

Oak Galls Exhibit Ant Dispersal Convergent with Myrmecochorous Seeds

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Submitted June 24, 2021; Accepted January 24, 2022; Electronically published June 15, 2022

ABSTRACT: Ants disperse oak galls of some cynipid wasp species similarly to how they disperse seeds with elaiosomes. We conducted choice assays in field and laboratory settings with ant-dispersed seeds and wasp-induced galls found in ant nests and found that seed-dispersing ants retrieve these galls as they do myrmecochorous seeds. We also conducted manipulative experiments in which we removed the putative ant-attracting appendages (“kapéllos”) from galls and found that ants are specifically attracted to kapéllos. Finally, we compared the chemical composition and histology of ant-attracting appendages on seeds and galls and found that they both have similar fatty acid compositions as well as morphology. We also observed seed-dispersing ants retrieving oak galls to their nests and rodents and birds consuming oak galls that were not retrieved by ants. These results suggest convergence in ant-mediated dispersal between myrmecochorous seeds and oak galls. Based on our observations, a protective advantage for galls retrieved to ant nests seems a more likely benefit than dispersal distance, as has also been suggested for myrmecochorous seeds. These results require reconsideration of established ant-plant research assumptions, as ant-mediated seed and gall dispersal appear strongly convergent and galls may be far more abundant in eastern North American deciduous forests than myrmecochorous seeds.

Keywords: *Aphaenogaster*, cynipid, convergent evolution, *Kokkocynips*, myrmecochory, woodlands.

Introduction

Ant-mediated seed dispersal (myrmecochory) is a well-described cosmopolitan interaction in which ants retrieve seeds to their nests (Gorb and Gorb 2003; Rico-Gray and

Oliveira 2007; Warren and Giladi 2014). In some cases, granivorous ants seek seeds as forage, but myrmecochory (sensu stricto) involves plants with seeds that have an appendage (elaiosome) that prompts omnivorous scavenging ants to retrieve them to subterranean nests, where they remove the elaiosome but leave the seed intact. Myrmecochory was first documented in 1906, and the elaiosome was described as an oily appendage that acted both as a food reward and as a handle well suited for ant mandibles (Sernander 1906; Beattie 1985). As it turns out, elaiosomes contain a suite of lipids that attract ants (Gammans et al. 2005; Fischer et al. 2008; Miller et al. 2020). The advantage for plants in attracting seed-dispersing ants remains debated, with the major potential benefits being distance (i.e., decreased density dependence) and/or protection from seed predators, fire, and pathogens (Warren and Giladi 2014; Tarsa et al. 2018).

Phasmid insects also appear to take advantage of ant foraging by producing an appendage (capitulum) that prompts egg retrieval by ants in much the same manner as elaiosomes prompt seed retrieval (Compton and Ware 1991; Hughes and Westoby 1992a). The phasmid egg capitulum was first described in 1898 (Sharp 1898), but the convergent interaction with ants was not recognized until decades later (Hughes and Westoby 1992a; Stanton et al. 2015). Some observers have noted that ants retrieve fallen *Kokkocynips* oak galls (Lyon 1970; Eiseman 2011) and found oak galls in ant nests (Warren et al. 2015). Whereas some wasp species induce oak galls that secrete “nectar” in exchange for ant protection (Stone et al. 2002; Aranda-Rickert et al. 2017; Nicholls et al. 2017), nectar-secreting galls remain arboreal, whereas elaiosomes and capitula fall to the ground—as do *Kokkocynips* galls. Moreover, arboreal ant species that are attracted to nectar are, mostly, a different

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group than the omnivorous ants attracted to elaiosomes and capitula.

We investigate the convergent interaction between oak galls and ants that parallels elaiosome- and capitulum-based dispersals. Two cynipid wasps, *Kokkocynips decidua* and *K. rileyi*, induce oak galls that also produce an appendage (hereafter, καπέλλο [“kapéllo”]; pronunciation *kapelo*; Greek for “cap”) that attracts ants and prompts retrieval after galls detach from trees and fall to the ground. Elaiosomes are phenotypes of the plants that produce them, whereas oak galls are extended phenotypes of cynipid wasps that induce the tumorlike growths in plants. Kapéllos are further extensions of these extended phenotypes, as the wasps ap-

pear to induce the plant to form an additional gall structure (paralleling elaiosomes and capitula) that attracts ant dispersers. The objective of our study was to investigate whether ant-mediated gall dispersal converges with ant-mediated seed dispersal (fig. 1). We asked whether seed-dispersing ants are attracted to oak galls as they are to myrmecochorous seeds, whether that attraction is driven by kapéllos, whether the galls are retrieved to ant nests, and whether myrmecochorous seeds and oak galls have similar chemical and histological compositions. We addressed these questions through field and laboratory observations and experiments and through chemical analysis of kapéllos and elaiosomes.

