The siren song of a sticky plant: Columbines provision mutualist arthropods by attracting and killing passerby insects

E. F. LoPresti,[1,4] I. S. Pearse,[2] and G. K. Charles[3]

[1]*University of California–Davis, Department of Entomology, One Shields Avenue, Davis, California 95616 USA*
[2]*Illinois Natural History Survey, 1816 South Oak Street, Champaign, Illinois 61820 USA*
[3]*University of California–Davis, Department of Plant Biology, One Shields Avenue, Davis, California 65616 USA*

Abstract. Many plants provide predatory arthropods with food or shelter. Glandular trichomes entrap insects and may provision predators with insect carrion, though it has not been clear whether this putative benefit functions with natural amounts of carrion, whether plants actively attract insect "tourists," and how common this provisioning system is. We tested the hypothesis that a sticky columbine (*Aquilegia eximia*: Ranunculaceae) attracts passerby arthropods (a siren song leading them to their demise); that these entrapped arthropods increased predators on the plant; and that these predators reduced damage to the plant. Sticky traps baited with columbine peduncles entrapped more arthropod carrion than unbaited control traps. Predator abundance correlated positively with carrion abundance observationally, and experimental removal of carrion reduced predator numbers. Experimental removal of carrion also increased damage to reproductive structures, likely due to reductions in predator numbers. This indirect defense may be common; we compiled a list of insect-trapping sticky plants that includes over 110 genera in 49 families, suggesting a widespread convergence of this trait, even in non-carnivorous plants. The ubiquity of this trait combined with these experiments suggest that carrion entrapment should be viewed as a common and active process mediated by the plant for indirect defense.

Key words: Aquilegia eximia; *carrion; columbine; herbivory; indirect defense; sticky plant; tritrophic interaction.*

Introduction

Plants often enlist helpers, mutualistic arthropods, to aid in defense against herbivores, pathogens, and competitors (Janzen 1967, Heil 2008). Examples include acacias, which provide shelter and food bodies to ants, which deter herbivory (Madden and Young 2002) and *Viburnum* species, which provide domatia and extrafloral nectar to predatory and mycophagous mites (Weber et al. 2012). Recent evidence suggests that arthropod carrion adhered to plant surfaces also provisions mutualistic predators (Ellis and Midgley 1996, Anderson 2005, Sugiura and Yamazaki 2006, Romero et al. 2008, Krimmel and Pearse 2013; Appendix A). Carrion provisioning usually begins with an adhesive surface, composed of glandular or hooked trichomes, which entraps insects (in addition to other functions of the trichomes). Predatory arthropods may seek out this carrion ephemerally or remain on plants with a reliable carrion food source. Predators then either repel (a nonconsumptive effect) or kill (a consumptive effect) herbivores. Thomas (1988) found that eliminating the sticky trap significantly reduced the abundance of the most common predator on *Cirsium discolor* (Aster-

aceae), but not on *Penstemon digitalis* (Plantaginaceae). In the most extensive test of this defense, Krimmel and Pearse (2013) demonstrated each of these links experimentally by adding insect carrion to *Madia elegans* (Asteraceae), and Romero et al. (2008) convincingly demonstrated predator-mediated herbivore reduction on a sticky plant.

Two observations suggest that carrion provisioning of predators may be a common indirect plant defense. First, numerous predatory arthropods have a strong association with sticky glandular plants. Many of these arthropods complete their life-cycle on these plants, feeding at several trophic levels: on the plant, entrapped carrion, herbivores of the plant, and other predators (e.g., Bérenger and Pluot-Sigwalt 1997, Anderson 2005, Romero et al. 2008, Voigt and Gorb 2008, Wheeler and Krimmel 2015). Second, a trend toward predator enrichment on carrion-covered plants has been shown in true carnivorous plants such as *Pinguicula* (Zamora 1990), and non-carnivorous plants such as the South African genus *Roridula* (Ellis and Midgley 1996, Anderson 2005), a glandular rhododendron (Sugiura and Yamazaki 2006), and a South American bromeliad (Gonçalves et al. 2011). In both the bromeliad and *Roridula* systems, at least some of predator enhancement benefit comes from nutrients supplied by their feces (Ellis and Midgley 1996, Gonçalves et al. 2011), though predators may also protect the plant from herbivores in

these systems. While carrion acts as a potent provision to predators in certain systems, the frequency of this indirect defense remains unknown.

