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## Arthropod entrapment increases specialist predators on a sticky crop and reduces damage

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## GRAPHICAL ABSTRACT



Predators feed on arthropods trapped in trichomes



Augmenting carrion increases predator density



Herbivore damage is reduced

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## ABSTRACT

Maximizing plant defensive strategies is integral to effective integrated pest management. Direct defenses, in the form of chemical and morphological components that inhibit pest damage, underlie host plant resistance, while indirect defenses including food provisioning and semiochemical production, improve biological control. Interactions between the two defensive strategies may be disruptive, complementary, or synergistic and are an important consideration for effective pest management programs. Glandular trichomes are plant structures that inhibit or entrap arthropods, protecting plants against herbivores, potentially at the cost of reducing natural enemy efficacy. Glandular trichomes may also contribute to indirect defense, as predatory arthropods adapted to "sticky" surfaces scavenge on entrapped arthropods. Scavenging increases predator abundance and reduces plant damage; this protective mutualism has been demonstrated with multiple sticky wild flowers but has not been assessed in an economically important plant, such as tobacco. We augmented dead arthropods (carrion) on tobacco plants grown under conditions similar to commercial production and assessed tri-trophic interactions. Carrion augmentation increased predator abundance, reduced damage to reproductive structures, and increased leaf yield, but did not reduce pest densities. We determined that systemic insecticide use did not affect carrion entrapment on tobacco plants. Review of the literature revealed that a variety of economically important plants entrap arthropods on their surfaces, indicating this mutualism has potential for development into a conservation biological control tactic.

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#### 1. Introduction

Plant defenses against herbivores fall into broad two categories: direct or indirect. Both defensive strategies have been exploited for agricultural pest management; direct defense is the foundation for host plant resistance (Painter, 1951), while indirect defense is intrinsic to biological control (Price et al., 1980). Host plant resistance and biological control are not exclusive in their effects on pests, and their interactions may be disruptive, complementary, or synergistic (Bottrell et al., 1998; Cortesero et al., 2000). For example, manipulating Pisum sativum L. epicuticular waxes increases resistance against Acyrthosiphon pisum (Harris) (Hemiptera: Aphididae) (Eigenbrode et al., 1997), improves predator effectiveness (Eigenbrode et al., 1998), but also reduces predator oviposition (Rutledge et al., 2003). Understanding interactions between plant resistance and biological control is crucial to developing integrated pest management programs, since both strategies are fundamental to the broad management approach (Cortesero et al., 2000; Peterson et al., 2016; Stern et al., 1959).

Trichomes are plant morphological features that exhibit a variety of shapes and sizes that can help regulate abiotic stress and are considered a primary defense against herbivores attacking plants (Levin, 1973). Glandular trichomes produce exudates that are repellent or toxic (Avé et al., 1987; Kauffman and Kennedy, 1989), aid natural enemies in locating herbivores (Weinhold and Baldwin, 2011), and entrap arthropods (LoPresti et al., 2015). Glandular trichomes may be targeted in the development of arthropod resistant crop varieties through selection for morphological and chemical attributes that inhibit pest activity (Glas et al., 2012; Kennedy, 2003). Predators and parasitoids may be affected by glandular trichomes in the same manner as target pests, potentially reducing protection provided by natural enemies (Riddick and Simmons, 2014a). Interactions with natural enemies may not always be antagonistic; in some cases, predation of herbivores is not affected by the presence of trichomes (Björkman and Ahrné, 2005; Obrycki and Tauber, 1984) or may be improved (Styrsky et al., 2006).

