The effectiveness of a lethal pitfall-trap pollination system: jack-in-the-pulpit versus mushroom flies

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Abstract

Jack-in-the-pulpit (*Arisaema triphyllum*) is a mostly unisexual species that uses a pitfall inflorescence to trap and release (males) or trap and kill (females) its pollinators, which are small mushroom flies and fungus gnats attracted by plant-produced odors. Pollinator behavior is an understudied feature of this system.

We devised experiments to test (a) whether flies visit male and female inflorescences at different rates, and (b) whether providing an exit hole in female inflorescences decreases pollination success. Neither experiment (conducted in Vigo County, Indiana) found significant differences, but sample sizes were small and will be enlarged in future work.

We identified flies captured in spathes, and compared visitor composition with flies captured in water-bowl traps. Both fly families that are known to be major pollinators of *Arisaema*, Mycetophilidae and Sciaridae, were common in spathes; other weak-flying Nematocera were present but uncommon (15% of captures). Water-traps captured these three taxa in significantly different proportions from spathes. Nevertheless, water-traps may prove useful in assessing mushroom fly abundance.

Background

Flowering plants commonly engage in mutualisms with animal pollinators, providing food rewards in exchange for pollen transfer. However, selection has also favored specialized nectar-robbing and other cheating mechanisms in certain animals (Inouye, 1980), and traits that deceive, exploit, and even kill pollinators in some plants (Renner, 2005). One such lineage is subfamily Aroideae of the monocot family Araceae, including species of *Arisaema* (ca. 150 species). Their reproductive shoot consists of a tubular and leaflike spathe surrounding a pole-like inflorescence (spadix) embedded with numerous tiny unisexual flowers, either all of one sex or a mixture (monoecious). The spadix bears an osmophore that emits odors attractive to small flies (Vogel and Martens, 2000). Flies attracted into the spathe are usually trapped, temporarily or permanently. Depending on species and the plant's sexual phase, there may be an exit hole, reached with difficulty after contact with anthers (male and monoecious spathes); or flies may be permanently trapped, their struggles perhaps improving pollen transfer to stigmas, if they arrive bearing pollen (all-female inflorescences; Vogel and Martens, 2000; Nishizawa et al., 2005). Jack-in-the-pulpit (*Arisaema triphyllum*), a common forest plant of the eastern United States, occurs in mainly dioecious populations; males have exit holes, females do not.

Fig. 1a, b. Male (left) showing escape hole and female (right) lacking exit hole

Question 1: Do flies discriminate between male and female spathes?

Successful pollination of *A. triphyllum* depends on some flies visiting both male and female inflorescences. Flies pick up pollen on their head and other body parts (see photo). Although flies are apparently deceived by both sexes, they may be more likely to visit one sex than the other because female inflorescences are larger, or because of other differences in attractiveness. Normally male inflorescences do not detain gnats for long. By plugging male escape holes with cotton, we collected visitors (with tweezers at 3 day intervals, over 9 days) and compared visit rates to the two sexes. Observations were made on 13 pairs of male and female plants (within 2 meters of each other) to control for spatial variation in fly abundance.

As other studies have shown (Clay 1993), **female spathes were significantly larger than males** in basal stem diameter (Fig. 1a; paired-sample *t* test, two-tailed P = 0.0002), and also in spathe height and osmophore length (data not shown).

However, the number of flies captured by **the two sexes did not differ significantly** (Fig. 1b; Wilcoxon paired-sample test, two-tailed P > 0.50). The median number captured was 2 flies (males) or 3 flies (females), in each case a rather small number. Thus, flies seem equally likely to visit the small male plants as large females.

Fig. 2a, b. Mean basal stem diameters of female and male inflorescences differed significantly (paired-sample t-test, P = 0.0002). Despite the size difference, the sexes did not differ significantly in number of flies captured (Wilcoxon paired-sample test, P > 0.50).

Question 2: Does the lethal trap feature improve pollination success for females?

Vogel and Martens (2000) hypothesized that lack of an escape hole in the female spathe increases fruit set by increasing mushroom fly contact with pistillate flowers. We tested this by comparing fruit set in three experimental treatments of female spathes

Natural: No manipulation (no exit hole)
Experimental: Anatomy made similar to male by surgically cutting a 1-2 mm-diameter escape hole in the bottom of the spathe.
Control: Escape hole cut, then plugged with cotton.

Each replicate treatment set was applied to plants in close proximity. Developing fruits and shriveled flowers were counted 30 and 45 days after flowering ended.

The three treatments showed similar distributions of fruit set (a mixture of low and high values), and did not differ significantly (Fig. 2; Kruskal-Wallis test, P = 0.65). Plants with artificial exit holes had high fruit set in 3 of 5 cases. However, sample sizes were low and we could not block on microsite because all three inflorescence types rarely survived deer herbivory. We plan to repeat this experiment more effectively in the future.

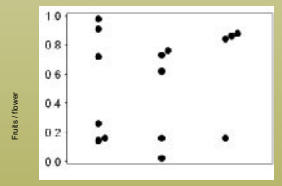

Fig. 3. Fruit set did not decline significantly when an exit hole was created in a female inflorescence (Kruskal Wallis test, P = 0.65).

Fig. 4. Female spathe displaying control treatment

Question 3: What fly taxa visit* Arisaema *spathes in western Indiana? Do water-filled bowl traps sample such flies adequately?

Vogel and Martens (2000), in the most extensive review of *Arisaema*'s insect visitors, found that two families of Nematocera – Mycetophilidae and Sciaridae – predominated as visitors of most Asian and American species, and that each family was often represented by much local species diversity. To determine if Indiana visitor assemblages followed this pattern, we collected flies from approximately 14 female spathes at a single site (Kieweg Woods), and identified specimens belonging to these families or to "other Nematocera".

We also set out water traps to see if they captured such flies and might serve as a useful index of mushroom fly abundance. Water traps were of the type commonly used to sample bees, colored styrofoam bowls filled with a water and detergent solution. Six were laid out at 10-meter intervals in a 50-m linear transect through *Arisaema*-rich areas at 4 sites, and exposed for 24 hours (since mushroom flies are active at twilight) on 2-4 dates per site.

Both fly families that are known to be major pollinators of *Arisaema* in other regions, Mycetophilidae and Sciaridae, were common in Indiana spathes. Other weak-flying Nematocera were present but uncommon (15% of captures; Fig. 3). Water-traps captured these three taxa in significantly different proportions from spathes at the site where spathe collections were made (Fig. 3; chi-square test, P < 0.0001), and results from 3 other sites were similar in showing low percentages of mycetophilids. Nevertheless, because they captured many Sciaridae, water-traps may prove useful in assessing abundance of *Arisaema* pollinators.

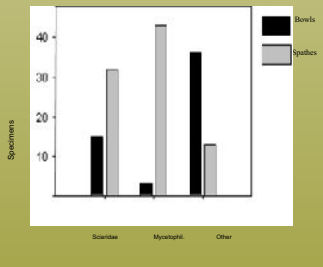

Fig. 5. Flies captured in Indiana plants were similar in taxonomic composition to collections from *A. triphyllum* in other regions, and from most *Arisaema* species worldwide, in consisting mainly of Sciaridae and Mycetophilidae, and lower numbers of other Nematocera. Water-traps captured significantly different proportions of these taxa.

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