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An immunological approach to distinguish arthropod viviphagy from necrophagy

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Abstract Scavenging activity of predators inhabiting agroecosystems has not been thoroughly investigated. Understanding the prevalence of necrophagy in predators is paramount to determining the effectiveness of biological control agents. A molecular predator gut content assay is described that can differentiate necrophagy from viviphagy. Cadaver sweetpotato whitefly, *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) and green lacewing, *Chrysoperla rufilabris* Burmeister (Neuroptera: Chrysopidae) serving as targeted prey items were marked with rabbit immunoglobulin G (IgG) protein and live prey items were marked with chicken IgG, respectively. The marked prey items were fed to convergent lady beetles, *Hippodamia convergens* Guérin-Méneville (Coleoptera: Coccinellidae) and soft-winged flower beetles, *Collops vittatus* (Say) (Coleoptera: Melyridae). The frequency of detection of the protein-marked prey items in the gut of the predaceous beetles was assessed at 0, 3, 6, 12, 24 and 48 h after feeding using a rabbit-IgG-specific or chicken-IgG-specific enzyme-linked immunosorbent assay (ELISA). Each IgG-specific ELISA detected the presence of the marker proteins in the gut of 90 % of the predators up to 12 h after prey consumption. A laboratory feeding study was also conducted to determine the propensity that each predator species engages in viviphagy and necrophagy. The laboratory feeding observations revealed that *C. vittatus* prefer carrion prey items. Finally, the laboratory observations of necrophagy were confirmed in a field study where *C. vittatus* was observed, directly and indirectly, feeding on *H. convergens* carcasses. The methodologies described here are useful for future studies on various aspects of insect predation.

Keywords Scavenging · Predation · *Collops vittatus* · *Hippodamia convergens* · Gut content analysis · ELISA

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Introduction

Many generalist predators have been identified as important contributors to the suppression of pest populations in agricultural systems (Hajek 2004). However, most generalists do not discriminate

between herbivorous, omnivorous or carnivorous prey. As such, in agroecosystems, predators may impede biological control services on herbivore and omnivore pest species if they frequently engage in intraguild predation or omnivory (Rosenheim et al. 1993; Holt and Lawton 1994; Holt and Huxel 2007; Pell et al. 2008). In addition, some generalist predators might engage in carrion feeding (Sunderland 1996). This too could interfere with effective biological control if a predator satiates by scavenging on non-living prey.

Vertebrate scavenging is relatively well studied (De Vault et al. 2003). However, with the exception of carrion beetles and flies, scavenging is narrowly studied among insect taxa. This is especially true for predators that inhabit agroecosystems (Steele 1927; Fellers and Fellers 1982; Blacklith and Blacklith 1990). The lack of data is due, in large part, to the fact that in situ insect feeding activity is difficult to observe and most predators do not leave evidence of attack (Hagler et al. 1991). Hence, several indirect predator gut content analysis methods have been developed for studying predator prey choice. The two most effective methods currently available for gut content analysis are enzyme-linked immunosorbent assays (ELISA) using prey-specific monoclonal antibodies (MAb) and polymerase chain-reaction (PCR) assays using prey-specific DNA primers (Sheppard and Harwood 2005; Fournier et al. 2008). Unfortunately, prey-specific assays cannot distinguish between live and carrion predation events (Foltan et al. 2005; Sheppard and Harwood 2005; Hagler 2011).

Recently, we observed the soft-winged flower beetle, *Collops vittatus* Say (Coleoptera: Melyridae), directly feeding on dead convergent lady beetles, *Hippodamia convergens* Guérin-Méneville (Coleoptera: Coccinellidae), in the field and dead sweetpotato whitefly, *Bemisia tabaci* Gennadius (Hemiptera: Aleyrodidae), in the greenhouse and laboratory. *C. vittatus* is a carnivore that is commonly found in Arizona agroecosystems (Naranjo et al. 2003), and has been identified via a *B. tabaci*-specific gut content ELISA as a voracious predator of whitefly (Hagler and Naranjo 1994). Because prey-specific gut content assays cannot differentiate between active predation and scavenging, the exact biological control services rendered by *C. vittatus* are difficult to estimate.

