INTRODUCTION

Plants those strongly depend on specific pollinators for pollination success adapt their floral traits to the characteristics of their pollinators. For example, previous studies have demonstrated that the flowering season matches the season when pollinators appear (Fleming, Sahley, Nolland, Nason, & Hamrick, 2001; Peter & Johnson, 2014; Queiroz, Quirino, Lopes, & Machado, 2016), that floral shapes fit the external characteristics of pollinators (Boberg et al., 2014; Nagano et al., 2014; Nilsson, 1988), that floral colors match the color vision of pollinators (Hoballah et al., 2007; Levin & Kerster, 1967; Sobel & Streisfeld, 2015), and that attractive traits of nectar secretion and...
odor emission patterns fit the activity patterns of pollinators (Cruz-Neto, Machado, Galetto, & Lopes, 2015; Heath, Landolt, Dueben, & Lenczewski, 1992; Krömer, Kessler, Lohaus, & Schmidt-Lebuhn, 2001). When the floral shape fits the external morphology of its pollinator, more pollen grains adhere to fixed positions on the pollinator, so that the plant transfers more pollen effectively (Bloch & Erhardt, 2008; Campbell, Waser, & Price, 1996). When the nectar secretion and odor emission patterns fit the activity patterns of pollinators, the plant can attract its pollinators more effectively, and the pollinator may visit more frequently, presumably increasing pollination success (Gijbels, van den Ende, & Honnay, 2014; Leiss & Klinkhamer, 2005).

Previous studies showed that pollinators induce selective pressures on floral traits. Plant adaptations to specific pollinators can occur when their distribution ranges closely overlap with those of their pollinators. However, when the distributional ranges of plants do not overlap with those of their specific pollinators, some plants change their flowering phenology, shape, color, nectar secretion pattern, and/or volatile components to attract another pollinator (Boberg et al., 2014; Nagano et al., 2014; Sun, Gross, & Schiestl, 2014). Finally, plants may speciate in each site (Fleming et al., 2001; Forest et al., 2014; Gowda & Kress, 2013). Otherwise, a plant might adapt its floral traits to several pollinator species (i.e., become generalized).

Insect- or bird-pollinated plants have been targeted in previous studies, and no studies have investigated the adaptations of mammal-pollinated plants to different mammalian pollinators in different regions. Although the diversity of mammal-pollinated plants is relatively low compared with insect-pollinated plants, there are many mammal-pollinated species throughout the world, especially in the tropics (Carthew & Goldingay, 1997; Fleming & Kress, 2013). However, pollination ecology of mammal-pollinated plants has been studied mainly in Australia and Africa, with only a few studies in Asia (Willmer, 2011).

*Mucuna macrocarpa* (Fabaceae) is a woody vine plant which is distributed from Southeast Asia to Kyushu, Japan (Tateishi & Ohashi, 1981). This flower is papilionaceous and utilizes a special pollination stage called "explosive opening" (Toyama, Kobayashi, Denda, Nakamoto, & Izawa, 2012). Stamens and pistils are tightly enclosed by the keel petals and are exposed when the flower opens explosively. The explosive opening is facilitated by different mammals (explosive openers) in different regions: Japanese macaques (*Macaca fuscata*) and Japanese martens (*Martes melampus*) in Kyushu; Formosan striped squirrels (*Callosciurus erythraeus*), Formosan striped squirrels (*Tamiops maritimus*), and masked palm civets (*Paguma larvata*) in Taiwan (Kobayashi, Denda, et al., 2015; Kobayashi et al. 2017; Toyama et al., 2012). Among them, Japanese macaques and red-bellied squirrels open the most flowers in Kyushu and Taiwan, respectively, compared with other explosive openers. Thus, these two species are the main pollinators in these regions (Kobayashi, Denda, et al., 2015; Kobayashi et al. 2017). Except for Japanese macaques, all explosive openers hold the wing petals with their forelegs and insert their snouts into the gap between the wings and banner petals and then push up the banner using their snout to feed on the nectar located inside the calyx. Japanese macaques open flowers using their hands. When all explosive openers open flowers successfully, many pollen grains adhere to them. In addition, the explosive opening is an indispensable stage for fruit set, as flowers do not open by themselves and no fruits are observed on unopened flowers (Kobayashi, 2017). Although bees collect pollen and stigma attaches to their body in some cases, most pollen grains are removed by explosive openers (Kobayashi, Denda, et al., 2015; Kobayashi et al. 2017; Toyama et al., 2012). Thus, explosive openers are considered as the main pollinators (Kobayashi, Denda, et al., 2015; Kobayashi et al. 2017; Toyama et al., 2012).

