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Arthropod carrion influences plant choice, oviposition, and cannibalism by a specialist predator on a sticky plant

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Abstract. 1. Dead arthropods, entrapped by trichomes on plant surfaces, are an underappreciated form of plant-provided food. Specialist predatory arthropods able to manoeuvre on plants covered in trichomes facultatively scavenge on the alternative food resource, increasing their abundance and reducing plant damage by herbivores.

2. This protective mutualism dependent on arthropod carrion has been demonstrated in several plant species, but the mechanisms driving the increase in predator abundance have not been identified. Through a series of greenhouse and laboratory experiments, the effect of arthropod carrion on predator behaviour was assessed.

3. The predator *Jalysus wickhami* preferred *Nicotiana tabacum* plants augmented with arthropod carrion, spending significantly more time and laying more eggs on those plants than plants without arthropod carrion.

4. Under low *J. wickhami* densities, arthropod carrion did not reduce egg cannibalism by adults. Under high densities, egg cannibalism by *J. wickhami* adults was reduced in the presence of arthropod carrion, but cannibalism by fifth instars was not.

5. Arthropod carrion may be utilised by a wide range of predatory arthropods that facultatively scavenge, and this research demonstrates its potential for influencing arthropod–plant and arthropod–arthropod interactions.

Key words. Arthropod–plant interactions, necrophagy, phylloplane resource, plant-provided food, scavenging, trichomes.

Introduction

Plants may defend themselves from herbivore attack by providing alternative food resources for natural enemies (plant-provided foods, PPFs). This indirect defensive strategy is utilised by numerous species and relies on the fact that many carnivorous arthropods are facultatively or obligately zoo-phytophagous, feeding on plant tissues at some point during their lives (Bugg *et al.*, 1991; Jervis *et al.*, 1996; Limburg & Rosenheim, 2001; Porter, 2018). By providing food, plants increase the abundance or efficacy of natural enemies which can lead to a reduction in herbivore density and damage (Bakker & Klein, 1992; Stapel *et al.*, 1997; van Rijn *et al.*, 2002; Wäckers, 2003). Some plant species have specialised food body structures to facilitate these interactions (Rickson, 1980; Heil *et al.*, 1998). More common types of PPFs utilised by natural enemies are pollen, floral, and extrafloral nectar (Wäckers, 2005).

Plants covered in trichomes can entrap arthropods on their surface (Romero *et al.*, 2008; Krimmel & Pearse, 2013). These 'tourists' (Moran & Southwood, 1982), unaccustomed to manoeuvring on the complex plant surfaces, are trapped by the outgrowths either via impalement on hooked trichomes (Pillemer & Tingey, 1978; Ricci & Ceppelletti, 1988; Riddick & Wu, 2011) or by capture in the sticky exudates of glandular trichomes (McKinney, 1938; Shade *et al.*, 1979; Romeis *et al.*, 1998). A guild of specialist predators able to manoeuvre on the plant surfaces without becoming entrapped facultatively feed on the dead arthropods, increasing their abundance and reducing damage to plants (Krimmel & Pearse, 2013; LoPresti *et al.*, 2015, 2018; Karban *et al.*, 2019; Nelson *et al.*, 2019).

Plant-provided foods may increase natural enemies on plants via multiple mechanisms. Volatiles produced by flowers can attract parasitoids to nectar (Wäckers, 2004), while pollen has been demonstrated to maintain predators during periods of

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low prey density, reducing emigration (van Rijn & Sabelis, 1990), and increase fecundity or shorten development time (Salas-Aguilar & Ehler, 1977; Cocuzza *et al.*, 1997; van Rijn *et al.*, 2002; Vandekerkhove & De Clercq, 2010). By providing food resources, plants may satiate natural enemies and decrease consumption of herbivores (Cottrell & Yeargan, 1998; Stenberg *et al.*, 2011). Alternatively, satiation may reduce cannibalism (Leon-Beck & Coll, 2007; Frank *et al.*, 2010), an important factor contributing to natural enemy population dynamics (Fox, 1975; Polis *et al.*, 1989). Whether arthropod carrion, entrapped on plants, functions similarly to any of the previously mentioned mechanisms is unknown; thus far authors have postulated that carrion either attracts or retains predators on the plants (Krimmel & Pearse, 2013; LoPresti *et al.*, 2015).

