal bovine serum and 10% DMSO (a cryoprotectant) in a Cryomed #910 programmable cell freezer (Thermo Fisher Scientific, Waltam, MA, USA), in liquid nitrogen, and tested the antibody-containing supernates from the 24-well plates with the aid of a Beckman Biomek 1000 pipetting robot (Beckman Coulter, Brea, CA, USA).

Table 1.—Insects assayed for cross-reactivity to MAb-*P. stultana*.

Order	Family	Species	Common name
Hemiptera	Cicadellidae	*Erasmoneura variabilis*	Variegated leafhopper
	Miridae	*Lygus* sp.	Lygus
Blattodea	Blattidae	*Blatta orientalis*	Oriental cockroach
Diptera	Drosophilidae	*Drosophila* sp.	Drosophila
Hymenoptera	Formicidae	*Solanopsis xyloni*	Southern fire ant
Orthoptera	Gryllidae	*Gryllus* sp.	Field cricket
	Tettigoniidae	*Scudderia furcata*	Fork-tailed katydid
Neuroptera	Chrysopidae	*Chrysoperla* sp.	Green lacewing
Lepidoptera	Tortricidae	*Choristoneura rosaceana*	Oblique-banded leafroller
		Grapholita molesta	Oriental fruit moth
		Cydia pomonella	Codling moth
	Pyralidae	*Amyelois transitella*	Navel orangeworm
		Cadra figulilella	Raisin moth

For the ELISAs, we coated 96-well Immulon #2 plates (Dynatech Laboratories, Chantilly, VA, USA) with 1 microgram/well of antigen in 100 microliter of pH 9.6 coating buffer (0.015 M Na_2CO_3-0.035 M $NaHCO_3$-0.003 M NaN_3, pH 9.6) and left them overnight at 4°C. After this, we removed the antigen and washed three times with PBS-Tween, and blocked by adding 1% bovine serum albumin (BSA) for 30 minutes. We repeated the PBS-Tween wash, added the MAb diluted in PBS with 0.05% Tween 20 and incubated it at room temperature for 1 hour. We repeated the PBS-Tween wash, and added goat anti-mouse Ig conjugated with alkaline phosphatase room temperature for 1 hour. We washed the plates again with PBS-Tween, and added p-nitrophenyl-phosphate (Sigma 104 substrate tablets), 1mg/ml, in 10% (w/v) diethanolamine hydrochloride (DEA) buffer.

We tested the MAb against several non-lepidopteran insects as well as other lepidopteran species which can be found in and around San Joaquin Valley vineyards and orchards (Table 1), using all ELISA ingredients except the antigen as a negative control, using at least five specimens per assay. We also tested the MAb on the four targeted spider species and conducted further assays on these spiders after they fed on *P. stultana* larvae in the laboratory.

We took spiders from two vineyards near the city of Fresno: the Chooljian vineyard, 14 km southeast, and the Smith vineyard, 15 km west, known to have significant late-season populations of *P. stultana* larvae. The managers of these vineyards applied cryolite (sodium hexafluoraluminate, a stomach poison), for control of *P. stultana* at bloomtime (in May), but did not apply any mid- or late-season insecticides. Cryolite is not known to have any negative effect on spiders. We collected spiders in July and August 1997 between the hours of 04:00 and 05:00, using a shake cloth method described by Costello & Daane (1997). We stored them immediately on dry ice, and, after transportation to the

Table 2.—Size categories for the field collected spiders.

	Size category (milligrams)		
Spider species	Small	Medium	Large
Hololena nedra	3–15	16–29	30–50
Trachelas pacificus	5–9	10–19	20–40
Oxyopes spp.	2–2.9	3–4.9	5–8

laboratory, at −80°C. We separated spiders by species and specimens by weight class (Table 2). We crushed them whole with a mortar and pestle, and assayed them at antigen dilutions of 1:100 and 1:1000. All assays were completed within one month of collection.

Data analysis.—We read the absorbance (optical density or OD) with an EIA microplate reader at 405 nm, taking three readings in 60 minutes and calculating the rate of the reaction (EIA rate = Δabsorbance @ 405nm/min × 10^3) by linear regression. The MAb dilution was 1:10, and the standard antigen dilution was 1:500. We scored the assay as not cross-reactive if there was at least a three-fold difference in EIA rate. For the field-collected spiders, assays were conducted at antigen dilutions of 1:100 and 1:1000, and scored as positive if the EIA rate was 10x that of the mean negative control.