In this study, we aimed to reveal the relationships between floral traits (shape and nectar) and characteristics of explosive openers (external morphology and daily activity patterns) in three regions. We examined the following hypotheses: (1) Floral shapes differ among the three regions; (2) face size, which is an important trait for opening flowers explosively, is different among explosive openers; (3) floral shape correlates with face size of explosive openers; (4) nectar secretion patterns differ among the three regions; and (5) nectar secretion patterns correlate with the activity patterns of the main explosive openers.

### 2 | MATERIALS AND METHODS

#### 2.1 | Study sites

This study was conducted from 2013 to 2016 at five sites in three different regions with different explosive openers: one site in Kyushu (KK: 32°45–46′ N, 131°51–52′ E), two sites on Okinawajima Island (northern site [OY]: 26°46–49′ N, 128°14–17′ E and southern site [OU]: 26°14′ N, 127°45′ E) in Japan, and two sites in Taiwan (northern site [TB]: 24°38–41′ N, 121°22–25′ E and southern site [TK]: 21°57′ N, 120°48′ E) (Figure 1). Kyushu is a large island, but distribution of *M. macrocarpa* is limited to the study site. This species grows in the southward steep slope (Kobayashi, Izawa, et al., 2015). The annual mean temperature (2008–2017) in Kamae, the nearest meteorological observation point, is 17.4°C, and annual mean precipitation is 2,401 mm (Japan Meteorological Agency, 2018). On Okinawajima Island, this species is distributed throughout the island and mainly grows along the valley (Kusumoto & Enoki, 2008). The annual mean temperature (2008–2017) in Oku, the nearest meteorological observation point of OY, is 20.8°C, annual mean precipitation is 2,611 mm, and those in Naha, the nearest meteorological observation point of OU, are 23.4°C and 2,159 mm (Japan Meteorological Agency, 2018). In Taiwan, this species is also distributed from north to south, but elevation of distribution area is ranging from 100 to 1,500 m (Herbarium of National Taiwan University, 2012). Annual mean temperature (2010–2017) in Fu Xing, the nearest meteorological observation point of TB, is 20.0°C and mean annual precipitation is 3,194 mm, while those in Heng Chun, the nearest meteorological observation point of TK, are 25.8°C and 2,166 mm (Central Weather
All study sites are evergreen forests, but the flora is quite different among these sites. In addition, the individual planted in TK originated from near the study site.

2.2 Measurements of flowers and explosive openers

Firstly, floral shape and size were compared among regions. Mature and dropped fresh flowers were collected from four individuals in Kyushu, six individuals (OY: 3, OU: 3) on Okinawajima, and eight individuals (TB: 7, TK: 1) in Taiwan. Flower length, the gap between banner petals, gap between wing petals, gap between the top of the banner and the top of wings, and the width of the calyx were measured (Figure 2a). Floral shape was compared among regions using principal component analysis (PCA).

Secondly, the height and width of the rhinarium and height and width of parts of the upper jaw at the top of the lower jaw of explosive openers were measured for external morphology of mammalian pollinators in each region (Figure 2b,c). Measured species were Japanese martens, Ryukyu flying foxes, red-bellied squirrels, Formosan striped squirrels, and masked palm civets, which use their snouts for explosive opening (Kobayashi, Denda, et al., 2015; Kobayashi et al. 2017; Toyama et al., 2012). Japanese macaques were the main openers in Kyushu; however, as they opened flowers using their hands, we did not measure any facial parts. Samples of Japanese martens (n = 16) and live individuals captured for ecological research (n = 10) on the Tsushima Islands, Japan. Captive Ryukyu flying foxes at the University of the Ryukyus were measured (n = 16). Eleven were rescued from the wild, and five were born in captivity.

Specimens of red-bellied squirrels (n = 31) and masked palm civets (n = 17) stored in the National Museum of Natural Science of Taiwan and Endemic Species Research Institute were measured. We could not find available specimens of striped squirrels, so we used the mean value of skull data (n = 4) measured by Chang (2011). The external morphology of opener snouts was compared using PCA.

Finally, the relationship between the floral gap size and snout size of the explosive openers was investigated in each region. When the explosive openers opened flowers using their snouts, the direction of snout insertion into the flower gap was almost fixed in the right-side upward direction (see Kobayashi, Denda, et al., 2015; Kobayashi et al. 2017; Toyama et al., 2012). Thus, the gaps of flower banners were compared using the width of rhinarium or width of upper jaw of openers, and the gaps between the tops of banners and the tops of flower wings were compared using the height of rhinarium or height of upper jaw of openers (see Figure 2).