Currently, the strongest evidence supporting carrion-mediated indirect defense in plants comes from experiments that artificially added carrion to plants (Krimmel and Pearse 2013) or comparisons among plant species that entrap or do not entrap carrion (Romero et al. 2008). Natural variation in glandularity and carrion abundance exists in and among individuals and populations of sticky plants (Krimmel and Pearse 2014), though it is unknown whether the natural amount of carrion on a plant enhances indirect defense above conspecifics that fail to trap carrion (or trap little).

Whether glandular plants actively attract and entrap insects or act as passive sticky traps is similarly unknown. Arthropods caught by carnivorous plants do not differ in abundance and identity from a simple passive trap (Ellison and Gotelli 2009), suggesting no attraction (but see Shaefer and Ruxton 2008). Although untested, many authors suggest this same passive entrapment in non-carnivorous species (Sutherst et al. 1982, Eisner et al. 1998, Suguira and Yamakazi 2006). Indeed, non-interacting arthropods are referred to as "tourists" (Krimmel and Pearse [2013] after the terminology in Moran and Southwood [1982]), suggesting little involvement with the plant (though creating a literal "tourist trap"). On the other hand, plants actively attract arthropods with volatile signals in a number of interactions including pollination (Raguso and Pichersky 1995) and defense by attraction of parasitoids (Van Poecke et al. 2001); this suggests a small evolutionary hurdle to attracting arthropods with which to provision predators. Because plants may benefit from carrion indirectly, we hypothesized that plants might actively attract these small arthropods, much like sirens, figures of classic mythology who lured sailors to their deaths with sweet songs.

We conducted a study on an herbaceous, glandular columbine (*Aquilegia eximia*: Ranunculaceae) and conducted a literature survey of carrion entrapment by plants in order to establish (1) if columbine peduncles attract non-interacting arthropods, which become carrion, (2) whether carrion entrapped by sticky columbine enhances indirect defense, and (3) whether carrion entrapment is common among plants that are not known to be carnivorous.

METHODS

System

Serpentine columbine, *Aquilegia eximia* (Ranunculaceae), grows in seeps and wet areas of California's northern coast range (Baldwin et al. 2012). At the University of California Davis's McLaughlin Reserve in Lake County, California, USA, columbine foliage grows from perennial rootstock in late winter, bolts in the spring, and flowers until the early fall; hummingbirds and bees visit the hanging red flowers. Peduncles, leaves,

petioles, buds, flowers, and fruit of the plants are extremely sticky and by June are covered by carrion of a variety of arthropods numbering up to several hundred on a single peduncle (Fig. 1D; E. F. LoPresti, *personal observation*; Appendix B). The primary herbivore on the columbine is *Heliothis phloxiphaga* (Lepidoptera: Noctuidae), a common polyphagous caterpillar that feeds primarily on the reproductive structures (buds, flowers, and fruit) of a variety of glandular plants at the site. A variety of omnivores, scavengers, and predators live on the plants (Fig. 1), the most common being a stilt bug, *Hoplinus echinatus* (Heteroptera: Berytidae), an assassin bug, *Pselliopus spinicollis* (Heteroptera: Reduviidae), a mirid, *Tupiocoris californicus* (Heteroptera: Miridae) and a crab spider, *Mecaphesa schlingeri* (Thomisidae). All true bugs were observed scavenging on entrapped carrion and we also observed consumed eggs of *Heliothis* and *Pselliopus* on the plants.

Attraction experiment

To determine whether the entrapped arthropods found on columbine peduncles were actively attracted to the plant by volatile cues, or had incidentally landed on the plant, we covered 9-cm diameter petri dishes with plastic mesh and placed inside three 5-cm sections of columbine peduncle, plus a single leaf, or nothing as a control. We coated the plastic mesh in a thin layer of Tanglefoot (ConTech; Victoria, British Columbia, Canada), which, in conjunction with the plastic mesh itself, effectively eliminated visual cues of the columbine. We placed the petri dishes along the side of a small meadow (38.858848° N, 122.432340° W) where columbines naturally grow, alternating treatments for maximum interspersion. We spaced the petri dishes >1 m from each other and >5 m from any columbines. After 24 hours, we assessed the number of arthropods (>1 mm) caught on the surface of the plastic mesh. Over the course of nine sampling nights between 13 July and 6 August, we placed 258 traps consisting of equal numbers of both treatments each trial. One trap was blown over and removed from the study.

