Sex-biased herbivory in Jack-in-the-pulpit (*Arisaema triphyllum*) by a specialist thrips (*Heterothrips arisaemae*)

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Abstract: We document through observational, correlative, and experimental studies evidence of sex-biased herbivory in the gender-labile, functionally dioecious plant, Jack-in-the-pulpit (*Arisaema triphyllum*). Jack-in-the-pulpit is the host for a specialist thrips, *Heterothrips arisaemae*. Second instar larvae of this thrips feed on the abaxial surface of Jack-in-the-pulpit leaves. We found that the level of herbivory by *H. arisaemae* was dependent on the gender expressed by plants. Significantly more damage was found on leaves of male plants than on leaves of female and asexual plants. Concentration of total phenols and nitrogen concentrations of leaf tissue did not explain different herbivory levels between genders. Spathe removal significantly reduced thrips damage, particularly in male plants. Our results suggests that adult feeding behavior and developmental phenologies of *H. arisaemae* are major factors in determining the observed patterns of male-biased herbivory in Jack-in-the-pulpit, rather than differences in levels in defensive chemicals or nutritional quality of leaf tissue. *Heterothrips arisaemae* was the most common insect in Jack-in-the-pulpit spathes, and male plants consistently contained significantly more adult thrips and thrips eggs than female flowers. Adult *H. arisaemae* carried more pollen than any than other insects and appeared to be the primary pollinator for Jack-in-the-pulpit at our study sites.

Key words: *Arisaema triphyllum*, C:N ratio, developmental phenology, herbivory, *Heterothrips arisaemae*, Jack-in-the-pulpit, nitrogen, phenolics, pollen, sex-biased herbivory, thrips

Introduction

Dioecious plants offer an opportunity to examine the susceptibility of male vs. female reproductive function to herbivory and the differential effects of herbivory on each sexual morph (Watson 1995). Several recent studies have compared damage by herbivores and pathogens between genders in a number of dioecious species. However, results are contradictory, and reported patterns of herbivory and attack by pathogens vary from male-biased (e.g., Danell et al. 1985, Ågren 1987, Elmqvist et al. 1988. Polhemus 1988, Alliende 1989, Jing & Coley 1990, Krischik & Denno 1990, Boecklen & Hoffman 1993, Wolfe 1997), to female-biased (Graetz 1981, Lovett Doust & Cavers 1982, Lovett Doust & Lovett Doust 1985, Parker 1987, Oyama & Dirzo 1991, Ågren 1997), to no preference (Boecklen et al. 1994, Araujo et al. 1995, Ågren 1997). These results suggest that different mechanisms underlie gender-biased herbivory, depending on the system. Variations in the level of herbivory may be explained by differences in the palatability of target organs, such as chemical and physical defenses (Ågren 1987, Krischik & Denno 1990, Jing & Coley 1990) and nutritional qualities (e.g., Danell et al. 1985, Boecklen & Hoffman 1993) of leaves in male vs. female plants. Variation in phenology, especially leafing phenology, between genders of the host plant may concentrate the herbivores on a specific gender (Boecklen et al. 1990). As a more entomocentric explanation, morphological and functional differences in reproductive organs of dioecious plants may alter behaviors of herbivores and consequently lead to gender-biased herbivore density. For example, if adults of a herbivore utilize resources specific to a certain gender (e.g., pollen in male plants) and their larvae feed on leaves, the level of herbivory may be determined by feeding behavior in the adult stage, influenced by the reproductive functions of host plants.

The objectives of the research presented here were to determine if there are gender-related differences in levels of herbivory in Jack-in-the-pulpit (*Arisaema triphyllum*: Araceae) and, if any, to quantify levels of herbivory in this species.