An immunomarking gut assay approach has been described for studying complex foodweb interactions. Specifically, Hagler (2006) marked different prey species, each with a unique protein, and released them into field cages containing the cotton predator complex. The predators were then collected and each individual was analyzed for the presence of the different protein marks by a multitude of protein-specific ELISAs. The present study assesses the feasibility of using prey immunomarking methodology to study arthropod scavenging. Specifically, two unique protein marks, rabbit immunoglobulin G (IgG) and chicken IgG, were used to mark cadaver and living prey, respectively. The targeted cadaver and living prey items included sweetpotato whitefly, a herbivorous pest, and green lacewing, *Chrysoperla rufilabris* Burmeister, a beneficial predator. In turn, a marked live or dead prey item was fed to an adult *C. vittatus* or *H. convergens*. The predators were held at various time intervals after feeding and then assayed for the presence of the marked prey items by IgG-specific ELISAs (Hagler 2011). In addition, a feeding choice study was conducted to determine if *C. vittatus* and *H. convergens* preferred living prey or carrion. Finally, a field study was conducted to determine the propensity of scavenging exhibited by the native *C. vittatus* population on sentinel *H. convergens* cadavers that were placed in an alfalfa field. The research methods presented here provide a foundation for future research studying complex predator–prey interactions.

Materials and methods

Predator feeding study

Predators

Adult *H. convergens* were purchased from Rincon-Vitova Insectories (Ventura, California, USA) or collected in 38-cm insect sweepnets from alfalfa fields located at the University of Arizona's Maricopa Agricultural Center located near Maricopa, Arizona, USA. Adult *C. vittatus* were collected from the same alfalfa fields described above. The predators were provided *Pectinophora gossypiella* Saunders (Lepidoptera: Gelechiidae) eggs as a food source and a wetted sponge as a water source.

Prey

Adult *B. tabaci* were reared on 'Delta Pine 5415' cotton in a greenhouse as described by Hagler et al. (2004). Immature *C. rufilabris* were purchased from Rincon-Vitova and subsequent generations were reared in the laboratory using the method described by Ridgway et al. (1970). These larvae were provided *P. gossypiella* eggs for a food source. The *C. rufilabris* used in the feeding studies were 2.0 to 3.0-mm long, third instar larvae. Prey items serving as cadaver prey were collected from the colonies and killed by freezing at −80 °C. Then, they were placed into a 50 °C oven for 6 h to simulate the desiccation of dead insects in the hot Arizona climate. The cadavers were stored at −80 °C to prevent further desiccation. Then, prior to presenting the cadavers to the predators in the feeding arenas (see below), they were removed from the freezer and thawed at 25 °C for 2 h. Live prey items were collected as needed from their respective colonies.

Prey retention tests

Rabbit IgG and chicken IgG were used to distinctly mark the cadaver and living prey items, respectively. Thirty individuals of each cohort were placed in separate 473-ml plastic containers and then externally marked with 2.0 ml of a 5.0 g ml^{-1} rabbit IgG or chicken IgG solution using a medical nebulizer (Hagler 1997).

Prior to conducting the feeding trials, cohorts of *H. convergens* and *C. vittatus* were placed in separate 3.5-cm Petri dishes and starved for 72 h, but they were allowed ad libitum access to a water soaked sponge. For the lacewing study, an individual predator was placed for up to 30 min in a 3.5-cm Petri dish containing either a single cadaver marked with rabbit IgG or a live lacewing marked with chicken IgG. Every 5 min, the arenas were checked to determine if the predator was feeding. If so, it was monitored continuously until it finished its meal. At that point, the predator was removed from its arena, isolated from food sources (but given water), and held for 0, 3, 6, 12, 24 or 48 h. For whiteflies, the predator was allowed to forage freely for 30 min in a 3.5-cm arena that was populated with either 10 rabbit IgG-marked cadaver or 10 chicken IgG-marked live prey items. After 30 min, the number of whiteflies remaining in each arena were recorded, the predator was removed, isolated from the food source (but given water), and held at the same time intervals given above. After each post-consumption time treatment interval, the individual predator was placed in a 1.5-µl micro-tube and frozen at −80 °C. During the 3-, 6-, 9-, and 12-h intervals, the predators were held under a constant light source at 25 °C. For the 24- and 48-h post-feeding time periods, the predators were held at a 16:8 h (L:D) photoperiod at 25 °C. Ten observations were conducted for each predator–prey combination and time interval.