RESULTS

Of the 360 cell lines screened against common vineyard-dwelling insects, we found one MAb (MAb-*P. stultana*) to have high specificity to *P. stultana*, as there was no cross-reactivity with any of the insects tested (Fig. 1a). There was some reaction with this MAb and the assay of other lepidopteran species, but only one which we considered cross-reactive with *P. stultana*, that being the co-tortricid *Choristoneura rosaceana*, which had a difference in OD of 2.78 (Fig. 1b). However, *C. rosaceana* is not a pest of grape, and the chance of encounter between this Lepidoptera and a vineyard-collected spider is negligible. The only other lepidopteran species that our study spiders may have encountered were the pyralids *Desmia funeralis* and *Cadra figulilella*. Although *D. funeralis* was not assayed in the cross-reaction tests, the other pyralids tested, *C. figulilella* and *A. transitella*, did not cross react. Initial assays showed no cross-reactivity with the four test spiders: *C. inclusum*, *T. pacificus*, *Oxypes* spp., and *H. nedra* (Fig. 1c). There was also no cross-reactivity for assays with *Oxyopes* spp. and *T. pacificus* which had been fed *P. stultana* vs. those not fed (Figs. 2a, b). There was some reaction for *H. nedra* fed *P. stultana* vs. not fed, although we did not consider this significant (3.16-fold difference in OD) (Fig. 2c). However, the *C. inclusum* assay for spiders fed *P. stultana* vs. not fed showed cross-reactivity which we considered significant (1.3-fold difference in OD) (Fig. 2d) and therefore, we decided not to include *C. inclusum* in the field sampled assays.

Of the field-sampled *H. nedra* specimens assayed, none of the small specimens were positive. However, of the 12 medium specimens, one was positive at 1:1000, and three were positive at 1:100 and 1:1000. Of the eight large *H. nedra* specimens, four were positive at 1:1000 (Table 3). In total, 33.3% of the medium- and large-sized *H. nedra* were positive.

Of the field-sampled *Oxyopes* spp. assayed, none of the small or large specimens were positive at either dilution (Table 3). Of the 34 medium specimens, two were positive at antigen dilution 1:100 and one was positive at 1:1000 (Table 3). In total, 8.8% of the medium-sized *Oxyopes* spp. specimens were positive.

Of the seven small *T. pacificus* assayed, one was positive at 1:100 and one was positive at 1:1000 (Table 3). Of the 28 medium specimens, one was positive at 1:100, three were positive at 1:100 and 1:1000, and ten were positive at 1:1000. Of the six large specimens, one was positive at 1:100 and 1:1000, and three were positive at 1:1000. In total, 28.5% of the small-, 57.1% of the medium- and 66.6% of the large-sized *T. pacificus* specimens tested positive.

DISCUSSION

Our results present the first direct evidence of spider predation on lepidopteran larvae in California vineyards. This work complements other recent studies documenting spider predation on lepidopteran larvae in laboratory settings (Pérez-Guerrero et al. 2013; Hogg et al. 2014), and those which have used gut analysis to document predation in the field (Furlong et al. 2014; Rendon et al. 2018).

It is important to point out the importance of serial dilutions when using ELISA, especially when assaying specimens with relatively high body mass, because excess antigen can interfere with the assay. In the current study, if we had relied on just one antigen dilution, for example, 1:100, only 14.6% of *T. pacificus*, regardless of size, would have been positive for MAb-*P. stultana*. With the inclusion of the 1:1000 dilution, the overall rate was increased to 48.7%.

This work provides information which allows us to better distinguish differences among vineyard spider species and their impacts as biological control agents of key pests. Although spiders are generalist predators, their impact on insect pest populations varies greatly by factors such as biology and size (see reviews by Bogya & Mols 1996; Nyffeler & Sunderland 2003). In the current study, we have results from spiders in three different families and three size classes, the combination of which played a role in the degree of attack on *P. stultana*. Overall, the hunting spider *T. pacificus* had the highest frequency of positives, >50% for medium- and large-sizes, whereas *Oxyopes* spp. had by far the lowest rate of positive tests, 8.8%, and only for medium-sized specimens. *Hololena nedra* was somewhere in-between, with 33.3% positive, but only for the medium- and large-sized classes.

In mid-summer, second generation *P. stultana* eggs are laid on or near ripening grape clusters, and newly eclosed larvae migrate to interiors of clusters, where they make feeding 'nests' by tying together berries and feeding from within. These cryptic habitats allow larvae to evade attack by web-spinning and ambush spiders. When we sampled for spiders in July and August, the majority of *P. stultana* larvae were in nests, rather than in the process of migration.

