

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/328162632>

# Regional differences in mammalian pollinators of *Mucuna macrocarpa* (Leguminosae): a Review

Article · September 2018

CITATIONS

0

READS

112

8 authors, including:



**Shun Kobayashi**

University of the Ryukyus

16 PUBLICATIONS 22 CITATIONS

[SEE PROFILE](#)



**Chi-Cheng Liao**

Chinese Culture University

15 PUBLICATIONS 72 CITATIONS

[SEE PROFILE](#)



**Somsak Panha**

Chulalongkorn University

531 PUBLICATIONS 1,122 CITATIONS

[SEE PROFILE](#)

Some of the authors of this publication are also working on these related projects:



Systematics and phylogeography of freshwater bivalves (Unionidae and Corbiculidae) in the mainland Southeast Asia [View project](#)

## Short Note

# Regional Differences in Mammalian Pollinators of *Mucuna macrocarpa* (Leguminosae): a Review

SHUN KOBAYASHI<sup>1\*</sup>, TETSUO DENDA<sup>1</sup>, CHI-CHENG LIAO<sup>2</sup>,  
JUMLONG PLACKSANOF<sup>3</sup>, SURACHIT WAENGSOTHORN<sup>3</sup>, CHITTIMA  
ARYUTHAKA<sup>4</sup>, SOMSAK PANHA<sup>5,6</sup>, MASAKO IZAWA<sup>1</sup>

<sup>1</sup>Faculty of Science, University of the Ryukyus, 1 Senbaru, Nishihara, Okinawa 903-0213 JAPAN

<sup>2</sup>Department of Life Science, Chinese Culture University, 55 Hwangang Road, Shilin, Taipei 11114 TAIWAN

<sup>3</sup>Sakaerat Environmental Research Station, Thailand Institute of Scientific and Technological Research, 1 Moo 9  
Udom, Wang Nam Khieo, Nakhon Ratchasima 30370 THAILAND

<sup>4</sup>Faculty of Fishery, Kasetsart University, 50 Ngam Wong Wan Road, Lat Yao, Chatuchak,  
Bangkok 10900 THAILAND

<sup>5</sup>Department of Biology, Chulalongkorn University, Payathai Road, Pathumwan, Bangkok 10330 THAILAND

<sup>6</sup>Center of Excellence on Biodiversity, Ministry of Education and Chulalongkorn University,  
Bangkok 10400 THAILAND

\* Corresponding Author: Shun Kobayashi (cheirotonus.jambar@gmail.com)

Received: 17 May 2018; Accepted: 7 August 2018

Many angiosperms are pollinated by animals<sup>1</sup>. Among them, certain species are pollinated exclusively by mammals, although mammal-pollinated plants are fewer in number than insect-pollinated plants<sup>2</sup>. Mammal-pollinated plants are known from many taxa which reviewed by Fleming and Kress<sup>3</sup>. In addition, specific groups of mammals are known pollinators. The most well-known of these are bats, but various non-flying mammals pollinate plants<sup>4</sup>.

This study focuses on *Mucuna* (Leguminosae). Genus *Mucuna* includes more than 100 species and this genus is distributed throughout tropics and subtropics<sup>5</sup>. *Mucuna* has inflorescences with relatively large flowers and this genus has been considered to be pollinated by bats or birds specifically<sup>6</sup>.

Among pollinators of *Mucuna* species, this study reviews the behavior of *Mucuna macrocarpa*'s mammalian pollinators and its flower structure. In addition, we discuss

the challenges of pollination studies in this genus. *Mucuna macrocarpa* is an evergreen woody vine. It produces 30–50 cm long inflorescences bearing 10–30 flowers with purple and pale green petals (Fig. 1). Matured flowers emit a fermentation-like odor. *Mucuna macrocarpa* is distributed from Southeast Asia to Japan<sup>7</sup>. In Thailand, it occurs in evergreen and mixed forests in the central to northern regions<sup>8</sup>. In the subtropics or temperate regions, it occurs in evergreen forests. The flowering season changes annually and locally, and is thought to take place over one or two months between January and May.