Nicotiana tabacum L. is an economically important annual crop covered in glandular trichomes (Bentley & Wolf, 1945) that trap numerous insect species (Marcovitch & Stanley, 1937; Rabb & Bradley, 1968; Severson *et al.*, 1985; Jackson *et al.*, 1989). The predator *Jalysus wickhami* Van Duzee (Hemiptera: Berytidae) is associated primarily with 'glandular-hairy' hosts, including *N. tabacum* (Wheeler & Henry, 1981), and readily scavenges on arthropod carrion entrapped on plant surfaces (Lawson, 1959; Elsey & Stinner, 1971; Elsey, 1972; Wheeler & Schaefer, 1982; Karban *et al.*, 2019; Nelson *et al.*, 2019). *Jalysus wickhami* responds positively to increased availability of arthropod carrion and is involved in defending plants against herbivore attack (Krimmel & Pearse, 2013; Lopresti & Toll, 2017; Nelson *et al.*, 2019).

Our goal was to assess how arthropod carrion influences predator behaviours, potentially contributing to increased abundance, on plants provisioning the resource. We hypothesised that arthropod carrion may influence multiple arthropod behaviours that can increase their abundance on plants. Through a series of experiments, we assessed the effect of arthropod carrion on predator plant preference, oviposition preference, and egg cannibalism by different life stages.

Materials and methods

We performed experiments with *J. wickhami* and *N. tabacum*. *Drosophila* spp. cadavers were selected as a surrogate for naturally occurring arthropod carrion as they have been utilised in other manipulative experiments and have been observed to be fed upon by *J. wickhami* (Krimmel & Pearse, 2013; LoPresti *et al.*, 2018; Nelson *et al.*, 2019). During our experiments, we observed *J. wickhami* adults and nymphs scavenging on *Drosophila* spp. cadavers numerous times in both the greenhouse and microcosms experiments.

Although we measured cannibalism in greenhouse experiments, these were designed to assess the effect of carrion on aggregation and egg laying, whereas microcosm experiments were designed to measure the effect of carrion directly on cannibalism.

Insect material

We collected *J. wickhami* from *N. tabacum* (var. NC 196) fields at the North Carolina Department of Agriculture and Consumer Services Lower Coastal Plain Research Station (Lenoir County, North Carolina: 35.297 404°N, 77.574 259°W) and Upper Coastal Plain Research Station (Edgecombe County, North Carolina: 35.894 264°N, 77.680 346°W), and established a laboratory colony. This colony was maintained in a 1.2 × 1.2 × 1.2 m (length × width × height) cage covered in overwintering fabric (Dewitt, Sikeston, Missouri) and provisioned the insects with four *N. tabacum* plants (var. K326) potted in 20-cm-tall, 11-litre plastic pots. Plants were infested with field-collected *Myzus persicae* (Sulzer, 1776) (Hemiptera: Aphididae), and we placed frozen, colony-reared *Manduca sexta* (Linneaus, 1763) (Lepidoptera: Sphingidae) eggs, *Heliothis virescens* (Fabricius, 1777) (Lepidoptera: Noctuidae) eggs, and frozen *Drosophila* spp. adults on plants every 1–2 weeks. We kept the colony in a greenhouse with temperatures fluctuating from 35 °C during the day to 22 °C at night with a photoperiod of LD 16:8 h.

We facilitated *J. wickhami* egg production by holding two females and one male in 30-ml plastic cups (Dart Container Corporation, Mason, Michigan) with a 2.5-cm-diameter disc of *N. tabacum* leaf placed adaxial side up on a 0.5-cm layer of 2% water agar (Alfa Aesar, Ward Hill, Massachusetts). Adults were provided with approximately six *Drosophila* spp. adult cadavers; cups were covered with a paper lid and were held in a growth chamber at 25 °C, LD 14:10 h, and RH 70%. We removed eggs daily for 4 days and stored them at 25 °C in *N. tabacum*-lined cups for no longer than 3 days before experimental use.

We collected *Drosophila* spp. adults from North Carolina State University genetics laboratory cultures and froze them until use.

Plant material

We used *N. tabacum* var. K326 in all experiments. *Nicotiana tabacum* was planted in 16-cm-diameter clay pots filled with 50:50 Fafard 4p mix (Sun Gro Horticulture, Agawam, Massachusetts):play sand and were fertilised with Osmocote 14-14-14 (The Scotts Company, Marysville, Ohio). Plants were grown for 6 weeks in the greenhouse and were *c*. 20 cm tall and 20 cm in diameter with eight to 10 leaves per plant at the time of use in experiments.

