Sticky plant traps insects to enhance indirect defence

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Abstract

Plant-provided foods for predatory arthropods such as extrafloral nectar and protein bodies provide indirect plant defence by attracting natural enemies of herbivores, enhancing top-down control. Recently, ecologists have also recognised the importance of carrion as a food source for predators. Sticky plants are widespread and often entrap and kill small insects, which we hypothesised would increase predator densities and potentially affect indirect defence. We manipulated the abundance of this entrapped insect carrion on tarweed (Asteraceae: Madia elegans) plants under natural field conditions, and found that carrion augmentation increased the abundance of a suite of predators, decreased herbivory and increased plant fitness. We suggest that entrapped insect carrion may function broadly as a plant-provided food for predators on sticky plants.

Keywords

Enemy free space, glandular trichomes, indirect defense, omnivory, scavenging.

INTRODUCTION

Extensive research has characterised the types of plant-provided foods used by predators (Wäckers et al. 2005) such as pollen (Salas-Aguilar & Ehler 1977; Wheeler 2001), extrafloral nectar (Janzen 1966; Bentley 1977; Heil et al. 2001) and protein bodies (Janzen 1966). In addition to these non-prey food sources, carrion has recently been proposed as a ubiquitous and important resource for predators (Wilson & Wolkovich 2011). Plant trichomes commonly entrap loosely associated invertebrates – ‘tourists’ (Moran & Southwood 1982; Southwood 1986), which die and become high-quality food sources for scavenging arthropods able to move on the sticky plant surface (Wheeler & Schaefer 1982; Southwood 1986; Anderson & Midgley 2002; Sugiu & Yamazaki 2006). The goal of our study was to test whether entrapped carrion functions as a plant-provided food for defence by enhancing indirect defence by scavenging predators.

Sticky plants are common – 20–30% of vascular plants are estimated to produce glandular trichomes (Duke 1994) and many more produce hooked trichomes. These trichomes are typically considered direct defences against herbivory (Levin 1973), but are thought to incur indirect costs by suppressing top-down control by predators, probably by diminishing their foraging efficacy (Eisner et al. 1998; Gassmann & Hare 2005). However, some of the few well-studied arthropods commonly found on sticky plants in nature (e.g. green lynx spiders, dicynphine plant bugs, stilt bugs, assassin bugs) can move across the sticky plant surfaces without becoming entrapped (Wheeler 2001; Voigt et al. 2007; Romero et al. 2008). Further, many are known to consume both living and dead prey items (Southwood 1973; Romero et al. 2008). Thus, we hypothesised that the benefits of attracting sticky plant-adapted predators for defence by producing glandular and hooked trichomes that entrap carrion (Figs. 1, 2) could outweigh the costs of excluding certain generalist predators.

MATERIALS AND METHODS

We experimentally augmented carrion on tarweed (Asteraceae: Madia elegans), an annual plant native to CA and OR. We then measured the responses of (1) predator abundance and diversity, (2) herbivore damage and (3) plant lifetime fitness. At our study site, tarweed’s major herbivore is the specialist caterpillar Heliothis diminutiva (Grote), which feeds largely on plant reproductive organs (Fig. 1) and can completely sterilise its host plants. The suite of predators commonly found on tarweed includes the assassin bug Preliopus spinicollis (Champion) (Fig. 1), two stilt bugs Hoplitus echinatus (Uhler) (Fig. 1) and Jalysus wickhami Van Duzee, the green lynx spider Peucetia sp. and the crab spider Mecaphesa schlegleri (Schick). All can navigate tarweed’s sticky surface.

Study site

This study was conducted in an oak savannah and chaparral community within Stebbins Cold Canyon Nature Reserve, Solano Co, CA., a part of the University of California Natural Reserve System (North 38.50, West 122.10.28). The dominant members of the plant community include blue oak (Quercus douglasii), grey pine (Pinus sabiniana), toyon (Heteromeles arbutifolia), poison oak (Toxicodendron spp), manzanita (Aroniaaptos growing spp.), buck brush (Ceanothus cuneatus), tarweed (M. elegans, Madia gracilis), California yerba santa (Eridericytis californicum) and gum plant (Grindelia camporum).