Carrion reduction experiment

To determine whether carrion mediated an indirect defense with predators, we conducted a carrion removal experiment on an isolated population of columbine (38.861694° N, 122.430288° W). On 2 July 2014, we marked 50 plants, alternating between two treatments. The first treatment was a carrion reduction, where we removed all arthropod carrion of ~1 mm or larger from the entire peduncle with a pair of fine-tipped forceps. The second group was a control, which we handled as in the manipulated group, but from which we did not remove any carrion. We repeatedly applied these treatments to the plants (9, 17, 22, and 31 July, 6, 17, and 25 August, 1, 8, and 19 September; treatments not reapplied the last two dates), each time recording the number of carrion (except at set-up) and predators, and

Reports

Reports

Fig. 1. (A–G) Arthropods entrapped on diverse sticky plants. (A) *Antirrhinum cornutum* (Scrophulariaceae), Lake County, California, USA. (B) *Mimulus layneae* (Phyrmaceae), Lake County, California, USA. (C) *Madia glomerata* (Asteraceae), Nevada County, California, USA. (D) *Aquilegia eximia* (Ranunculaceae), Lake County, California, USA. (E) *Boerhavia* unknown sp. (Nyctaginaceae), Lambayeque, Peru. (F) *Arctostaphylus viscida* (Ericaceae), Lake County, California, USA. (G) *Petunia* x *hybrida* domestic (Solanaceae), Yolo County, California, USA. (H–K) Common arthropods of columbine. (H) *Heliothis phloxiphaga* and characteristic florivory. (I) *Tupiocoris californicus* nymph. (J) *Hoplinus echinatus* nymph. (K) Two just-hatched *Pselliopis spinicollis* and their eggs. All photos: E. F. LoPresti.

the number and status (damaged [any chewing damage] or undamaged) of all reproductive structures (flower buds, flowers, fruit) on the plant.

Statistical analysis

We performed all analyses and prepared all figures in R version 3.0.2 (R Foundation for Statistical Computing 2013) using package lme4 (Bates et al. 2014). For all statistical analyses, we checked data for oversdispersion and employed Poisson (for count data), negative binomial (for overdispersed count data), or binomial error distributions when appropriate. All reported means include standard error.

We performed two main analyses in our study. First we tested whether columbine volatile cues attracted arthropods. We evaluated the impact of columbine presence on arthropod count data using a generalized linear mixed-effect model (GLMM) with a Poisson error distribution. Our response variable was count of arthropods entrapped over a 24-hour period, with the

PLATE 1. More insect-entrapping plants, clockwise from top left: sticky flower buds of *Erica* sp. (Ericaceae), UC–Santa Cruz Arboretum, California; *Micranthes californicus* (Saxifragaceae), McLaughlin Reserve, Yolo County, California; *Mentzelia* sp. (Loasaceae), Arches National Park, Utah; *Salvia spathaceae* (Lamiaceae), UC–Davis Arboretum, Yolo, California; *Cerastium* sp. (Caryophyllaceae), Parque Nacional Altos de Lircay, Chile; *Leucheria* sp. (Asteraceae), Parque Nacional Altos de Lircay, Chile; *Boerhavia diffusa* (Nyctaginaceae), Santiago, Chile. Photo credits: top left, W. Krimmel; all others, E. F. LoPresti.

independent variable of columbine presence or absence. Since we ran multiple traps each day and did this several times, we used date of trapping as a random effect with varying intercept.

Our second set of analyses quantified the effects of experimental carrion removal on predator abundance and damage to reproductive structures. We modeled the treatment effect of carrion removal on predator abundance using a GLMM with a negative binomial error and date as a random effect with varying intercept. When considering the growing season as a whole we calculated the mean predator abundance over all sampling dates, and we tested for an effect of carrion removal using a GLM with a quassipoisson error distribution (as means were not integers). We checked for non-additivity between observation date and treatment by considering observation date as a continuous fixed factor and checked its interaction with treatment, which was a nonsignificant interaction with predator abundance.