Greenhouse experiments

We performed both greenhouse experiments under the previously described environmental conditions, using 1.0 × 0.5 × 0.5-m cages covered in overwintering fabric.

Plant and egg laying choice. In order to test the effect of carrion presence on egg laying in the absence of prey items, we placed two potted *N. tabacum* plants 15 cm from longitudinal cage edges and randomly assigned following treatments to the plants: no carrion or carrion addition (four *Drosophila* spp. cadavers added to each leaf). We introduced six adult *J. wickhami* at a female:male ratio of 50:50 into the centre of cages and assessed the number of insects on each plant at 2, 4, 8, 12, 24, and 48 h after introduction. At 48 h we removed all *J. wickhami* and destructively sampled the plants to count the number of eggs laid on the plants. We used a randomised complete block design with five blocks and replicated the experiment on five dates.

No-choice egg cannibalism. We placed a single potted *N. tabacum* plant in the centre of a cage and added three *J. wickhami* eggs to the adaxial leaf surface along the midrib of each of two haphazardly selected leaves (observations made during the previous experiment indicate that *J. wickhami* egg laying is clustered, predominantly on adaxial leaf surfaces, and frequently along leaf midribs). Plants were assigned to one of two treatments: no carrion or carrion addition (three *Drosophila* spp. cadavers added per leaf with *J. wickhami* eggs). We introduced six *J. wickhami* adults at a 50:50 female:male ratio into the centre of cages and assessed egg cannibalism after 48 h. We used a randomised complete block design with four blocks and replicated the experiment on five dates.

No-choice microcosm egg cannibalism

We performed microcosm experiments using the previously described cups lined with agar and *N. tabacum* leaves. We assessed egg cannibalism by adult *J. wickhami* by adding five colony-reared eggs to cups and one of two carrion treatments: no carrion or carrion addition (five *Drosophila* spp. cadavers). A single adult *J. wickhami* was introduced to each of the cups, which were then covered with paper lids. We assessed egg cannibalism at 24, 48, and 72 h and replicated the experiment on five dates with at least four repetitions per treatment. We assessed egg cannibalism by fifth-instar *J. wickhami* by adding three colony-reared eggs to cups and the same carrion treatments (carrion addition: three *Drosophila* spp. cadavers). A single fifth-instar *J. wickhami* was introduced to the cups which were then covered with paper lids. We assessed egg cannibalism at 24, 48, and 72 h and replicated the experiment on four dates, blocking by date, with at least four repetitions per treatment.

Statistical analyses

We performed all statistical analyses using SAS v.9.4 (SAS Institute, Cary, North Carolina) and used Tukey's test ($\alpha < 0.05$) for *post-hoc* mean separations. Response variables were transformed to meet assumptions of normality as needed, but non-transformed data are presented for clarity.

We analysed adult log-transformed [$\log_{10}(x + 1)$] *J. wickhami* counts with a linear mixed model (PROC MIXED) with repeated measures, using the following structure: carrion treatment, assessment time, and their interactions as fixed effects, and replicate and block nested within replicate as random effects. The interaction among block, replicate, and assessment time was the subject of repeated measures, using compound symmetry. Mean *J. wickhami* eggs per plant were square-root-transformed and analysed with the following model: carrion treatment as the fixed effect and replicate, block nested within replicate, and the interaction between treatment and block as random effects.

Egg cannibalism by *J. wickhami* in the greenhouse experiments was evaluated using a linear mixed model. We log-transformed the number of eggs cannibalised and used the following model structure: carrion treatment as the fixed effect, and replicate and block nested within replicate as random effects. Egg cannibalism by nymphs and adults in microcosm experiments was analysed using separate linear mixed models with repeated measures. The number of eggs cannibalised was log-transformed and carrion treatment and assessment date and their interactions were fixed effects. We assigned replicate as the random effect and utilised a repeated statement with compound symmetry structure, with the interaction of repetition and replicate as the subject.