Recent research investigating arthropod-plant interactions on wildflowers with glandular trichomes has revealed that trichomes can provide alternative food for natural enemies (Krimmel and Pearse, 2013; LoPresti et al., 2018, 2015). A group of predatory arthropods adapted to maneuvering on such "sticky" plants exists, utilizing a variety of adaptions to avoid entrapment on surfaces generally treacherous to arthropods (Voigt et al., 2007; Voigt and Gorb, 2010, 2008). These predators take advantage of arthropods entrapped on the sticky surfaces, frequently scavenging on the carrion. Arthropod carrion on sticky plants functions similarly to plant provided foods: carrion increases predator abundance, reduces herbivory, and improves plant fitness (Krimmel and Pearse, 2013; LoPresti et al., 2018, 2015). As arthropod carrion is found on the surface of many sticky plants (LoPresti et al., 2015), including economically important plants, such a protective mutualism could improve biological control in economically important plants.

Grown worldwide (FAO, 2018), *Nicotiana tabacum* L., cultivated tobacco, is an economically valuable crop (USDA-NASS, 2018) and, along with its wild relatives, an important system for studying plant biology, genetic engineering, and arthropod-plant interactions (Baldwin, 2001; Ganapathi et al., 2004; Zhang et al., 2011). Tobacco exhibits multiple trichome types that decrease in density as leaves grow (Bentley and Wolf, 1945), including glandular trichomes that do or do not produce exudates (Johnson et al., 1985). Trichomes play a critical role in insect resistance in tobacco, with glandular trichomes impairing movement and limiting the establishment of lepidopteran pests and other small insects (Jackson et al., 1989; Severson et al., 1985). Likewise, glandular trichomes may entrap lepidopteran egg parasitoids (Marcovitch and Stanley, 1937; Rabb and Bradley, 1968) and reduce the mobility of several generalist predators (Belcher and Thurston, 1982; Elsey, 1974; Shah, 1982).

Jalysus wickhami, the most abundant predatory arthropod in

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tobacco, prefers stickier tobacco varieties (Jackson et al., 1989, 1988), on which it can maneuver easily due to leg morphology (Henry, 1997; Southwood, 1986). J. wickhami preys on eggs and small instars of *Heliothis virescens, Manduca sexta*, and *Manduca quinquemaculatua*, the primary lepidopteran pests of tobacco in the southeastern U.S. (Elsey, 1972; Elsey and Stinner, 1971). In addition to predation, J. wickhami has been reported to scavenge on dead arthropods trapped in tobacco glandular trichomes (Elsey, 1972; Elsey and Stinner, 1971; Lawson, 1959; Wheeler and Schaefer, 1982).

LoPresti and Toll (2017) established criteria for observational data to indicate that a protective mutualism exists between arthropod predators and sticky plants, and observations in tobacco satisfy two of these: (1) the most abundant predator, *J. wickhami*, readily scavenges on entrapped carrion and (2) *J. wickhami* can reduce populations of *H. virescens* and *Manduca* spp. (*M. sexta* and *M. quinquemaculata*). Thus, our goal was to assess whether such a mutualism exists in cultivated tobacco, which could be generalized to other economically-important plants covered in glandular trichomes.

Utilizing arthropod carrion as an alternative food source for predatory arthropods could improve biological control on sticky plants, taking advantage of plant traits typically involved in direct defense. We performed field experiments under agronomically relevant conditions in which tobacco plants were augmented with carrion, and evaluated *J. wickhami* and pest abundance, plant damage, yield, and carrion entrapment on insecticide-treated plants. Finally, we reviewed the literature to survey economically important plants that trap arthropods on their surface to illustrate the potential of this tactic.

## 2. Materials and methods

## 2.1. Experimental design

We performed research in 2016 and 2017 at the North Carolina Department of Agriculture and Consumer Services Lower Coastal Plain Research Station (Lenoir County, North Carolina 35.297404, -77.574259) and Upper Coastal Plain Research Station (Edgecombe County, North Carolina, 35.894264, -77.680346). Tobacco variety NC 196 was used in all experiments.