To measure the effect of carrion removal on risk of damage to a given reproductive structure, we used a binomial response of either intact or damaged. We used a binomial GLMM with treatment and date as predictor variables, with plant ID as a random effect with a variable intercept. We allowed the slope of the treatment effect to vary by date. We checked for non-additivity between observation date and treatment by considering observation date as a continuous fixed factor and checking for its interaction with treatment. For damage to reproductive structures, a significant interaction was detected. We therefore assessed the effect of carrion removal treatment on reproductive structure damage for each observation date.

RESULTS

Survey of carrion-entrapping plants

Many taxonomically unrelated plants (over 110 genera in 49 families) entrap arthropods on adhesive surfaces (Table 1, Fig. 1, Appendix A). A small subset of these plants utilize this resource directly as carnivores, absorbing nutrients from the carrion (e.g., the sundews, *Drosera*; Chase 2009). Another subset absorb nutrients from entrapped arthropods, either directly or indirectly, but are not considered carnivorous (Spomer 1999). However, most carrion-entrapping plants are not known to benefit directly from nutrients absorbed from carrion. Natural history observations from the published literature and the authors' experiences with other sticky plants are summarized in Appendix A.

Reports

TABLE 1. Plants that are known to entrap arthropods on adhesive surfaces.

Family	Genera
Anacardiaceae	*Rhus*[49]
Asteraceae	*Ageratina*[86], *Arnica*[5], *Brickellia*[6], *Cirsium*[8], *Daubatia*[9], *Grindelia*[76], *Haplopapus*[11], *Helichrysum*[62], *Hemizonia*[77], *Hieracium*[12], *Holocarpha*[79], *Hulsia*[80], *Kyhosia*[78], *Layia*[13], *Lessingia*[75], *Leucheria*[7], *Madia*[50], *Senecio*[68], *Trichogoniopsis*[15]
Boraginaceae	*Eriodictyon*[17]
Brassicaceae	*Capsella*[36]
Bromeliaceae	*Vriesea*[4]
Byblidaceae	*Byblis*†[16]
Calceolariaceae	*Calceolaria*[51]
Cannabaceae	*Cannabis*[60]
Caryophyllaceae	*Cerastium*[5,52], *Dianthus*[81], *Holosteum*[81], *Lychnis*[81], *Silene*[10], *Spergularia*[33], *Stellaria*[5]
Cephalotaceae	*Cephalotus*[16]
Cleomaceae	*Cleome*[26]
Cucurbitaceae	*Sicana*[61]
Dioncophyllaceae	*Triphyophyllum*†[16]
Droseraceae	*Drosera*†[26,67]
Drosophyllaceae	*Drosophyllum*†[26]
Ericaceae	*Arctostaphylos*[50], *Befaria*[20], *Comarostaphylis*[21], *Erica*[22,67], *Kalmia*[66], *Rhododendron*[23]
Euphorbiaceae	*Croton*[40], *Dalechampia*[41]
Fabaceae	*Adesmia*[53], *Cajanus*[59], *Chapmannia*[37], *Ononis*[68], *Phaseolus*‡[63], *Schizolobium*[38], *Stylosanthes*[39]
Geraniaceae	*Geranium*§[5], *Pelargonium*[16]
Grossulariaceae	*Ribes*[5]
Haemodoraceae	*Wachendorfia*[3]
Lamiaceae	*Origanum*[28], *Salvia*[28]
Lentibulariaceae	*Genlises*†[26], *Pinguicula*†[16]
Limeaceae	*Limeum*[34]
Loasaceae	*Eucnide*‡[18], *Mentzelia*‡[19]
Lythraceae	*Cuphea*[48], *Lythrum*[67]
Malvaceae	*Abutilon*[43], *Gossypium*[17], *Hermannia*[44]
Martyniaceae	*Ibicella*[27], *Martynia*[16], *Proboscidia*[26]
Melastomataceae	*Bellucia*¶[45]
Nyctaginaceae	*Abronia*[55], *Allionia*[35], *Anulocaulis*[47], *Boerhavia*[50], *Mirabilis*[10,67], *Pisonia*[26], *Plumbago*[26]
Orobanchaceae	*Castilleja*[5], *Parentucellia*[56]
Passifloraceae	*Passiflora*[16]
Paulowniaceae	*Paulownia*[30]
Phyrmaceae	*Mimulus*[5,50]
Plantaginaceae	*Antirrhinum*[50], *Penstemon*[5,82], *Stemodia*[31]
Polemoniaceae	*Allophyllum*[24], *Collomia*[57], *Gilia*[5], *Microsteris*[58], *Navarretia*,[84] *Polemonium*[25]
Primulaceae	*Primula*[16]
Proteaceae	*Protea*[65]
Ranunculaceae	*Aquilegia*[50]
Rhamnaceae	*Ceanothus*[46]
Roridulaceae	*Roridula*§[26]
Rosaceae	*Drymocallis*/*Potentilla*§[5], *Rosa*[5]
Sapindaceae	*Aesculus*[67]
Saxifragaceae	*Heuchera*[5], *Micranthes*[69], *Saxifraga*[67]
Scrophulariaceae	*Euphrasia*[74], *Lyperia*[32], *Verbascum*[70]
Solanaceae	*Calibrachoa*[71], *Datura*[64], *Hysocyamus*[26], *Nicotiana*[67], *Petunia*[5,50], *Salpiglossus*[72], *Solanum*[5,54], *Schizanthus*[73]
Stylidiaceae	*Stylidium*†[16]
Tofieldiaceae	*Tofieldia*[2]
Verbenaceae	*Glandularia*[1]