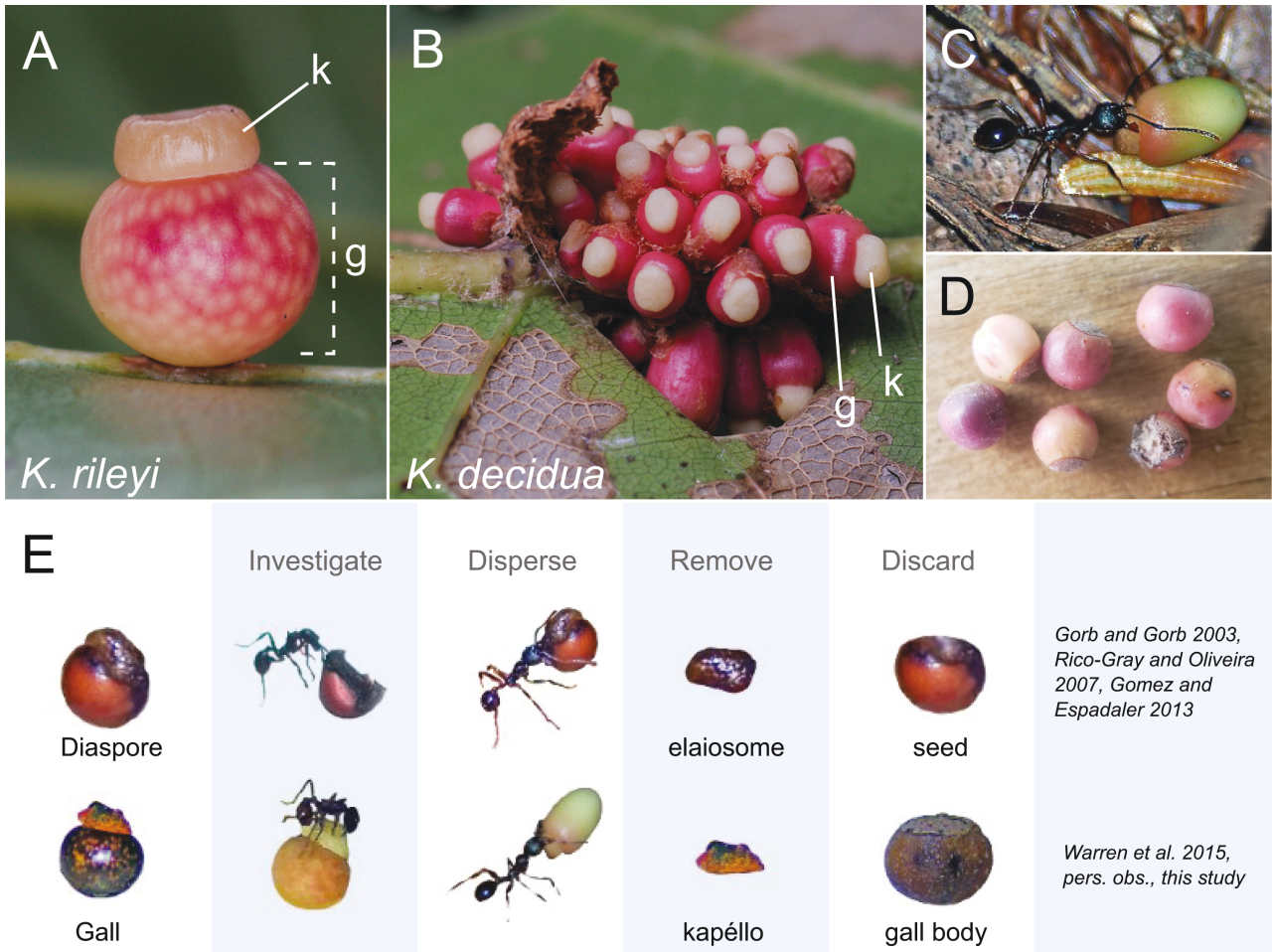


Figure 1: Evolutionary convergence in interactions between *Kokkocynips rileyi* and *K. decidua* galls and ants and myrmecochorous seeds. The galls of *K. rileyi* (A) and *K. decidua* (B) grow on midveins of *Quercus rubra* leaves (gall; g) and are topped by an ant-attracting tissue (we name “kapéllo”; k). C, *Aphaenogaster* sp. transporting *K. decidua* gall by holding the kapéllo. D, *K. rileyi* galls collected in an ant nest (kapéllos are absent, presumably removed by the ants). E, Comparison between oak gall dispersal and myrmecochory. For both seeds and oak galls, ants investigate the item, focusing respectively on the elaiosome (seed) or kapéllo (gall); pick it up and retrieve the item back to their nest, usually using the elaiosome or kapéllo as a handle that fits in their mandibles; remove the elaiosome or kapéllo; and discard or store the seed or gall intact. Photo credits: A, B, A. Guiguet; D, A. R. Deans; C, E, R. J. Warren II.

