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NOTES AND INSIGHTS

PLANT SPECIES BIOLOGY WILEY

The glandular hairs within the floral tube of *Paederia foetida* (Rubiaceae) and their influence on ant accessibility

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Abstract

Hairs that grow on plant organs have been shown to play a variety of roles. *Paederia foetida* (Rubiaceae) is a perennial vine with many glandular hairs in the floral tube. The hairs of *P. foetida* are thought to play a role in preventing ants from entering the floral tube, but this has not been tested. We aimed to test this hypothesis by trimming the glandular hairs in the floral tube in the field. The results showed that trimming the glandular hairs increased the success rate of ants entering the floral tube. Thus, our findings indicate that the presence or absence of glandular hairs in the floral tube of *P. foetida* has an effect on an ant's ability to enter a flower and suggest that the glandular hairs in the floral tube of *P. foetida* might have played a role in preventing ants from entering.

KEYWORDS

floral function, glandular hairs, *Paederia foetida*, plant-ant interaction, Rubiaceae

1 | INTRODUCTION

Hairs (including glandular hairs and trichomes) of flowers and leaves are known to play an important role in protecting the floral parts involved in reproduction, the reduction of feeding by insects, and the promotion of pollination by flower-visiting insects; for example, hairs on the young leaves in *Mallotus japonicus* (L.f.) Müll.Arg. (Euphorbiaceae) are useful for preventing feeding damage by beetles (Coleoptera) and the larvae of butterflies (Lepidoptera) (Yamawo et al., 2012). Hairs inside the floral tube of *Aristolochia* sp. (Aristolochiaceae) facilitate pollination by flies (Matallana-Puerto et al., 2024; Sugawara et al., 2016), hairs on the petal surfaces of *Menyanthes trifoliata* L. (Menyanthaceae) defend against ants attempting to enter the floral tube (Tagawa, 2018). The morphological characteristics of each species indicate highly diverse functions associated with insects.

Many plants engage in defensive mutualisms with ants by offering nectar as a reward (Weber & Keeler, 2013). Ants visiting flowers without bringing benefits to the plant are often considered to be nectar thieves or have a negative effect on pollination (Willmer et al., 2009). Among the negative effects on pollination by ants are direct attacks on pollinators or ants reducing the duration of visits of pollinators (Hansen & Müller, 2009; Lach, 2008; Takeda et al., 2021; Tsuji et al., 2004; Willmer et al., 2009). Ants can damage the reproductive organs of plants and antibiotics secreted from the ant's body decrease pollen viability (Beattie et al., 1984; Dutton & Frederickson, 2012; Willmer et al., 2009). The amount of pollen attached to an ant's body is low, thereby not contributing to pollination (Komamura et al., 2021; Willmer et al., 2009). In addition, the consumption of nectar by ants has been reported to reduce nectar yield, resulting in poor rewards for pollinators (Fritz & Morse, 1981; Norment, 1988; Willmer et al., 2009). Thus several floral functions have been proposed as chemical or physical barriers to ants (Willmer et al., 2009).

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Paederia foetida L. (Rubiaceae) has dense glandular hairs in the floral tube (Figure 1a,b,e). We found that ants frequently visit the flowers of *P. foetida* in a preliminary field survey, but many ants did not enter the floral tube. Glandular hairs of *P. foetida* have been considered to defend against ants entering the floral tube much the same as in *Menyanthes trifoliata* (Tada, 2021; Yaoi, 2011). However, it has not been verified that the glandular hairs of *P. foetida* prevent ants from entering the floral tube. Therefore, determining the function of the glandular hairs of *P. foetida* is necessary for understanding if they are a defense mechanism to prevent ants from entering the floral tube.

In our study, we aimed to clarify whether the glandular hairs inside the floral tube of *P. foetida* prevented ants from entering. We also postulated that hair trim could increase the success rate (SR) to enter inside the floral tube, and the staying time in the floral tube was longer than the control. To test the hypothesis, we conducted the experimental analyses of the hair functions by removing the floral hairs.