The plant

Common tarweed (M. elegans) is an annual flowering plant in the family Asteraceae. In Cold Canyon, it is very sticky, producing abundant glandular trichomes. It generally emerges in the spring and flowers in mid-late summer, from approximately June through September.

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The herbivore

Tarweed’s major herbivore in Cold Canyon is the noctuid moth *H. diminutiva*. Eggs are deposited primarily on developing buds and the caterpillars feed mostly on reproductive parts of the plant. Early and mid-instar larvae tend to develop inside flower buds. Single caterpillars are capable of sterilising entire tarweed plants by consuming all of their flowers and buds.

The predators

We encountered five abundant species of predatory arthropod on tarweed: the assassin bug *P. spinicollis*, two stilt bugs *H. echinatus* and *J. wickhami*, the crab spider *M. schlingeri* and the lynx spider *Peucetia*. *P. spinicollis* nymphs and adults are highly mobile, and can be observed feeding both on *H. diminutiva* caterpillars and on insect carrion under natural field conditions. We observed *H. echinatus* scavenging on insect carrion in the field, but have not observed it preying upon live insects; little is known about the ecology of this bug. *J. wickhami* is a predator of Lepidoptera (Jackson & Kester 1996), although we did not observe it feeding. *M. schlingeri* was observed feeding on early instar *H. diminutiva* caterpillars in the field. Although we did not observe *Peucetia* feeding, *Peucetia* spp. consume carrion and live prey items varying in size and taxonomic composition and are known to associate with glandular plants across broad geographical ranges (Vasconcellos-Neto et al. 2007).

Glandular trichomes

\[ \text{Glandular trichomes} \xrightarrow{+} \text{Carriion} \xrightarrow{+} \text{Predator abundance} \xrightarrow{-} \text{Herbivore damage} \xrightarrow{-} \text{Plant fitness} \]

*Figure 2* Hypothesised interactions connecting glandular trichomes to plant fitness via carrion entrapment, increased predator abundance and reduced herbivory. The directions of the expected interactions are shown as +/- . The expected indirect effect of carrion addition on plant fitness is shown with a dashed line. Other indirect effects, such as trophic cascades, are expected to occur but not depicted in the flowchart for simplicity.

Experimental design

*Carrion-addition experiment*

To manipulate carrion availability we selected 82 plants in a natural field and randomly assigned them to experimental (5 *Drosophila* spp.
fruit flies added per week) and control treatments (no fruit flies added) (Online Supplementary Information). Our addition of 5 fruit flies fell well within the natural variation of carrion on tarweed, which ranged from 0 to 40 entrapped insects per observation and averaged 2.6. The experiment was initiated in early June, prior to colonisation by adult assassin bugs and moths, and continued until plants senesced in September. As tarweed is a small plant, we were able to count all arthropods and, for some species, their eggs, as well as plant reproductive organs on all plants each week. Additionally, we recorded the number of chewed buds as a measure of caterpillar damage, and the number of successfully dehisced fruits as a measure of plant fitness; since tarweed is an annual that does not reproduce clonally, changes in fruit production are likely to have strong fitness and population consequences. We also estimated the density of secreting glandular (viscid) trichomes and abundance of naturally entrapped carrion on all plants each week.

The carrion-addition experiment was established on June 7, 2011 as a complete randomised design where half of 82 M. elegans plants were randomly assigned to either control or carrion addition treatments. Each week through July, five freeze-killed fruit flies (Drosophila spp.) were placed onto the glandular trichomes of each carrion augmented plant. Throughout the season, plants were monitored weekly to measure the abundance of carrion (experimentally and naturally entrapped), plant growth (# buds and flowers), herbivore damage to buds and predator abundance (including P. spinicollis eggs, H. echinatus adults, nymphs and eggs, J. wickhami adults and nymphs, and the spiders Penetia sp. and M. schlingeri). How sticky a plant is depends both on the number of glandular trichomes it bears and the extent to which they are actively secreting exudates. To capture a functional combination of these two characteristics, we recorded rank-order estimates between 0 and 5 for each plant based on natural variation in viscid (actively secreting) trichome density each week (Online Supplementary Information). For all analyses, we condensed weekly field observations into season-wide measurements on each M. elegans plant (Online Supplementary Information).