Gut assays

Each predator sample was homogenized in 500 µl tris buffered saline (TBS) buffer and assayed for either the presence of the targeted protein mark by the rabbit or chicken IgG ELISAs described by Hagler (2011). Samples were scored positive for marked prey remains if they yielded an ELISA response greater than three SD above the mean of their negative control (unmarked predators).

Feeding choice study

Feeding arena

Individual *C. vittatus* and *H. convergens* adults were observed continuously for 30 min in a 3.5-cm Petri dish feeding arena containing both live and cadaver prey. Prior to observation, each predator was removed from its food source for 72 h, but provided water ad libitum. For whitefly, five live prey and five cadavers were placed in each arena. For lacewing, only one live prey and one cadaver item was placed in each arena. Twenty 30-min observations were conducted for each predator–prey combination. We recorded the number of carrion and live prey consumed over the 30 min period.

Data analysis

Significant differences between the feeding frequencies exhibited by the predators on live versus carrion prey were determined using the χ^2 test.

Field study

Sentinel cadavers

Adult *H. convergens* were purchased *en masse* from Arbico (Oracle, Arizona, USA). Upon arrival, the beetles were killed by freezing at −80 °C. After freezing, 15 cadaver beetles were glued (Elmer's Glue-All™, Elmer's Products Inc, Columbus, OH, USA) to 9.0-cm long × 2.0-cm wide plastic twist-lock "bread" tags (Hummert Int., Topeka, KS, USA). The 15 cadavers attached to each tag were situated so that five individuals occupied each third of the tag. The beetles were glued on the tags so their dorsal surface was facing up.

Study site

The study was conducted in a 0.76-ha blooming alfalfa field, grown using standard agronomic practices, located at the University of Arizona's Maricopa Agricultural Center. The alfalfa plants containing the sentinel cadavers (see below) were 68.7 ± 12.6 cm (mean ± SE) tall at the time of the study.

Experimental design

The alfalfa field consisted of 48 plots arranged in a randomized block design consisting of four linear blocks, each of which contained 12, 6-m × 12-m plots. It should be noted that the scavenging data obtained for this study was serendipitous as this experimental design was for a separate experiment with different objectives. On 15 June 2011, six randomly selected alfalfa plants were "tagged" with bread tags containing the 15 cadavers in each of the 48 plots. Two cadaver tags were placed on each plant: one on the lower half (≈20 cm from the ground) and one on the upper half of each plant (≈20 cm from the top of the plant). The lower and upper cadaver treatments served to measure the degree of scavenging as a function of the cadaver's location on the plant.

Cadaver sampling procedure

On 16 June, the day after the cadavers were placed in the field, the first cadaver samples were collected by cutting the outer third of each bread tag ($n = 5$ beetles) on the lower and upper portion of the plant. Each sample was placed in an envelope that was labeled with the date of collection, plot number, plant number, and location on the plant. Subsequently, the middle third and bottom third of each bread tag sample was collected four (19 June) and seven days (22 June) after placement in the field. The cadavers were examined visually in the laboratory for evidence of scavenging. It should be noted that *C. vittatus* scavenging activity is obvious and unique because they tunnel through their food item. It should be also noted that during the collection process we: (1) frequently observed adult *C. vittatus* feeding on the cadavers and (2) did not observe any other predator species feeding on the cadavers.