### Methods of Observation

Previous observations have been either direct, in which observers stay in front of the target flowers, or via video cameras<sup>9,10</sup>. However, these methods have limitations, given the wariness of mammal visitors and influence of observers on their flower-visiting behavior and staying time. In addition, night-vision scopes are needed,

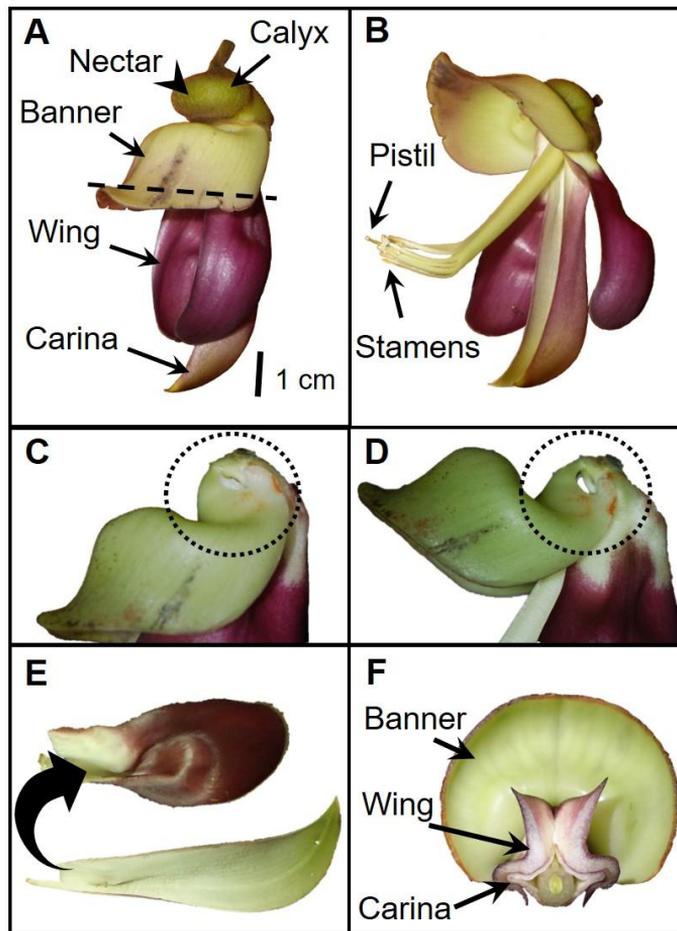


**FIGURE 1.** Inflorescences of *Mucuna macrocarpa*.

and observation of detailed flower-visiting behavior is difficult. Video cameras are expensive and battery life is short, placing a limitation on observation time. In the 1990s, automatic camera traps were developed for observation of mammalian flower visitors<sup>11</sup>. However, detailed observation of flower-visiting behavior is required, because not all flower visitors contribute to pollination, and some visitors rob nectar or drop flowers<sup>12-14</sup>, and this method does not allow for

description of flower-visiting behavior from photographs.

We used automatic video camera traps to resolve these problems<sup>15</sup>. There are various types of trigger<sup>16</sup>. Among them, cameras with infrared sensors which detect differences between air temperature and animal (surface) temperature are often used for field surveys of mammals. In this method, 1) mammals do not change their behaviors, 2) researchers can observe



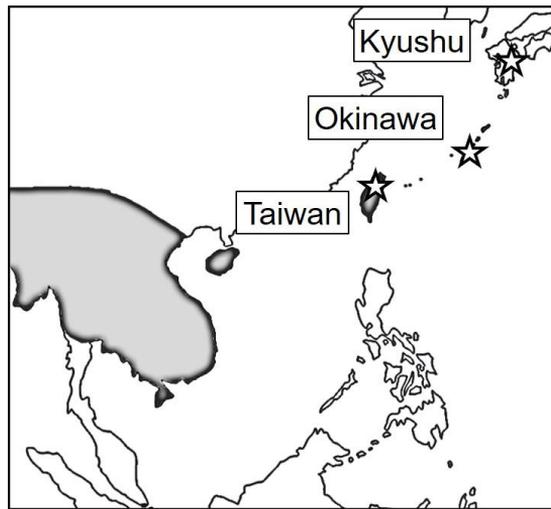
**FIGURE 2.** Flower of *Mucuna macrocarpa* and floral structures. Banner petal is pale green, wing petals are purple, and carina petals are pale purple. (A): Before flower opening, (B): After flower opening, (C): Hook-like structure (before flower opening), (D): Hook-like structure (after flower opening), (E): Connected part of wing and carina petals, (F): Section of the broken line in Fig. 2A. Large amount of sweet nectar is located inside the calyx (see Fig. 2A). When the flower opens and the banner faces upward, nectar flows down from the hook-like structure (see Fig. 2D) to the tip of the carina. Dotted circle in Figs. 2C and D shows the location of the hook-like structure.

throughout the day and night, and 3) flower-visiting behaviors are recorded in detail. This method has been successfully used to observe flower-visiting mammals<sup>17-19</sup>.

