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Arisaema: Pollination by lethal attraction

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1 | INTRODUCTION

The genus *Arisaema* contains approximately 180 species of deciduous or evergreen perennial herbs that are commonly known as "jack-in-the-pulpit" (Murata et al., 2018). The majority of *Arisaema* species are found in subtropical to cool temperate regions of Asia, but a few are endemic to North America and tropical East Africa (Murata et al., 2018). The Japanese archipelago is known to be a hotspot for *Arisaema* (Murata et al., 2018). The sexual expression of individual plants is determined by their nutrient status. As sequential hermaphrodites, small *Arisaema* plants tend to be only males; however, sex expression changes from male to female as plants grow in size (Kinoshita, 1986). The inflorescences of *Arisaema* consist of a spadix, on which fertile flowers are arranged at the base, and a spathe that wraps around the spadix and forms a hood that covers the spadix tip (Figure 1). In addition, the upper part of each spadix is modified into a well-developed sterile appendix, similar to several other tribes in the family Araceae.

Interestingly, there is a striking similarity between the inflorescences of certain *Arisaema* species and the leaves of carnivorous pitcher plants, such as *Nepenthes* (Nepenthaceae) and *Sarracenia* (Sarraceniaceae) (Suetsugu & Sato, 2020; Thorogood et al., 2018). Since the main function of both the pitchers of carnivorous plants and the inflorescences of *Arisaema* is to capture insects (i.e., pitcher plants to sequester nitrogen and *Arisaema* to transmit genetic material), the morphological similarity arguably represents a case of convergent evolution, rather than coincidence (Figure 1). Yet, even though *Arisaema* pollination is generally lethal to pollinating insects, little is known about the mechanisms by which these plants lure insects to their inflorescences. Thus, the aim of this paper is to review current advancements in the understanding of the unique pollination biology in the genus *Arisaema*.

2 | INFLORESCENCES AS POLLINATOR TRAPS

Pollination typically involves mutualistic relationships between flowering plants and insects, in which the plant usually provides a reward for the pollinator (such as nectar) and the pollinator transfers pollen while collecting the reward. However, plant–insect interactions are not always mutualistic (Urru et al., 2011). Some plants deceptively exploit signals to pollinators by advertising rewards but providing none. For example, diverse orchids, encompassing 6000 species across 47 genera, produce beautiful rewardless flowers that rely on pollination by naive insects (Jersáková et al., 2006). In addition, several species of *Arum* (Araceae), *Aristolochia* (Aristolochiaceae), and *Ceropegia* (Apocynaceae) possess deceptive flowers that attract and temporarily trap fly pollinators by chemically mimicking food sources (Ollerton et al., 2009; Vogel & Martens, 2000). However, they release pollinators after a fixed, species-specific period, during which pollination and/or pollen removal occurs (Vogel & Martens, 2000). In this respect, *Arisaema* employs one of the most unique pollination systems by permanent imprisonment of its pollinators.

The inflorescences of *Arisaema* species trap insects to ensure pollination (Vogel & Martens, 2000) and their victims are handled differently between *Arisaema* sexual morphs. Visitors of *Arisaema* inflorescences are typically fungus gnats belonging to the families Mycetophilidae and Sciaridae. They enter through the upper opening and then move to the lower portion of the spathe tube, which is brighter than the upper portion and thus mimics an exit point. This leads the gnats to an area of the inflorescence that contains many flowers; the appendix and inner spadix surface are coated with slippery wax, which prevents the gnats from climbing out (Vogel & Martens, 2000). A similar mechanism exists in carnivorous pitcher plants (Thorogood et al., 2018). In male morph inflorescences, the