Data analysis

Differences in the frequencies of scavenging activity exhibited by *C. vittatus* on the upper versus lower plant canopy was determined using a proportions *Z* test calculation with Yates correction for continuity (Glanz 1997; SigmaPlot Ver. 11, San Rafael, CA, USA).

Results

Predator feeding study

The predators were offered either ten living or ten cadaver whiteflies over a 30 min time interval. On average, the *H. convergens* consumed 9.50 (±0.87) and 8.92 (±1.30) living and cadaver whiteflies, respectively. For *C. vittatus*, the average number of living and cadaver whiteflies consumed was 8.00 (±1.24) and 8.96 (±1.39), respectively. The mean (±SE) ELISA OD value yielded and percentage of predators that scored positive for rabbit IgG or chicken IgG after feeding on several protein-marked *B. tabaci* and a single *C. rufilabris* (±SE) are presented in Fig. 1. The presence of protein-marked prey was detected for both prey types in almost all the beetles for 6 h ($n = 10$ for each interval) after feeding. With the exception of the *C. vittatus* that fed on the chicken IgG-marked *B. tabaci*, ≥90 % of the immunolabels were detectable 12 h after feeding.

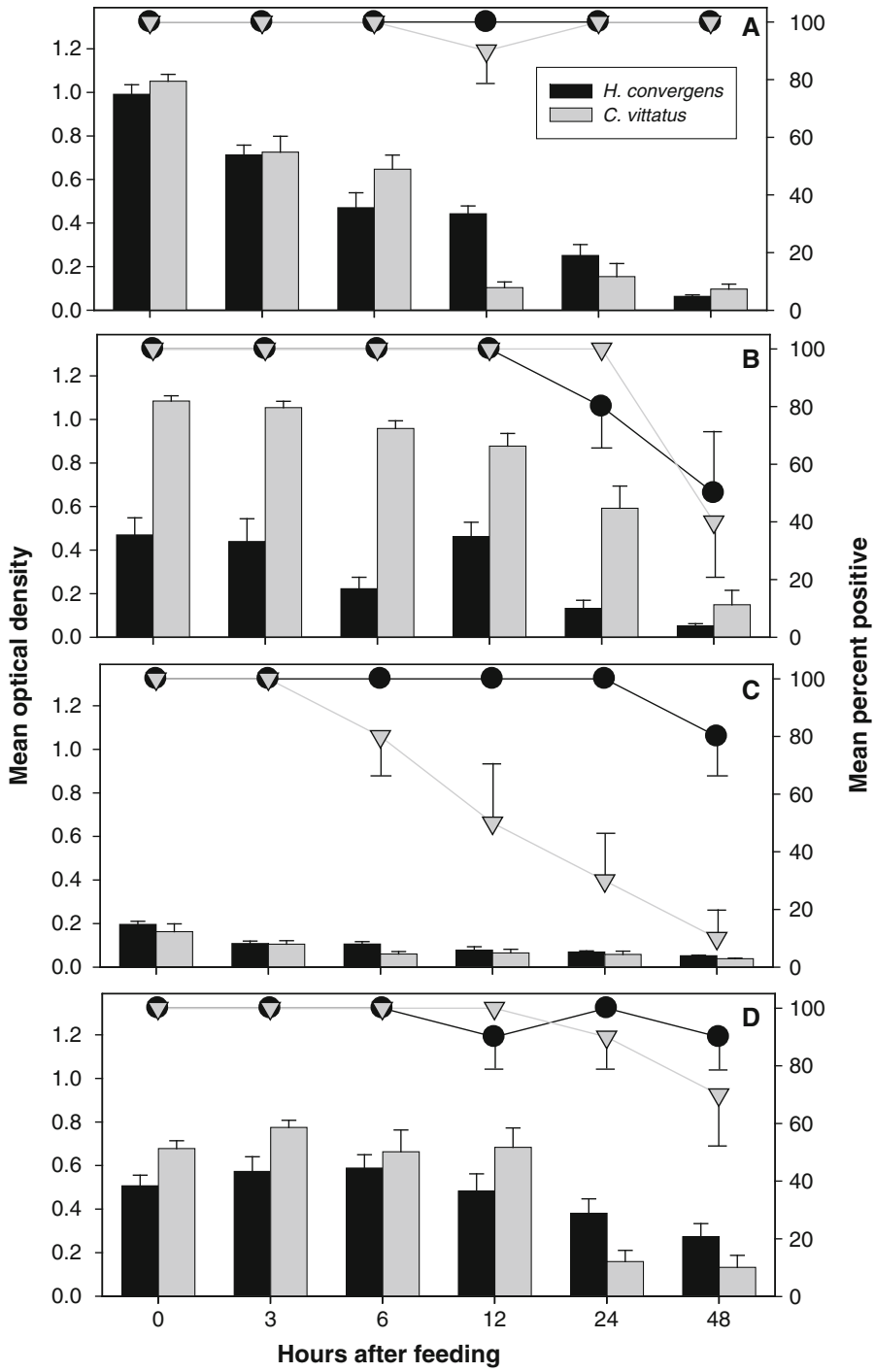

Fig. 1 Mean (+SE) sandwich ELISA optical density values (bars read from left *y*-axis) and mean (+SE) percentage of predators (scatter plot read from right *y*-axis) scoring positive for the presence of **a** rabbit IgG-marked *B. tabaci*, **b** rabbit IgG-marked *C. rufilabris*, **c** chicken IgG-marked *B. tabaci*, and **d** chicken IgG-marked *C. rufilabris* ($n = 10$ for each time treatment interval). Note that the rabbit IgG and chicken IgG-marked prey were cadaver and living prey items, respectively

Feeding choice study

The data showing the predator's preference for live prey versus cadavers are given in Table 1. Adult *H. convergens* did not exhibit a significant feeding preference for live or cadaver whiteflies ($\chi^2 = 1.22, \text{df} = 1, P = 0.269$). Moreover, these beetles were reluctant to feed on *C. rufilabris* larvae. Specifically, over the course of the 10 h of direct observation, only four live and four cadaver lacewings were consumed by *H. convergens*. As such, there were