Methods

Study Species

Kokkocynips rileyi (Ashmead, 1896) and *K. decidua* (Beutenmueller, 1913), both formerly considered in *Dryocosmus*, are oak gall wasps (Hymenoptera, Cynipidae, Cynipini) that are closely related but not sister taxa (Nicholls et al. 2018; Nieves-Aldrey et al. 2021). There are approximately 1,000 described cynipid wasps, tiny parasites that typically oviposit into oak meristematic tissues (i.e., *Quercus*; Espírito-Santo and Fernandes 2007; Ronquist et al. 2015). Species of tribe Cynipini typically induce galls on one or a few closely related oak species, and their distributions (mostly within Asia, Europe, and North America) track their hosts at evolutionary timescales (Stone et al. 2002, 2009). Ovipositing females, eggs, and larvae prompt plant tissue to lyse and then grow, tumorlike, around developing insect larvae. Eggs are usually deposited in spring. Galls grow during summer and detach from leaves in the fall; wasps are presumed to emerge from galls early in spring after 1 or 2 years (Weld 1959; R. J. Warren II, A. Guiguet, C. Mokadam, J. F. Tooker, and A. R. Deans, personal observations).

For comparison between gall and seed dispersal, we focused on *Aphaenogaster* ants, the most common ants, by number and biomass, in eastern deciduous forests (Ness et al. 2009; Lubertazzi 2012; King et al. 2013). Whereas several ant genera will pick up myrmecochorous seeds, *Aphaenogaster* are the most effective seed dispersers in this range, typically collecting 75% of available seeds (Ness et al. 2009; Warren et al. 2014).

Field Observations

As part of other studies, we observed intact *K. rileyi* galls (sans kapéllos) in nine *Aphaenogaster picea* (Wheeler, W.M., 1908) colonies at seven locations in Western New York and three *Aphaenogaster* sp. colonies at one site in central Pennsylvania. These galls were similar to previous observations in the southern Appalachian Mountains (Warren et al. 2015). In addition to observing ant/gall interactions at our bait stations, we also set up video cameras to capture additional animal/gall interactions. Rodents eat seeds with elaiosomes (Heithaus 1981; Ness and Bressmer 2005), so we included nocturnal videos.

Field Cafeteria Experiment

On September 19 and 26, 2020, we established 10 seed/gall bait stations at Franklin Gulf County Park (Collins, NY; 42.606, -78.908) in a mixed deciduous forest stand (video S1, available in the Dryad Digital Repository [<https://doi.org/10.5061/dryad.9ghx3ffk2>; Warren et al.

2022]). On each date, we placed ten 4 × 4-cm polystyrene weighing dishes on the forest floor at 10-m intervals and added to each dish 10 *Sanguinaria canadensis* L. seeds and 10 *K. rileyi* galls. We monitored the bait stations and surrounding area for 90 min for dispersing ants. We purchased *S. canadensis* seeds from Prairie Moon Nursery (Winona, MN), whereas we collected *K. rileyi* galls in September 2020 from localities in Stormstown (40.797, -77.956) and Pine Grove Mills (40.730, -77.884), Pennsylvania. The seeds and galls were used within 14 days of procurement or collection and stored at 4°C before being placed in the field.

We treated each bait station as a replicate ($n = 10$) and each sampling date as a block ($n = 2$). Seed/gall removal was analyzed as a function of bait type (seed or gall) and block (sampling date) using a generalized linear model (GLM) assuming a quasi-Poisson error distribution (as the data were overdispersed; $\phi = 4.2$). We evaluated the GLM terms using analysis of deviance, a maximum likelihood approach using an analysis of variance model with a χ^2 test. We also included a bait × block interaction term to test whether bait preference varied by sampling date.

Laboratory Cafeteria Experiment 1

In September 2020, we placed five *A. picea* workers from five different colonies in each of five 100 × 20-mm polystyrene petri dishes to assess ant interest in myrmecochorous seeds and galls with kapéllos. We allowed ants to acclimate for 10 min and then added 10 *S. canadensis* seeds and 10 *K. rileyi* galls to each petri dish. We immediately started video recording each dish to quantify ant/bait interactions for 60 min. We quantified interactions using an ordinal index modified from Culver and Beattie (1978) to score ant interest in seeds and galls: (1) antennate—ant investigates seed or gall with antennae; (2) inspect—ant more thoroughly examines bait with mandibles; and (3) pickup—ants picks up or moves bait.

For the laboratory cafeteria experiments, we used a cumulative link mixed model to analyze the ant interest index (ordinal data) as a function of bait (seed or gall) using the ordinal package (Christensen 2019) in the R statistical program (ver. 3.5.1; R Development Core Team 2020). Cumulative link models employ a regression framework that treats ordinal data as categorical but recognizes that the data are ordered. Given that there were repeated measures within each petri dish, we included dish identity as a random effect to account for autocorrelation.