Jack-in-the-pulpit is a gender-labile, functionally dioecious perennial herb, which is common in mesic, deciduous forests throughout much of eastern North America. The sexual state of a plant (i.e., male, female, and asexual) is closely related to the size of its corm, a perenneating organ of this species, with the largest individuals in a population being females (Policansky 1981, Bierzychudek 1982, Ewing & Klein 1982, Lovett Doust & Cavers 1982). Plant growth and gender, therefore, have been correlated with resource availability (e.g., soil nutrient and moisture) in the environment (Lovett Doust & Cavers 1982, Lovett Doust et al. 1986), and previous year's sex, size, seed production, and herbivory (Bierzychudek 1984). The aboveground portion of Jack-in-the-pulpit consists of a single annual ramet with one or two leaves, each with three leaflets, and an inflorescence. Female plants almost always have two leaves. Males can have either one or two leaves. Asexual plants typically have one leaf (Lovett Doust & Cavers 1982). A male or female inflorescence is enclosed in a spathe located at the end of a scape. Inside the spathe, sessile flowers occur at the base of an erect, cylindrical spadix. Male flowers appear as a cluster of dark brown anthers, while the females are a cluster of green ovaries with short stiles and fuzzy white stigmas. Subtle sexual dimorphism occurs in the external morphology of the spathe. In male plants, the spathe has a small gap, 1-2 mm in diameter, at the base of the inflorescence near the peduncle where the sides of the spathe fold together. In female plants, the spathe folds over smoothly and does not form a gap. Bierzychudek (1982) suggested that the sexual dimorphism of the spathe in Jacks vs. Jills is an adaptation to a pollinator assemblage of fungus gnats and that the gap at the base of the male spathe provides an escape route for these insects. The flowers of Jack-in-the-pulpit are visited by a number of insects, including thrips (Thysanoptera) and flies (Diptera: Mycetophilidae, Phoridae, Sciaridae). By most accounts, fungus gnats (dipterans) are assumed to be the major pollinators for this species (Bierzychudek 1982, Meeuse 1985). A specialist thrips, *Heterothrips arisaemae* Hood (Thysanoptera: Heterothripidae), is the most abundant floral visitor and also has been implicated as a pollinator for Jack-in-the-pulpit (Rust 1980). However, it had been unknown whether this specialist thrips acts as a major herbivore of Jack-in-the-pulpit. We discovered in our preliminary observations on the leaf herbivores of Jack-in-the-pulpit that larvae of *H. arisaemae* can cause serious damage to the plants in our study site.

In this paper, we examine the relationship of the thrips at different stages (i.e., adults, eggs, and larvae) with Jack-in-the-pulpit, and the levels of leaf herbivory for three genders of host plants, i.e., asexual, male, and female. We also tested two hypotheses that explain sex-biased herbivory. The first hypothesis states that the level of herbivory is determined by gender-dependent quality of leaves (Danell et al. 1985, Ågren 1987, Krischik & Denno 1990, Jing & Coley 1990, Boecklen & Hoffman 1993). To test this hypothesis, we quantified concentration of carbon (C), nitrogen (N), and total phenols in leaf tissue. This hypothesis predicts the highest levels of herbivory in the gender (asexual, male, or female) that possesses leaves with less defense and/or higher nutrition. An alternative hypothesis states that morphological and functional differences in reproductive organs of host plants lead to gender-biased herbivory (Boecklen et al. 1990). To test this hypothesis, we experimentally removed reproductive organs of male and female plants and observed changes in the levels of herbivory. To test the function of the gap at the base of the male spathe in herbivory, in females, a gap was created in the base of the spathe and in males the gap was closed. This hypothesis predicts that differences in floral morphology will result in differences in rates of herbivory.

Materials and methods

This study was conducted in southern Maryland in forests associated with the Smithsonian Environmental Research Center (SERC), Edgewater, MD, USA (N38°59′: W76° 33′), a 1000 ha long-term research site along the Chesapeake Bay. The landscape at SERC includes coastal plain forests in varying seral stages, agricultural fields, fresh and brackish water wetlands and marshes, and open estuarine waters. Several studies provide detailed descriptions of the vegetation, geomorphology, geochemistry, and hydrology of this research site (e.g., Pierce 1982, Jordan & Correll 1985, Parker 1995).