### Explosive Opening

The flower shape of *M. macrocarpa* is papilionaceous. Papilionaceous flowers have

five petals — a banner, a pair of wings, and a pair of carina petals (Fig. 2A). Nectar, a reward for visitors, is stored inside the calyx. The stamens and pistil are enclosed by a pair of carina petals, preventing automatic pollination. However, specific mammals are able to open the flower,



**FIGURE 3.** Distribution map of *Mucuna macrocarpa* and study regions. Shaded areas show distribution. Stars indicate study sites.

exposing stamens and pistil (Fig. 2B) so that pollination can occur. Once the flower of *M. macrocarpa* is opened in this manner the stamens and pistil are not enclosed again. Additionally, the opening of the flower is accompanied by explosive release of pollen, referred to as “explosive opening”. This mechanism is also known from other, bee-pollinated genera<sup>20</sup>. The flowers of these plants cannot open on their own, and at least cross-pollination by an animal, or explosive opener, is obligatory.

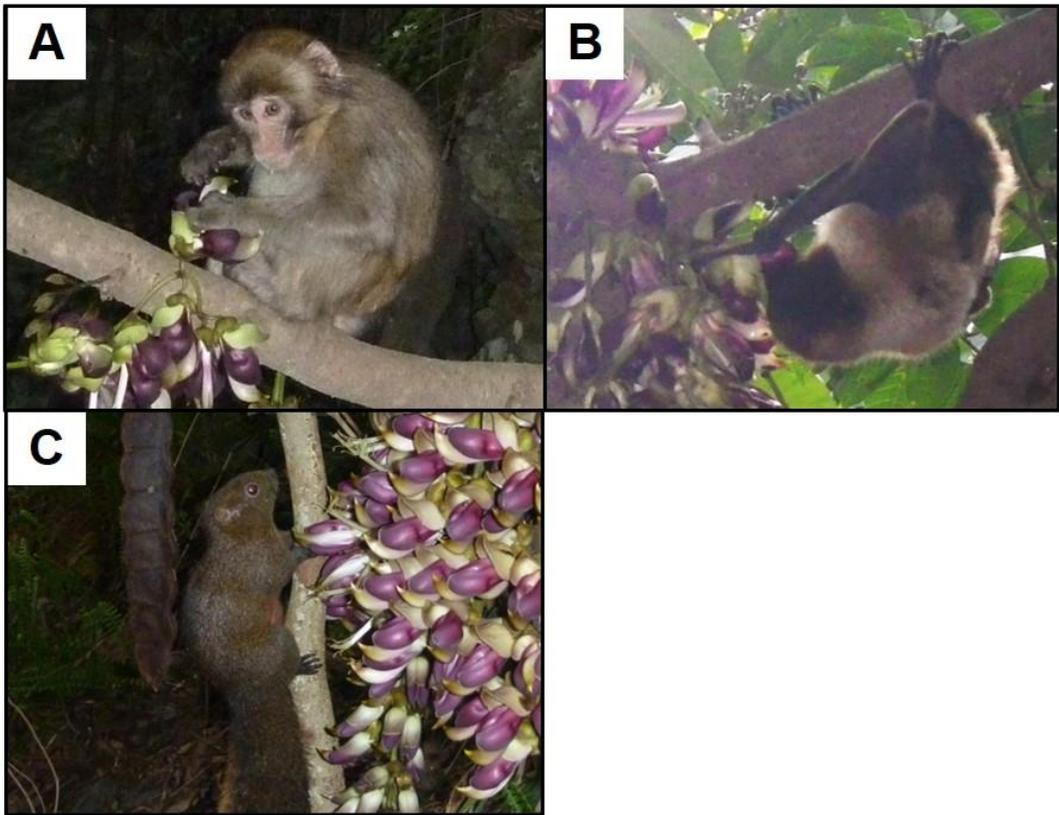
In *M. macrocarpa*, flower opening takes place when the wing petal is pressed downward, and the banner petal simultaneously pressed upward<sup>21</sup>. Thus, explosive openers must be able to accomplish this movement. Successful pollinators must also be able to release the pair of hook-like structures at the base of the banner petal, which press the wing petals from both sides, preventing the flower from opening automatically<sup>21</sup> (Fig. 2C). When these hook-like structures are released (Fig. 2D), nectar flows away from the calyx,

allowing the explosive opener to feed<sup>21</sup>. In addition, because of the wing petal’s attachment to the carina (Fig. 2E, F) depressing the wing petal has the simultaneous effect of pushing the carina down. Thus, flower opening requires the strength of a mammal pollinator, as even large bees, such as carpenter bees *Xylocopa appendiculata circumvolans*, cannot open *M. macrocarpa* flowers<sup>22</sup>.

Explosive openers were considered pollinators, but their role had not been experimentally verified<sup>9,23,24</sup>. While our observations on fruit set following artificial pollination in this genus suggest self-compatibility, fruits were not observed when flowers did not open<sup>25</sup>. Thus, we assume that explosive opening is necessary for pollination in this genus, even though only one species was tested.