Laboratory Cafeteria Experiment 2

In October 2020, we used a similar laboratory experimental design with *K. decidua* galls (which senesce from

oak leaves about 1 month after *K. rileyi*) in three treatments: entire gall, gall body with kapéllo removed, and kapéllo with body removed. We also included entire *Andricus dimorphus* (Beutenmüller, 1913) galls as a control (these similarly sized and shaped galls have no kapéllos and are distantly related to *Kokkocynips*). Five *A. picea* ants from five colonies were added to five petri dishes and acclimated, and then 10 each of the galls and gall parts were added; we then videotaped ant behavior for 60 min. We collected the *K. decidua* galls in September 2020 in New Hampshire (Lincoln; 44.041, –71.680) and Pennsylvania (Halfmoon Township; 40.785, –77.989).

Data and statistical code underlying the field and laboratory experiments have been deposited in the Dryad Digital Repository and Zenodo (<https://doi.org/10.5061/dryad.9ghx3ffk2>; Warren et al. 2022).

Chemical Analysis

Elaiosome chemistry is well studied and strongly influences ant attraction and effectiveness of seed dispersal. Seed-dispersing ants appear to prefer elaiosomes that contain fatty acids, particularly oleic acid, which attracts ants and initiates dispersal (O'Dowd and Hay 1980; Brew et al. 1989). Because free fatty acids (FFAs) can be the most abundant and critical form of fatty acids for ant dispersal (Lanza et al. 1992; Miller et al. 2020), we used gas chromatography (GC) to measure them in galls, their kapéllos, and the elaiosomes and seeds of two common myrmecochorous plant species, *S. canadensis* and *Asarum canadense* L. (each was analyzed separately). Using previously described methods (Schmelz et al. 2004), we extracted FFAs from galls of *K. rileyi* and their kapéllos and from elaiosomes and seeds of *S. canadensis* and *A. canadense* (four to six replicates per tissue type) and converted them to methyl esters. We quantified the abundance of fatty acid methyl esters on the basis of an internal standard (500 ng octadecane sample⁻¹) with GC equipped with a flame ionization detector, confirming the identity of compounds by comparing retention times to those of pure standards and spectra produced via GC coupled with mass spectrometry.

Histology

Cross sections of galls of *K. decidua* and *K. rileyi* were cut with a surgical scalpel and fixed with 2.5% paraformaldehyde and 0.4% glutaraldehyde in phosphate-buffered saline. After dehydration in a graded series of ethanol, samples were embedded in LR White resin (London Resin Company). Semithin sections (1 μ m) were obtained and stained with toluidine blue O 0.1% (w/v in water). Images were as-

sembled using the MosaicJ plug-in of ImageJ (Thévenaz and Unser 2007).

Results

Field Observations

We frequently observed on oak leaves *Kokkocynips* galls that naturally fall to the ground; we did not observe any ant species “tending” them before they fell to the ground. We also observed *Aphaenogaster picea* workers retrieve *Kokkocynips* galls to their nests in Western New York and central Pennsylvania, and we found intact *Kokkocynips* galls (i.e., not visibly damaged) in *A. picea* nests in both Western North Carolina (Warren et al. 2015) and Western New York (this study). In all cases, kapéllos were removed. We also used video traps that captured rodents and birds eating galls (with kapéllos intact) that were not dispersed by ants (Deans 2021).

Field Cafeteria Experiment

We observed *A. picea* ants remove from stations as many *Kokkocynips rileyi* galls as *Sanguinaria canadensis* seeds, suggesting no difference in ant preference (table S2, pt. A [table S2 is available in the Dryad Digital Repository; <https://doi.org/10.5061/dryad.9ghx3ffk2>; Warren et al. 2022]; fig. 2A). There also was no difference in removal between sampling dates nor an interaction between bait and sampling data (table S2, pt. A).

Laboratory Cafeteria Experiment 1

We observed 94 interactions between *A. picea* ants and *K. rileyi* galls and 48 interactions between ants and *S. canadensis* seeds. Ants interacted with galls and seeds similarly, suggesting no difference in ant interest (table S2, pt. B; fig. 2B). We also observed that in gall interactions ants focused on kapéllos (vs. gall bodies) 64% of the time and that in seed interactions ants focused on elaiosomes (vs. seed bodies) 42% of the time.

Laboratory Cafeteria Experiment 2

In the second laboratory experiment, we observed 36 interactions between *A. picea* workers and *Andricus dimorphus* (control) galls, 95 interactions with *Kokkocynips decidua* gall bodies (kapéllos removed), 58 interactions with *K. decidua* kapéllos (bodies removed), and 109 interactions with entire *K. decidua* galls. Ant interest did not differ between control galls and *K. decidua* with kapéllos removed, but ant interest was greater for *K. decidua* kapéllos than the control as well as greater for entire *K. decidua* galls than the control (table S2, pt. C; fig. 2C).