Jack-in-the-pulpit is a spring-blooming, perennial, gender-labile, functionally dioecious, perennial herb. Its perenneating organ is a corm. Although this species is typically dioecious, a small percentage of monecious individuals occur within populations (Ewing & Klein 1982, Bierzychudek 1982). However, the pollen produced by infloresences that have both male and female flowers is not fertile (Bierzychudek 1982). Jack-in-the-pulpit also may reproduce vegetatively by underground cormlets (Bierzychudek 1982).

To compare the level of herbivory among the male, female, and asexual Jack-in-the-pulpit plants, we surveyed and measured leaf damage to plants (N = 33 female, 35 male, 34 asexual) occurring in natural conditions within a 1-m wide belt transect in a closed forest at SERC. We also measured leaf area, leaf height, and basal diameter of each plant for which thrips damages were investigated. Measurements were made in early June. Leaves from each plant were harvested, and the number of damaged patches per leaf was counted. Percent leaf area damaged was determined with Image Software (NIH). We also examined each gender to determine behavior and feeding patterns of its herbivores.

To determine the insect fauna associated with inflorescences of Jack-in-the-pulpit, the spathes from 32 female and 37 male plants were collected. Each spathe was harvested and immediately sealed in a plastic bag so that none of the associated insects could escape before they could be counted. To determine the insect fauna that was carrying Jack-in-the-pulpit pollen at our study sites, we trapped flying insects on 7.5 cm × 13 cm sticky traps (N = 20), over a 24 hr period at two sites during early May 2000 and May 2001. We identified to family all insects stuck to both sides of the traps and counted the number of Jack-in-the-pulpit pollen grains adhering to their bodies. To make certain that we could distinguish pollen, we collected and identified the pollen of all plants in bloom within a 0.5 km radius around the experimental sites.

As a measure of chemical defence in Jack-in-the-pulpit leaves, we determined phenolic concentration in male, female, and asexual plants using a microFolin-Denis method (Arnold et al. 1995). Leaf tissue samples from plants randomly selected along our belt transect (N = 18 female, 20 male, 19 asexual) were harvested and immediately frozen in liquid nitrogen. For each leaf sample, approximately 100 mg of tissue were ground while still frozen and thawed in 200 µl trichloroacetic acid solution (1.2 g TCA/ml DW) to precipitate proteins. After further grinding, 1000 µl of 50% acetone were added to each sample to extract phenolic compounds. Following an extraction period of 4 h, samples were assayed for Folin-Denis positive reactants. After centrifuging, 20 µl of extract were combined with 1000 µl of 1: 10 Folin-Denis reagent (Association of Official Analytical Chemists 1970). After 3 min, 100 µl of sodium carbonate, saturated at 25°C, were added. At the end of 1 h, assay tubes were centrifuged, and the absorbance of the supernatant was read at 725 nm. Dry weights were determined by drying tissue/extract samples at 100°C to constant weight. Phenolic content in units of tannic acid equivalents (mg TAE/g dry wt) was calculated by comparison to a tannic acid standard curve.

To determine the effects of flowering and floral characteristics on herbivory, we altered floral morphology of male and female plants in a factorial experimental: sex (2) × floral characteristics (3). The three levels of floral characteristics that we manipulated were: 1) spathes were completely removed; 2) in females, a gap was created in the base of the spathe and, in males, the gap was closed; 3) control (plants were not altered), with 30 replicates, for a total of 180 plants. To create the gap in females, a 2-mm diameter circular hole was cut into the base of the spathe, just distal to the peduncle, in a position similar to the gap in male spathes. To close the gap in males, Tanglefoot® was used to seal the pre-existing opening at the base of their spathes. This experiment was set up in early May and harvested in mid-June.