Notes: This table does not include other methods of arthropod entrapment, e.g., pitchers. Table references (footnote numbers) and natural history literature and observation comprise Appendix A.

† Carnivorous, sensu Spomer (1999).

‡ Hooked, not glandular, entrapping trichomes.

§ Protocarnivorous, sensu Spomer (1999).

¶ *Rhycanthera* in citation, synonymy unclear in the Integrated Taxonomic Information System at www.ITIS.gov.

Carrion attraction experiment

Petri dishes baited with columbine peduncles entrapped ~21% more arthropods than controls (Poisson mixed model, date as a random effect, coefficient of treatment, $z = -2.22$, $P = 0.026$; sample size, control = 129, columbine = 128). Because the mesh visually obstructed the columbine, this effect was likely due to a volatile cue of the columbine peduncles.

Carrion reduction experiment

The mean number of predators encountered per check was 74% higher in controls than on carrion-removal plants (Fig. 2; negative binomial model, likelihood ratio test, $\chi^2 = 13.54$, $P < 0.001$). Reproductive structures (flowers, flower buds, and fruits) of carrion-removed plants were more likely to sustain damage than those of control plants, especially in the

latter half of the season (Fig. 2). Carrion removal the increased the chance of damage to reproductive structures. The odds of reproductive structures being damaged was 121% higher (95% CI, 6–391%) in the carrion removal treatment than in the control group (binomial mixed model, likelihood ratio test, $\chi^2 = 8.2$ $P = 0.04$,), which likely accounted for the marginally higher seeds per fruit found in the control group (Appendix C). However, in an initial test with both sampling date and carrion removal as fixed effects, we found that the effect of treatment depended on sampling date (date × treatment interaction, quassi-poisson mixed model, $t_{1, 151} = 2.301$, $P = 0.02$). Therefore, we looked for an effect of carrion removal on each sampling date, and found that carrion removal increased the probability of damage to reproductive structures in the final five observation dates, but not in the first five (Fig. 2).

DISCUSSION

Many diverse plants entrap arthropods on their surfaces (Table 1, Fig. 1; see Plate 1); this experiment demonstrated a "siren song" indirect defense of one of these plants. Columbines attracted and entrapped usually noninteracting, neither herbivore nor predatory, arthropods, which increased predator presence on plants and reduced damage to the plant. Direct attraction of natural enemies of herbivores using volatile cues is a common defense strategy in plants (Kessler and Heil 2011); luring in non-interacting arthropods has not been reported previously for non-carnivorous plants. Past studies have relied on species comparisons or carrion addition to suggest carrion-mediated indirect defense (Romero et al. 2008, Krimmel and Pearse 2013). Observationally, predators correlated with carrion abundance in a natural population (Appendix D) and in our experiment natural carrion abundance caused indirect resistance, suggesting that carrion provisioning operates with amounts of carrion observed in the field. We suggest that this siren song, attraction of tourist arthropods, provisions beneficial natural enemies in order to retain their predator services.