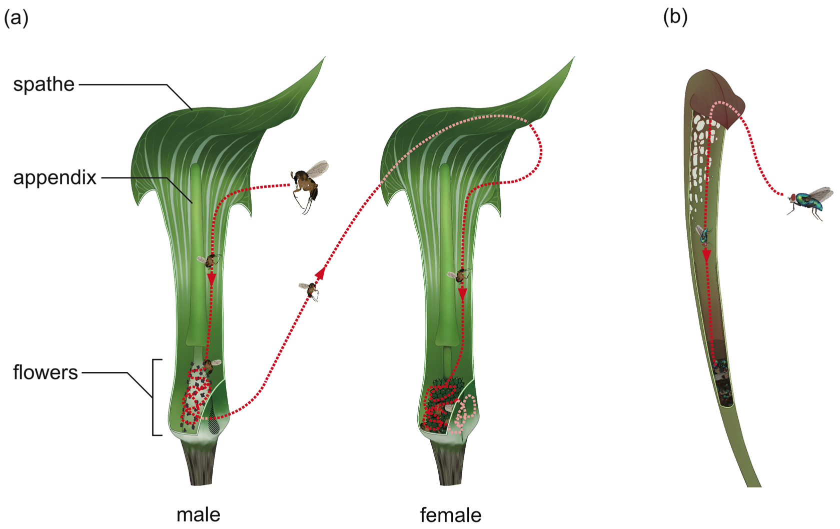

FIGURE 1 Schema of the mechanism of insect trap in *Arisaema* (a) and carnivorous pitcher plant *Sarracenia* (b). *Arisaema* and carnivorous pitcher plants show a remarkable convergence to trap insects for different purposes. Both the hood of the spathe and pitcher lid act as a shelter against rain to prevent wastage of pollen grains and dilution of the digestive fluid, respectively. Both *Arisaema* and *Sarracenia* possess slippery surfaces to retain captured insects. Finally, transparent patterns (fenestrations) on the trap chamber may be involved in long range attraction of prey and/or disorientation of captured insects. Illustrations not to scale. Illustration: Hiroki Nishigaki

gnats accumulate an increasing number of pollen grains while struggling to escape, until finally locating and exiting through a small opening at the base of the spathe. However, female morphs lack such exit holes in their spathes. Thus, the fungus gnats that visit female morph inflorescences are unable to escape, and the gnats deposit pollen grains on the stigmas and eventually die. Hence, female individuals of the genus *Arisaema* are the only known plants that permanently imprison their victims within their floral traps (Figure 1; Suetsugu & Sato, 2020; Vogel & Martens, 2000).

Even though the pollination system is well-known, the reason *Arisaema* females kill their pollinators remains a mystery. It has been proposed that the lack of an exit hole on the female spathe increases the time spent by flies around the floret, resulting in more pollen deposition (Vogel & Martens, 2000). Although a manipulative field experiment failed to provide evidence that a lack of an exit hole improves the fruit set of *Arisaema triphyllum* (Pettit, 2009), increased reproductive success may be found in specific localities and/or over years with favorable pollinator densities. The alternative but mutually nonexclusive hypothesis involves permanently trapping pollinators to reduce the chance of other individuals setting fruits and thereby preventing competition. Further investigations will be required to elucidate why *Arisaema* females kill their pollinators.

The mechanism by which *Arisaema* species lure pollinators into their inflorescences is also somewhat unclear. Mushroom mimicry has historically been considered an important pollination strategy for the genus, since most reported pollinators of *Arisaema* spp. are fungus gnats, which are typically mycophagous during their larval stage (Vogel & Martens, 2000). Certainly, the sterile appendix of a few distinctive species, such as *Arisaema sikokianum*, resembles a mushroom in both appearance and odor (Figure 2; Kakishima et al., 2019). The insect assemblages trapped in *A. sikokianum* were strikingly similar to those attracted to the fruiting bodies of polyporous fungi such as *Ganoderma applanatum* (Kakishima et al., 2019). On the other hand, there is little evidence that many other *Arisaema* inflorescences mimic mushroom fruiting bodies. The inflorescence scents of many *Arisaema* species are nearly imperceptible to the human nose (Suetsugu et al., 2021), whereas most mushroom mimicry involves scent cues associated with C_8 aliphatics, which are readily discernible by humans (Kakishima et al., 2019; Policha et al., 2016). Thus, it is unlikely that mushroom mimicry is typical of the *Arisaema* species, except for a few species such as *A. sikokianum*.

3 | POLLINATOR-MEDIATED RADIATION IN JAPAN

The Japanese archipelago is a hotspot for *Arisaema* diversity (Iwatsuki et al., 2016). Murata et al. (2018) reported that 64 *Arisaema* taxa (53 species, 9 subspecies, and 2 varieties) are native to Japan, of which 58 taxa are endemic. Interestingly, most taxa (50/56) of the *Arisaema* section *Pistillata* are endemic to Japan, and it could be argued that the diversification of *Pistillata* is centered in Japan (Ohi-Toma et al., 2016). Moreover, *Pistillata* is considered to have radiated recently based on the limited genetic distances even among morphologically distinct species (Ohi-Toma et al., 2016). Therefore, there is particular interest in understanding how the diverse group has established reproductive isolation (Kakishima et al., 2019; Matsumoto et al., 2019; Matsumoto et al., 2021; Suetsugu et al., 2021).