In 2016, we manipulated carrion abundance on individual plants in plots treated with systemic imidacloprid treatments (Admire Pro, 42.8% imidacloprid, Bayer Crop Sciences, Research Triangle Park, NC, USA) in a split-plot, randomized complete block design. Main plots consisted of eight rows spaced 1.22 m apart, 15.24 m long, with 25 tobacco plants per row. Plants in main plots were left untreated or treated with Admire Pro (42.8% imidacloprid, Bayer Crop Sciences, Research Triangle Park, NC, USA) at 17.76 ml/1000 plants via a greenhouse tray drench or in-furrow application, and treatments were replicated four times. Split-plots were randomly assigned to two plants near both ends of rows three and six of main plots. We manipulated arthropod carrion by sprinkling 0.05 g of frozen Drosophila spp. adults (~30 individuals, sourced from NCSU genetics laboratory colonies) from 0.5 m above plants assigned to carrion augmentation treatments; plant assigned to ambient treatments received no Drosophila spp. carrion. Colony-reared Drosophila spp. carrion has been used in other manipulative experiments (Krimmel and Pearse, 2013; LoPresti et al., 2018), and we had previously observed Drosophila spp. naturally on tobacco plants (Nelson, personal observation). Carrion was applied weekly from 15 June to 23 August.

In 2017, we repeated individual plant experiments and performed whole plot experiments in which two carrion densities were manipulated on a larger scale. All plants in both experiments were treated with imidacloprid in a greenhouse tray drench (17.76 ml/1000 plants) to reduce interference of non-lepidopteran pests with treatments, and replicate plots consisted of three 6.5 m long rows, spaced 1.22 m apart with 10 plants per row. Individual plant experiments received the same carrion treatments applied in 2016, replicated eight times, in a

randomized complete block design. Carrion treatments were assigned to two plants near either end of row two and were applied weekly from 15 June to 8 August. Whole plot experiments received the following carrion treatments replicated eight times in a randomized complete block design: ambient carrion (no addition), low carrion (0.05 g frozen *Drosophila* spp. adults), and high carrion (0.20 g frozen *Drosophila* spp. adults). We applied carrion treatments to all plants in plots weekly from 15 June to 8 August.

## 2.2. Arthropod carrion entrapment survey

In 2016, we surveyed dead arthropods trapped on tobacco plants to evaluate the effect of systemic imidacloprid applications on arthropod entrapment. We performed weekly visual inspections of plants in main plots of the individual plant experiment to compare entrapment between untreated, greenhouse tray drench, and transplant water drench treated plots. We performed four 60-second surveys per plot, counting the number of dead arthropods greater than 1 mm in length trapped on the surface of tobacco plants, excluding those typically associated with tobacco (*M. persicae, H. viresecens, Manduca* spp., *J. wickhami*, etc). Carrion entrapment was assessed weekly from 30 May, when *J. wickhami* first appear in tobacco fields (Elsey and Stinner, 1971; Nelson et al., 2019), to 4 July, at which point imidacloprid efficacy against early season pests is reduced (Semtner and Srigiriraju, 2005). We did not survey carrion on plants assigned to carrion manipulation treatments.

## 2.3. Arthropod surveys

We surveyed arthropods in individual plant and whole plot experiments by inspecting entire plants for *J. wickhami, H. virescens,* and *Manduca* spp. Plants assigned carrion manipulation treatments were surveyed in individual plant experiments, while all plants in row two were surveyed in whole plot experiments. Surveys were performed weekly, beginning at the start of carrion augmentation, and concluded one week after augmentation ended.

#### 2.4. Plant damage assessment

We evaluated the effect of carrion manipulation on plant injury by assessing reproductive structure (flower and seed capsule) damage and green leaf weight. Reproductive structures were harvested from individual plant experiments on 1 September 2016 (Edgecombe Co), 23 August 2016 (Lenoir Co.), 9 August 2017 (Edgecombe Co), and 15 August (Lenoir Co.). Damage was estimated in the laboratory by inspecting structures for evidence of caterpillar feeding and assigning one of two responses: damaged or undamaged. In 2017, we measured green leaf weight in whole plot experiments. Six tobacco leaves were collected from lower, mid, and upper stalk positions from seven plants in row three of plots, and their combined mass was measured by stalk position on 8 August (Edgecombe Co.) and 15 August (Lenoir Co.).

