

# Do larger pollinators have higher pollination efficiency for a generalist plant *Hibiscus mutabilis*?

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## Abstract

Many insect species provide pollination services for flowering plants. However, the pollination efficiency of various pollinator species varies greatly due to differences in body size, foraging behavior, and visitation rate. Here, we investigated a generalist plant *Hibiscus mutabilis*, and we compared the body size, visitation rate, and pollination efficiency of five pollinator species. Our observations revealed that the pollination efficiency of the moth species was relatively lower than all bee species. The body length of five pollinator species increased the amount of transferred pollen, and larger bees tended to remove more pollen from anthers and deposit more pollen on stigmas, resulting in higher pollination efficiency. However, there was no correlation between the intertegular distance and pollination efficiency of visitors in *H. mutabilis*. Body length may be a better index of body size than intertegular distance.

## Introduction

Ninety percent of flowering plants are pollinated by animals (Ollerton *et al.* 2011; Tong *et al.* 2023). Without pollinators, many plants could not set seed and reproduce; and without plants to provide pollen, nectar, and other floral rewards, many animal populations would decline (Kearns *et al.* 1998). Pollinators tend to move both within and among neighboring plants, and the pollen transfer efficiency of pollinators varies markedly, so that most plants end up with a mixed mating strategy at the point of being pollinated (Harder and Barrett 1996; Goodwillie *et al.* 2005). Vogler and Kalisz (2001) reviewed available data to show that most plants achieve a mixture of selfing and outcrossing. Plants can control their mating opportunities by the way they manipulate their visitors. Attracting a larger number of pollinators is mainly determined by the advertising traits and floral rewards of plants. Therefore, understanding the pollination efficiency of various pollinators can help predict how different floral visitors could influence plant reproduction.

In animal-pollinated plants, the contribution of different pollinator species to plant's reproductive fitness differs significantly because their pollination efficiency varies greatly due to differences in body size, foraging behavior, and visitation rate (Chang *et al.* 2023). Fewer pollinator visits or less pollen delivered per visit may reduce the reproductive success of plants (Olsen 1996; Ashman *et al.* 2004; Sahl and Conner 2007). Body size is an important functional characteristic that underlies pollination-related ecological processes (Kendall *et al.* 2019). The body size of pollinators such as body length and intertegular distance can influence the amount of deposited pollen (Goulson *et al.* 2002; Földesi *et al.* 2020). The intertegular distance is a useful body size index established by Cane (Cane, 1987). Goulson *et al.* (2002) found that the amount of pollen transferred by bees was influenced by the intertegular distance. Larger bees tended to deposit more pollen on stigmas at each visit than smaller bees, and the interspecific body length and intertegular distance of bees had a positive effect on pollen deposition (Földesi *et al.* 2020; Chang *et al.*

2023). There was no correlation between intertegular distance and pollen deposition among individuals of the same species (Chang *et al.* 2023). However, whether pollen removal and pollination efficiency (pollination efficiency = pollen deposition/pollen removal, see Li *et al.* 2022) are affected by body size of pollinators is still unknown.

In this study, we used a generalist plant *Hibiscus mutabilis* as an example to investigate the impact of pollinators' body size on pollination efficiency. We measured the floral traits of plants and the body length and intertegular distance of various pollinator species. We identified the breeding system of *H. mutabilis* by imposing four pollination treatments. We compared the visitation rates of various pollinator species. To assess pollination efficiency, we examined pollen deposition and pollen removal of each pollinator species. Based on field investigations, we aimed to address the following three questions: (1) Are there differences in visitation rate and pollination efficiency among various pollinator species in *H. mutabilis*? (2) Does the species *H. mutabilis* have a mixed mating system? (3) Is the body size of pollinators related to pollination efficiency?

## Materials and Methods

### Study species and site

*Hibiscus mutabilis* (Malvaceae) is a hermaphroditic perennial shrub or small tree cultivated in many areas of both north and south China. This species is almost certainly native to China but was domesticated a long time ago. Flowering individuals can grow up to 2.5 m high. Flowers are solitary and axillary on the upper branches. Each flower is actinomorphic, with five petals, one staminal column, five styles, and one campanulate calyx. The corolla is white or reddish. The nectary is located at the base of the calyx. Flowering generally occurs from July to November. The flower longevity of one single flower lasts only 1–2 days. This study was conducted during the flowering season of 2023 in a field located at 104deg45'29" E, 30deg40'45" N, 433.1 m above sea level, about 39 km southeast of Jintang County, Sichuan Province, China.