We used a one-way analysis of variance (ANOVA) to look for differences in herbivory and leaf chemistry among female, male, and asexual plants. When an ANOVA found a significant effect, we used a pairwise contrast matrix to locate differences among the three genders (Systat®, Wilkinson 1990). We used Pearson's correlation to determine if there were relationships between plant size and level of thrips damage. Counts of thrips and eggs in female and male spathes were analyzed as a Kruskal-Wallis nonparametric analysis of variance. We analyzed the 2 × 3 factorial experiment in which we altered floral morphology as a two-way ANOVA. To analyze for heteroscedasticity, probability plots of all variables and ANOVA residuals were examined. For heterogeneous variances, we transformed continuous data using logarithms and transformed noncontinuous data (counts) using the square root. Proportions were transformed using arcsine-square root to correct for platykurtosis.

Results

We found a distinct pattern of herbivory on the leaves of Jack-in-the-pulpit, which was caused by the thrips *H. arisaemae.* The second instar larvae (larvae II) of this thrips fed by piercing and sucking in the mesophyll on the abaxial surface of leaves. Under low magnification, several larval thrips were observed feeding within each feeding patch. By late spring, thrips feeding patches, which were dispersed on the undersurfaces of leaves, could be seen clearly without magnification. Over the next few weeks, these patches also became visible on the adaxial leaf surface as small yellow-green to white spots (Fig. 1). By early summer, the leaf tissue above the feeding patches had died and desiccated, which caused these areas to open up to form distinct holes in the leaves. Other than the damage by larval *H. arisaemae*, we found very little evidence of any other insect herbivore's feeding on Jack-in-the-pulpit.

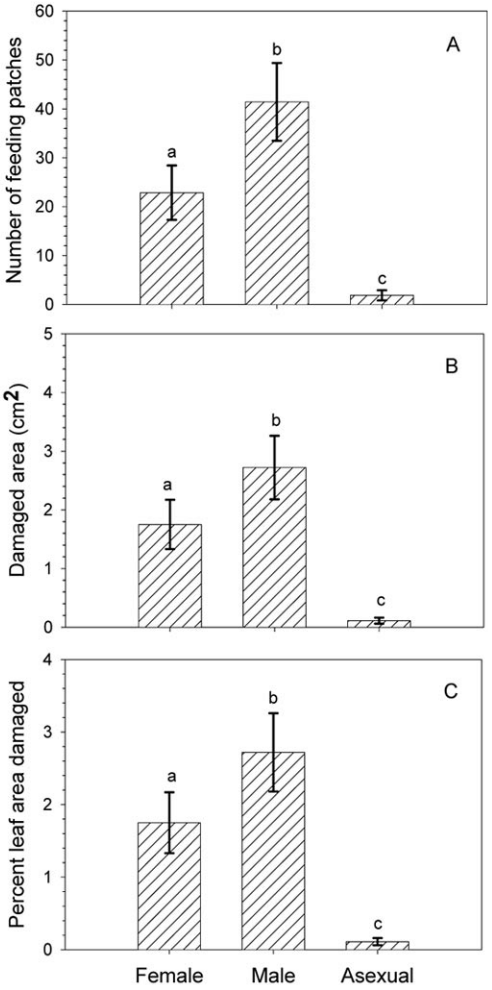
Beginning in early spring, adults of *H. arisaemae* were commonly found inside the spathes and were most abundant in male plants (Fig. 2). They were typically found crawling through the pool of pollen that collected beneath the male flowers at the base of the spadix. These tiny insects can enter a flower through the gap at the base of male spathe as well as along the slit where the spathe folds over on itself in both male and female plants. Inside male spathes, adults thrips were often observed completely covered in pollen grains and appeared to feed on pollen. Adults, eggs, and two larval instars (larvae I and II) were associated with the spathe, in particular the pollen-producing male spathe. Thrips embedded their eggs into the tissue of the inside wall of the spathe. Larvae I remained in the spathes, congregated on the anthers, and appeared to feed on pollen. When larvae II emerged, they migrated out of the spathe to the undersurface of leaves where they fed on leaf tissue. Thrips' activity and damage to leaves of Jack-in-the-pulpit were not uniformly distributed among all plants in the population at our study site.