2 | MATERIALS AND METHODS

2.1 | Plants and study site

Pederia foetida L. (Rubiaceae) is a climbing perennial in thickets and grasslands in temperate regions of eastern Asia (Yamazaki, 1993). It has a white funnel-shaped corolla (floral tube) about 1 cm long, is deep purplish red inside with the inner surface covered with dense glandular hairs for 2/3 of its length (Figure 1). Nectar is produced deep within the tube. Honey bees and halictid bees have been reported to be pollinators of *P. foetida* (Liu et al., 2006; Tada, 2021; Yaoi, 2011). This plant has been tested in the United States, where it grows as an exotic species and is self-incompatible (Liu et al., 2006).

Field observations of the flowers of one individual of *Paederia foetida* at each site were conducted at four sites in Okayama Prefecture, western Japan; one at Okayama University of Science (35°41′49″N, 133°55′44″E) and the other three in Handayama Botanical Garden in Okayama City (35°41′34″N, 133°55′49″E) for 23 days during the flowering period from the end of July to mid-September 2023.

2.2 | Experimental analysis of hair functions of *P. foetida* for ants

Three treatments of the glandular hairs inside the floral tube were used in this study: (1) hairs untouched (control) (number of flowers observed: $N = 61$), (2) hairs trimmed for 5 mm from the entrance of the floral tube ($N = 42$), and (3) all glandular hairs trimmed ($N = 56$) (Figure 1). We carried out treatment (2) to examine