Results

Greenhouse experiments

Jalysus wickhami abundance was significantly greater on plants with added carrion ($F_{1,216} = 132.14$, $P < 0.0001$), and abundance on plants regardless of carrion treatment was greatest at 24 h ($F_{1,4} = 22.95$, $P < 0.0001$; Fig. 1). Further, plants receiving carrion additions had four times the number of eggs as control plants ($F_{1,4} = 27.42$, $P = 0.0064$; Fig. 2). Egg cannibalism by *J. wickhami* adults in caged experiments was infrequent and did not differ in the presence of carrion ($F_{1,19} = 0.21$, $P = 0.6526$; Fig. 3).

Microcosm experiments

Egg cannibalism was significantly lower in the presence of arthropod carrion ($F_{1,128} = 53.71$, $P < 0.0001$) and was highest during the last assessment period (72 h) ($F_{2,128} = 9.18$, $P = 0.0002$; Fig. 4). The presence of carrion did not alter egg cannibalism by *J. wickhami* nymphs ($F_{1,105} = 0.95$, $P = 0.3315$), but cannibalism did increase over time ($F_{2,105} = 13.05$, $P < 0.0001$) and was highest at 48 and 72 h (Fig. 5).

Discussion

Plant-provided foods exist in a variety forms (floral and extrafloral nectar, pollen, food bodies, elaiosomes, etc.) (Wäckers, 2005) and supplement the diet of natural enemies, thereby enlisting them in defence against herbivores. Plant-provided foods influence natural enemy behaviour, including interactions with plants and other arthropods (Stapel *et al.*, 1997; Eubanks & Denno, 2000; Jamont *et al.*, 2014), and can enhance performance (Kiman & Yeargan, 1985; Fouly *et al.*, 1995). Dead arthropods, entrapped on plant surfaces by trichomes, are another form of PPF utilised by predatory arthropods able to navigate the plant surfaces without becoming ensnared (Krimmel & Pearse, 2013, 2014; LoPresti *et al.*, 2015, 2018; Lopresti & Toll, 2017; Nelson *et al.*, 2019).

Our results demonstrate that this food source influences the behaviour of the predator *J. wickhami*. In greenhouse experiments performed to assess the effect of carrion on

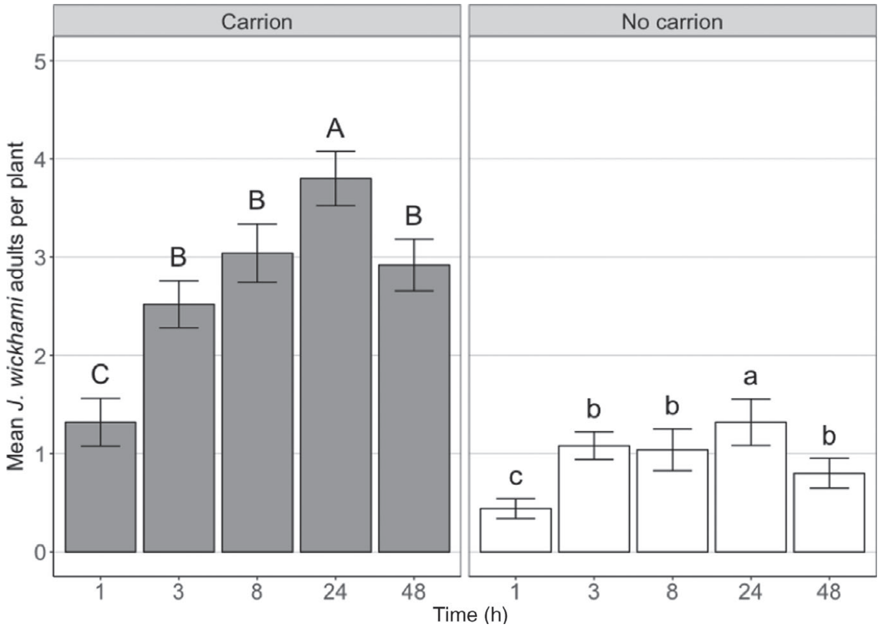

Fig. 1. Mean (SEM) *Jalysus wickhami* adults per plant in greenhouse plant choice caged experiments. Differences in *J. wickhami* between treatments were statistically significant; different letters indicate statistically significant differences in assessment time within a treatment (Tukey's honestly significant difference, $\alpha \leq 0.05$).