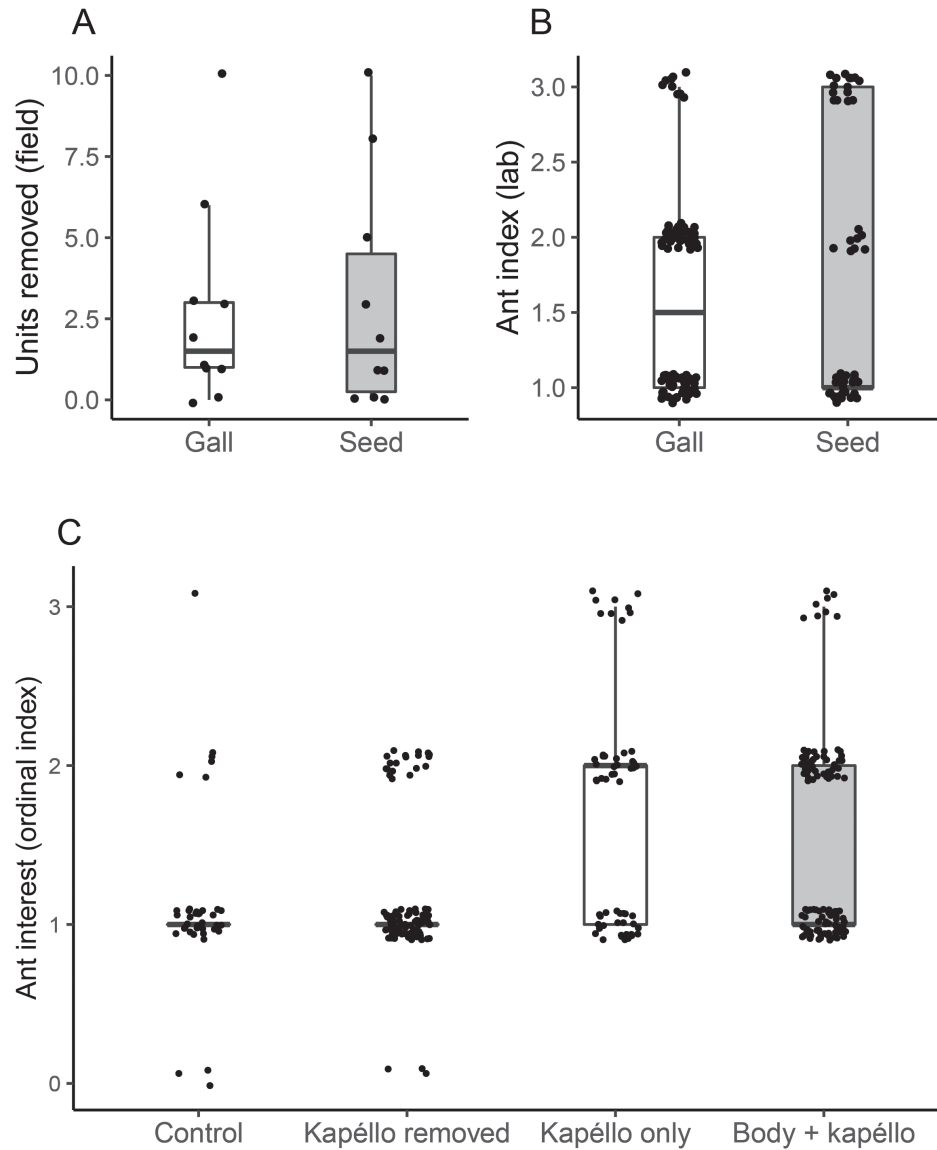


Figure 2: Results of the cafeteria experiments. A, B, Experiment 1: boxplots showing *Aphaenogaster picea* ant removal of *Kokkocynips rileyi* galls and *Sanguinaria canadensis* seeds from field bait stations (A) and *A. picea* interest (ordinal index) in *K. rileyi* galls and *S. canadensis* seeds in laboratory behavioral assays (B). In both cases, ants were as likely to remove (A) or show interest in (B) galls as they were seeds. C, Experiment 2: boxplots showing *A. picea* ant interest (ordinal index) in *Andricus dimorphus* galls (no kapéllos), *K. decidua* galls with kapéllos manually removed, *K. decidua* kapéllos with gall body removed, and entire *K. decidua* galls in behavioral choice experiments in which all were placed together in laboratory bait stations. There was little ant interest (and hence little variance) in the control galls and *K. decidua* galls with kapéllos removed, and ant interest in these did not differ. The ants exhibited much greater interest in *K. decidua* kapéllos and *K. decidua* galls with kapéllos than the control.