Fig. 1. Thrips larvae II of *Heterothrips arisaemae* feed in small areas (~3-5 mm diameter), on the abaxial leaf surface. By mid-June, these feeding areas form distinct patches visible through the leaf. Later in the summer, the damaged areas coalesce to form larger holes.

g. 2. Adult thrips of *Heterothrips arisaemae* are typically found crawling through the pollen that collects inside the spathe beneath the inflorescence at the base of the spadix.

At our study site at SERC, leaves on male plants had more than twice as many feeding patches by *H. arisaemae* as on female plants and more than 20 times as many as on asexual plants (ANOVA, F = 48.068, P < 0.000; Fig. 3A). The damaged area (cm^2) and percent leaf area damaged by larval thrips were also significantly higher on leaves of male plants than of females and asexual plants (ANOVA, F = 56.721, P < 0.000; Fig. 3B-C). Female plants were significantly larger than either male or asexual plants, and male plants were significantly larger than asexual plants (Table 1). Measures of plant size (leaf area, leaf height, basal diameter) were most closely correlated with each other. Each measure of plant size also showed significant correlations with thrips damage, measured as damaged area (cm^2) and number of feeding patches, but not with percent leaf area damaged (Table 2).

Male spathes contained significantly more adult and larval thrips than did female spathes (Kruskal-Wallis, $\chi^2 = 6.413$, df = 1, P ≤ 0.01; Fig. 4A-B). *Heterothrips arisaemae deposited many more eggs in the spathes of male plants than in female plants (Kruskal-Wallis,* $\chi^2 = 20.410$, df = 1, P ≤ 0.001; Fig. 4C). The density of eggs was particularly high near the base of the male spathe. These eggs are visible as reddish spots on the tissue surface. In early June, first instar larvae were observed emerging from these eggs. Other insects found inside Jack-in-the-pulpit spathes included dipterans (mean ± 1 SE, 1.6 ± 0.3 per female spathe; 0 per male spathe), caterpillars (0.3 ± 0.1 per female; 0 per male), and collembolans (0 per female; 0.5 ± 0.3 per male). For the 252 insects that we collected on sticky traps, 53% of



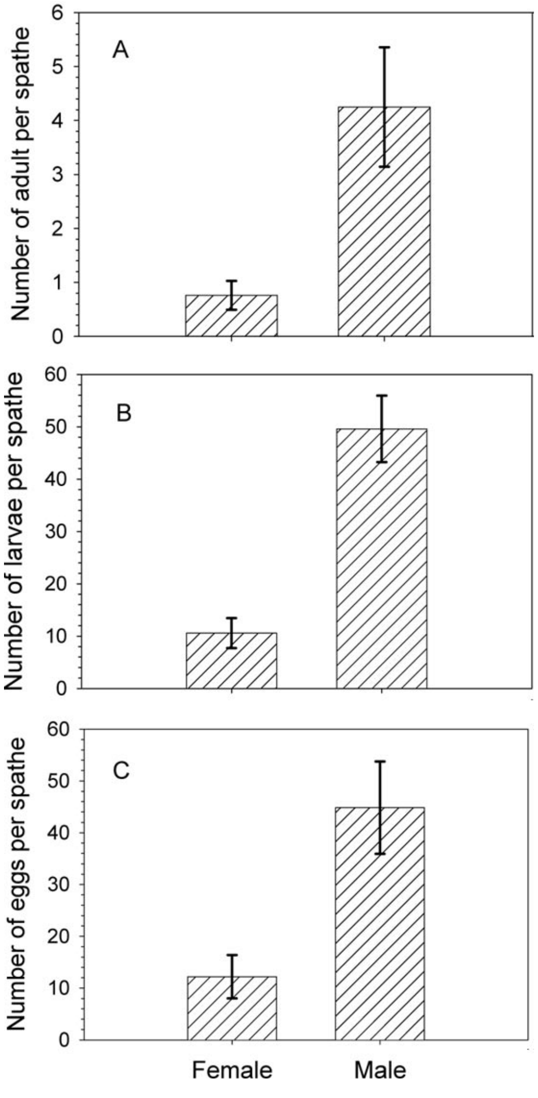
Figs. 3A-C. (A) The number of thrips larvae II of *Heterothrips arisaemae* feeding patches on female, female, and asexual Jack-in-the-pulpit plants; (B) Damaged area (cm^2) caused by thrips per plant gender; (C) Percent leaf area damaged by thrips on leaves of male, female, and asexual plants. Values are means ± 1 SD. N = 30 plants per gender.