Predators reduced damage in the experiment, though there was a lag between the time when damage was initiated and when an effect of the carrion-removal treatment was detected (Fig. 2 and Appendix D). We believe that the natural history of the herbivores caused this lag. *Heliothis phloxiphaga* has more than one generation a year; the individuals of the first generation seemed to escape predation by provisioned predators, probably because these predators feed on eggs and small larvae, and these herbivores were already large when we initiated carrion treatments. Carrion provisioning did reduce later herbivore damage, caused by second generation *H. phloxiphaga*. We did not test whether consumptive or nonconsumptive effects of the predators (Thaler and Griffin 2008) caused the reduction in herbivory. Predators may have deterred the
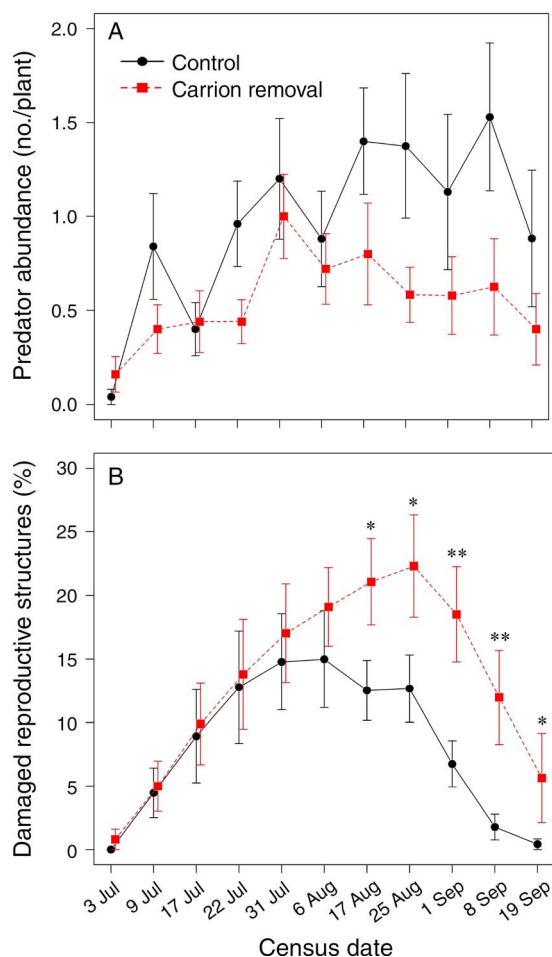

FIG. 2. (A) Predator abundance on columbines with experimentally removed carrion and on controls with natural carrion abundance over the growing season. (B) Percentage of reproductive structures damaged on columbines with experimentally removed carrion and controls with natural carrion abundance over the growing season. Values are means ± SE. Asterisks (* and **) indicate a significant increase in damage at that observation date due to carrion removal at $P < 0.05$ and $P < 0.01$, respectively.

mobile caterpillars from feeding on a plant, deterred ovipositing female moths or consumed eggs and early-instar larvae.

In other systems, glandular trichomes act as a costly direct defense against herbivores (Hare et al. 2003) and impede the efficacy of predators (Eisner et al. 1998). While we did not explicitly test the effect of stickiness (our experiment manipulated only carrion) the experimental results suggest that these specialized predators are effective bodyguards on this plant; an exudate removal experiment, which also removed carrion, found the same results (Appendix E). The same suite of predators are found on other glandular plants in the same habitat including *Madia* (Krimmel and Pearse 2013), and glandular *Arctostaphylos*, *Hemizonia*, *Holo-*

Reports

Reports

carpha, *Calycidenia*, *Cordelanthus*, *Castilleja*, *Mimulus*, *Trichostema*, and *Grindelia* near the columbine populations (E. F. LoPresti, *personal observation*). This suggests this suite of predators are generalist feeders that are associated with glandular plants (Wheeler and Krimmel 2015), and may act in similar ways on all these plants.