## 2.5. Statistical analysis

We performed all statistical analyses in SAS v 9.4 (SAS Institute, Cary NC). Carrion survey, season-long arthropod counts, and plant damage for all experiments were analyzed with independent linear mixed models (PROC MIXED), using the Kenward and Roger (1997) procedure to calculate degrees of freedom. We performed post-hoc mean separations using Tukey's test at  $\alpha < 0.05$ . All means and standard errors reported are untransformed data; data was back transformed if necessary.

We log-transformed  $(\log + 1)$  weekly arthropod carrion counts for analysis of variance with repeated measures. The transformed data was the response variable and imidacloprid treatment, week after treatment, and their interactions were fixed effects. The model included location and block nested within location as random effects and the repeated measures statement utilized compound symmetry with the interaction of replicate plots and location as the subject.

We divided arthropod counts and reproductive structure damage assessments in 2016 individual plant experiments by the number of plants per split-plot (two) to account for pseudo-replication. Seasonlong counts of *J. wickhami*, *H. virescens*, and *Manduca* spp. were squareroot transformed for analysis of variance in separate models. Imidacloprid treatment (main plot), carrion augmentation treatment (split-plot), and their interactions were fixed effects in the models, and random effects included location, block nested within location, and the interaction of imidacloprid treatment and block. The proportion of damaged reproductive structures was calculated and was analyzed using the same model structure as season-long arthropod counts.

We accounted for pseudo-replication in 2017 individual plant experiments in the same manner described for 2016 experiments and square-root transformed season-long arthropod counts. Independent models for each arthropod had the same structure: carrion treatment as the fixed effect and location and block nested within location as random effects. The proportion of damage to reproductive structures was arcsine transformed and analyzed using the same model structure. Seasonlong arthropod counts in whole plot experiments were log-transformed, green leaf weight was square root transformed, and both were analyzed using the same model structure described for 2017 individual plant analyses.

## 3. Results

#### 3.1. Arthropod entrapment literature review

A variety of economically important plant entrap arthropods on their surface, including flowers, herbs, and annual and perennial crops (Table 1). Our review drew heavily from and expanded upon the survey by LoPresti et al. (2015), identifying 26 species or varieties that trap insects, typically with glandular or hooked trichomes. Citations and photographs of observations are included in the Supplementary Material.

## 3.2. Arthropod carrion entrapment survey

Arthropod carrion, entrapped on the surface of tobacco plants, was not influenced by imidacloprid treatments (F = 0.72; df = 2,98; P = 0.4893) but did vary significantly by week (F = 30.77; df = 4,98; P < 0.0001). Carrion abundance initially decreased, peaked in week eight and decreased again (Fig. 1). The interaction between imidacloprid treatment and week was not significant (F = 0.51, df = 8,98; P = 0.8491).

#### 3.3. Individual plant experiment: 2016

*Jalysus wickhami* abundance was influenced by imidacloprid (F = 9.51; df = 2, 8.64; P = 0.0066) and carrion (F = 29.19; df = 1, 26.5; P < 0.0001) treatments but the interaction between the two effects was not significant (F = 0.13; df = 2, 26.5; P = 0.8772) (Fig. 2a). *Jalysus wickhami* counts were greatest in main plots not treated with imidacloprid and were greater on plants augmented with arthropod carrion. As expected, caterpillar densities were not influenced by imidacloprid (*Heliothis virescens* F = 2.82; df = 2, 21; P = 0.0842; *Manduca* spp. F = 3.23; df = 2, 35; P = 0.0515), but carrion treatments (*Heliothis virescens* F = 0.86; df = 1,21; P = 0.3635; *Manduca* spp. F = 0.483; df = 1, 35; P = 0.4943), and their interaction with imidacloprid were also not significant (*Heliothis virescens* F = 0.17; df = 2,21; P = 0.8446; *Manduca* spp. F = 0.04; df = 2,35; P = 0.9585) (Fig. 2).