The few positives found for *H. nedra*, the web-spinning spider in this study, could be the result of the capture of *P. stultana* moths, since this spider is unlikely to encounter migrating larvae. Although we selected MAb-*P. stultana* using larval antigen, it is probable that the MAb reacted to adults as well. In addition, the lack of small-sized *H. nedra* positives suggest that *P. stultana* moths are too large to be successfully handled by them, or that small-sized *H. nedra* webs are not large enough to trap moths. It is also possible that some *P. stultana* larvae may have dropped from their nests onto the broad, funnel-shaped webs of *H. nedra*

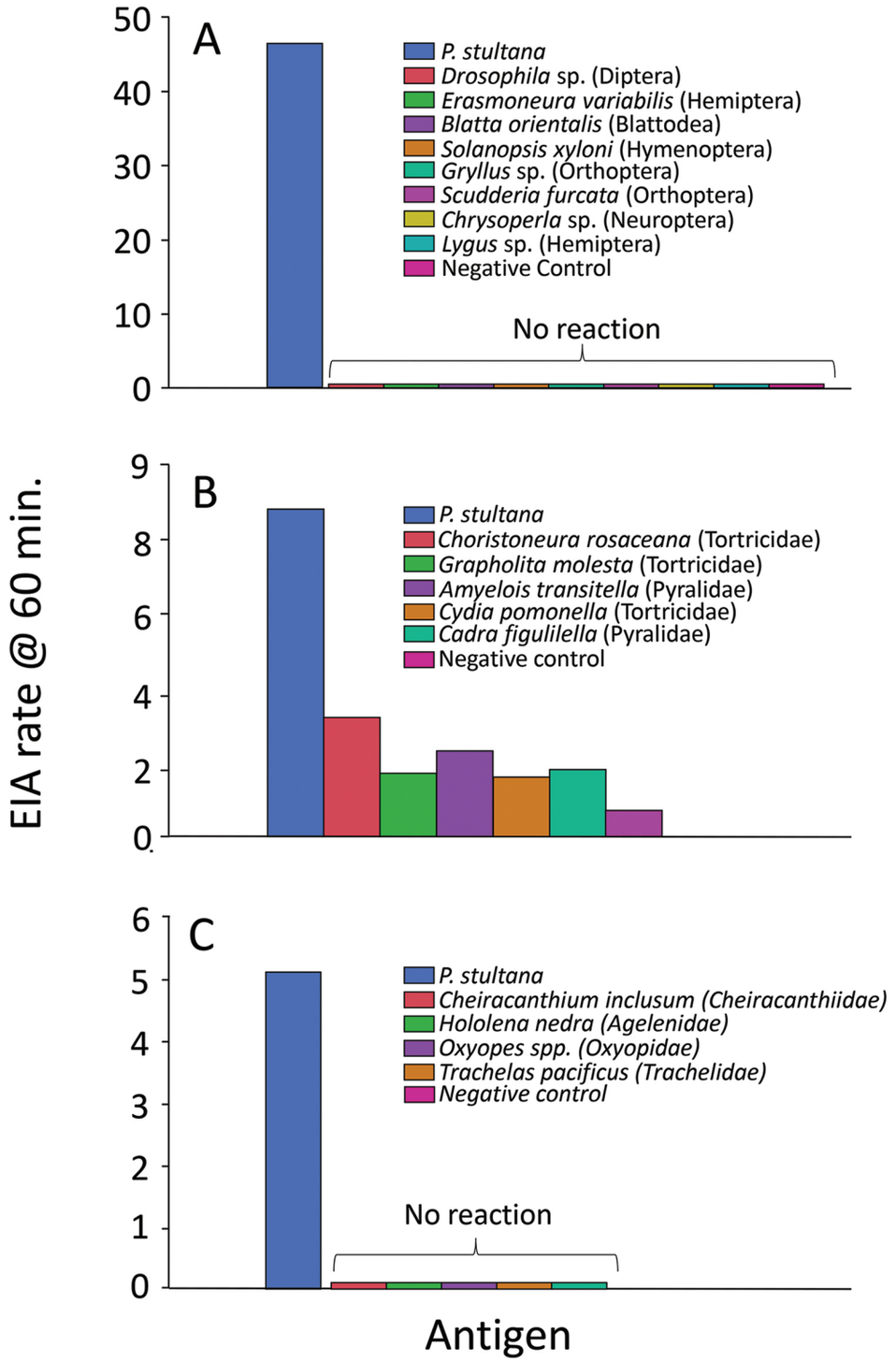

Figure 1.—Cross-reactivity of MAb-*P. stultana* with (a) vineyard insects excluding Lepidoptera, (b) select lepidopteran larvae found in San Joaquin Valley vineyards and orchards, and (c) the four test spiders. In each graph blue bars represent positive controls (cross-reactivity of MAb-*P. stultana* with *P. stultana* extracts), magenta bars show cross-reactivity with negative controls.

and been caught, although this occurrence is probably not common.