Insect entrapment has evolved repeatedly in plants (Table 1). The phenomenon of insect entrapment is common, but rarely reported. Roughly 50% of genus-level records of carrion entrapment in Table 1 are new to the literature, suggesting that the list of carrion-entrapping plants is vastly incomplete. Anecdotally, a brief trip to Chile by E. F. LoPresti added nine genera to this list, suggesting a great deal more await discovery, even in well-studied locations. The list includes many economically important horticultural and crop genera such as *Petunia* and *Nicotiana*, suggesting that this type of indirect defense may be applicable to pest management in agricultural systems (Krimmel 2014). In most of the listed genera, insect entrapment is a derived feature found in one or few species, often within large, widely distributed genera (e.g., Asteraceae: *Cirsium discolor*; Lamiaceae: *Salvia* spp., Phyrmaceae: *Mimulus* spp.), though, in some cases, the trait is likely basal to several genera (e.g., Asteraceae: Madiinae: *Kyhosia*, *Madia*, *Holocarpha*, *Hemizonia*). The great majority of insect-entrapping plants have not been examined for this indirect resistance, and the simple methodology presented here could be easily adapted to many other systems. Adaptations to locomotion on sticky plants occur in various groups of arthropod predators worldwide (Romero et al. 2008, Voigt and Gorb 2008, Wheeler and Krimmel 2015). Glandular trichomes serve a variety of functions (LoPresti 2015). Carrion entrapment and this indirect defense may not be the selective agent responsible for the evolution of this trait, and its benefit may be totally incidental. Further research should directly examine fitness correlates as in Krimmel and Pearse (2013) to build a stronger adaptive case for entrapment. In combination, the commonness of insect entrapment (Table 1), and experimental evidence from four model systems: predator enrichment on thistle (Illinois, Asteraceae; Thomas 1988), predator enrichment and damage reduction in: columbine, (California, Ranunculaceae; present study), *Trichogoniopsis* (Brazil, Asteraceae; Romero et al. 2008), and tarweed (California, Asteraceae; Krimmel and Pearse 2013) suggest that carrion provisioning is phylogenetically and geographically widespread.

In what may be a common indirect interaction in plants, columbines attracted and entrapped small arthropods, which either attracted or retained predators, reducing herbivore damage on carrion-covered plants. The two prior tests of this indirect defense (Romero et al. 2008, Krimmel and Pearse 2013) were on asters; this current experiment suggests a similar strategy in a columbine. This was the first experiment demonstrating that non-carnivorous sticky plants attract carrion, a novel yet logical extension of beneficial predator attraction to the carrion. We suggest that this indirect defense strategy should be accepted as a normal consequence of stickiness in plants despite the deterrence of generalist predators (Eisner et al. 1998, Hare et al. 2003, but see Krimmel and Pearse 2014) and there exists an entire guild of phylogenetically and geographically diverse predators on sticky plants (Romero et al. 2008, Krimmel and Pearse 2013, Wheeler and Krimmel 2015).

LITERATURE CITED

Anderson, B. 2005. Adaptations to foliar absorption of faeces: a pathway in plant carnivory. Annals of Botany 95:757–761.

Baldwin, B., and D. H. Goldman, editors. 2012. The Jepson manual: vascular plants of California. University of California Press, Berkeley, California, USA.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2014. lme4: linear mixed-effects models using Eigen and S4. R package version 1.1-6. http://CRAN.R-project.org/package=lme4

Bérenger, J., and D. Pluot-Sigwalt. 1997. Special relationships of certain predatory Heteroptera Reduviidae with plants. First known case of a phytophagous Harpactorinae. Comptes Rendus de l'Académie des Sciences—Series III—Sciences de la Vie 320:1007–1012.

Chase, M. 2009. Murderous plants: Victorian Gothic, Darwin and modern insights into vegetable carnivory. Botanical Journal of the Linnean Society 161:329–356.

Eisner, T., M. Eisner, and E. R. Hoebeke. 1998. When defense backfires: detrimental effect of a plant's protective trichomes on an insect beneficial to the plant. Proceedings of the National Academy of Sciences USA 95:4410–4414.

Ellis, A., and J. Midgley. 1996. A new plant–animal mutualism involving a plant with sticky leaves and a resident hemipteran insect. Oecologia 106:478–481.

Ellison, A. M., and N. J. Gotelli. 2009. Energetics and the evolution of carnivorous plants— Darwin's "most wonderful plants in the world." Journal of Experimental Botany 60:19–42.

Gonçalves, A. Z., H. Mercier, P. Mazzafera, and G. Q. Romero. 2011. Spider-fed bromeliads: seasonal and interspecific variation in plant performance. Annals of Botany 107:1047–1055.

Hare, J. D., E. Elle, and N. M. van Dam. 2003. Costs of glandular trichomes in *Datura wrightii*: a three-year study. Evolution 57:793–805.

Heil, M. 2008. Indirect defence via tritrophic interactions. New Phytologist 178:41–61.