2.3 Measurement of nectar

To investigate the daily change in nectar secretion, the volume, weight, and sugar concentration of nectar were measured every 3 hrs. Mature flowers were picked from four individuals in Kyushu, five individuals (OY: 1, OU: 4) on Okinawajima and six individuals (TB: 5, TK: 1) in Taiwan. Nectar was collected from inside the calyx, and volume was measured using a microsyringe (MS-N100; Ito Corporation, Tokyo, Japan). Nectar weight was measured using a digital portable balance (TR-SC30; Pepaless, Hyogo, Japan) and sugar concentration (Brix index) was measured using a handheld.
refractometer with special compensating thermometer (HSR-500; Atago, Tokyo, Japan).

In addition, the sugar composition was analyzed using high-performance liquid chromatography (HPLC). Nectar used for HPLC was collected from 12 flowers at 0900 and 2100 hr in each region and put into microtubes and stored in the freezer (−20°C) until analysis. Firstly, the acetonitrile solution (nectar:distilled water:acetonitrile = 2:33:65) was prepared. Then, the acetonitrile solution was percolated using a Mini-UniPrep syringeless filter (UN203NPUAQU; GE Healthcare companies, Buckinghamshire, UK). The percolated acetonitrile solution was analyzed using an HPLC analysis machine (LC-20AD; Shimadzu Corporation, Kyoto, Japan). The Sugar-D column (Nacalai Tesque, Kyoto, Japan) was used, and 80% acetonitrile solution was delivered at a flow rate of 0.5 ml/min. Sugar was identified from a chromatogram, which had been calculated previously from the components of each sugar found in our samples.

ANOVA was used to compare the volume, weight, and sugar concentration of nectar in flowers from each region, and the chi-square test was used to compare the sugar components over time and across regions. All statistical analyses were conducted using the statistical software R ver. 3.4.0 (R Core Team, 2017).

3 | RESULTS

3.1 | Comparison between floral and opener shapes

All flower parts were significantly different among regions, with the longest length observed in Kyushu and the shortest on Okinawajima (ANOVA for each flower trait; p < 0.05) (Table 1). The maximum and minimum values of each part were observed in the different regions. The PCA of floral parts showed that floral shape had the least difference among the three regions (Figure 3). In addition, the external morphology of the openers’ snouts differed among the three regions. Snouts of Japanese martens and masked palm civets were larger than those of squirrels (Figure 4). Snouts of Ryukyu flying foxes were medium-sized; however, the rhinarium was larger than that of any other opener (Figure 4).

The snout sizes of Ryukyu flying foxes and red-bellied squirrels were smaller than the flower gaps (gaps between banner petals and gaps between the tops of the banner and the tops of wings; see Figure 2a) into which explosive openers inserted their snouts (Figure 5). The rhinarium sizes of Japanese martens and masked palm civets were smaller than their respective flower gaps; however, their upper jaw sizes were larger than the flower gaps (Figure 5). The mean size of the flower gap of flower and the mean size of the snout of the main explosive openers were not positively correlated with each other (Figure 5a–c), except for height of upper jaw versus gap between the top of the banner and top of the wings (Figure 5d), although flower gaps showed high variation in all regions (Figure 5).

3.2 | Nectar production pattern

The nectar volume, weight, and nectar concentration did not change throughout the day in any of the regions (ANOVA; p > 0.05) (Table 2, Figure 6). Also, nectar was stored inside the calyx throughout the day. Nectar volume was 429.4 ± 112.14 (mean ± SD), 437.1 ± 86.6, and 429.5 ± 99.2 μl, and weight was 499.1 ± 126.4, 489.9 ± 91.2, and 484.8 ± 112.0 mg in Kyushu, Okinawajima, and Taiwan, respectively; neither were different among the three regions (ANOVA; volume: F2,215 = 0.41, p = 0.67, weight: F2,635 = 1.02, p = 0.36) (Figure 6). However,
Nectar concentration was 28.2 ± 1.5% in Kyushu, which was significantly higher than that in Okinawajima (24.5 ± 1.4%) and Taiwan (25.4 ± 2.0%) (ANOVA; $F_{2,721} = 330.97, p < 0.05$) (Figure 6). The analysis of sugar component ratio showed that sucrose was dominant in all regions. The ratio of sucrose was over 65%, and the range of mean sugar ratio was 1.93-2.07 in the three regions (Figure 7). In addition, the sugar component ratio between morning and night was the same in all regions (chi-square test; Kyushu: $\chi^2 = 0.00, p > 0.05$, Okinawajima: $\chi^2 = 0.00, p > 0.05$, Taiwan: $\chi^2 = 0.05, p > 0.05$) (Figure 7).