Chemical Analysis

Kapéllos and galls of *K. rileyi* contained a subset of the FFAs found in elaiosomes and seeds of *S. canadensis* and *Asarum canadense* (table 1). Notably, kapéllos and elaiosomes contained substantial amounts of lauric, palmitic, oleic, and stearic acids (table 1), the latter three of which

are known to mediate attraction and preference of ants for elaiosomes.

Histology

Sections of *K. decidua* and *K. rileyi* galls (fig. 3) revealed a clear contrast between the kapéllo and the gall body: the

Table 1: Fatty acid composition of elaiosomes and seeds of *Sanguinaria canadensis* and *Asarum canadense* plants and kapéllos and galls of *Kokkocynips rileyi*

Free fatty acid	<i>S. canadensis</i>		<i>A. canadense</i>		<i>K. rileyi</i>	
	Elaiosome	Seed	Elaiosome	Seed	Kapéllo	Gall body
Lauric	2.2 ± .7	.34 ± .04	.95 ± .33	.42 ± .11	.73 ± .11	.65 ± .15
Myristoleic	d	d				
Myristic	d	d				
Palmitoleic	d	d				
Palmitic	27.2 ± 13.2	2.6 ± .4	4.4 ± 1.2	2.4 ± 1.2	2.1 ± .4	1.9 ± .53
Linoleic	d	d	d	d	d	d
Oleic	247.9 ± 151.3	56.4 ± 36.5	6.4 ± 4.6	.76 ± .08	14.0 ± 4.2	36.3 ± 27.7
Stearic	17.3 ± 9.1	1.0 ± .1	3.9 ± 1.0	1.2 ± .6	1.1 ± .2	1.0 ± .3
cis-11-eicosenoic	d	d	d	d		
Arachidic	d	d	d	d		
Heneicosanoic	d	d				
Erucic	d	d				
Behenic	d	d	d	d		

Note: The letter *d* indicates that the compound was detected, but concentrations were too low to be reliably quantified with our methods; no *d* indicates that the compound was not detected. Concentrations (mg g⁻¹; mean ± SE) are provided for lauric acid and three fatty acids (palmitic, oleic, stearic) known to be important for ant attraction. For elaiosomes and kapéllos, these fatty acids accounted for on average >94.1% (95% confidence interval: 92.6%–95.5%) of the fatty acids detected. Amounts of these fatty acids in seeds and the gall bodies are presented for context, but the key comparison is between elaiosomes and kapéllos. Even though it has not been implicated in ant attraction, lauric acid was included because it was abundant in both the elaiosomes and the kapéllos. The fatty acids are arranged in order of their retention times (earlier to later) in gas chromatography. Linoleic acid also was present in the elaiosomes and kapéllos, but more research is required to quantify its concentrations appropriately.

vacuoles of kapéllo cells stained blue whereas most gall body parenchymal cells had weak vacuole staining, suggesting that the chemical composition of the vacuoles of kapéllo cells differ from the gall body. The interface between kapéllo and gall body is highly lignified in mature galls of both species (fig. 3B, 3E). In *K. rileyi*, at early stages the interface between the kapéllo and the rest of the gall presents lines of small cells with relatively large nuclei, characteristic of procambial activity. At intermediate and mature stages, kapéllo cells contained unstained organelles absent from parenchymal cells (fig. 3C, 3D). Lignification of the interface between kapéllo and gall body is first visible at the intermediate stage (fig. 3D) and continues until the mature stage, when the entire interface is lignified (fig. 3E). A similar lignification is encountered at the interface between the seed and the elaiosome (fig. 3F–3H) (Mayer and Svoma 1998; Ciccirelli et al. 2005; González and Pabón-Mora 2017).

Discussion

Our results demonstrate a striking parallel between ant dispersal of galls and seeds. Galls of *Kokkocynips rileyi* and *K. decidua* and myrmecochorous seeds employ a distinct ant-attracting appendage that induces retrieval to ant colonies without collateral damage to seeds or galls. Indeed, parallel to experiments with seeds or phasid eggs with elaiosomes

or capitula experimentally removed (Hughes and Westoby 1992a, 1992b), our experiments with kapéllos removed from galls decisively demonstrated their role as ant attractants. These results elucidate an intriguing species interaction and raise stirring questions about a century of myrmecochory research.