### Floral traits

To understand the floral traits of *H. mutabilis*, 30 bagged flowers from 15 plants were examined on 10 October 2023. The flowers are single- or double-flowered on a 5–8 cm pedicel on the upper branches (Fig. 1A). The *H. mutabilis* flower displays a color change from white to red (Fig. 1B). First, corolla diameter, corolla height, sepal length, sepal width, petal length, petal width, stamen length, pistil length, ovary height, and ovary diameter of each flower were measured with a digital caliper to 0.01 mm. The base circumference was measured by a thread, then the length of the thread was determined by a digital caliper to 0.01 mm. The anther and ovule number of each flower were counted. To examine the production of pollen grains per flower, the anthers of each flower were dissected and washed in 400 mL of distilled water to dislodge the pollen grains from the anthers. The suspensions were stirred for 2 min, and three 1-mL samples of suspension were drawn respectively on the plankton counting chambers, after which the number of pollen grains in the samples was counted under a light microscope at x10 magnification. The pollen count of the three sub-samples (1 mL each) was averaged and multiplied by the dilution factor (400) to obtain the total number of pollen grains per flower. To evaluate the production of nectar volume per flower (open one day), nectar volume was measured using 10- $\mu$ L glass microcapillary tubes during the period of 17:00–18:00 p.m. on 10 October.

### Breeding system

To identify the breeding system of *H. mutabilis*, 160 flowers from 30 individual plants experienced four pollination treatments in September 2023. Flowers were randomly chosen from different plants to reduce the possible effect of resource reallocation on the fruit set, and were enclosed with fine-mesh polyester bags to exclude any visitors before the artificial treatments. To test for potential autogamy, 40 flowers were caged to exclude any insects. In addition, 40 flowers were hand-pollinated with self-pollen grains from flowers of the same individual, and another 40 flowers were hand-pollinated with outcross pollen grains from multiple flowers of other individuals to test for any differences in seed production between selfing and outcrossing.

The remaining 40 flowers without any treatment were exposed to open pollination as a natural control. Four weeks later, the fruits produced by these flowers were harvested, and the seeds and undeveloped ovules in each fruit were counted.

### Foraging behavior observations

To estimate the types of floral visitors and their foraging behaviors (for pollen or/and nectar) in *H. mutabilis*, we (four observers) observed the foraging behaviors of various visitors in the periods from 08:30 to 17:30 on sunny days in October 2023. Four plots (2m × 2m) were randomly established, each including 10 flowers. These plots were observed daily for 30 min. A total of 128 observation sessions were conducted. Using a camera (Nikon D7000), we recorded the foraging behaviors of various visitors. Moreover, we recorded the number of visits and the number of flowers visited by various visitors per 30 min, after which we calculated the visitation rates of each visitor (visits per flower per 30 min) by dividing the total number of observed flowers by the number of flowers visited per 30 min. The main pollinators were determined by the number of visits and the foraging behaviors.

### Measurements of body size of pollinators

To measure the body size of various pollinators, we captured 10 individual insects of each species visiting the flowers of *H. mutabilis* during peak flowering. The insect specimens were pinned and dried in a specimen box. Specimens were photographed using a stereoscopic microscope JSZ6S (Nanjing Jiangnan Yongxin Optical Co. Ltd., Nanjing, China) with a digital camera. After imaging, the body length and intertegular distance were measured using ImageJ 1.8.0 software (NIH Image, Research Services Branch, USA) (Fig. 2).

### Pollination efficiency

Our field surveys showed that there were five pollinator species of *H. mutabilis* during our experiments. To compare the pollen removal, pollen deposition, and pollination efficiency of various pollinator species, more than 200 flowers of *H. mutabilis* were selected randomly from different individuals and were bagged with fine-mesh polyester bags before blooming in October 2023. When the flowers bloomed, all flowers were exposed to pollinators. When the flowers had been visited a single time in the field, we harvested the flowers immediately. To estimate pollen grains deposited on the stigmas of the flowers, each stigma was dissected and washed in 5 mL of 75% alcohol to dislodge the pollen grains from the stigma. The suspension was stirred for 2 min, and the sample of suspension was drawn on the plankton counting chamber, after which the number of pollen grains in the sample was counted under a light microscope at ×10 magnification. Moreover, we counted pollen grains remaining in the anthers of the flowers following the methods described above. Pollen removal per flower was calculated as the mean number of pollen grains per flower minus the remaining grains per flower. Finally, pollination efficiency was calculated by dividing pollen deposition by pollen removal.