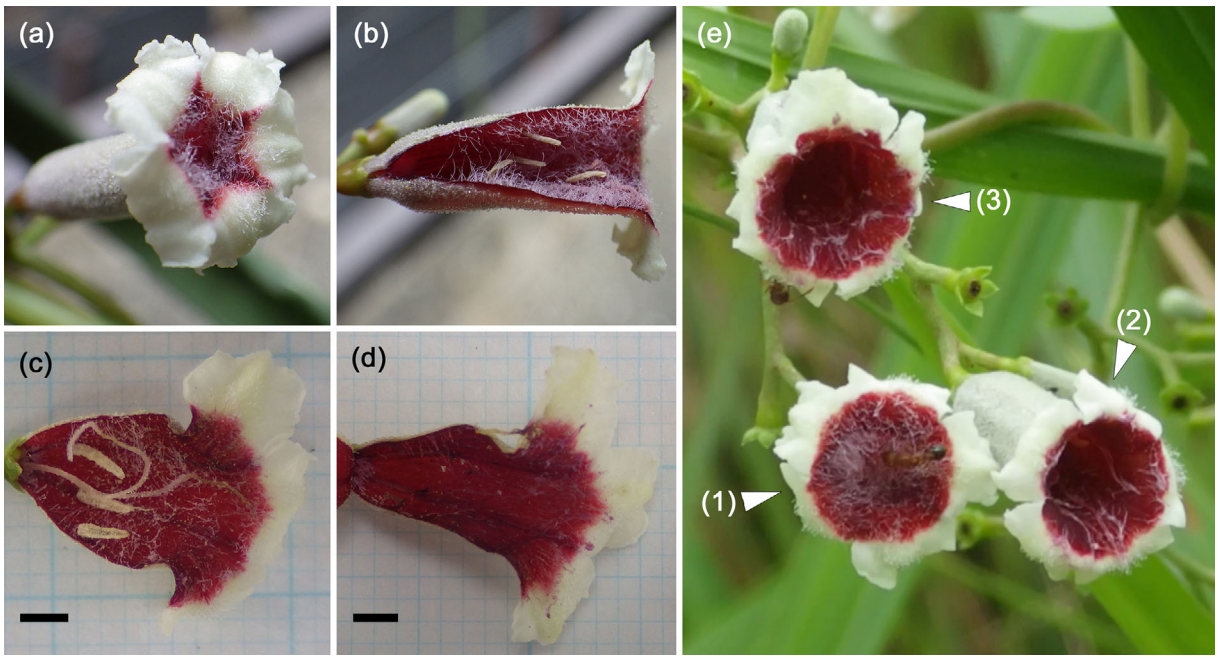


FIGURE 1 Floral tube of *Paederia foetida*. (a, b) White funnel-shaped corolla (floral tube); inside deep purplish red, with dense glandular hairs on upper 2/3. (c) Floral tube with glandular hairs trimmed to 5 mm from entrance. (d) Floral tube with all glandular hairs trimmed. (e) Field observations using three treatments of glandular hairs inside floral tube. Arrowhead indicates floral tube used as control (1), floral tube with glandular hairs trimmed to 5 mm from entrance (2) and floral tube with all trimmed glandular hairs (3). Scale bars: (c) and (d) 2 mm.

whether the hairs inside as well as at the entrance to the floral tube are involved in the success or failure of ant entry. Because, if the glandular hairs of *P. foetida* prevent ants from entering the floral tube, it is predicted that in the case of (2), ants stay only near the entrance of the floral tube, but in the case of (3), they will be able to enter deeply inside.

To trim the glandular hairs, they were moistened with a wet paper towel 10 mm × 10 mm in size, wiped off using dry paper towels, and then removed using a sticky cotton swab. Observations were conducted 63 times (one to four times per 1 day) for 30 min between 9:00 a.m. and 4:30 p.m. Observations of the ants that approached the floral tube were video recorded using a digital camera (RICOH WG-5) from which the behavior of ants was analyzed in the laboratory to determine if the ants entered the floral tube. Video recorded one to a maximum of 12 sessions during the 30 min. In one video session, two to four flowers were photographed. We photographed the same or different treatments in two flowers, at least two different treatments in three, and at least three different treatments in four. Thus, each video session did not necessarily include control flowers. Flowers used in one observation were not repeated in the next 30 minutes. The surrounding flowers were not treated and not observed in this study.

For 30 flowers of the control at four sites, the length and diameter of the entrance, the maximum width of the middle part of the tube and the width of the lower part of the tube were also measured using a ruler after 30 min of observation.

To determine if the ants entered the floral tube we categorized four main behaviors of ants. (1) successful entry if the entire body of the ant deeply entered the floral tube and remained there for more than 1 s; (2) although the entire body of the ant entered the floral tube for more than 1 s, failure if it only remained near the entrance of the floral tube; (3) failure if only half of the body of the ant entered the floral tube and only investigated the inside of the flower or just walked on the petals; (4) unclear entry if the entire body of the ant entered the floral tube, but remained there for less than 1 s.

We identified the species of ants that visited the flowers to understand the relationship the ant's size and SR in entering the floral tube. We classified observed ants into large (more than 5 mm long) and medium to small (less than 5 mm long) by identifying ants species from videos. We also investigated SR of ants entering the floral tube of each type of flower treatment and the size of the ant. To determine significant differences in SR of ants entering, we conducted a Fisher's exact test using R version 4.4.1 (R Core Team, 2024) and indicated *p*-value. Furthermore, we noted that the length of staying time of ants within the floral tubes of successful visits for each treatment from video session. Wilcoxon signed rank tests were carried out to determine significant differences the length of staying time of ants within floral tubes among three treatments of the glandular hairs inside the floral tube.

3 | RESULTS

3.1 | Floral tube size of *Paederia foetida* L. ($N = 30$)

The floral tube ranged from 8.5 to 13 mm (Mean ± SD: 11.1 ± 1.15 mm) long. The diameter of the entrance of the floral tube ranged from 3.5 to 9 mm (6.23 ± 1.04 mm) wide. The maximum width of the middle part of the floral tube ranged from 3.5 to 5 mm (4.28 ± 0.52 mm) wide; the width of the lower part of the floral tube ranged from 2 to 3 mm (2.27 ± 0.31 mm) wide.