4 | DISCUSSION

Floral shape and size of *M. macrocarpa* differed among the three regions. Although the sample size of striped squirrel was small, size and external morphology of snouts of explosive openers were

**FIGURE 4** Principal component analysis of shape of the tip of the nose of explosive openers. PC1 indicates the size of the tip of the nose, and PC2 indicates the height-to-width ratio.
different; however, the sizes of flower gaps and the rhinarium size of the main explosive openers were not correlated. Nectar was stored inside the calyx throughout the day, and daily nectar secretion patterns were not different among regions. Therefore, these results confirmed hypotheses 1 and 2, while hypotheses 3, 4 and 5 were rejected.

Many previous studies clarified that some plants adapt their floral shapes to the main pollinators in each region when the main pollinator differs among regions (Anderson & Johnson, 2008; Boberg et al., 2014; Johnson & Steiner, 1997). In this study, the floral shape and size of *M. macrocarpa* slightly differed among regions. In addition, there were specific mammalian openers in each region (Kobayashi, Denda, et al., 2015; Kobayashi et al. 2017; Toyama et al., 2012), and snout sizes of these openers were also different among regions. However, contrary to our third hypothesis, floral dimensions did not correlate with snout sizes of main openers. Thus, we concluded that this plant did not adapt its floral shapes to individual pollinators. One possible reason might be that mammals have a higher intraspecific size variation (including differences between sexes or among ages) than insects or birds and cannot exert sufficient selection pressure on the plants they pollinate.

Nectar secretion patterns were not adapted to mammalian openers in each region in this study. Bat-pollinated plants generally secrete nectar at night (Fægri & van der Pijl, 1979; Willmer, 2011). This characteristic is also observed in *Mucuna* species (Table 2); for example, *M. urens*, whose explosive opening depends on tiny nectar-feeding bats (*Glossophaga soricina*), secretes nectar only at night (Agostini, Sazima, & Galetto, 2011). In contrast, *M. japira* and *M. sempervirens*, which are explosively opened by passerine birds (*Cacicus haemorrhous*) and squirrels (*Dremomys pernyi* and *C. erythraeus*), respectively, secrete nectar throughout the day (Agostini et al., 2011; Liu, Shah, Zha, Mohsin, & Ishtiaq, 2013) (Table 3). However, contrary to our fourth and fifth hypotheses, the nectar secretion patterns of

---

**TABLE 2** Results of ANOVA comparing among sampling times of nectar

|          | Kyushu |          | Okinawajima |          | Taiwan |
|----------|--------|----------|-------------|----------|--------|
|          | n      | F value  | p value     | n        | F value  | p value |
| Volume   | 275    | 1.33     | 0.23        | 198      | 0.73    | 0.66 |
| Weight   | 274    | 1.53     | 0.15        | 120      | 0.55    | 0.82 |
| Concentration | 283 | 1.93     | 0.06        | 197      | 0.91    | 0.51 |

**FIGURE 6** Nectar volume, weight, and concentration in flowers from Kyushu (a, d, and g), Okinawajima (b, e, and h), and Taiwan (c, f, and i). Error bars indicate SD.

**FIGURE 7** Proportions of sugar components in nectar of flowers from Kyushu (a), Okinawajima (b), and Taiwan (c) at 0900 and 2100 hr. Error bars indicate standard deviation.
M. macrocarpa did not coincide with the activity patterns of each explosive opener in each region. Furthermore, nectar secretion patterns were not different among regions even when either diurnal or nocturnal pollinators occurred (Kobayashi, Denda, et al., 2015; Kobayashi et al. 2017; Toyama et al., 2012). In comparison, plants pollinated by pteropodid bats were reported to have higher sucrose content (Baker & Baker, 1983; Baker, Baker, & Hodges, 1998), which might also be the case in the nonflying mammal-pollinated plants, although the sample size of previous studies is small (Willmer, 2011).