Ant-dispersed seeds produce a suite of lipids (e.g., stearic, oleic, and palmitic acids) that attract ants (Gammans et al. 2005; Fischer et al. 2008; Miller et al. 2020); oak galls induced by *K. rileyi* produced kapéllos that contained a similar suite of ant-attracting fatty acids. Similarly, some phasids produce eggs with capitula that contain a similar chemical composition that is also attractive to ants (Hughes and Westoby 1992a). For *Kokkocynips* galls, kapéllos separate from gall bodies during development because of lignification at the interface with the gall body similar to how elaiosomes separate from seeds (Mayer and Svoma 1998; Ciccirelli et al. 2005). The lipids contained in elaiosomes are similar to insect hemolymph (Hughes et al. 1994; Gammans et al. 2005; Fischer et al. 2008), and dead insects attract seed-dispersing ants (Warren and Giladi 2014). Hence, the impetus for convergent evolution of elaiosomes, capitula, and kapéllos appears primed by insect scavenging by ants. Still, these are not the only ant/gall interactions that parallel other ant interactions. Many ants are attracted to sugar solutions released by plants (nectar) or soft-bodied insects (honeydew) in exchange for protection; similarly, some gall wasp species induce oak

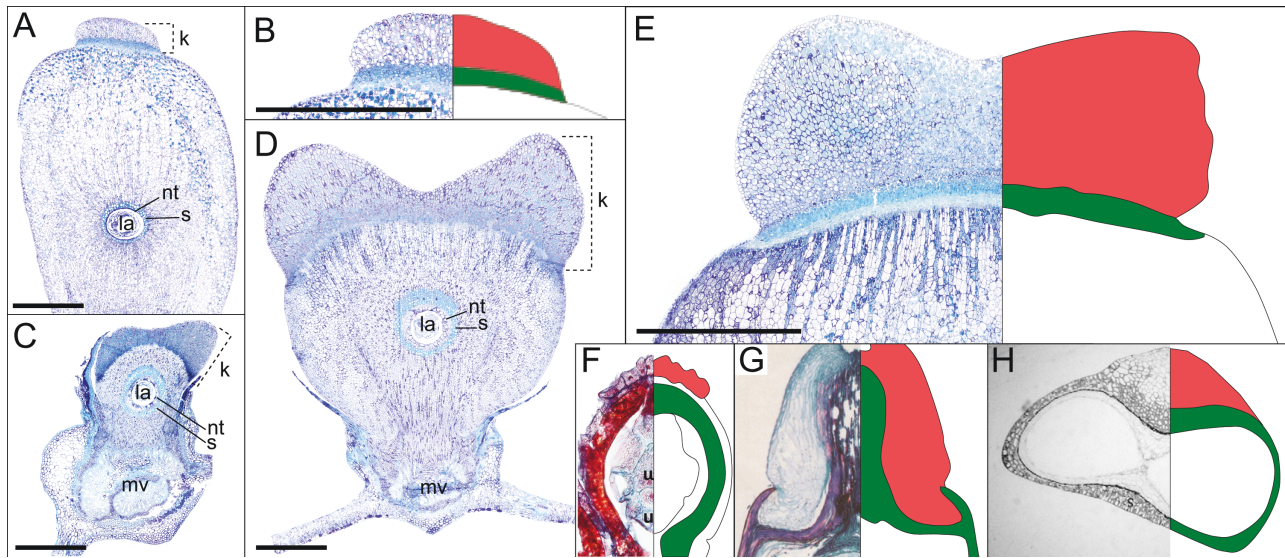


Figure 3: Compared anatomy of *Kokkocynips decidua* and *K. rileyi* galls and seeds with elaiosomes. A, Cross sections of *K. decidua* gall at mature stage. B, Detail of the kapello of *K. decidua* gall. C–E, Cross sections of *K. rileyi* galls at early stage (C), intermediate stage (D), and mature stage (E). F–H, Cross sections of seeds with elaiosomes: *Pilostyles boyacensis* (F), *Knautia dipsacifolia* (G), and *Myrtus communis* (H; modified from Mayer and Svoma 1998; Ciccarelli et al. 2005; González and Pabón-Mora 2017). Scale bars: 500 μ m (A–E). Red = kapello or elaiosome; green = sclerenchyma; k = kapello; la = larva; mv = midvein; nt = nutritive tissue; s = sclerenchyma.

galls that produce sweet liquid that is consumed by ants or other predators that protect the galls from natural enemies (Stone et al. 2002; Aranda-Rickert et al. 2017; Nicholls et al. 2017). In this regard, it is interesting to note that *K. rileyi* and *K. decidua* may be closely related to *K. attractans*, a species inducing a nectar-secreting gall (Nicholls et al. 2018).

The potential benefits for myrmecochorous plants from ant-mediated dispersal can be summarized as distance versus directed dispersal (Giladi 2006; Warren and Giladi 2014). Distance dispersal potentially provides benefit by alleviating negative parent-offspring and sibling density dependence, whereas directed dispersal benefits plants when seeds are placed in “safe” sites protected from seed predators and/or harsh environmental conditions (e.g., fire). For galls, then, distance dispersal seems an unlikely driver given that adult cynipids can fly much farther than the 0.5–2 m that ants typically carry seeds (Gómez and Espadaler 2013). That said, if senesced cynipid galls accumulate below the dripline of trees, there might be negative density consequences from optimally foraging parasitoids and gall predators.