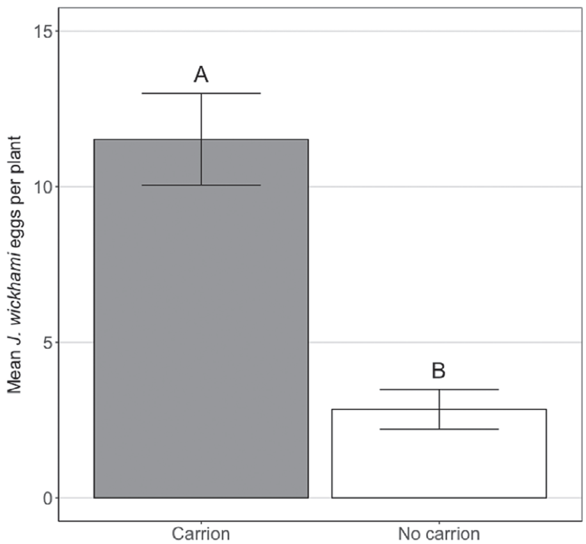

Fig. 2. Mean (SEM) *Jalysus wickhami* eggs oviposited on plants in greenhouse plant choice caged experiments. Different upper-case letters indicate statistically significant differences in carrion treatments (Tukey's honestly significant difference, $\alpha \leq 0.05$).

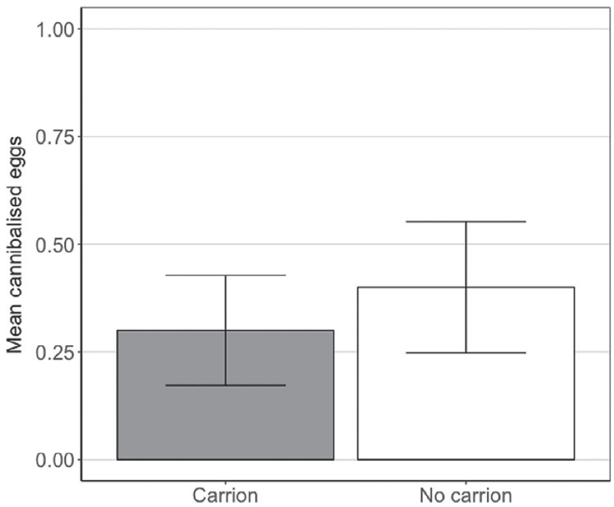

Fig. 3. Mean (SEM) *Jalysus wickhami* eggs cannibalised by adults in greenhouse no-choice caged experiments.

arthropod–plant interactions, *J. wickhami* adults were observed on *N. tabacum* plants augmented with *Drosophila* spp. carrion at greater frequencies, and *J. wickhami* oviposited more eggs on these plants as well. *Drosophila* spp. carrion reduced egg cannibalism by *J. wickhami* adults, but only at the higher density assessed in microcosm experiments, and did not reduce egg cannibalism by nymphs.

Natural enemy abundance typically increases with the availability of PPF. This numerical response is due in part to the aggregation of natural enemies to food resources (Solomon, 1949), and a variety of predators are attracted to and feed on nectar and pollen, increasing their abundance (Bentley, 1977; Sutherland *et al.*, 1999; Nomikou *et al.*, 2010; Wong & Frank, 2013). Our results indicate that *J. wickhami* respond similarly to arthropod carrion, as more adults were observed on *N. tabacum* plants augmented with *Drosophila* spp. cadavers than those without. Aggregation is the result of attraction