3.2 | Flower visitors and visitation frequency

A total of 142 video sessions were taken during 1890 min of observations (63 times for 30 min), five species of ants visited the floral tube of *Paederia foetida* 663 times (Table 1). Among the visiting ants, most were *Formica japonica* Motschoulsky (313 visits; 47.2% of all visits) followed by *Pheidole nodus* Smith (256 visits; 38.6% of all visits) (Table 1, Figure 2). *Formica japonica* was over 5 mm long (Figure 2) and was the only ant over 5 mm that visited the floral tube. *Pheidole nodus* was less than 5 mm long and was considered to be medium-small. Three additional species of ants, *Tetramorium bicarinatum* Nylander, *Camponotus vitiosus* Smith., *Pristomyrmex punctatus* Smith. and unidentified were medium-small (less than 5 mm long) and visited infrequently (Table 1). The large and medium-small sized ants often visited the same floral tube once or twice during each 30-min observation period (Table S1).

Among the 663 visits to the floral tube by ants, the number visiting for each treatment of glandular hairs inside the floral tube was 237 (35.7%) for the control, 167 (25.2%) for hairs trimmed to 5 mm from the entrance of the floral tube, and 259 (39.1%) for glandular hairs fully trimmed (Table 2). In Fisher's exact test, SR of entry when all the hairs were trimmed (3; 61.8%) was significantly higher than in the control (1; 35.0%) and the hairs trimmed to 5 mm from the entrance (2; 35.9%) ($p < 0.001$; Figure 3). However, there was no significant

TABLE 1 Species of ants that visited floral tube of *Paederia foetida* and their frequency.

Ants body size	Ants species	Number of times of visits to floral tube	Total
Large (body length 5 mm-)	*Formica japonica*	313 (47.2%)	313
Medium and small (>5 mm in length)	*Pheidole noda*	256 (38.6%)	350
	Tetramorium bicarinatum	33 (5.0%)	
	Camponotus vitiosus	7 (1.1%)	
	Pristomyrmex punctatus	3 (0.5%)	
	Unidentified	51 (7.7%)	

Note: Ants were categorized by body size into large and medium-small.

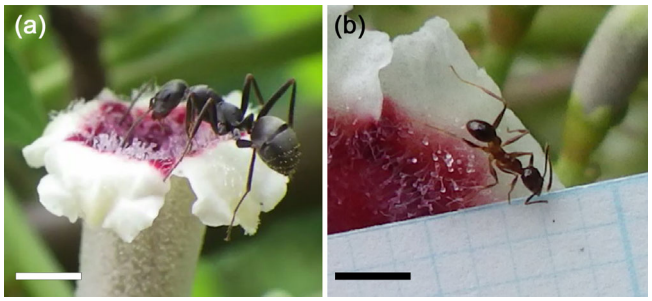


FIGURE 2 Two species of the most frequent visiting ants to the flowers of *Paederia foetida*. (a) Large ants, *Formica japonica*. (b) Medium-small ants, *Pheidole noda*. Scale bars: (a) and (b) 2 mm.

difference in SR between hairs trimmed to 5 mm from the entrance (2) and the control (1) ($p = 0.92$; Figure 3).

In 313 visits by large ants, *Formica japonica*, SR for hairs all trimmed (3) was significantly greater than in the control (1) and the hairs trimmed to 5 mm from the entrance (2) ($p < 0.001$; Figure 3) in Fisher's exact test. However, SR of the hairs trimmed to 5 mm from the entrance (2) was lower than the control (1) ($p < 0.05$; Figure 3). The length of staying time of large ants within the floral tubes for each treatment ranged from 1.7 to 199.7 s (Mean ± SE: 30.5 ± 6.0 s, $N = 46$) for the control (1), ranged from 7.2 to 96.5 s (44.3 ± 9.5 s, $N = 10$) for hairs trimmed to 5 mm from the entrance (2) and ranged from 1.4 to 236.8 s (25.7 ± 4.8 s, $N = 70$) for hairs all trimmed (3). The length of staying time of large ants in floral tubes was longer for hairs trimmed to 5 mm (2) than in the control (1) and the hairs all trimmed (3) ($p < 0.05$; Figure 4) in Wilcoxon signed rank test. However, there was no significant difference in staying time between hairs all trimmed (3) and the control (1) ($p = 0.31$; Figure 4).