Table 1 The number and χ^2 values (df = 1) found for each predator under direct observation in the laboratory

Predator	Target prey									
	No. of *Bemisia tabaci* consumed					No. of *Chrysoperla rufilabris* consumed				
	Total	Live	Cadaver	χ^2	*P* value	Total	Live	Cadaver	χ^2	*P* value
Hippodamia convergens	118	53	65	1.22	0.269	8	4	4	n/a	n/a
Collops vittatus	110	45	65	3.64	0.057	25	8	17	3.24	0.072

insufficient data for analysis. The data did reveal that *C. vittatus* had a marginally significant preference for cadaver whiteflies ($\chi^2 = 3.64$, df = 1, $P = 0.057$) and cadaver lacewings ($\chi^2 = 3.24$, df = 1, $P = 0.072$).

Field study

As expected, the percentage of *H. convergens* cadavers consumed by *C. vittatus* increased as the cadaver exposure time in the field increased. A total of 9.1, 21.6, and 40.2 % of the cadavers were consumed after one, four, and seven days in the field, respectively (Table 2). Overall, 23.5 % of the sentinel cadavers were preyed upon during the study. Also, there was a significantly higher frequency of cadavers consumed on the upper (28.2 %) canopy than on the lower (18.8 %) canopy ($z = 10.2$, $P < 0.001$).

Discussion

Use of foreign protein markers in tandem with post-mortem gut content immunoassays to examine predation was described nearly 20 years ago (Hagler and Durand 1994). It has since been used to examine the feeding patterns of predators on several prey types (Hagler 2006, 2011; Buczkowski and Bennet 2007; Mansfield et al. 2008; Kelly et al. 2013). Moreover, the efficacy of the rabbit IgG ELISA compared favorably to a prey-specific ELISA in both laboratory and field settings. Rabbit IgG ELISA had a greater prey detection rate for rabbit IgG marked *Helicoverpa armigera* (Hübner) than a *H. armigera*-specific ELISA designed to detect an *H. armigera*-specific protein (Mansfield et al. 2008).