### Shift of Explosive Openers

Explosive openers were identified *M. macrocarpa*’s range, in Kyushu, Okinawa, and Taiwan<sup>15,18,21</sup> (Fig. 3). Explosive openers are Japanese macaques *Macaca*



**FIGURE 4.** Explosive openers (effective pollinators) in three study regions. (A): Japanese macaque (*Macaca fuscata*), (B): Ryukyu flying fox (*Pteropus dasymallus*), (C): Red-bellied squirrel (*Callosciurus erythraeus*).

*fuscata* (Fig. 4A) and Japanese martens *Martes melampus* in Kyushu; Ryukyu flying foxes *Pteropus dasymallus* (Fig. 4B) in Okinawa; and red-bellied squirrels *Callosciurus erythraeus* (Fig. 4C), Formosan striped squirrels *Tamiops maritimus* and masked palm civets *Paguma larvata* in Taiwan. Although the openers described above are available, Japanese macaques are the main openers in Kyushu and red-bellied squirrels are the main openers in Taiwan, by virtue of the large number of flowers they open when compared to other openers. Explosive openers differ among regions, but all known

openers are mammals. When these species open a flower large amounts of pollen are removed. Supported by the results of experiments, we conclude that explosive openers are effective pollinators.

In *Mucuna*, explosive openers comprise either one or 2–3 species from the same group, as reported in Table 1. Almost all of them are bats or birds (Table 1). On the other hand, mammals from different orders act as pollinators in different regions of *M. macrocarpa*'s range. There were other examples of plants pollinated by different mammals at different sites. Traveler's trees *Ravenala madagascariensis* are pollinated

TABLE 1. Explosive openers or flower visitors of *Mucuna* spp.

Plant name	Study region/Country	Explosive opener (Flower visitor**)		Pollinator observation method	Literature
		Species name	Common name		
<i>M. macrocarpa</i>	Kyushu (Japan)	<i>Macaca fuscata</i> ***	Japanese macaque	Video camera trap / Direct observation	15
		<i>Martes melampus</i>	Japanese marten		
	Okinawa (Japan)	<i>Pteropus dasymallus</i>	Ryukyu flying fox	Direct observation	21
	Taiwan	<i>Callosciurus erythraeus</i> ***	Red-bellied squirrel	Video camera trap	18
<i>Tamiops maritimus</i>		Formosan striped squirrel			
<i>Paguma larvata</i>		Masked palm civet			
<i>M. sempervirens</i>	Kunming (China)	<i>Callosciurus erythraeus</i>	Red-bellied squirrel	Direct observation	49
		<i>Dremomys pernyi</i>	Perny's long-nosed squirrel		
<i>M. birdwoodiana</i> *	Hongkong	( <i>Rousettus leschenaulti</i> )	(Leschenault's rousette bat)	Direct observation	50,51
		( <i>Paguma larvata</i> )	(Masked palm civet)		
<i>M. macropoda</i>	Papua New Guinea	<i>Syncteris australis</i>	Queensland blossom bat	Direct observation	24
<i>M. gigantea</i> *	Indonesia		(Bat ?)	Estimate from the claw mark on flower	23
<i>M. reticulata</i> *	Indonesia		(Bat ?)	Estimate from the claw mark on flower	23
<i>M. macrophylla</i> *	Indonesia		(Bat ?)	Estimate from the claw mark on flower	23
<i>M. monosperma</i> *	Indonesia		(Bat ?)	Estimate from the claw mark on flower	33
<i>M. flagellipes</i>	Kamerun	<i>Megaloglossus woermanni</i>	Woermann's fruit bat	Direct observation	52
<i>M. urens</i>	Brazil	<i>Glossophaga soricina</i>	Pallas's long-tongued bat	Direct observation	53
<i>M. holtonii</i>	Costa Rica	<i>Glossophaga commissarisi</i> ***	Commissaris's long-tongued bat	Direct observation / Video camera	10,54
		<i>Hylonycteris underwoodi</i>	Underwood's long-tongued bat		
		<i>Lichonycteris obscura</i>	Dark long-tongued bat		
<i>M. rostrata</i>	Colombia	<i>Cacicus cela</i>	Yellow-rumped cacique	Direct observation	55
<i>M. japira</i>	São Paulo (Brazil)	<i>Cacicus haemorrhous</i>	Red-rumped cacique	Direct observation	9
<i>M. sloanei</i> *	No information	<i>Glossophaga soricina</i>	Pallas's long-tongued bat	Direct observation	56
<i>M. mutisiana</i> *	No information		(Bat ?)	No information	57****
<i>M. reptans</i> *	Australia		(Rat or Bird ?)	Estimate from the floral characteristics	58
<i>M. pruriens</i> *	No information		(Bat ?)	No information	57****

\*Quantitative observations were not conducted to identify the pollinator. \*\*Parentheses indicate that explosive opening behavior was not observed for this species. \*\*\* This is a main pollinator in the region, even when multiple pollinators occur in the region.