GENDER	N	LEAF AREA (cm^2)	LEAF HEIGHT (cm)	BASAL DIAMETER (mm)
Female	33	467^{a} (+140, -122)	413^{a} (+72, -66)	9.9^{a} (+1.9, -1.7)
Male	35	170^{b} (+91, -72)	301^{b} (+65, -58)	6.5^{b} (+1.5, -1.4)
Asexual	34	92^{c} (+68, -49)	222^{c} (+79, -67)	4.2^{c} (+1.4, -1.2)

Table 1. Leaf area per individual, leaf height, and basal diameter of plants for which thrips damages were investigated along a 1-m wide belt transect. Mean (± standard deviations) are listed. Different letters indicate significant differences in mean value among gender (P ≤ 0.05), based on analysis of variance.

	FEEDING PATCHES	DAMAGED AREA	DAMAGED AREA (%)	LEAF AREA	LEAF HEIGHT
Damaged area	0.93*				
Damaged area (%)	0.86*	0.88*			
Leaf area	0.36*	0.35*	0.07		
Leaf height	0.40*	0.38*	0.20	0.88*	
Basal diameter	0.41*	0.40*	0.18	0.96*	0.90*

Table 2. Pearson's correlations between measurements of thrips' damage and size measurements of individual plants. All plants of the three genders were used in this analysis (N = 102). Asterisks indicate significant deviations of correlation coefficient from zero at $P \leq 0.01$.



Figs. 4A-C. The number of *Heterothrips arisaemae* (A) adults, (B) larvae, and (C) eggs found in male and female spathes of Jack-in-the pulpit. Values are means ± 1 SD. N = 30 plants per gender.

the Jack-in-the-pulpit pollen was on *H. arisaemae* adults (Table 3), with up to nine pollen grains per individual. Although flies carried approximately 38% of the pollen, the two families of fungus gnats (Mycetophilidae, Sciaridae) carried less than 8%. A small amount of the Jack-in-the-pulpit pollen was found on beetles and tiny parasitic wasps. However, no pollen was found on the collembolans, hemipterans, homopterans, spiders, and mites that were trapped by the sticky traps.

There were no significant differences in the percent N or in the C:N ratio among male, female, and asexual plants (Table 4). Similarly, there were no significant differences in phenolic concentrations among genders (ANOVA, F = 0.565, $P > 0.05$). There were also no significant differences in leaf mass per unit area among genders.

Alteration of the spathe morphology had a significant effect on subsequent herbivory by *H. arisaemae* larvae II on leaves (ANOVA, F = 23.881, $P < 0.000$; Fig. 5). In male plants, spathes completely removed caused a significant decrease in the percent leaf area damaged. There was no difference in leaf damage in female with spathes completely removed and female control plants. Male plants with their flowers removed had herbivory levels similar to female control plants. Closing the gap at the base of the male spathe caused a slight, but non-significant, decrease in level of damage, whereas opening a gap in female spathes caused a slight and non-significant increase in level of damage. In the controls, male plants had significantly more thrips damage than female plants.