Caterpillar addition experiment

On July 15, 2011, we set up an additional experiment aimed at quantifying the impact of herbivory on plant fitness in this system. We selected 14 pairs of additional plants and randomly assigned them to experimental (one caterpillar added, without any cage) and control (no caterpillar added) treatments. In the first week of the experiment, two plants were lost for reasons that could not be attributed to caterpillar feeding, resulting in 12 control and 14

Figure 3 (3a–b): Results from carrion-augmentation experiment. Carrion increases predator abundance, reduces herbivory and increases plant fitness. (a) Carrion attracts predators. The effects of experimentally added carrion to M. elegans plants on the abundance of four types of predatory arthropod: the assassin bug P. spinicollis (df = 1,80; P < .001), spiders P. viridus and M. schlingeri (df = 1,80; P = .01), the stilt bug H. echinatus (eggs: df = 1,80; P = .004; nymphs and adults: df = 1,80; P < .001) and the stilt bug J. wickhami (df = 1,80; P = .006). P. spinicollis was recorded as egg deposition on plants over the season. Spiders and J. wickhami were recorded as adult and nymph encounters over the season. H. echinatus was recorded as eggs, adults and nymphs over the season. Predatory arthropods were surveyed on 41 control and 41 carrion-augmented plants. Asterisks denote a significant effect of carrion addition (*P < 0.1, *P < 0.05, **P < 0.01, ***P < 0.001). (b) Carrion decreases herbivore damage and increases plant fitness. The effects of experimentally added carrion to M. elegans plants on herbivore damage to plant buds caused by H. diminutiva caterpillars and plant lifetime fitness, as measured by total dehisced fruits produced. Plant damage and fitness were surveyed on 41 control and 41 carrion-augmented plants. Asterisks denote a significant effect of carrion addition (*P < 0.1, *P < 0.05).
caterpillar-augmented plants. These plants were scored each week in the same way as in the carrion-addition experiment.

RESULTS

The addition of 5 dead fruit flies (carrion) to plants each week over the growing season increased the abundance of all surveyed predatory arthropods associated with M. elegans plants by 76% to 450% (Fig. 3a). For P. spinicollis, the most abundant predator, this effect was strongest during the early growth season in June and July (Fig. 5).

The addition of carrion to M. elegans plants produced a 60% decrease in bud damage caused by H. diminutiva, the dominant lepidopteran herbivore in this system (df = 2,69; P = 0.013, Fig. 3b), and increased lifetime fruit production by 10% (df = 2,69; P = 0.048, Fig. 3b). The number of damaged buds increased overall throughout the season as H. diminutiva abundance increased and more plants became reproductive (Fig. 6).

Plants that had higher densities of viscid trichomes tended to entrap more carrion than less viscid plants (df = 2,68; P < .001, Fig. 4a). Within the control plants, the abundance of P. spinicollis eggs was greater on plants that had more naturally entrapped

Figure 4 The density of viscid trichomes, carrion abundance and predator eggs. (a) A regression of observed natural carrion accumulation on plant viscid trichome density (stickiness) on M. elegans plants (N = 82). Entrapped carrion was counted weekly over the growing season of M. elegans, viscid trichome density was assessed at the same intervals, and both measures were integrated over the growing season. Both measures were square-root transformed prior to linear regression. (b) The relationship between naturally entrapped carrion on M. elegans control plants (N = 41) and the accumulation of P. spinicollis eggs over the growing season. The trend line shows the predicted values of a zero-inflated Poisson regression model. P. spinicollis egg observations were square-root transformed in the model but not in the Figure.

Figure 5 A time series by month showing: (a) the accumulation of P. spinicollis eggs on M. elegans plants for the carrion addition treatment (dashed line, triangles) and control treatment (solid line, circles) over the season; and (b) natural entrapment of carrion (dotted line, squares) and bud damage from herbivory (solid line, circles). Error bars are +/− SE.