Plants receiving carrion augmentation had a lower proportion of damaged reproductive structures than ambient treatments (F = 14.95; df = 2, 27.7; P = 0.0006), but plant damage was not affected by

#### Table 1

Economically important plants reported to entrap arthropods on their surface. Data presented is derived partially from the survey of carrion entrapping families and genera by LoPresti et al. (2015). References are presented in Appendix B. GT: glandular trichomes, HT: hooked trichomes, NGT: non-glandular trichomes.

Binomial name	Common name	Family	Genus	Entrapment mechanism	References
Abelmoschus esculentus (L.) Moench	Okra	Malvaceae	Abelmoschus	GT	Duraimurugan and Regupathy (2005)
Cajanus cajan (L.) Millsp.	Pigeon pea	Fabaceae	Cajanus	GT	Romeis et al. (1998)
Cannabis sativa L.	Marijuana	Cannabaceae	Cannabis	GT	Potter (2009)
Cicer arietinum L.	Chickpea	Fabaceae	Cicer	GT	Romeis et al. (1999)
Cucumis sativus L.	Cucumber	Curcubitaceae	Cucumis	HT	Ricci and Ceppelletti (1988)
Pelargonium x hortorum L.H.Bailey	Garden geranium	Geraniales	Geraniaceae	GT	Walters (1988)
Glycine max (L.) Merr.	Soybean	Fabaceae	Glycine	NGT	Panizzi (1987)
Gossypium spp.	Cotton	Malvaceae	Gossypium	NGT	LoPresti et al. (2015)
Lagenaria siceraria (Molina) Standl.	White-flowered gourd	Curcubitaceae	Lagenaria	NGT	Kishaba et al. (1992)
Medicago sativa L.	Alfalfa	Fabaceae	Medicago	GT	Small (1985), Shade et al. (1979)
Nicotiana tabacum L.	Tobacco	Solanaceae	Nicotiana	GT	Lawson (1959), Marcovitch and Stanley (1937)
Origanum x intercedens Rech.	Oregano	Lamiaceae	Origanum	GT	Bosabalidis and Skoula (1998)
Petunia spp. Juss.	Petunia	Solanaceae	Petunia	GT	Davidson et al. (1992)
Phaseolus coccineus L.	Scarlett runner bean	Fabaceae	Phaseolus	HT	Ricci and Ceppelletti (1988)
Phaseolus lunatus L.	Lima bean	Fabaceae	Phaseolus	HT	Riddick and Wu (2011)
Phaseolus vulgaris L.	French bean	Fabaceae	Phaseolus	HT	Quiring et al. (1992), Pillemer and Tingey (1978)
Phaseolus vulgaris L. var. Sortex process	Bush bean	Fabaceae	Phaseolus	HT	Shah (1982)
Rhododendron macrosepalum Maxim., 1870	Azalea	Ericaceae	Rhododendron	GT	Sugiura and Yamazaki (2006)
Rosa hybrida L.	Rose	Rosaceae	Rosa	NGT	Yamazaki et al. (2014)
Salvia officinalis L.	Sage	Lamiaceae	Salvia	GT	Corsi and Bottega (1999)
Salvia sclarea L.	Clary sage	Lamiaceae	Salvia	GT	Nelson observation
Sicana odorifera (Vell.) Naudin	Cassabanana	Curcubitaceae	Sicana	GT	Kellogg et al. (2002)
Solanum tuberosum L. x berthualtii	Potato	Solanaceae	Solanum	GT	Obrycki and Tauber (1984)
Solanum lycopersicum L.	Tomato	Solanaceae	Solanum	GT	McKinney (1938)
Sorghum bicolor (L.) Moench	Sorghum	Poaceae	Sorghum	NGT	Taneja and Woodhead (1987)
Theobroma cacao L.	Cocoa	Malvaceae	Theobroma	GT	Wheatley (1952)
Vitis romanetii Rom.Caill.	Grape	Vitaceae	Vitis	GT	Ma et al. (2016)