Gene flow among the Japanese *Arisaema* species is likely to be restricted by premating barriers. Indeed, even though artificial cross experiments have determined the cross-compatibility among species belonging to the *Pistillata* species (Murata et al., 2018), these *Arisaema* species often co-occur in apparent reproductive isolation. Pollinator specialization contributes to the reproductive isolation of these species (Kakishima et al., 2019; Kakishima et al., 2020; Matsumoto et al., 2019; Matsumoto et al., 2021; Suetsugu et al., 2021). For example, Suetsugu et al. (2021) reported that the mycetophilid fungus gnats trapped by inflorescences of the sympatric, co-blooming, and closely related species *Arisaema angustatum* and *Arisaema peninsulae* differed significantly. *Cordyla murina* accounted for >90% of mycetophilids found in *A. angustatum*, while *Brevicornu* sp. 1 and *Mycetophila* sp. 1 accounted for >80% of the mycetophilids found in

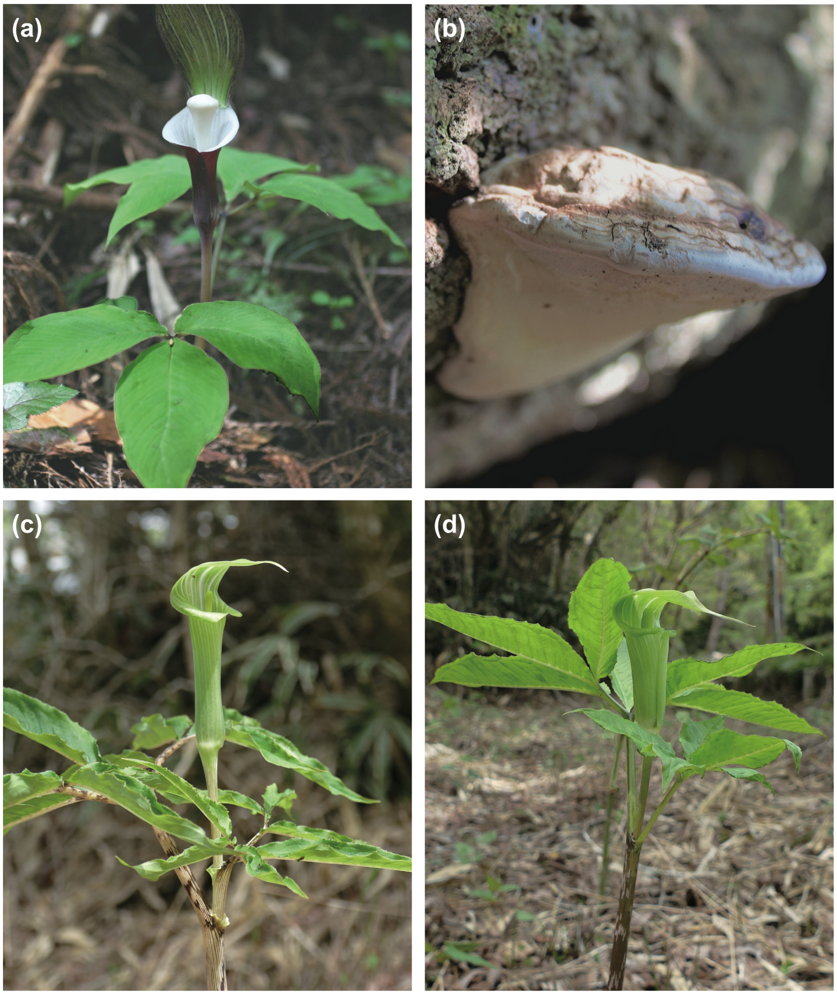

FIGURE 2 Diversity of *Arisaema* inflorescences. (a) *Arisaema sikokianum*, which has a snow-white and distinctly capitate sterile appendix that resembles a fungal fruiting body, such as that of the bracket fungus *Ganoderma applanatum* (b), and emits a distinct fungus-like smell. (c, d) Other *Arisaema* species (*Atrichum angustatum* and *Apodemus peninsulae*, respectively) typically possess a pale green, slightly clavate sterile appendix that does not resemble mushrooms and lure specific male fungus gnats by scents that are almost imperceptible to humans. Photographs: (a) Hisanori Takeuchi, (b) Hidehito Okada, and (c, d) Kenji Suetsugu

A. peninsulae, with no common mycetophilid species observed among them. Similarly, Matsumoto et al. (2021) reported that the geographic and phenological isolation of five species belonging to *Pistillata* was significantly weaker than pollinator isolation. Therefore, pollinator specificity has possibly played an important role in the speciation and diversification of the section *Pistillata* in Japan.