Figure 6 The effect of a single experimentally added H. diminutiva caterpillar on M. elegans plants. Caterpillar addition (a) increased bud damage to plants and (b) decreased lifetime fitness, as measured by total dehisced fruits. Plant damage and fitness were surveyed on 12 control and 14 caterpillar addition plants in a paired design. Asterisks denote a significant effect of caterpillar addition (*P < 0.05, ***P < 0.001).

Plants that had higher densities of viscid trichomes tended to entrap more carrion than less viscid plants (df = 2,68; P < .001, Fig. 4a). Within the control plants, the abundance of P. spinicollis eggs was greater on plants that had more naturally entrapped
carrion (df = 1,34; P < .0001, Fig. 4b). The abundances of other predators were too low to assess temporal trends or correlations with naturally entrapped carrion on control plants. On average, we recorded 2.6 pieces of naturally entrapped carrion per plant each week. Natural carrion entrapment by plants remained fairly constant throughout the season, though it peaked in July (Fig. 5).

In a separate experiment, we added a single H. diminutiva caterpillar to M. elegans plants to quantify the impact of herbivory on plant fitness. Plants with a caterpillar experienced 50% more bud damage than control plants (df = 14,11; P = 0.02, Fig. 6), and lifetime fruit production fell by 50% (df = 14,11; P < 0.001, Fig. 6).

**DISCUSSION**

Our results show that carrion entrapment by plants can enhance top-down control of herbivores by increasing the densities of their natural enemies. This indirect defence is not species-specific: experimental plants attracted 5 species of predatory bugs and spiders. Given the widespread distribution of glandular and hooked trichomes across flowering plants and the ubiquity of scavenging by predators, we suggest that carrion is a widespread type of plant-provided food for predators. This could help to explain why glandular plants are so abundant, which is at odds with the conventional view that stickiness is costly in the presence of predators (Eisner et al. 1998; Gassmann & Hare 2005). When protein is costly for plants to produce, carbon-rich glandular exudates or hooked trichomes – ‘tourist’ traps – could be a relatively cheap means of providing protein-rich foods for predators.

Although nectar and other well-known plant-provided foods for predators are produced directly by plants, insect carrion is captured from the external environment. This changes the resource economics of plant defence since the nutritional quality of the plant-provided food is separate from the cost of producing it. Nectar tends to be very nutrient-poor, which can make plant bodyguards more effective predators by fuelling them with carbohydrates while depriving them of proteins they need to get from herbivores of the plant (Ness et al. 2009). As insect carrion is high in protein, the particular mechanisms resulting in herbivore suppression on tarweed as a result of carrion provisioning are likely to differ from systems where nectar is provisioned. Future research is needed to determine whether fear or actual predation is the key mechanism at work.

Our study shows that the costs that plants incur from trichomes stemming from the exclusion of some generalist predators (e.g. lacewings Gassmann & Hare 2005, lady beetles Eisner et al. 1998, parasitoids Price et al. 1980) can be offset by benefits from the increase in sticky plant-adapted arthropods attracted to the carrion resources (e.g. assassin bugs Berenger & Plat-Sigwalt 1997, stilt bugs Wheeler & Schafer 1982, dichypinid mirid bugs Wheeler 2001 and lynx spiders Vasconcellos-Neto et al. 2007). This indirect benefit has been proposed for certain tropical plants with resident lynx spiders (Romero et al. 2008; Morais-Filho & Romero 2010), but has never been tested. Our study is the first to test the effects of entrapped carrion availability on predator abundance, herbivore damage and plant fitness. Importantly, our study demonstrates that diverse groups of predatory arthropods are involved in the protective mutualism. Invertebrate carrion provided by sticky plants may be a broadly important but previously unrecognised form of indirect plant defence.

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**AUTHOR CONTRIBUTIONS**

B.A.K. designed the study, assisted with fieldwork and wrote the manuscript. I.S.P. contributed to the experimental design, assisted with fieldwork, conducted the statistical analyses, prepared Figures and wrote the original results and Online Supplementary Information. Both authors discussed the results and commented on the manuscript.

**REFERENCES**


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