Oxyopes spp., even though they are hunting spiders, appear to have a limited ability to capture *P. stultana* larvae. This may be due to *Oxyopes* spp. small size in general (see Table 2), and because they do not have the ability to extract *P. stultana* larvae from their nests in the grape clusters. An explanation for the few *Oxyopes* spp. positives is that these are a result of spiders

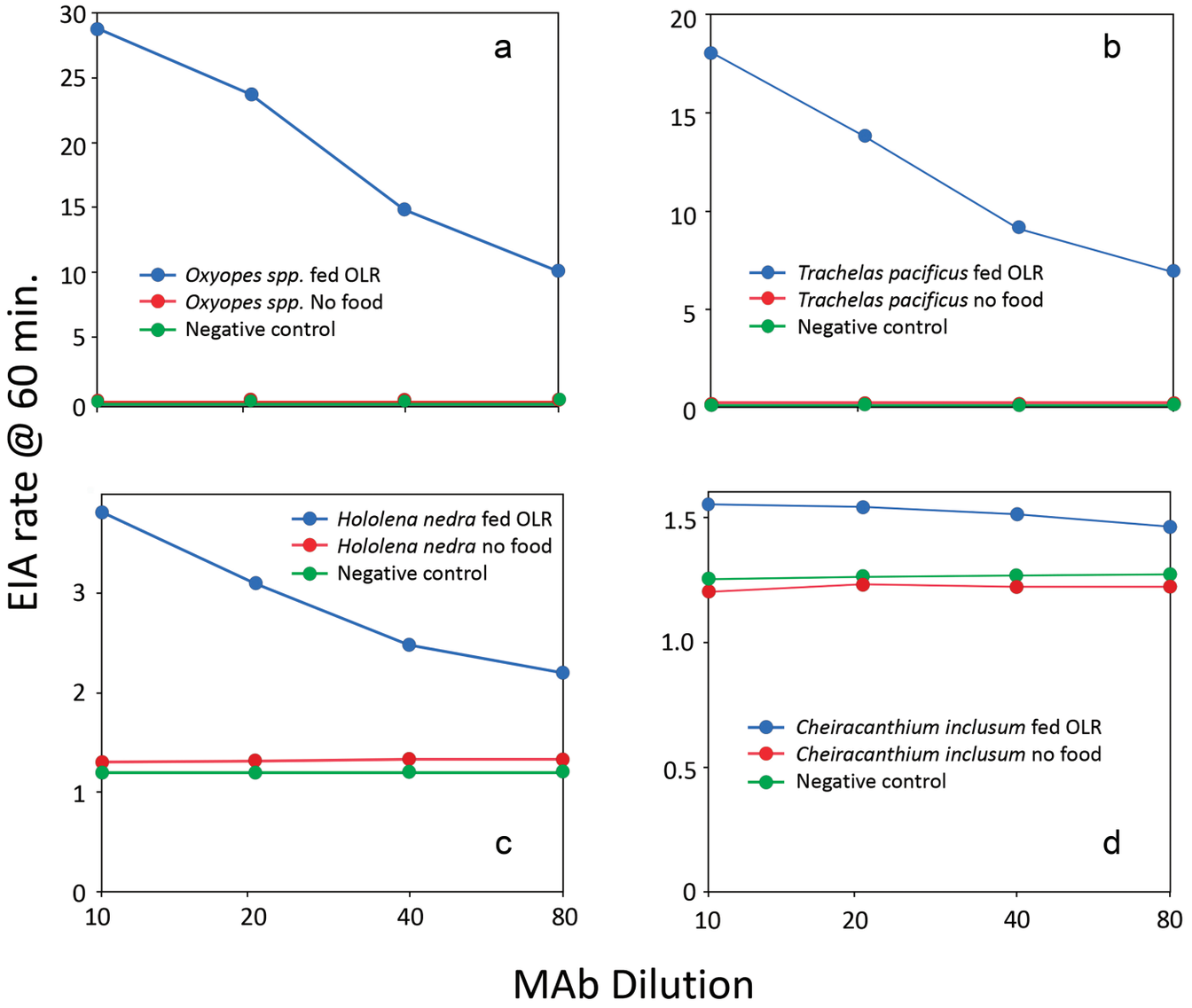

Figure 2.—Linear relationship between MAb-*P. stultana* diluted at 1:10, 1:20, 1:40 and 1:80 and enzyme activity (EIA rate), of spider species fed *P. stultana* larvae compared to spiders not fed. Individual graphs: (a) *Oxyopes* spp., (b) *Trachelas pacificus* (c) *Hololena nedra* (d) *Cheiracanthium inclusum.*