\*\*\*\*Article suggested the pollinator, but we could not find any evidence of field observation.

by ruffed lemurs *Varecia variegata* in their naturally-occurring range, and by gray-headed flying foxes *Pteropus poliocephalus* in Australia where traveler's trees have been introduced<sup>26,27</sup>. However, to our knowledge, pollinator shifts from one mammal to another within a species' natural range are not known. Pollinator shifts from bats to non-flying mammals or vice versa are also rare.

### Comparisons of Explosive Opening Behaviors

In *M. macrocarpa*, it is necessary to simultaneously raise banner and push down wing petals for explosive opening to occur. Does explosive opening behavior differ among openers? Our observations clarified that explosive opening behavior is common among openers, who hold wing petals with their forelimbs and raise the banners with their snouts by inserting them into the gap between wing and banner<sup>15,18,21</sup>; a single exception is the Japanese macaque, which holds the wing petal in one hand and raises the banner petal with the other hand<sup>15</sup>.

This difference in opening behavior may affect pollination success. The Ryukyu flying fox, the only opener in Okinawa, and the red-bellied squirrel, the main opener in Taiwan, always inserted their snouts into the gap between wing and banner at a similar angle<sup>18,21</sup>. This method results in both the adherence of pollen grains to, and contact of the plant's stigma with the pollinator, on the same part of the pollinator's body, with obvious consequences for pollination efficacy i.e. the pollinator's method maximizes the likelihood of pollen deposition on the stigma. In contrast, when Japanese macaques open flowers, pollen grains may adhere to their hands or faces, depending on the precise opening stance employed i.e. the distance between face and flower when opening occurs. The stigma

always attached to the face and does not touch on hand. Thus, the site of attachment of pollen and stigma is not always same in the case of macaques.

Explosive opening behaviors have been described for other *Mucuna* species. In *M. japira*, which is pollinated by red-rumped caciques *Cacicus haemorrhous*, Agostini et al.<sup>9</sup> noted that birds used their heads to "press the base of the wing and carina petals at the same time". In bat-pollinated *M. macropoda*, Hopkins and Hopkins<sup>24</sup> described pollen release when the pressure (exerted by the bat with its head) on the base of the petals released the androecium and gynoecium from within the carina. Other leguminous explosive openers are known among bee-pollinated species in which the weight of bees on the plant's wings appears sufficient to trigger explosive opening without any specialized behavior<sup>20,28</sup>. Compared to these species, the mechanism of explosive opening in *M. macrocarpa* is more complex, its reliance on the use of the mammalian forelimb suggesting co-evolution with mammal pollinators.

### Flower Visitors Other than Explosive Openers

Flower visitors other than explosive openers were also recorded in the three regions sampled<sup>15,18,21</sup>. While Japanese macaques (in Kyushu) could open and pollinate flowers as described, Formosan rock macaques *Macaca cyclopis* could not open flowers<sup>18</sup>. In a survey spanning at Nanrenshan Ecological Reserve Area, southern Taiwan<sup>16</sup> we used camera traps (Ltl-Acorn 5210; Shenzhen Ltl Acorn Electronics Co., Ltd., China) to ascertain the fate of *M. macrocarpa* inflorescences, discovering that 92.9% (n = 14) of inflorescences were picked and eaten by Formosan rock macaques prior to maturation, while Formosan rock macaques

visited mature flowers in northern Taiwan. Because of regional differences in vegetation in Taiwan<sup>29</sup> food sources exploited by macaques vary with area, and their reliance on *Mucuna* relative to other foods may also vary as a reflection of these differences. Resource requirements may also differ on the basis of troop size, which varies among troops<sup>30</sup> and may influence which food sources are most regularly visited.

Secondly, visitors to opened flowers were observed in all regions. One of them, the honeybee, *Apis cerana* visits to collect pollen, sometimes coming into contact with the stigma<sup>15,18</sup> and potentially acting as a secondary pollinator, although efficiency is unknown. In addition, honeybees frequently visited flowers immediately after explosive opening. Diurnal Japanese macaques and red-bellied squirrels frequently visited flowers in the early morning<sup>25</sup>, thus attracting the visits of honeybees at this time.