ARTHROPODS		**PERCENT OF POLLEN CARRIED**	
		BY FAMILY	**BY ORDER**
Coleoptera:			7.9%
	Chrysomelidae	5.9%	
	Staphylinidae	4.6%	
	Coccinellidae	1.3%	
Collembola:			0
Diptera:			38.2%
	Anisopidae	3.3%	
	Cecidomyidae	0.7%	
	Drosophilidae	2.6%	
	Empididae	8.6%	
	Muscidae	6.6%	
	Mycetophylidae	3.9%	
	Otitidae	0.7%	
	Phoridae	1.3%	
	Sciaridae	3.9%	
	Sepsidae	3.9%	
	Unknown	2.0%	
Hemiptera:			0
Homoptera:			0
Hymenoptera:		1.3%	
	Tiny parasitic wasps (Family unknown)	1.3%	
Araneae and Acari:			0
Psocoptera:			0
Thysanoptera:			52.6%
	Heterothripidae: *Heterothrips arisaemae*	52.6%	

Table 3. Percent of Jack-in-the-pulpit pollen grains carried by arthropods (N = 236 arthropods; N = 252 pollen grains) collected on 20 sticky traps placed 30 cm above the ground, 0.5 m from the nearest plant in May 2000. Arthropods were categorized by order and family.

	PLANT GENDER		
PARAMETERS	**FEMALE**	**MALE**	**ASEXUAL**
N (%)	2.89 ± 0.06	2.80 ± 0.05	2.74 ± 0.04
C:N	15.81 ± 0.30	16.16 ± 0.25	16.47 ± 0.23
Phenolics (mg/g dry wt)	6.18 ± 0.52	5.24 ± 0.84	5.28 ± 0.54
Leaf mass per area (mg/cm^2)	2.23 ± 0.05	2.13 ± 0.05	2.05 ± 0.05

Table 4. Percent nitrogen (N), carbon (C):N ratios, phenolic concentrations (expressed as tannic acid equivalents), and leaf mass per unit area for leaves from female, male, and asexual Jack-in-the-pulpit plants. N = 30 per gender.

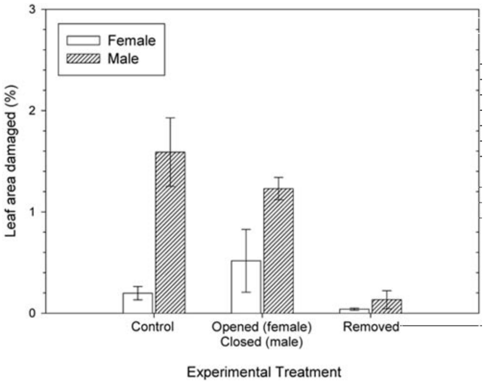


Fig. 5. Herbivory (means ± 1 SD) by thrips larvae II of *Heterothrips arisaemae*, expressed as percent leaf area damaged in Jack-in-the-pulpit, by Sex (male, female) x Floral Characteristics (spathe opened in female plants or closed in male plants, spathe completely removed, control). N = 30 plants per Sex × Floral Characteristic level.

Discussion

A specialist thrips, *H. arisaemae*, exhibited a distinct pattern of sex-biased herbivory on it host, Jack-in-the-pulpit. Male plants consistently had higher levels of damage than either female or asexual plants. Sex-biased herbivory has been reported in a number of plants species (e.g., Jing & Coley 1990, Boecklen et al. 1990, 1994, Boecklen & Hoffman 1993, Watson 1995). In most cases, male plants suffer higher levels of damage than female plants (Boecklen & Hoffman 1993, Watson 1995). In some studies, the patterns of damage correlated with plant defensive chemistry (e.g., Jing & Coley 1990) or nutritional quality of leaves (e.g., Boecklen & Hoffman 1993). In other studies, the damage pattern was determined by plant characteristics that are associated with herbivore developmental phenologies (e.g., Boecklen et al. 1994).