The concentration and sugar ratio of nectar in Mucuna are determined by the species of pollinator (Agostini et al., 2011; Liu et al., 2013), except for M. macrocarpa (Table 3). Although the squirrel-pollinated M. sempervirens has some similarities in nectar secretion patterns (i.e., nectar concentration, sugar ratio, and daily variation) (Table 3), the nectar secretion patterns of M. macrocarpa are unique among Mucuna species. In conclusion, M. macrocarpa may attract both diurnal and nocturnal mammals. Although M. macrocarpa uses explosive openers, a special pollination mechanism, and restricts pollinator species, the floral shapes and nectar secretion dynamics do not match the main explosive openers in each region. Therefore, mammalian pollinators may not be selective pressures for floral traits in this plant.

Although the floral traits of M. macrocarpa, such as shape and nectar secretion patterns, did not match the main pollinators in each region, there were small differences among regions. Floral traits only differed in biotic factors, but also in abiotic factors (e.g., Campbell, 1996; Petanidou, Goethals, & Smets, 2000). Therefore, abiotic factors, such as temperature, precipitation, and soil conditions, should be considered as well as genetic drift caused by bottlenecks and/or founder effects on floral traits in future.

In the eastern Caribbean, bird-pollinated plants have different pollinators in different regions and have evolved their floral traits depending on the traits of the pollinator in each region (Gowda & Kress, 2013; Temeles & Kress, 2003). In the Sonoran Desert, bat-pollinated cactus species are known to adapt to both bird and bat pollinators (i.e., become more generalized) (Fleming et al., 2001). Examples of vertebrate pollinator shifts are reported from the New World, and these plants adapt to their new bird pollinators through speciation. However, no reports have demonstrated that mammal-pollinated plants have different mammalian pollinators in different regions, except for M. macrocarpa. The Mucuna group is distributed throughout tropics and subtropics (Schrire, 2005), and many species are pollinated specifically by birds or bats (Agostini, Sazima, & Sazima, 2006; Cotton, 2001; Grünmeier, 1993; Hopkins & Hopkins, 1993; Sazima, Buzato, & Sazima, 1999). However, plants pollinated by multiple mammals are found only in Asia (Kobayashi, Denda, et al., 2015; Kobayashi et al. 2017; Toyama et al., 2012). One reason why bat-pollinated plants have become specialized or adapted to local vertebrate pollinators in the New World is the high diversity of nectar-feeding specialist birds and bats (Fleming & Kress, 2013). Conversely, the diversity of nectar-feeding mammals is low in the Old World, especially in Asia (see Fleming & Kress, 2013), while the diversity of omnivorous mammals, such as squirrels, macaques, and civets, is high in

### TABLE 3

Comparison of components of nectar secretion patterns among species

| Species          | Study sites | Explosive opener | Volume (μl)a | Weight (mg)b | Sugar ratio S/(F + G)a | Concentration (%)a | Dominant sugar  | Secretion pattern               |
|------------------|-------------|------------------|--------------|--------------|------------------------|--------------------|-----------------|---------------------------------|
| M. macrocarpa    | Kyushu      | Japanese macaque | 429.4        | 499.1        | 1.93                   | 28.2               | Sucrose         | Throughout the day             |
|                  | Okinawajima | Ryukyu flying fox | 437.1        | 499.9        | 2.07                   | 24.5               | Sucrose         | Throughout the day             |
|                  | Taiwan      | Red-berried squirrel | 439.5      | 484.8        | 1.97                   | 25.4               | Sucrose         | Throughout the day             |
|                  |             | Squirrels        | 20–80        | 310          | 5.38                   | 29                 | Constant        | Throughout the day             |
| M. sempervirens  |             | Tiny bats        | 340          | 340          | 0.37                   | 10                 | Fructose        | Throughout the day             |
| M. urens         |             | Passe-renière    | 340          | 340          | 0.26                   |                    |                 |                                  |

a Each value shows average.

b Present study. c Liu et al. (2013). d Agostini et al. (2011).
Southeast Asia (Corlett, 2007). Therefore, in case the nectar-feeding specialist bats and birds are lacking, plants have evolved nonflying mammal-dependent and/or generalist-like pollination systems.

However, this hypothesis is based on the information of one specific genus. Mammalian pollinators are not well clarified in Asian regions. Further researches clarifying pollinators of mammal-pollinated plants are needed to establish this hypothesis.

ACKNOWLEDGMENTS

We thank Atsushi Nakamoto (Okayama University of Science), Yoko Okawara, Hiroaki Ui, Keiichiro Abe (University of the Ryukyus), National Museum of Natural Science (Taiwan), and Taiwan Endemic Species Research Institute for supporting this study. HPLC analysis was supported by the Center for Research Advancement and Collaboration, University of the Ryukyus. We also thank the reviewers for giving us valuable comments. This study was partly supported by KAKENHI (Grant Numbers 25·114 and 16H05771).