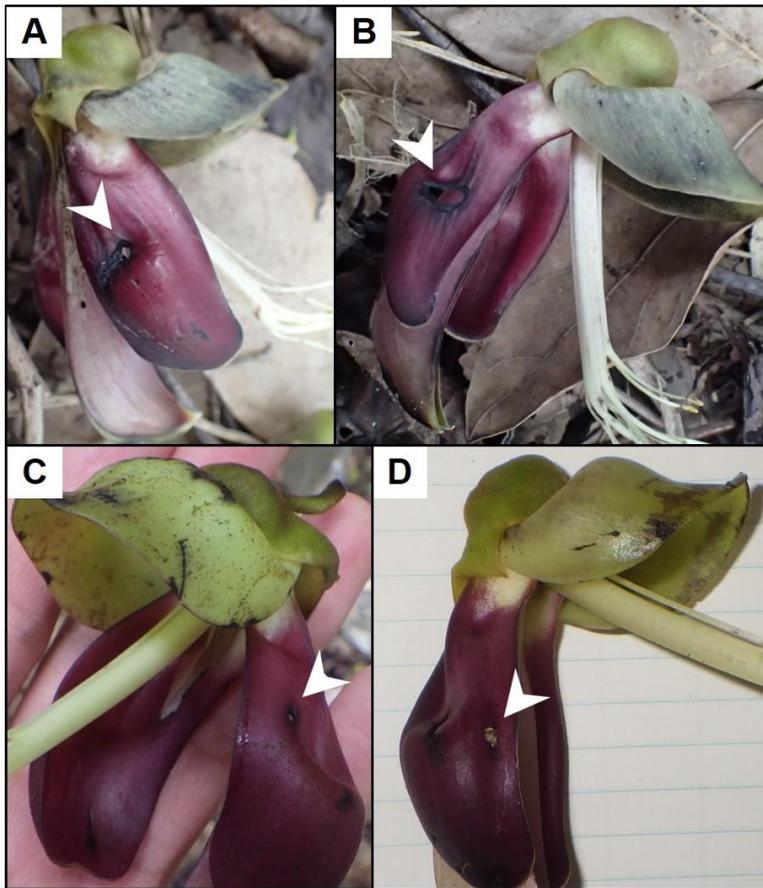
Interestingly, birds seldom visited *M. macrocarpa* flowers. Japanese white-eyes *Zosterops japonicus* and brown-eared bulbuls *Hypsipetes amaurotis* visited flowers less frequently than explosive openers both in Kyushu and Okinawa, and did not open flowers at all<sup>15,18,21</sup>. In Taiwan, no birds visited flowers<sup>18</sup>. These results suggest that *M. macrocarpa* relies solely on mammal pollinators. While the Okinawa woodpecker *Sapheopipo noguchii* visited relatively frequently and fed on nectar<sup>31</sup> this may reflect a feeding habit related to evolution on a small island<sup>32</sup>, and insignificant in terms of pollination.

### Future Challenges

It will be instructive to identify the pollinators of *Mucuna* spp. A large number of vertebrate-pollinated plant species occur in the tropics<sup>3</sup>, and *Mucuna* is a good target

group for studies on the diversity and evolution of mammal-dependent pollination systems. Pollinators of several *Mucuna* species have been clarified (Table 1). However, some of these pollinators were identified only by the observations confirmed visits by these species but not necessarily visits resulting in pollination (Table 1). This genus has been considered to be pollinated by bats or birds<sup>6</sup>, but this suggestion is not based on enough surveys. For example, although van der Pijl<sup>23,33</sup> conducted pioneering studies, he concluded that bats were pollinators based on the claw marks on flowers. While claw marks of fruit bats may differ from those of other mammals, squirrels and macaques also mark flowers (Fig. 5) and it is sometimes difficult to distinguish between the marks of bats and those of other mammals. In addition, information on flower-visiting frequency and flower-visiting behavior is lacking, and van der Pijl<sup>23</sup> did not consider other possible visitors. Furthermore, the genus *Mucuna* requires specific flower-visiting behaviors (this requirement does not apply only to *M. macrocarpa*). Thus, detailed observations are needed especially in those species. Otherwise, *Mucuna* species may have other additional pollinators, and pollinators may differ in different parts of *Mucuna*'s range.

The genus *Mucuna* originated in tropical Asia<sup>34</sup>. Therefore, in order to understand the pollination system of *Mucuna*, Southeast Asia is the most important region. The fauna in the tropical zone is more diversified than that in the temperate zone, and squirrels and carnivores are the most diversified group in Southeast Asia<sup>35</sup>. The importance of flying foxes<sup>36-38</sup> and squirrels<sup>38,39</sup> as pollinators in Southeast Asia has been noted. In fact, diurnal tree squirrels act as pollinators of number of plants besides *Mucuna*<sup>40-42</sup>. Most studies of non-flying mammal-pollinated



**FIGURE 5.** Claw marks of explosive openers. (A) and (B): Ryukyu flying-fox, (C): Japanese macaque, (D): Red-bellied squirrel. Arrows indicate the claw marks of each opener.

plants have been conducted in Australia, and South Africa, and more research into mammal-dependent pollination systems in Southeast Asia are needed.