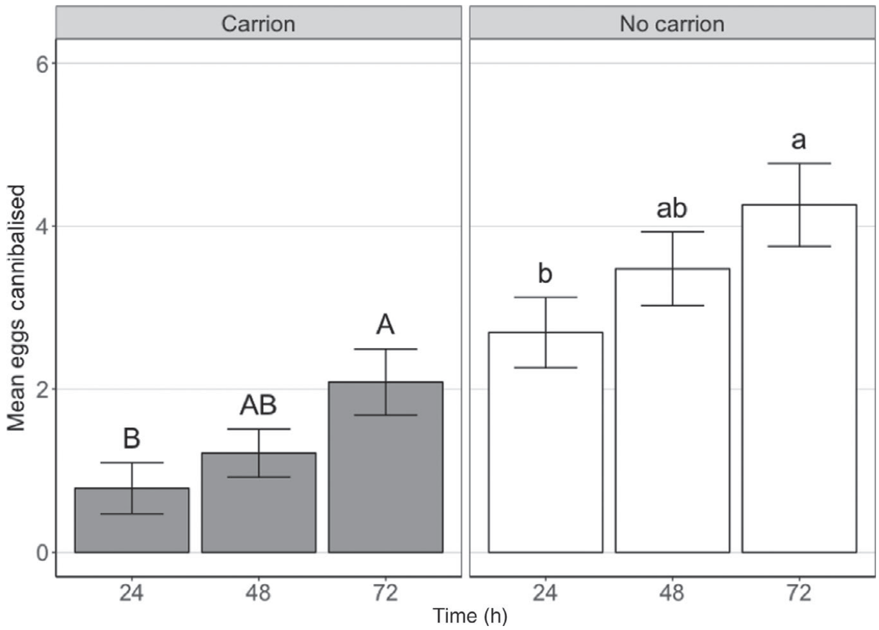

Fig. 4. Mean (SEM) *Jalysus wickhami* eggs cannibalised by adults in microcosm experiments. Differences in egg cannibalism by adults were statistically significant between treatments; different letters indicate statistically significant differences in assessment time within a treatment (Tukey's honestly significant difference, $\alpha \leq 0.05$).

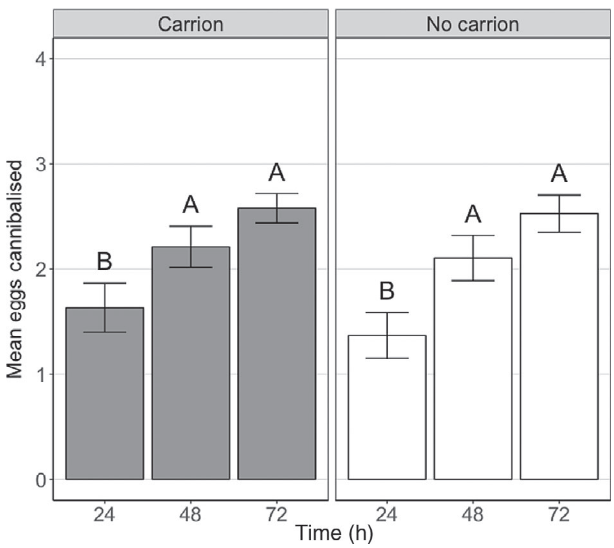

Fig. 5. Mean (SEM) *Jalysus wickhami* eggs cannibalised by fifth instars in microcosm experiments. Egg cannibalism did not differ significantly between carrion treatments; different letters indicate statistically significant differences in assessment time (Tukey's honestly significant difference, $\alpha \leq 0.05$).

(Wäckers, 2004) and retention (Stapel *et al.*, 1997). Although we observed greater frequencies of *J. wickhami* adults on plants with carrion, we did not attempt to parse out sensory modalities contributing to attraction or assess retention rates. Olfactory cues are involved in the attraction of scavenging grasshoppers to carrion (Bomar, 1993); assessing whether *J. wickhami* respond positively to volatiles produced by carrion or the interface of plants and carrion could help to elucidate aggregation mechanisms.

In addition to aggregation, egg laying by natural enemies may contribute to numerical responses (Solomon, 1949) and can increase with the availability of alternative foods (van Rijn & Sabelis, 2005). Consumption of PPF by natural enemies may overcome dietary deficiencies and increase fecundity (Kiman & Yeargan, 1985; Cocuzza *et al.*, 1997; Eubanks & Styrsky, 2005; Jacometti *et al.*, 2010). We observed a significant increase in the number of eggs laid on plants with arthropod carrion, which is probably due to adults aggregating on the same plants. Similar short-term effects of PPF availability on Coccinellidae (Coleoptera) predator oviposition have been observed in the field (Cottrell & Yeargan, 1999) and may be explained, in part, by PPF functioning as an oviposition stimulant (Evans & Dixon, 1986). Our experimental design precluded assessing the influence of arthropod carrion on fecundity, as we did not rear *J. wickhami* on different diets. Further research investigating this is warranted.