CONFLICT OF INTEREST

None declared.

AUTHOR CONTRIBUTIONS

S. K., T. D., and M. I. conceived and designed the study. S. K. contributed to all surveys and analysis. T. D. and M. I. surveyed in Okinawajima, and C.-C. L. and S.-H. W surveyed in Taiwan. All authors contributed to make up the draft and approved for publication.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.nv5cr00

ORCID

Shun Kobayashi http://orcid.org/0000-0003-3167-3358

REFERENCES

Agostini, K., Sazima, M., & Galetto, L. (2011). Nectar production dynamics and sugar composition in two Mucuna species (Leguminosae, Faboideae) with different specialized pollinators. Naturwissenschaften, 98, 933–942. https://doi.org/10.1007/s00114-011-0844-6

Agostini, K., Sazima, M., & Sazima, I. (2006). Bird pollination of explosive flowers while foraging for nectar and caterpillars. Biotropica, 38, 674–678. https://doi.org/10.1111/j.1744-7429.2006.00191.x

Anderson, B., & Johnson, A. D. (2008). The geographical mosaic of coevolution in a plant-pollinator mutualism. Evolution, 62, 220–225.

Baker, H. G., & Baker, I. (1983). Floral nectar sugar constituents in relation to pollinator type. In C. E. Jones & R. J. Little (Eds.), Handbook of experimental pollination ecology (pp. 117–141). New York, NY: Nostrand Reinhold.

Baker, H. G., Baker, I., & Hodges, S. A. (1998). Sugar composition of nectars and fruits consumed by birds and bats in the tropics and subtropics. Biotropica, 30, 559–586. https://doi.org/10.1111/j.1744-7429.1998.tb00997.x

Bloch, D., & Erhardt, A. (2008). Selection toward shorter flowers by butterflies whose proboscides are shorter than floral tubes. Ecology, 89, 2453–2460. https://doi.org/10.1890/06-2023.1

Boberg, E., Alexandersson, R., Jonsson, M., Maad, J., Ågren, J., & Nilsson, L. A. (2014). Pollinator shifts and the evolution of spur length in the moth-pollinated orchid Platanthera bifolia. Annals of Botany, 113, 267–275. https://doi.org/10.1093/aob/mct1217

Campbell, D. R. (1996). Evolution of floral traits in a hermaphroditic plant: Field measurements of heritabilities and genetic correlations. Evolution, 50, 1442–1453. https://doi.org/10.1111/j.1558-5646.1996.tb03918.x

Campbell, D. R., Waser, N. M., & Price, M. V. (1996). Mechanisms of hummingbird-mediated selection for flower width in Ipomopsis aggregata. Ecology, 77, 1463–1472. https://doi.org/10.2307/226543

Carthew, S. M., & Goldingay, R. L. (1997). Non-flying mammals as pollinators. Trends in Ecology and Evolution, 12, 104–108. https://doi.org/10.1016/S0169-5347(96)10067-7

Central Weather Bureau (2018). Search for past meteorological data. Retrieved from http://e-service.cwb.gov.tw/HistoryDataQuery/index.jsp

Chang, S.-W. (2011). Molecular phylogenetics of the genus Tamiops and geographic variation in genetics and morphology of Tamiops maritimus formosanus in Taiwan. Ph.D. thesis, Tonghai University, Taichung.

Corlett, R. T. (2007). What’s so special about Asian tropical forests? Current Science, 93, 1551–1557.

Cotton, P. A. (2001). The behavior and interactions of birds visiting Erythrina fusca flowers in the Colombian Amazon. Biotropica, 33, 662–669. https://doi.org/10.1111/j.1744-7429.2001.tb00223.x

Cruz-Neto, O., Machado, I. C., Galetto, L., & Lopes, A. V. (2015). The influence of nectar production and floral visitors on the female reproductive success of Inga (Fabaceae): A field experiment. Botanical Journal of the Linnean Society, 177, 230–245. https://doi.org/10.1111/bot.12236

Fægri, K., & van der Pijl, L. (1979). The principles of pollination ecology, 3rd ed. Oxford, UK: Pergamon Press.