Of 350 visits by medium-small sized ants, in Fisher's exact test, SR of (3) all trimmed was significantly higher than in the control (1) ($p < 0.001$; Figure 3) and higher than the hairs trimmed to 5 mm from the entrance ($p < 0.01$; Figure 3). However, SR between hairs trimmed to 5 mm from the entrance (2) and the control (1) was insignificant ($p = 0.21$; Figure 3). The length of staying time of medium-small sized ants within the floral tubes for each treatment ranged from 9.4 to 136.5 s (Mean ± SE: 61.5 ± 8.0 s, $N = 23$) for the control, ranged from 3.2 to 284.2 s (76.0 ± 18.4 s, $N = 19$) for hairs trimmed to 5 mm from the entrance (2) and ranged from 2.4 to 108.5 s (22.1 ± 2.6 s, $N = 67$) for hairs all trimmed (3). In Wilcoxon signed rank test, the length of staying of medium-small sized ants within floral tube was significantly longer in the control (1) than hairs all trimmed (3) ($p < 0.001$; Figure 4). Staying time for hairs trimmed to 5 mm from the entrance (2) was longer than hairs all trimmed (3) ($p < 0.01$; Figure 4). However, there was no significant difference in staying time between hairs trimmed to 5 mm from the entrance (2) and the control (1) ($p = 0.60$; Figure 4).

When two species of ants, one individual of *Formica japonica* in the floral tube of a control (1) and several individuals of *Pheidole noda* in a flower with hairs trimmed to 5 mm (2), stayed in the floral tube, small bees, did not enter the floral tube (Figure S1a). We observed *P. noda* carrying the anthers from the floral tube of a control (1) and from a flower with hairs trimmed to 5 mm (2) (Figure S1b). We also observed four species of ants licking the nectar on the calyx at the base of the floral tube 17 times after the corolla had fallen (Figure S1c): *P. noda* (7 times), *F. japonica* (5 times), *T. bicarinatum* (3 times), and *P. punctatus* (2 times).

4 | DISCUSSION

Several features of plants that enable them to defend themselves from the negative effect of ants have been reported: for example, hairs on the surface of the petals in *Menyanthes trifoliata* (Tagawa, 2018) and the slippery perianth in *Codonopsis lanceolata* (Siebold et Zucc.) Trautv. (Campanulaceae) and *Fritillaria koidzumiana* Ohwi (Liliaceae) (Takeda et al., 2021). Glandular hairs in

TABLE 2 Number of times and entry rates (%) of ants visiting floral tube for each patterns of glandular hairs in *Paederia foetida*.

	Successful entry deeply inside			Only near the entrance entry		
Treatment	**Total**	**Large sized ants**	**Medium and small sized ants**	**Total**	**Large sized ants**	**Medium and small sized ants**
(1) Control	83 (35.0%)	49 (35.3%)	34 (34.7%)	10 (4.2%)	8 (5.8%)	2 (2.0%)
(2) 5 mm trimmed	60 (35.9%)	10 (19.2%)	50 (43.5%)	37 (22.2%)	8 (15.4%)	29 (25.2%)
(3) All trimmed	160 (61.8%)	75 (61.5%)	86 (62.8%)	22 (8.5%)	7 (5.7%)	14 (10.2%)
Total	303	134	169	69	23	46
	Failure entry			**Unclear entry**		
Treatment	**Total**	**Large sized ants**	**Medium and small sized ants**	**Total**	**Large sized ants**	**Medium and small sized ants**
(1) Control	143 (60.3%)	82 (59.0%)	61 (62.2%)	1 (0.4%)	0 (0.0%)	1 (1.0%)
(2) 5 mm trimmed	68 (40.7%)	33 (63.5%)	35 (30.4%)	2 (1.2%)	1 (1.9%)	1 (0.9%)
(3) All trimmed	72 (27.8%)	36 (29.5%)	36 (26.3%)	5 (1.9%)	4 (3.3%)	1 (0.7%)
Total	283	151	132	8	5	3