Fig. 1. Mean (  $\pm$  SEM) Arthropod carrion on tobacco plants receiving systemic imidacloprid applications.

imidacloprid treatment (F = 2.24; df = 2, 8.5; P = 0.1658) or the interaction of the two effects (F = 2.01; df = 2, 27.7; P = 0.1534) (Fig. 3).

#### 3.4. Individual plant experiment: 2017

Plants augmented with carrion had higher season long *J. wickhami* densities than ambient treatments (F = 46.30; df = 1, 29; P < 0.0001) (Fig. 4a). Both *H. virescens* and *Manduca* spp. season-long counts were not influenced by carrion treatments (F = 0.55; df = 1,15; P = 0.4681; F = 3.37; df = 1, 15; P = 0.0863, respectively) (Fig. 4a &b), while the proportion of damaged reproductive structures was significantly reduced on plants augmented with carrion (F = 7.43; df = 1, 29; P = 0.0107) (Fig. 5).

#### 3.5. Whole plot experiment: 2017

Low and high carrion augmentation treatments had significantly higher J. wickhami abundance than the ambient treatment but the two augmentation rates were not significantly different from each other (F = 53.33; df = 2, 26.4; P < 0.0001; Fig. 4a). Season-long means of H. virescens did not differ significantly due to carrion treatments (F = 1.42; df = 2,30; P = 0.2568 (Fig. 4b), nor did Manduca spp. (F = 0.60; df = 2,32.4; P = 0.5539) (Fig. 4c). Green leaf weight was significantly influenced by both carrion treatment (F = 12.26; df = 2, 122; P < 0.0001) and stalk position (F = 52.71; df = 2, 119; P < 0.0001) but the interaction of the two factors was not significant (F = 1.59; df = 4, 119; P = 0.1813). Overall, green leaf weight was significantly greater on plants augmented with arthropod carrion compared to ambient treatments, and there was no difference between low and high carrion augmentation rates (Fig. 6). Green leaf weight was greatest at low stalk positions, followed by mid and upper stalk positions (Fig. 6).

## 4. Discussion

Arthropod carrion trapped by trichomes is an underappreciated form of plant-provided food that influences trophic interactions. Trichome entrapment is typically considered a direct defense against herbivores, but research indicates trichomes are also involved in indirect defense. Augmenting carrion on tobacco plants increased densities of *J. wickhami*, reduced damage to reproductive structures, and increased green leaf weight. This is the first report of a carrion-mediated protective mutualism with a member of the Solanaceae and with an economically important plant grown under agronomically-relevant conditions. Our review of the literature revealed that numerous economically important plants trap arthropods on their surface, suggesting this phenomenon has potential to enhance biological control in a variety of cropping systems.

Provisioning natural enemies with alternative food is predicted to



Fig. 2. Season-long mean ( $\pm$  SEM) A) *Jalyus wickhami* B) *Heliothis virescens* and C) *Manduca* spp. in 2016 individual plant experiments. Different capital letters indicate statistically significant differences in imidacloprid treatments, different lowercase letters indicate statistically significant differences in carrion treatments (Tukey's HSD,  $\alpha \leq 0.05$ ).