Fleming, T. H., & Kress, W. J. (2013). The ornament of life: Coevolution and conservation in the tropics. Chicago, IL: The University of Chicago Press. https://doi.org/10.7208/chi9780226023328.001.0001

Fleming, T. H., Sahley, C. T., Nason, J. N., Nason, J. D., & Hamrick, J. L. (2001). Sonoran Desert columnar cacti and the evolution of generalized pollination systems. Ecological Monograph, 71, 511–530. https://doi.org/10.1890/0012-9615(2001)071[0511:SDCCAT]2.0.CO;2

Forest, F., Goldblatt, P., Manning, J. C., Baker, D., Colville, J. F., Devy, D. S., ... Buerki, S. (2014). Pollinator shifts as triggers of speciation in painted petal irises (Lapeirousia: Iridaceae). Annals of Botany, 113, 357–371. https://doi.org/10.1093/aob/mct248

Gijbels, P., van den Ende, W., & Honnay, O. (2014). Landscape scale variation in nectar amino acid and sugar composition in a Lepidoptera pollinated orchid species and its relation with fruit set. Journal of Ecology, 102, 136–144. https://doi.org/10.1111/j.1365-2745.2012.12183

Gowda, V., & Kress, W. J. (2013). A geographic mosaic of plant-pollinator interactions in the Eastern Caribbean Islands. Biotropica, 45, 224–235. https://doi.org/10.1111/j.1744-7429.2012.00915.x

Grünmeier, R. (1993). Bestäubung der Fabaceae (Fabaceae): A field experiment. In W. Barthlott, C. M. Naumann, K. Schmidt-Loske, & K.-L. Schuchmann (Eds.), Animal-plant interactions in tropical environments (pp. 29–39). Bonn, Germany: Museum A. Koenig.

Heath, R. R., Landolt, P. J., Dueben, B., & Lenczewski, B. (1992). Identification of floral compounds of night-blooming jessamine...
attractive to cabbage looper moths. *Environmental Entomology*, 21, 854–859. https://doi.org/10.1093/ee/21.4.854

Herbarium of National Taiwan University (2012). *Plant of Taiwan*. Retrieved from http://tai2.ntu.edu.tw

Hoballah, M. E., Gübitz, T., Stuurman, J., Broger, L., Barone, M., Mandel, T., ... Kuhlemeyer, C. (2007). Single gene-mediated shift in pollinator attraction in *Petunia*. *Plant Cell*, 19, 779–790. https://doi.org/10.1105/tpc.10.048694

Hopkins, H. C. F., & Hopkins, M. J. G. (1993). Rediscovery of *Mucuna macropoda* (Leguminosae: Papilionoideae), and its pollination by bats in Papua New Guinea. *Kew Bulletin*, 48, 297–305. https://doi.org/10.2307/4117936

Japan Meteorological Agency (2018). *Search for past meteorological data*. Retrieved from http://www.data.jma.go.jp/obd/stats/etrn/index.php

Johnson, S. D., & Steiner, K. E. (1997). Long-tongued fly pollination and evolution of floral spur length in the *Disa draconis* complex (Orchidaceae). *Evolution*, 51, 45–53. https://doi.org/10.1111/j.1558-5646.1997.tb02387.x

Kobayashi, S. (2017). Mammal-dependent pollination system of *Mucuna macrocarpa* (Fabaceae). Ph.D. thesis, University of the Ryukyus, Okinawa.

Kobayashi, S., Denda, T., Liao, C.-C., Wu, S.-H., Lin, Y.-S., & Izawa, M. (2017). Squirrel pollination of *Mucuna macrocarpa* (Fabaceae) in Taiwan. *Journal of Mammalogy*, 98, 533–541. https://doi.org/10.1093/jmammal/gyw189

Kobayashi, S., Denda, T., Mashiba, S., Iwamoto, T., Doi, T., & Izawa, M. (2015). Pollination partners of *Mucuna macrocarpa* (Fabaceae) at the northern limit of its range. *Plant Species Biology*, 30, 272–278. https://doi.org/10.1111/1442-1984.12065

Kobayashi, S., Izawa, M., Denda, T., Mashiba, S., Doi, T., & Iwamoto, T. (2015). Appearance of new relationship between *Mucuna macrocarpa* (Fabaceae) and Japanese macaques as pollination partner: Indirect effect of afforestation policy. *Primate Research*, 31, 39–47. (In Japanese with English summary). https://doi.org/10.2354/psj.31.003

Krömer, T., Kessler, M., Lohaus, G., & Schmidt-Lebuhn, A. N. (2001). Nectar sugar composition and concentration in relation to pollination syndromes in *Bromeliaceae*. *Annals of Botany*, 87, 267–273.