Table 2 The percentage of cadaver *Hippodamia convergens* that were scavenged on the upper and lower half of alfalfa plants by *Collops vittatus*

Days in the field	Canopy location	*n*[a]	No. eaten	%
1	Upper	1434	179	12.5
	Lower	1435	82	5.7
	Total	2869	261	9.1
4	Upper	1431	380	26.6
	Lower	1432	239	16.7
	Total	2863	619	21.6
7	Upper	1417	650	45.9
	Lower	1384	477	34.5
	Total	2801	1127	40.2
Grand total		8533	2007	23.5

[a] Number of *H. convergens* cadavers examined

This paper describes a novel application of prey immunomarking to study scavenging activity. Our laboratory feeding trial showed that IgG-marked cadaver and live prey items were readily detectable in the gut of the majority of the predators for at least 6 h (in most cases for 24 h) after feeding. This time frame is similar to that reported by Hagler (2011) on protein-marked *Lygus hesperus* Knight. In that study, field cage methodology was combined with the prey marking methodology to quantify predation on live rabbit IgG and chicken IgG-marked prey over a 6 h period. Our results indicate that this method can also be reliably used in concert with field cage methodology for examining predator scavenging activity for up to 6 h.

The laboratory feeding choice study showed that *H. convergens* and *C. vittatus* are equally adept at capturing and consuming adult whitefly, and that *C. vittatus* has a proclivity toward whitefly carrion. In contrast, both predators rarely fed on *C. rufilabris* in the laboratory, but *C. vittatus* fed on twice as many lacewing cadavers as live lacewings.

The discovery that *C. vittatus* is a voracious scavenger of *H. convergens* was serendipitous. Specifically, sentinel *H. convergens* cadavers were strategically placed in the field within the alfalfa canopy to test the efficacy of a protein spray application for a mark-capture study. It was only when we were

collecting the samples that we noticed that a large proportion of our sentinel samples had been, or were being, preyed on by the native *C. vittatus* population. The data showed that *C. vittatus* scavenging activity was significantly more prevalent on the upper portion of the plant canopy. This was somewhat surprising because *C. vittatus* is known to dwell in the soil and plant foliage (pers. obs.).

As mentioned above, this prey marking methodology overcomes one of the major pitfalls associated with conventional prey-specific ELISA and PCR gut assays. Specifically, it can be used to distinguish between predation and scavenging. The laboratory studies showed that *C. vittatus* had a slight preference for dead whitefly and lacewing and the field study showed that they had a voracious appetite for dead lady beetles. Whether *C. vittatus* will readily feed on cadavers under natural conditions (e.g., the cadavers will likely fall to the ground) deserves further investigation. Specifically, more studies are needed to fully understand *C. vittatus* foraging patterns within the plant canopy and at ground level. This study raised questions regarding the natural spatial distribution of carrion foodstuffs. More precisely, do cadavers remain on the plant or do they fall to the ground? Finally, it would be interesting to ascertain whether carrion or insect predators feeding on carrion emit chemical signals that might serve as an attractant to beetles. Clearly, future field studies using this protein marking methodology are needed to determine the biological control services provided by *C. vittatus* and other predaceous natural enemies in the agroecosystem.

In summary, the prey immunomarking technique provides researchers with a flexible tool for conducting a wide variety of predation studies that cannot be conducted with conventional prey-specific gut assay systems (Hagler 2006, 2011). This study indicates that prey-immunomarking can be adapted to study arthropod scavenging activity. Moreover, the method does not require the development of costly and time consuming prey-specific MAb or DNA probes. Finally, the processing of samples by ELISA is much more user-friendly, less costly, and less time consuming than the PCR gut assay procedure (Fournier et al. 2008; Aebi et al. 2011; Hagler et al. 2012; Hagler and Blackmer 2013). The results from the laboratory and field study suggest that *C. vittatus* is a voracious predator and scavenger on several types of prey. As such, this predator is an ideal candidate for future field research using the methods described in this study.

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