### Statistical analyses

For the pollination treatments, a generalized linear model (GLM) with binomial distribution and logistic-link function was used to detect the effects of the treatments on the seed set (with seed number as event variable, total ovule number as trial variable and different treatments as factors) and fruit set (with fruit number as event variable, total treated flower number as trial variable, and different treatments as factors). We also performed a GLM with normal distribution and identity-link function to test for differences in the visitation rates (with visitation rate as the dependent variable, and pollinator species as factors) and pollination efficiency (with pollination efficiency as the dependent variable, and pollinator species as factors) of various pollinator species. To compare pollen removal and pollen deposition among pollinator species, data were analyzed with a GLM with Poisson distribution and loglinear-link function (with pollen number as a dependent variable and different treatments as factors). We carried out a Pearson correlation analysis to determine the relationship between the body size and the pollination efficiency of various pollinator species in *H. mutabilis*. All statistical analyses were performed in SPSS V. 19.0 (SPSS Inc., USA).

### Results

## Floral traits

On average, each *H. mutabilis* flower produced  $72813 \pm 1221$  pollen grains and  $24.61 \pm 1.08$   $\mu\text{L}$  nectar volume (Table 1), suggesting that flowers offered plenty of floral rewards for visitors. Each flower produced  $241 \pm 3$  ovules, and the pollen/ovule ratio was  $303 \pm 6$ . The Corolla diameter is  $128.79 \pm 0.54$  mm and the corolla height is  $30.97 \pm 1.15$  mm, suggesting that this species has a large corolla.

## Breeding system

The GLM analysis showed that pollination treatments have significant influences on fruit set (Wald  $\chi^2 = 9.348$ ,  $df = 3$ ,  $P = 0.009$ ) and seed set (Wald  $\chi^2 = 22.018$ ,  $df = 3$ ,  $P < 0.001$ ) (Fig. 3). Under natural conditions, the fruit set and seed set were  $65 \pm 7.6$  % ( $N = 40$ ) and  $80.4 \pm 2.6$  % ( $N = 26$ ) respectively, which were significantly lower than hand self-pollination ( $87.5 \pm 5.3$  %,  $N = 40$ ,  $P = 0.004$ , and  $90 \pm 0.9$  %,  $N = 35$ ,  $P < 0.001$ , respectively) and cross-pollination ( $85 \pm 5.7$  %,  $N = 40$ ,  $P = 0.014$ , and  $87.3 \pm 1$  %,  $N = 34$ ,  $P = 0.002$ , respectively). It suggested that there was a pollen limitation under natural conditions. There was no significant difference in the fruit set between self-pollination and cross-pollination, indicating that *H. mutabilis* is highly self-compatible (Fig. 3). The fruit set of bagged flowers was zero ( $N = 40$ ), which indicated that neither spontaneous autogamy nor apomixis occurs in this species.

## Foraging behavior of pollinators

At our study site, *H. mutabilis* was visited by five insect species (Fig. 4), including four bee species (*Xylocopa appendiculata*, *Xylocopa dissimilis*, *Bombus breviceps*, and *Apis mellifera*) (Fig. 4A-F) and one moth species (*Macroglossum pyrrhosticta*) (Fig. 4G and H). The body length ( $12.58 \pm 0.18$  mm,  $N = 10$ ) and intertegular distance ( $3.29 \pm 0.07$  mm,  $N = 10$ ) of *A. mellifera* were the smallest among five visitor species (Wald  $\chi^2 = 4738.98$ ,  $df = 4$ ,  $P < 0.001$ , and Wald  $\chi^2 = 1877.37$ ,  $df = 4$ ,  $P < 0.001$ ) (Fig. 5B and C), but the visitation rate ( $0.92 \pm 0.08$  visits per flower per 30 min,  $N = 128$ ) of *A. mellifera* was the highest among five visitor species (Wald  $\chi^2 = 253.16$ ,  $df = 4$ ,  $P < 0.001$ ) (Fig. 5D). The body length ( $31.72 \pm 0.18$  mm,  $N = 10$ ) and intertegular distance ( $6.52 \pm 0.08$  mm,  $N = 10$ ) of *M. pyrrhosticta* were relatively larger than that of *X. dissimilis* ( $21.37 \pm 0.22$  mm and  $5.59 \pm 0.09$  mm,  $N = 10$ ,  $P < 0.001$ ) (Fig. 5A and B), *B. breviceps* ( $17.96 \pm 0.22$  mm and  $5.52 \pm 0.03$  mm,  $N = 10$ ,  $P < 0.001$ ) (Fig. 5B and C), and *A. mellifera* ( $P < 0.001$ ) (Fig. 5B and C), but the visitation rate ( $0.12 \pm 0.02$  visits per flower per 30 min,  $N = 128$ ) of *M. pyrrhosticta* was relatively lower than that of *B. breviceps* ( $0.38 \pm 0.05$  visits per flower per 30 min,  $N = 128$ ,  $P < 0.001$ ) (Fig. 5D), and *A. mellifera* ( $P < 0.001$ ) (Fig. 5D). All visitor species did not actively collect the pollen grains of *H. mutabilis*. When they entered the corolla of flowers to forage for nectar, they would remove pollen grains from mature anthers and deposit pollen grains on the stigma. Therefore, all visitor species served as effective pollinators of *H. mutabilis*.