4 | PUTATIVE SEXUAL DECEPTION SYSTEM

Plants that mimic mushrooms, including the exceptional fungal mimetic *Arisaema* species (*A. sikokianum*), are visited by various fungivorous insects such as *Mycodrosophila* species (Drosophilidae) and staphylinids (Coleoptera; Kakishima et al., 2019; Matsumoto et al., 2019; Matsumoto et al., 2021). In contrast, many other *Arisaema* species (especially *Pistillata* taxa) are exclusively pollinated by a limited number of fungus gnat species (one or two) (Suetsugu et al., 2021). This raises the question of whether most *Arisaema* species have evolved to mimic mushrooms.

Suetsugu et al. (2021) have provided reasoning for the *Arisaema* species attracting just one or two pollinating fungus gnat species, proposing the possibility of sexual deception. Sexual deception is a pollination system where pheromones of female insects are mimicked by plants to attract and deceive specific male insects into attempting to mate with their flowers (Gaskett, 2011). Notably, Suetsugu et al. (2021) reported that the pollinators of *A. angustatum* and *A. peninsulae* were strongly male-biased (57/58 and 38/38, respectively). It is unlikely that such male bias would be associated with mushroom mimicry, which generally involves signals that mimic mating or brood sites and thus would be equally or more likely to attract female gnats (Suetsugu, 2018). Suetsugu et al. (2021) also demonstrated that olfactory cues emitted by the spadix appendix are the basis for the attraction of each specific fungus gnat, although the scent is nearly imperceptible by humans (Suetsugu et al., 2021). Furthermore, it has recently been shown that the flowers of *Pterostylis* species (Orchidaceae), which are morphologically similar to *Arisaema* inflorescences, are pollinated by male fungus gnats that are attracted by the emission of specific sex pheromones (long-chain unsaturated hydrocarbons; Hayashi et al., 2021; Phillips et al., 2014; Reiter et al., 2019).

Although pollination systems that involve sexual deception have only historically been observed in the Orchidaceae, sexual deception has also been recently reported to occur in certain members of the

Asteraceae and Iridaceae (Ellis & Johnson, 2010; Vereecken et al., 2012). Since the Araceae contains the largest number of deceptively pollinated species after Orchidaceae (Chartier et al., 2014), it is not unreasonable to hypothesize that pollination systems of Araceae could also involve sexual deception. In addition, a remarkable feature of plants with sexually deceptive pollination systems is that reproductive isolation can occur rapidly through minor modifications to floral scent chemistry that correspond to the chemicals mediating reproductive isolation in the associated pollinators, thereby promoting speciation (Peakall & Whitehead, 2014; Xu et al., 2011). Accordingly, the characteristics such as the specific attraction of male pollinators, absence of food rewards, attraction using compounds that are imperceptible by humans, and the rapid diversification of closely related species are in agreement with the hypothesis that *Arisaema* taxa that do not mimic mushrooms instead utilize sexually deceptive pollination systems.

5 | CONCLUDING REMARKS

Despite attracting the interest of both evolutionary biologists and naturalists, the mechanisms underlying the lethal pollination system used by most *Arisaema* species have only recently begun to be understood. Further investigation is needed to unequivocally demonstrate sexual deception in *Arisaema* pollination. For example, it would be interesting to examine whether some *Arisaema* species exhibit characteristics more directly associated with sexual deception, such as signals that elicit premating behaviors or the production of chemicals that mimic sex pheromones. In addition, the high morphological diversity of genus *Arisaema* indicates that novel deception mechanisms, beyond mushroom mimicry and sexual deception, possibly exist. Future research into these aspects will facilitate a deeper understanding of the mechanisms underlying the group's rapid reproductive isolation and radiation.

KEYWORDS

deceptive pollination, floral mimicry, fungus gnat, lethal kettle trap, radiation, reproductive isolation, sexual deception, trap flower

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

KS designed the review, collected and interpreted the data, and wrote the paper.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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