We conclude that the clear pattern of male-biased herbivory observed in this study resulted from the reproductive function of host plants and feeding behavior of different developmental stages of *H. arisaemae*, which are closely associated with the spathe morphology and availability of pollen of its host plant, Jack-in-the-pulpit. Our data do not support the hypothesis that suggests that defensive or nutritional aspects of leaf chemistry explain patterns of sex-biased herbivory. Specifically, adult thrips appear to feed on pollen and, thus, they become concentrated in the spathes of male plants. Consequently, they place their eggs primarily in these male spathes. When larvae I emerge, they congregate on the male flowers of these spathes where they also appear to eat pollen. When the foliphagous larvae II emerge, they migrate out of the spathes and onto the leaves of the plant on which they developed. Although adult *H. arisaemae* are winged and can fly among plants (Rust 1980), the first and second instar larvae lack wings. Thus, it is most likely that they remain on the individual plants where they developed, which are predominantly male plants.

Thrips are widely recognized for their importance as herbivores, particularly for crop plants (Kirk 1997). This study demonstrates conclusively that they are the primary herbivores of Jack-in-the-pulpit at our study sites and that they feed in a distinct pattern of male-biased herbivory. Larvae II, which feed on the undersurface of leaves, caused the leaf damage. A distinctive pattern of damage on the leaves became apparent by early to mid-June when thrips were already in the adult stage and had disappeared from their host plants. The impact of this leaf damage increased as the summer progressed, and male and female Jack-in-the-pulpit plants were distinguishable from their patterns of leaf damage by July. There are few reports of herbivory in Jack-in-the-pulpit, and most accounts are anecdotal. Crystals of calcium oxalate in the leaves, corm, and berries are thought to keep herbivory at relatively insignificant levels (Bierzychudek 1982, 1984). This species is susceptible to a systemic fungal pathogen, *Uromyces ari-triphylli* (Schw.) Seeler (Basidiomycetes), which appears to attack a disproportionately greater number of female plants than either male or asexual plants (Lovett Doust & Cavers 1982, Parker 1987).

The gender-biased herbivory may cause a shift in sex ratio of Jack-in-the-pulpit populations. Jack-in-the-pulpit is gender-labile and the sexual state of a plant is closely related to the amount of resources in the corm, accumulated by the end of previous year's growing season (Bierzychudek 1982). Therefore, serious damage on photosynthetic organs of male plants may prolong the male phase in the gender cycle of Jack-in-the-pulpit individuals, and consequently increase the male/female ratio of the populations. We need further comparative studies of gender ratios using multiple populations with and without thrips to evaluate this prediction.

Although several sources list fungus gnats as the primary pollinators of Jack-in-the-pulpit (e.g., Bierzychudek 1982, Meeuse 1985), Rust (1980) reported that *H. arisaemae* is the most abundant floral visitor and suggested that it may be the principal pollinator. Our data support his observations and provide evidence that *H. arisaemae*, rather than fungus gnats, is the primary carrier of Jack-in-the-pulpit pollen. Pollination by thrips has been demonstrated in a number of other plants, including Zamiaceae (Terry 2001, Mound & Terry 2001), Annonaceae (Momose et al. 1998), and the Moraceae (Sakai 2001). Because the adults appear to feed on the pollen, we suggest that pollen may be serving as a floral reward. Furthermore, the larvae feed on leaf tissue. This close relationship between thrips and Jack-in-the-pulpit demonstrates clearly that herbivory and pollination are not independent of each other. However, several questions remain to be answered regarding *H. arisaemae*'s relationship with Jack-in-the-pulpit. For example, if *H. arisaemae* adults consume pollen, how much of Jack-in-the-pulpit's pollen is emptied by these thrips and thereby rendered inviable? High rates of pollen feeding would reduce the amount of pollen available for pollination and may result in insufficient pollen to pollinate females in the vicinity. Alternatively, thrips may feed on pollen and also act as efficient pollinators. Although their feeding would reduce the amount of pollen available for pollination, the act of pollination would compensate for this loss, and further counterbalance the cost of leaf herbivory. If pollen is the floral reward attracting thrips to male flowers, what is their incentive to visit female flowers? Future studies will focus on these questions.

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