Janzen, D. 1967. Interaction of the bull's-horn acacia (*Acacia cornigera* L.) with an ant inhabitant (*Psuedomyrmex ferruginea* F. Smith) in eastern Mexico. University of Kansas Science Bulletin 47:315–558.

Kessler, A., and M. Heil. 2011. The multiple faces of indirect defences and their agents of natural selection. Functional Ecology 25:348–357.

Krimmel, B. A. 2014. Why plant trichomes might be better than we think for predatory insects. Pest Management Science 70: 1666–1667.

Krimmel, B. A., and I. S. Pearse. 2013. Sticky plant traps insects to enhance indirect defence. Ecology Letters 16:219–224.

Krimmel, B. A., and I. S. Pearse. 2014. Generalist and sticky plant specialist predators suppress herbivores on a sticky plant. Arthropod–Plant Interactions 8:403–410.

LoPresti, E. F. 2015. Chemicals on plant surfaces are a heretofor unrecognized, but ecologically-informative, class for investigations into plant defense. Biological Reviews *in press*. http://dx.doi.org/10.1111/brv.12212

Madden, D., and T. P. Young. 1992. Symbiotic ants as an alternative defense against giraffe herbivory in spinescent *Acacia drepanolobium*. Oecologia 91:235–238.

Moran, V., and T. Southwood. 1982. The guild composition of arthropod communities in trees. Journal of Animal Ecology 51:289–306.

R Development Core Team. 2013. R version 3.0.2. R Foundation for Statistical Computing, Vienna, Austria. www.R-project.org

Raguso, R., and E. Pichersky. 1995. Floral volatiles from *Clarkia breweri* and *C. concinna* (Onagraceae): recent evolution of floral scent and moth pollination. Plant Systematics and Evolution 194:55–67.

Romero, G., J. Souza, and J. Vasconcellos-Neto. 2008. Anti-herbivore protection by mutualistic spiders and the role of plant glandular trichomes. Ecology 89:3105–3115.

Schaefer, H. M., and G. D. Ruxton. 2008. Fatal attraction: carnivorous plants roll out the red carpet to lure insects. Biology Letters 4:153–155.

Spomer, G. G. 1999. Evidence of protocarnivorous capabilities in *Geranium viscosissimum* and *Potentilla arguta* and other sticky plants. International Journal of Plant Sciences 160:98–101.

Sugiura, S., and K. Yamazaki. 2006. Consequences of scavenging behaviour in a plant bug associated with a glandular plant. Biological Journal of the Linnean Society 88: 593–602.

Sutherst, R., R. Jones, and H. Schnitzerling. 1982. Tropical legumes of the genus *Stylosanthes* immobilize and kill cattle ticks. Nature 295:320–321.

Thaler, J. S., and C. A. Griffin. 2008. Relative importance of consumptive and non-consumptive effects of predators on prey and plant damage: the influence of herbivore ontogeny. Entomologia Experimentalis et Applicata 128:34–40.

Thomas, P. A. 1988. The function of insect-trapping by *Penstemon digitalis* and *Cirsium discolor*. Dissertation. University of Illinois at Urbana-Champaign, Champaign, Illinois, USA.

Van Poecke, R., M. Posthumus, and M. Dicke. 2001. Herbivore-induced volatile production by *Arabidopsis thaliana* leads to attraction of the parasitoid *Cotesia rubecula*: chemical, behavioral, and gene-expression. Journal of Chemical Ecology 27:1911–1928.

Voigt, D., and S. Gorb. 2008. An insect trap as habitat: cohesion-failure mechanism prevents adhesion of *Pameridea roridulae* bugs to the sticky surface of the plant *Roridula gorgonias*. Journal of Experimental Biology 211:2647–2657.

Weber, M. G., W. L. Clement, M. J. Donoghue, and A. A. Agrawal. 2012. Phylogenetic and experimental tests of interactions among mutualistic plant defense traits in *Viburnum* (Adoxaceae). American Naturalist 180:450–463.

Wheeler, A. G., and B. A. Krimmel. 2015. Miridae (Hemiptera: Heteroptera) as sticky-plant specialists: adaptations, interactions and ecological implications. Annual Review of Entomology 60:393–414.

Zamora, R. 1990. Observational and experimental study of a carnivorous plant-ant kleptobiotic interaction. Oikos 59:368–372.

Supplemental Material

Ecological Archives

Appendices A–E are available online: http://dx.doi.org/10.1890/15-0342.1.sm

Reports