One of the important issues for discussion of the evolution of mammal-pollinated plants is that of floral traits. Many plants that are considered bat-pollinated species have floral traits reflecting this pollination syndrome, causing researchers to overlook the possibility of other pollinators. Pollination syndrome is the concept that plants pollinated by same pollinator have

common floral traits such as shape, nectar secretion dynamics, and odor (volatile components). Although several *Mucuna* species fit bat-pollination syndromes<sup>10,24,43</sup>, floral traits are seldom quantitatively assessed for their fit with pollinators. This represents a significant gap in our knowledge, and there are instances in which pollinators predicted for a species, based on floral characteristics and pollination syndromes, differ from observed pollinators. Many such exceptions have recently been described<sup>44-46</sup> and it appears that prediction

of pollinators based on the pollination syndrome is unrealistic. However, it is known that a specific floral trait attracts a specific pollinator. In mammal-pollinated plants, volatile components are one of the most important attractive traits<sup>47</sup>. Further research on *Mucuna* is needed to clarify floral traits such as shape, nectar production dynamics, and volatile components, and to examine the relationship of these traits with pollinators.

### Conclusion

Pollinators of *M. macrocarpa* differ among regions but all of them initiate explosive opening, with the exception of the Japanese macaque. Such commonness of behavior indicates that the ability of *M. macrocarpa* to open explosively makes it available to a number of potential pollinators. However, in all regions, non-mammal flower visitors are infrequently observed, suggesting a reliance on mammals at the expense of other groups, and the evolution of flower strength useful for prohibiting small animals from robbing nectar.

The explosive opening behavior of Japanese macaques is distinctive, and this pollinator occurs at the northern limit, or edge, of *M. macrocarpa*'s range<sup>15</sup>, where pollinator shift is more likely to occur<sup>48</sup>. In addition, Japanese macaques dropped flowers frequently<sup>15</sup> and other *Macaca* monkeys cannot open and pollinate flowers. Thus, Japanese macaques might have become pollinators as a secondary consequence of learning to prey on *Mucuna* flowers.

In Southeast Asia, non-flying mammals are known to pollinate plants reported as bat-pollinated species<sup>18,44</sup>. Thus, we need to clarify the pollinators of other *Mucuna* species in Asia. In addition, clarifying pollination systems, including floral traits, is

needed to enhance understanding of the evolution of mammal pollination.

### ACKNOWLEDGEMENTS

We appreciate to T. Doi, T. Iwamoto, S. Mashiba, J. Kawano, H. Ui, Y.-H. Lin, K.-F. Lin, and S.-H. Wu for supporting field surveys. This study was partly supported by JSPS KAKENHI (Grant number 16H05771).

### LITERATURE CITED

- Ollerton, J., Winfree, R. and Tarrant, S. 2011. How many flowering plants are pollinated by animals?. *Oikos* 120:321-326.
- Devy, M.S. and Davidar, P. 2003. Pollination system of trees in Kakachi, a mid-elevation wet evergreen forest in Western Ghats, India. *American Journal of Botany* 90:650-657.
- Fleming, T.H. and Kress, W.J. 2013. *The Ornament of Life: Coevolution and Conservation in the Tropics*. The University of Chicago Press, Chicago. 588 pages.
- Carthew, S.M. and Goldingay, R.L. 1997. Non-flying mammals as pollinators. *Trends in Ecology and Evolution* 12:104-108.
- Schrire, B.D. 2005. Tribe Phaseoleae. In: Lewis, G., Schrire, B.D., Mackinder, B. and Lock, M. (eds.). *Legumes of the World*. Royal Botanic Gardens, Kew, London, UK. pp. 393-431.
- Fægri, K. and van der Pijl, L. 1979. *The Principles of Pollination Ecology*, 3rd edition. Pergamon Press, Oxford, UK. 256 pages.
- Tateishi, Y. and Ohashi, H. 1981. Eastern Asiatic species of *Mucuna* (Leguminosae). *The Botanical Magazine, Tokyo* 94:91-105.
- Wilmot-Dear, C.M. 2008. *Mucuna* Adans. (Leguminosae) in Thailand. *Thai Forest Bulletin (Botany)* 36:114-139.
- Agostini, K., Sazima, M. and Sazima, I. 2006. Bird pollination of explosive flowers while foraging for nectar and caterpillars. *Biotropica* 38:674-678.
- von Helversen, D. and von Helversen, O. 2003. Object recognition by echolocation: a nectar-feeding bat exploiting the flowers of a rain forest vine. *Journal of Comparative Physiology*