Kusumoto, B., & Enoki, T. (2008). Contribution of a liana species, *Mucuna macrocarpa* Wal., to litterfall production and nitrogen input in a subtropical evergreen broad-leaved forest. *Journal of Forest Research*, 13, 35–42. https://doi.org/10.1007/s10310-007-0046-4

Leiss, K. A., & Klinkhamer, P. G. L. (2005). Spatial distribution of nectar production in a natural *Echium vulgare* population: Implications for pollinator behaviour. *Basic and Applied Ecology*, 6, 317–324. https://doi.org/10.1016/j.baae.2005.02.006

Levin, D. A., & Kerster, H. W. (1967). Natural selection for reproductive isolation in *Phlox*. *Evolution*, 21, 679–687. https://doi.org/10.1111/j.1558-5646.1967.tb03425.x

Liu, T., Shah, A., Zha, H.-G., Mohsin, M., & Ishfaq, M. (2013). Floral nectar composition of an outcrossing bean species *Mucuna sempervirens* Hemsl (Fabaceae). *Pakistan Journal of Botany*, 45, 2079–2084.

Nagano, Y., Abe, K., Kitazawa, T., Hattori, M., Hirao, A. S., & Itino, T. (2014). Changes in pollinator fauna affect altitudinal variation of floral size in a bumblebee-pollinated herb. *Ecology and Evolution*, 4, 3395–3407. https://doi.org/10.1002/ece3.1191

Nilsson, L. A. (1988). The evolution of flowers with deep corolla tubes. *Nature*, 334, 147–149. https://doi.org/10.1038/334147a0

Peter, C. I., & Johnson, S. D. (2014). A pollinator shift explains floral divergence in an orchid species complex in South Africa. *Annals of Botany*, 113, 277–288. https://doi.org/10.1093/aob/mct216

Queiroz, J. A., Quirino, Z. G. M., Lopes, A. V., & Machado, I. C. (2016). Vertebrate mixed pollination system in *Encholirium spectabile*: A bromeliad pollinated by bats, opossum and hummingbirds in a tropical dry forest. *Journal of Arid Environments*, 125, 21–30. https://doi.org/10.1016/j.jaridenv.2015.09.015

R Core Team (2017). *R: A language and environment for statistical computing*. Vienna: Austria: R Foundation for Statistical Computing. Retrieved from http://www.R-project.org

Sazima, M., Buzato, S., & Sazima, I. (1999). Bat-pollinated flower assemblages and bat visitors at two Atlantic forest sites in Brazil. *Annals of Botany*, 83, 705–712. https://doi.org/10.1093/abo.1999.0876

Schrière, B. D. (2005). Tribe *Phaseoleae*. In G. Lewis, B. D. Schrire, B. Mackinder, & M. Lock (Eds.), *Legumes of the world* (pp. 393–431). London, UK: Royal Botanic Gardens, Kew.

Sobel, J. M., & Streisfeld, M. A. (2015). Strong pre-mating reproductive isolation drives incipient speciation in *Mimulus aurantiacus*. *Evolution*, 69, 447–461. https://doi.org/10.1111/evo.12589

Sun, M., Gross, K., & Schiestl, F. P. (2014). Floral adaptation to local pollinator guilds in a terrestrial orchid. *Annals of Botany*, 113, 289–300. https://doi.org/10.1093/aob/mct219

Tateishi, Y., & Ohashi, H. (1981). Eastern Asian species of *Mucuna* (Leguminosae). *Journal of Plant Research*, 94, 91–105.

Temeles, E. J., & Kress, W. J. (2003). Adaptation in a plant-hummingbird association. *Science*, 300, 630–633. https://doi.org/10.1126/science.1080003

Toyama, C., Kobayashi, S., Denda, T., Nakamoto, A., & Izawa, M. (2012). Feeding behavior of the Orii’s flying-fox, *Pteropus dasymallus inopinatus*, on *Mucuna macrocarpa* and related explosive opening of petals, on Okinawajima Island in the Ryukyu Archipelago, Japan. *Mammal Study*, 37, 205–212. https://doi.org/10.3106/041.037.0304

Willmer, P. (2011). *Pollination and floral ecology*. Princeton, NJ: Princeton University Press. https://doi.org/10.1515/9781400838943

How to cite this article: Kobayashi S, Denda T, Liao C-C, Lin Y-H, Wu S-H, Izawa M. Floral traits of mammal-pollinated *Mucuna macrocarpa* (Fabaceae): Implications for generalist-like pollination systems. *Ecol Evol*. 2018:8:8607–8615. https://doi.org/10.1002/ece3.4404