## Pollination efficiency

The GLM analysis showed that the pollen removal ( $22750 \pm 456$ ,  $N = 20$ ) and pollen deposition ( $748 \pm 33$ ,  $N = 20$ ) of *X. appendiculata* were the most among five visitor species (Wald  $\chi^2 = 428.94$ ,  $df = 4$ ,  $P < 0.001$ , and Wald  $\chi^2 = 369.91$ ,  $df = 4$ ,  $P < 0.001$ ) (Fig. 6A and B). The pollination efficiency of *X. appendiculata* ( $0.033 \pm 0.002$ ) and *X. dissimilis* ( $0.032 \pm 0.002$ ) were relatively higher than that of the other three pollinator species (Wald  $\chi^2 = 187.35$ ,  $df = 4$ ,  $P < 0.001$ ) (Fig. 6C). In terms of four bee species, the pollen removal ( $11556 \pm 548$ ,  $N = 20$ ) and pollen deposition ( $306 \pm 19$ ,  $N = 20$ ) of *A. mellifera* were the fewest (Wald  $\chi^2 = 181.87$ ,  $df = 4$ ,  $P < 0.001$ , and Wald  $\chi^2 = 164.78$ ,  $df = 3$ ,  $P < 0.001$ ) (Fig. 6A and B), and the pollination efficiency of *A. mellifera* were the lowest (Wald  $\chi^2 = 10.17$ ,  $df = 4$ ,  $P = 0.02$ ) (Fig. 6C). The pollen removal ( $5896 \pm 459$ ,  $N = 20$ ) and pollen deposition ( $19 \pm 4$ ,  $N = 20$ ) of *M. pyrrhosticta* were relatively fewer than that of four bee species ( $P < 0.001$ ) (Fig. 6A and B), and the pollination efficiency ( $0.004 \pm 0.001$ ,  $N = 20$ ) of *M. pyrrhosticta* was also relatively lower than that of four bee species ( $P < 0.001$ ) (Fig. 6C).

## Relationships between pollen transfer and body size of pollinators

Pearson correlation analysis showed that there were significant positive correlations between the body length of five pollinator species and pollen removal, pollen deposition, and pollination efficiency ( $P < 0.05$ ) (Table

2), suggesting that the body length increased the amount of transferred pollen. When the moth species was excluded, the intertegular distance of four bee species was significantly and positively correlated to pollen removal and pollen deposition ( $P < 0.05$ ) (Table 2), suggesting that the larger bees tended to remove more pollen from anthers and deposit more pollen on stigmas. However, there was no correlation between the intertegular distance and pollination efficiency (Table 2).

## Discussion

Our investigations demonstrated that the species *H. mutabilis* showed a mixed mating system, and its sexual reproduction depended on pollinators. The floral reward (nectar) of *H. mutabilis* was consumed by various visitors, including four bee species and one moth species. The pollination efficiency of the moth species was relatively lower than all bee species. The body length of five pollinator species increased the amount of transferred pollen, and larger bees tended to remove more pollen from anthers and deposit more pollen on stigmas, resulting in higher pollination efficiency. However, there was no correlation between the intertegular distance and pollination efficiency of visitors in *H. mutabilis*. Body length may be a better index of body size than intertegular distance.