Cannibalism is pervasive amongst arthropods, including carnivorous (Elgar, 1992) and non-carnivorous taxa (Richardson *et al.*, 2010), and it can be the result of a variety of density-dependent and independent factors (Fox, 1975; Polis, 1981; Richardson *et al.*, 2010). Cannibalism by natural enemies may be increased when prey abundance is reduced or low in quality (Hironori & Katsuhiro, 1997; Snyder *et al.*, 2000; Denno *et al.*, 2004; Moreno-Ripoll *et al.*, 2012) and is ameliorated by alternative foods, including PPFs (Cottrell & Yeargan, 1998; Leon-Beck & Coll, 2007; Frank *et al.*, 2010). Arthropod carrion had mixed effects on egg cannibalism by *J. wickhami*: at low adult densities, egg cannibalism was infrequent and did not decrease when carrion was present. At higher densities, egg cannibalism by adults was reduced in the presence of carrion, but nymph cannibalism did not differ. Increased population density is frequently linked to cannibalism (Fox, 1975; Polis, 1981; Richardson *et al.*, 2010) and is a plausible explanation for differences observed in egg cannibalism by *J. wickhami* in our experiments. Microcosm cannibalism experiments had substantially higher *J. wickhami* densities (one per 30 cm^3) compared with greenhouse experiments (one per 41 666 cm^3). We have counted as many as 22 *J. wickhami* per *N. tabacum* plant and observed cannibalism in the field. Assessing cannibalism was not our main goal in carrying out greenhouse experiments, and relatively lower densities of carrion were adequate to observe effects on egg laying.

Predation is frequently an asymmetrical interaction, as size hierarchies (interspecific, due to ontogeny, or intraspecific) can drive cannibalism and intraguild predation (Polis, 1981; Polis *et al.*, 1989). Similarly, scavenging by *J. wickhami* could be driven by differences in size between the predators and arthropod carrion. Egg cannibalism by *J. wickhami* nymphs was not reduced in the presence of *Drosophila* spp. cadavers, which were approximately the same length as the fifth-instar predators. Scavenging by *Loxosceles reculsa* Gertsch & Mulaik, 1940 (Aranae: Sicariidae) is dependent on the size of carrion relative to live prey (Vetter, 2011), and assessing similar interactions with *J. wickhami* nymphs is warranted. Diet mixing can differ between arthropod life stages, and life-history omnivory amongst predators and parasitoids is not uncommon (Coll & Guershon, 2002). *Jalysus wickhami* nymphs may have different nutritional requirements from those of adults, which prevent them from scavenging as readily.

Carrion consumption, or scavenging, is a predominantly facultative predatory behaviour and can have significant effects on trophic interactions (Wilson & Wolkovich, 2011; Barton *et al.*, 2012; Beasley *et al.*, 2012). Scavenging on vertebrate carrion by arthropod decomposers (Benbow *et al.*, 2015) and conspecifics by social arthropods (Sun & Zhou, 2013) is well studied, but facultative scavenging by arthropods on arthropod carrion has been neglected. Facultative scavenging by a diverse group of arthropods has been reported (Lavigne & Pfadt, 1964; Wheeler, 1974; Coelho & Hoagland, 1995; Pierce, 1995; Foltan *et al.*, 2005; Vetter, 2011) but few studies have assessed the effects of scavenging on individuals and communities (Wilson & Wolkovich, 2011; Peng *et al.*, 2013; LoPresti, 2018; LoPresti *et al.*, 2018; Nelson *et al.*, 2019). Our study indicates that scavenging by predators can reduce cannibalism, probably via satiation on arthropod carrion, potentially increasing their abundance. Whether or not predators remain sated on carrion and are thus less likely to feed on herbivores is unknown; experiments assessing the effect of carrion augmentation in tobacco fields revealed that, whereas *J. wickhami* abundance increased and plant damage was reduced, herbivore abundance was not reduced (Nelson *et al.*, 2019). Future research could utilise molecular techniques (Mansfield & Hagler, 2016) to evaluate relative rates of herbivore and carrion consumption by predators.

Plant trichomes are typically considered to be detrimental to herbivorous and carnivorous arthropods (Levin, 1973; Riddick & Simmons, 2014), but recent research has begun untangling the intricacies of arthropod–plant interactions on these complex plant surfaces. Our efforts contribute to the growing body of literature demonstrating that specialist predators thrive on these typically treacherous plants, taking advantage of alternative food resources found on the phylloplane. Although the importance of alternative food for predators is understood, empirical studies with such resources are predominantly limited to plant tissues (van Baalen *et al.*, 2001; Wäckers *et al.*, 2005). Arthropod carrion is a type of PPF made available due to plant morphology, similar to pollen and fungus (Roda *et al.*, 2003; Pozzebon & Duso, 2008). Future efforts recognising and assessing the importance of different forms of alternative foods and their interactions with plants could improve the study of predator–prey dynamics.

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