	Total amount		
Treatment	**Total**	**Large sized ants**	**Medium and small sized ants**
(1) Control	237 (35.7%)	139 (44.4%)	98 (28.0%)
(2) 5 mm trimmed	167 (25.2%)	52 (16.6%)	115 (32.9%)
(3) All trimmed	259 (39.1%)	122 (39.0%)	137 (39.1%)
Total	663	313	350

Note: Behavior of ants is indicated as (1) successful entry of floral tube, (2) only near the entrance enter, but not a successful entry, (3) failure to enter, (4) unclear entry, and total entry. Ants were categorized by body size into total, large, and medium-small.

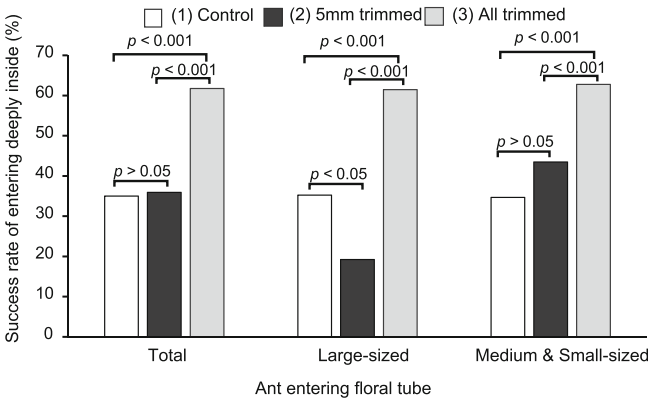


FIGURE 3 Success rate (SR) of ants entering floral tube for each treatment of glandular hairs in *Paederia foetida* (%). Ants were categorized by size into total, large, and medium-small; *p* value by Fisher's exact test comparing per condition of glandular hairs is shown above the line.

the floral tube of *Paederia foetida* have also been considered to prevent ants from entering the floral tube at personal observations (Tada, 2021; Yaoi, 2011). In this study, trimming all the glandular hairs in the floral tube resulted in about a 1.5 times greater increase in both large and medium-small sized ants entering the floral tube as compared with the control (Figure 3, Table 2). Thus, our results indicated that the glandular hairs in the floral tube of *P. foetida* have an effect on ants' ability to enter the flower. However, we predicted that the entry SR might be equal to or higher than that of control after trimming the 5 mm long hairs from the entrance of the floral tube; SR for large ants was lower than for medium-small ants in deeply entering the flowers (Figure 3, Table 2). The lower SR of large ants entering flowers with hairs trimmed to 5 mm at the entrance was unclear; future study is needed.