Directed dispersal seems a more promising explanation for galler benefits because protection from natural enemies is among the driving selective forces on galls (Stone et al. 2002) and a factor favoring ant-attracting mechanisms on seeds and phasid eggs (Hughes and Westoby 1992a; Warren and Giladi 2014). For galls, parasitoids cause high mortality on developing larvae (Stone et al. 2002); whether

ant nests provide safe harbor from cynipid parasitoids is unknown, but for seeds and phasid eggs, seed predation and egg parasitism decreases when harbored inside ant nests (Hughes and Westoby 1992a; Warren and Giladi 2014). Moreover, we observed nocturnal rodents and diurnal phasianid birds eating galls with kapellos, and given that such galls are readily consumed by livestock (Kotinsky 1902; Fagan 1918), there may be a plethora of gall predators. We did not observe any indication that the dispersing ants tried to eat anything more than the kapellos, and phasid nymphs emerge from active ant nests without being harmed (Compton and Ware 1991). Whereas direct observations are lacking, adult cynipids that emerge in active ant nests may be able to cloak themselves or pacify the ants, as do an estimated 10,000 species of social parasites that safely enter and exploit ant nests using chemical mimicry, morphological similarity, and/or nectar rewards (Hölldobler and Wilson 1990; Lenoir et al. 2001; Thomas and Settele 2004). Finally, seed-dispersing ants move their nests quite often (Smallwood 1982; Warren et al. 2018) and hence might be absent during emergence of adult gall wasps one or two seasons after retrieval.

A complication for directed dispersal is that *Aphaenogaster* ants do not always keep dispersed seeds in their nests after removing elaiosomes. Indeed, more than 90% seeds can be “redispersed” outside of nests (Canner et al. 2012). As such, protection from enemies may be fleeting, although it might alleviate an initial wave of attack when

numerous galls accumulate under oaks. Another important consideration is that most myrmecochorous seeds become available in spring and summer, when ant colonies are increasing in size and activity, whereas these two species of cynipid oak galls become available in autumn, when ant colonies are slowing and preparing for winter diapause (likely deeper in the forest floor than the nest location). An additional possibility is that galls benefit from the antibiotic nature of ant nest environments. Fungal pathogens can cause mortality for gall larvae (Taper et al. 1986; Stone et al. 2002); ants, however, have glands that continually produce antimicrobial chemical compounds to protect themselves from pathogenic bacteria and fungi (Hölldobler and Wilson 1990). The secretions reduce entomopathogenic microbes and help protect plant seeds by reducing phytopathogenic fungi (Guimaraes and Cogni 2002; Tarsa et al. 2018).

Given that myrmecochory was described more than a century ago (Sernander 1906) and has received considerable research effort (Warren and Giladi 2014), it might be assumed that ant-mediated seed dispersal is the “type” interaction with phasmids and galls coming after, but that assumption may be folly for several reasons. First, we describe two wasp species that induce ant-attracting galls (*K. rileyi* and *K. decidua*), and based on gall morphology (Stone et al. 2002) we suspect that several more species may do the same. Second, myrmecochorous plants make up only about 4.5% of all plant species (Lengyel et al. 2010) and may not contribute an appreciable amount of food resources to drive ant selection (Warren et al. 2021). In contrast, oak galls can be staggeringly abundant. For example, the abundance of *K. decidua* has been so great that it was called “black oak wheat” and used to fatten livestock (Kotinsky 1902; Fagan 1918). Ant-mediated gall dispersal is a potentially widespread and abundant plant-insect interaction that may require a reevaluation of the functions and origin of ant-mediated seed dispersal.

Acknowledgments

We thank Daniel Murphy and Hugo Deans for observations of *Kokkocynips rileyi* galls in *Aphaenogaster* ant nests. This material is based, in part, on work supported by the National Science Foundation under grant DEB-1856626. Any opinions, findings, and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of the National Science Foundation. We also thank Edmund D. Brodie III and two anonymous reviewers for constructive and complete critiques of the manuscript. The authors declare no competing interest.

Statement of Authorship

R.J.W., A.R.D., J.F.T., A.G., and C.M. designed and performed the research; R.J.W. analyzed the data and wrote the manuscript; and A.R.D., J.F.T., A.G., and C.M. reviewed and edited the manuscript.

Data and Code Availability

The data generated and analyzed for the current study and the R software code are available in the Dryad Digital Repository and Zenodo (<https://doi.org/10.5061/dryad.9ghx3ffk2>; Warren et al. 2022).

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Natural History Editor: Edmund D. Brodie III



Aphaenogaster picea carrying a *Kokkocynips rileyi* (oak wasp gall) by its petiole through eastern deciduous forest ground litter at Franklin Gulf Park (Collins, NY). Photo credit: Robert Warren.