encountering newly hatched larvae migrating to clusters, rather than hunting them in established nests. It does not appear that relative size was a factor here, given that only medium- but not large-sized *Oxyopes* spp. were found positive; given the low frequency overall, this may just have been a stochastic effect. Other studies have documented predation by *Oxyopes* spp. on lepidopteran larvae (Young & Lockley 1985; Pérez-Guerrero 2013), but the current study is the first to identify feeding in the field by this genus on a species of Tortricidae. Still, these results suggest that the impact of *Oxyopes* spp. on *P. stultana* larvae in vineyards is low.

The relatively high percentage of *T. pacificus* which were positive across all size categories suggests that this is an effective predator, capable of finding and consuming *P. stultana* larvae hidden in their nests. Other studies have shown that spiders of the families Corinnidae, Miturgidae and Anyphaenidae, hunting spiders of the same guild, readily feed on lepidopteran larvae in the laboratory, (Hogg et al. 2014; Corrigan & Bennett 1987; Pérez-Guerrero 2013). Amalin et al. (2001) recorded spiders in these families aggressively attacking and consuming well-hidden leaf miner larvae. Spider size likely plays a role in the impact of *T. pacificus* on *P. stultana*, as a higher percentage of medium- and large-sized spiders were positive compared to small-sized ones. The explanation for this may be that only larger *T. pacificus* are capable of attacking *P. stultana* larvae in their nests; small-sized spiders, similar to what we suggested for *Oxyopes* spp., may only be capable of attacking migrating larvae, which are at a lower density in the vineyard for a shorter time period. *Trachelas pacificus* is also noteworthy in that it is the only species we found that had higher population density on grapevines grown with summer ground cover (Costello & Daane 2003).

It is unclear what role *T. pacificus* plays in population regulation of *P. stultana*; understanding this would require a broader

Table 3.—ELISA assays positive by spider species and size category, at antigen dilutions of 1:100 and 1:1000.

			1:100		1:1000		
Spider species	Size	N	Number positive	Percent positive	Number positive	Percent positive	Overall positive [n] (%)
Hololena nedra	Large	8	0	0.0	4	33.0	[4] (33.3%)
	Medium*	12	3	25.0	4	33.0	[4] (33.3%)
	Small	9	0	0.0	0	0.0	0
Oxyopes spp.	Large	68	0	0.0	0	0.0	0
	Medium	34	2	5.8	1	2.9	[3] (8.8 %)
	Small	27	0	0.0	0	0.0	0
Trachelas pacificus	Large#	6	1	1.6	4	66.6	[4] (66.6%)
	Medium+	28	4	14.2	13	46.4	[15] (53.5%)
	Small	7	1	1.4	1	1.4	[2] (28.5 %)

Specimens were scored as positive for *P*. *stultana* antigen if the optical density reading was 10x the average of the negative controls on all plates.
*3 samples tested positive at 1:100 and 1:1000.
#1 sample tested positive at 1:100 and 1:1000.
+3 samples tested positive at 1:100 and 1:1000.

study, controlling for densities of both species over an extended time period. However, given the evidence that *T*. *pacificus* feeds on *P*. *stultana*, and doing so at a relatively high frequency of detection, we believe that *T*. *pacificus* species may play a positive role in lowering population density of *P*. *stultana*. Although our results are specific to *P*. *stultana*, there are two other tortricid species that can be found in California vineyards and that are in the same guild: *Argyrotaenia franciscana* (orange tortrix), which is a significant pest of grape on the coast, and *Epiphyas postvittana* (light brown apple moth), which is established in several coastal counties but is not at present considered a major pest of grape. We believe that *T*. *pacificus* may have a similar impact on these lepidopteran pests. It is also likely that the cheiracanthid *Cheiracanthium* spp. (*C*. *inclusum*, and the more recent immigrant *Cheiracanthium mildei* L. Koch, 1864), which are common in San Joaquin Valley vineyards, in the same guild as *T*. *pacificus,* and of comparable size, have a similar impact on *P*. *stultana* populations.

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