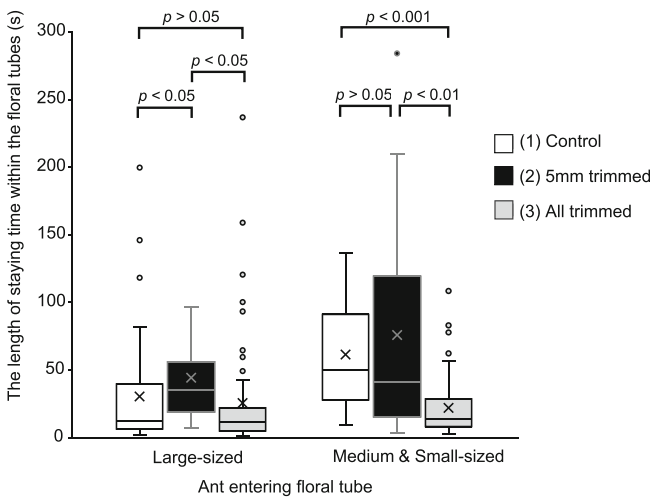


FIGURE 4 The length of staying time of ants successfully entering the floral tube of *Paederia foetida*. Ants were categorized by size into large and medium-small. Cross marks show the mean of the length of the staying times.

Tagawa (2018) also reported that ants, *Lasius japonicus*, could not walk smoothly due to dense hairs on the petals of *M. trifoliata* and stayed longer on hairy flowers than on hair-removed flowers. Thus he suggested that the dense hairs on the petals of *M. trifoliata* acted as a physical barrier against ants (Tagawa, 2018). In our study, medium-small-sized ants that entered the floral tube stayed longer in the control with hairs and in the floral tube with hairs trimmed to 5 mm from the entrance than in the tube with all the glandular hairs trimmed (Figure 4). On the other hand, the staying times of large ants in the floral tube were not significantly different between the control with hairs and the floral tube with all glandular hairs trimmed (Figure 4). These results suggest that the glandular hairs in the floral tube of *P. foetida* have a function to hinder the movement of at least small and medium-sized ants, as in *M. trifoliata*. In addition, Tagawa (2018) reported that the existence of ants on the petals of *M. trifoliata* for a longer time might cause pollinators to keep away. For medium to small-sized ants that tended to stay longer in the glandular-haired floral tube (Figure 4), the glandular hairs in the floral tube of *P. foetida* might also prolong the residence time of ants, potentially increasing the likelihood of encountering pollinators.

Ants visiting flowers without benefiting the plant are often considered nectar thieves or have negative effects on pollination (Willmer et al., 2009). In our study, we observed ants licking nectar on the calyx in *P. foetida* (base of floral tube) after the corolla had fallen (Figure S1c). The floral nectar of *P. foetida* may be attractive to ants. Interestingly, two species of ants, *Formica japonica* and *Pheidole nodus*, frequently visited the flowers of *P. foetida* (Table 1). In general, however, the ants are small in comparison with the size of the flower and rarely serve as pollinators (Dutton & Frederickson, 2012; Willmer et al., 2009). In our study, the floral tube of *P. foetida* was significantly larger than the two species of ants that entered the flowers. Ants successfully entering the floral tube of *P. foetida* are therefore thought to be nectar thieves and potentially affect pollination negatively and may not themselves be pollinators. Honey bees and halictid bees have been reported to be pollinators of *P. foetida* (Liu et al., 2006; Tada, 2021; Yaoi, 2011). The pollinator needs to enter the floral tube of *P. foetida*, but when ants are inside the floral tube, bees do not enter (Figure S1a). The negative effect of ants on pollination in which they interfere with the effective pollinators is known (Willmer et al., 2009). Our findings suggest that ants in the floral tube interfere with effective visitors such as pollination of *P. foetida*. Moreover, ants damage the reproductive organs by removing anthers (Willmer et al., 2009). We also confirmed that ants removed the anthers from the floral tube of *P. foetida* (Figure S1b). Thus, the glandular hairs in the floral tube of *P. foetida* may be partially effective in preventing ants from entering the floral tube, since they did not completely prevent entry. The relationship between *P. foetida* and ants needs to be studied in more detail. Additionally, the role of glandular hairs is not limited to ants; they may also be involved in the effectiveness of pollinators. Further research is needed to determine the role of glandular hairs in the floral tube of *P. foetida* on bees as pollinators.

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CONFLICT OF INTEREST STATEMENT

The authors declare that there are no conflicts of interest.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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