Fig. 3. Mean ( $\pm$  SEM) damage to reproductive structures in 2016 individual plant experiments. Different letters indicate statistically significant differences between carrion treatments (Tukey's HSD,  $\alpha \leq 0.05$ ).

increase their abundance (van Baalen et al., 2001; van Rijn et al., 2002) and carrion augmentation in individual plant and whole plot experiments boosted *J. wickhami* populations compared to ambient carrion treatments. In whole plot experiments, *J. wickhami* numbers did not differ between low and high carrion augmentation treatments. Natural enemy populations grow partly in response to food supplementation via increased reproductive rates (van Rijn and Sabelis, 2005) however, this mechanism may be more readily observed in organisms with shorter generation times (Sabelis, 1992; van Rijn et al., 2002). *J. wickhami* have two generations per growing season (Elsey and Stinner, 1971) which may not provide enough time for raised reproductive rates to increase abundance. Plots assigned to high augmentation treatments received four times the amount of carrion as low treatment plots; this difference may not have been great enough to increase *J. wickhami* numbers. Testing a wider range of augmentation rates could identify the limits at which this mutualism increases predator abundance.

Plants benefit from provisioning carrion to predators by increasing their own fitness, assessed by measuring damage to reproductive structures (Krimmel and Pearse, 2013; LoPresti et al., 2018, 2015). In our study, carrion augmentation reduced damage to tobacco flowers and seed capsules, indicating tobacco benefits in this same manner. In addition to improving plant fitness, reductions in damage to these structures has economic implications for tobacco grown for seed in nursery production. Tobacco, like many domesticated plants, is grown to produce large amounts of leaf mass (Brown et al., 2018). By measuring green leaf weight, a proxy for yield, we determined that carrion augmentation increases leaf mass. This is the first report of this protective mutualism reducing damage to vegetative plant structures, indicating carrion augmentation could improve biological control of foliar pests as well as flower and fruit pests.

Despite the reduction in plant damage, lepidopteran pest (H. virescens and Manduca spp.) numbers did not differ in response to carrion augmentation. Over shorter periods of time, supplying alternative food may reduce prey consumption, especially if that food is substitutable (Tillman, 1982; van Rijn and Sabelis, 2005). Alternately, a reduction in damage without a change in pest numbers indicates that the effect of J. wickhami on pests may be non-consumptive (Thaler and Griffin, 2008; Werner and Peacor, 2003). Non-consumptive effects of natural enemies are becoming increasingly valued for their role in pest management (Eubanks and Finke, 2014; Hermann and Landis, 2017) and may contribute to reductions in herbivory in other sticky plant mutualisms (LoPresti et al., 2015). Evaluating the relative importance of predator non-consumptive effects would clarify trophic interactions on sticky plants. Determining the potential for substitutability of arthropod carrion is necessary for further development into a conservation biological control tactic.

This is the first report of a carrion-mediated protective mutualism assessed in an agroecosystem. Excessive pesticide use in agroecosystems can simplify food webs and destabilize predator dynamics (Croft and Brown, 1975; Ripper, 1956). Systemic imidacloprid applications are frequently used in North Carolina flue-cured tobacco production for early season pest management (Burrack and Toennisson, 2018); these applications are compatible with J. wickhami (Nelson et al., 2019), but reduce the availability of the prey Myzus persicae (Merchán and Burrack, 2017). Arthropod carrion on tobacco plant surfaces did not differ between imidacloprid treatments, suggesting carrion may be available for J. wickhami when prey is absent due to imidacloprid use. LoPresti et al. (2015) reported that volatile cues produced by Aquilegia eximia Van Houtte ex Planch. Attract arthropods, leading them to their demise (but see Appendix A). Systemically applied insecticides may translocate to exudates of glandular trichomes and impair arthropods (Cherry and Pless, 1969; Reddy et al., 1970), thus evaluating the effect of insecticide use on carrion entrapment in other crops is warranted.