The nectar of *H. mutabilis* was not displayed at the base of the petals but at the base of the ovary. So the flower structure of *H. mutabilis* shielded visitors with shorter proboscis. The best match between the length of the proboscis and the circumference of the nectar secretion at the base of the flower is the *M. pyrrhosticta*, which suggests the *M. pyrrhosticta* should be the most important pollinator in its native habitat (Fig. 5A). However, the investigation results found that bees were still important pollinators of *H. mutabilis*. Although the proboscis length does not match the circumference of the basal nectar, they can suck in nectar from the gap between the front petals. Different proboscis lengths of bees could absorb different amounts of nectar, which can improve the chances of pollen removal and pollen deposition.

Although the moth species *M. pyrrhosticta* had the longest body length among the five visitor species, its pollination efficiency was relatively lower than all bees. The interpretation of the relationship between body size and pollination efficiency may depend on the influence of other morphological traits of *M. pyrrhosticta*. Unlike bees, the moth without hairiness may carry a few pollen grains. Moreover, the moth has a long proboscis so that they can get nectar easily without entering deep into the corolla of flowers. In this case, the moth may have little contact with floral sex organs. In terms of four bee species, the body length of *X. appendiculata* was  $1.8\times$  longer than that of honey bee *A. mellifera* (Fig. 5B). Moreover, the pollen removal and pollen deposition of *X. appendiculata* were  $1.9\times$  and  $2.4\times$  more than that of *A. mellifera* (Fig. 6A and B), and the pollination efficiency of *X. appendiculata* was  $1.2\times$  more than that of *A. mellifera* (Fig. 6C). These results demonstrated that larger bees removed and deposited more pollen than smaller bees in a single visit, and larger bees were more efficient pollinators in *H. mutabilis*. The reason was that larger bees were more likely to come into contact with floral sex organs. This finding is partly consistent with a previous study, which indicated that larger bee species deposited more pollen grains onto stigmas than smaller bees in *Brassica napus* (Chang *et al.* 2023), but they did not consider the effect of body size on pollen removal and pollination efficiency. Besides, we found that the intertegular distance was not an effective index of body size, because there was no correlation between the intertegular distance and pollination efficiency of visitors in *H. mutabilis*. Only the moth species was excluded, the intertegular distance of four bee species was significantly and positively correlated to pollen removal and pollen deposition. However, there were always significant positive correlations between the body length of four or five pollinator species and pollen removal, pollen deposition, and pollination efficiency. We concluded that body length may be a better index of body size than intertegular distance.

The visitation rate of bees is another important behavioral parameter. Honey bee *A. mellifera* was the most frequent visitor to flowers of *H. mutabilis*. The visitation rate of *A. mellifera* was  $5.1\times$  more than that of *X. appendiculata*, even though the pollination efficiency of *A. mellifera* was relatively lower. The high visitation rate of bees to flowers may increase the pollinator's interaction with the stigma or pollen transfer, so *A. mellifera* was also a very efficient pollinator in *H. mutabilis*. Although the pollination efficiency of *X. appendiculata* was higher than honey bees, they visited fewer flowers than honey bees. Therefore, it is

difficult to comprehensively assess which insect species contributes more pollination service to flowers in *H. mutabilis*, and further study is needed to investigate the pollination service of various pollinators to flowers throughout the flowering period of plants.

The flowers of *H. mutabilis* had a generalist pollination system and attracted various pollinator species by providing plenty of nectar rewards. Although *H. mutabilis* was highly self-compatible, there was pollen limitation under natural conditions. The sexual reproduction of *H. mutabilis* depended on pollinators. The visitation rate and pollination efficiency of various pollinator species were greatly different. The species *H. mutabilis* with a mixed mating system may be an adaptation to variable pollinator visiting.

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### Conflicts of interests

The authors declare that they have no conflict of interest.

### Authors contribution

Authors of the article include: Xiao-Qing Shi, Bin Zheng, Xiao-Li Liu, Qiu-Mei Quan, Yun-Xiang Li. The experimental design of this article is guided by Qiu-Mei Quan; Experimental site survey, receipt collection and analysis were completed by Xiao-Qing Shi and Bin Zheng; The article was illustrated by Xiao-Li Liu; Yun-Xiang Li provided guidance and objective proofreading for the article, and all authors contributed to further revisions. All authors read and approved the final manuscript.

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