Inhibiting insect movement is one mechanism of antixenosis in host plant resistance (Kogan and Ortman, 1978; Painter, 1951). Insect entrapment by plants has been reported in over 110 genera in 49 families (LoPresti et al., 2015); our species-specific review includes flowers, herbs, agronomic, and horticultural crops (Table 1). Selecting or breeding for varieties with trichomes could benefit integrated pest management programs, as insect entrapment may contribute to both



Fig. 4. Season-long mean ( $\pm$  SEM) A) Jalyus wickhami B) Heliothis virescens and C) Manduca spp. in 2017 individual plant and whole plot experiments. Asterisk denotes a significant effect of carrion treatment. Different letters indicate statistically significant differences between carrion treatments (Tukey's HSD,  $\alpha \leq 0.05$ ).





Fig. 5. Mean ( $\pm$  SEM) damage to reproductive structures in 2017 individual plant experiments. Asterisk denotes a significant effect of carrion treatment.

direct (resistance) and indirect plant defenses (biological control). Domestication may reduce plant defenses (Chen et al., 2015) and assessing wild relatives of crops for arthropod entrapment could initiate development of this feature into an efficacious conservation biological

**Fig. 6.** Mean ( $\pm$  SEM) green leaf weight harvested from plants in 2017 whole plot experiments. Different upper case letters indicate statistically significant differences in carrion treatments, different lowercase letters indicate statistically significant differences in stalk position (Tukey's HSD,  $\alpha \leq 0.05$ ).

control tactic. For instance, wild tomato (Gentile et al., 1968; Simmons et al., 2004) and potato (Gibson and Turner, 1977; Obrycki and Tauber, 1984) relatives are "stickier" (increased trichome density) than their

domesticated counterparts and trap arthropods on their surfaces.

Trichomes may produce harmful effects against natural enemies and reduce their efficacy in controlling herbivores (Eisner et al., 1998; Kennedy, 2003; Riddick and Simmons, 2014a) but this narrative of morphology mediating arthropod-plant interactions is incomplete. Predatory arthropods able to maneuver on sticky plant surfaces without ill effects have been observed on multiple wild hosts (Krimmel and Pearse, 2013; LoPresti et al., 2018, 2015; Lopresti and Toll, 2017); we have found members of this group (berytids, reduviids, oxyopids) on tobacco plants as well (Nelson et al., 2019). Natural enemy interaction with glandular trichomes may be nuanced and requires ecologicallyrelevant studies to determine if this direct defense impedes predators and parasitoids. Coccinellid movement may be impaired by glandular trichomes (Cottrell and Yeargan, 1999; Shah, 1982), however, their efficacy in reducing aphid abundance was increased on sticky versus non-sticky races of the same plant (Krimmel and Pearse, 2014).

Provisioning natural enemies with food is a conservation biological control tactic; utilizing non-crop plants to provide extra-floral nectar or pollen is one approach (Berndt et al., 2002; Hansen, 1983; Lee and Heimpel, 2003; Wong and Frank, 2013). Arthropod carrion could be developed into a similar resource via exploitation of plant morphology or application of artificially reared carrion to augment alternative food for predatory arthropods. Evaluating a range of augmentation rates and varietal differences in carrion entrapment could advance the development of this tactic. Trichomes are not a dead end for biological control, but considering appropriate natural enemies and their interactions with plants in crop-specific context is necessary to prevent the failure of such efforts (Davidson et al., 1992; Krimmel, 2014; Riddick and Simmons, 2014b).

#### CRediT authorship contribution statement

**Peter N. Nelson:** Conceptualization, Investigation, Methodology, Formal analysis, writing - original draft. **Hannah J. Burrack:** Conceptualization, Funding acquisition, writing - review & editing. **Clyde E. Sorenson:** Conceptualization, Funding acquisition, writing review & editing.

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## Author contributions

P.N.N. contributions: conceptualization, investigation, methodology, formal analysis, and writing-original draft. H.J.B. and C.E.S. contributions: conceptualization, funding acquisition, and writing-review & editing.

#### Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocontrol.2019.104021.

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