- A 189:327-336.
11. Carthew, S.M. 1991. Monitoring animal activity with automated photography. *Journal of Wildlife Management* 55:689-692.
  12. Grand, T.I. 1972. A mechanical interpretation of terminal branch feeding. *Journal of Mammalogy* 53:198-201.
  13. Janson, C.H., Terborgh, J. and Emmons, L.H. 1981. Non-flying mammals as pollinating agents in the Amazonian forest. *Biotropica* 13:1-6.
  14. Deng, X.-B., Ren, P.-Y., Gao, J.-Y. and Li, Q.-J. 2004. The striped squirrel (*Tamias swinhoii hainanus*) as a nectar robber of ginger (*Alpinia kwangsiensis*). *Biotropica* 36:633-636.
  15. Kobayashi, S., Denda, T., Mashiba, S., Iwamoto, T., Doi, T. and Izawa, M. 2015. Pollination partners of *Mucuna macrocarpa* (Fabaceae) at the northern limit of its range. *Plant Species Biology* 30:272-278.
  16. Swann, D.E., Kawanishi, K. and Palmer, J. 2011. Evaluating types and features of camera traps in ecological studies: a guide for researchers. In: O'Connell, A.F., Nichols, J.D. and Karanth, K.U. (eds.). *Camera Traps in Animal Ecology, Methods and Analyses*. Springer Japan, Tokyo, Japan. pp. 27-43.
  17. Hobbhahn, N., Steenhuisen, S.L., Olsen, T., Midgley, J.J. and Johnson, S.D. 2017. Pollination and breeding system of the enigmatic South African parasitic plant *Mystropetalon thomii* (Mystropetalaceae): rodents welcome, but not needed. *Plant Biology* 19:775-786.
  18. Kobayashi, S., Denda, T., Liao, C.-C., Wu, S.-H., Lin, Y.-H. and Izawa, M. 2017. Squirrel pollination of *Mucuna macrocarpa* (Fabaceae) in Taiwan. *Journal of Mammalogy* 98:533-541.
  19. Kühn, N., Midgley, J. and Steenhuisen, S.-L. 2017. Reproductive biology of three co-occurring, primarily small-mammal pollinated *Protea species* (Proteaceae). *South African Journal of Botany* 113:337-345.
  20. Westerkamp, C. 1997. Keel blossoms: Bee flowers with adaptations against bees. *Flora* 192:125-132.
  21. Toyama, C., Kobayashi, S., Denda, T., Nakamoto, A. and 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.
  22. Kobayashi, S., Hirose, E., Denda, T. and Izawa, M. 2018. Who can open the flower? Assessment of the flower opening force of mammal-pollinated *Mucuna macrocarpa*. *Plant Species Biology*. DOI: 10.1111/1442-1984.12221
  23. van der Pijl, L. 1941. Flagelliflory and cauliflory as adaptations to bats in *Mucuna* and other plants. *Annals of the Botanic Gardens, Buitenzorg* 51:83-93.
  24. Hopkins, H.C.F. and 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.
  25. Kobayashi, S. 2017. Mammal-dependent pollination system of *Mucuna macrocarpa* (Fabaceae). Ph.D. Thesis, University of the Ryukyus, Okinawa, Japan. 139 pages.
  26. Calley, M., Braithwaite, R.W. and Ladd, P.G. 1993. Reproductive biology of *Ravenala madagascariensis* Gmel. as an alien species. *Biotropica* 25:61-72.
  27. Kress, W.J., Schatz, G.E., Andrianifahanana, M. and Morland, H.S. 1994. Pollination of *Ravenala madagascariensis* (Strelitziaceae) by lemurs in Madagascar: evidence for an archaic coevolutionary system? *American Journal of Botany* 81:542-551.
  28. Kishi, S. 2015. Flower-visiting behavior of native and alien *Xylocopa* carpenter bees to Japanese *Wisteria* flowers. *Japanese Journal of Entomology (New Series)* 18:31-38. In Japanese with English summary.
  29. Liao, C.-C., Liu, M., Su, M.-H. and Wang, J.-C. 2014. Compression and overlap of unique vegetation system of subtropical mountain resembling tropical and temperate forests along elevation. *Journal of Forest Research* 19:215-225.
  30. Hsu, M. and Lin, J.-F. 2001. Troop size and structure in free-ranging Formosan macaques (*Macaca cyclopis*) at Mt. Longevity, Taiwan. *Zoological Studies* 40:49-60.
  31. Kobayashi, S., Denda, T. and Izawa, M. 2014. Okinawa Woodpeckers *Sapheopipo noguchii* (Picidae) robbing *Mucuna macrocarpa*. *Strix* 30:135-140. In Japanese with English summary.
  32. Kotaka, N., Ozaki, K., Toguchi, Y., Kinjo, M. and Ishida, K. 2006. Extraordinary sexual differences in foraging niche in the Okinawa woodpecker on a subtropical island. *Journal of Ornithology* 147:196.
  33. van der Pijl, L. 1956. Remarks on pollination by bats in the genera *Freycinetia*, *Duabanga*, and *Haplophragma*, and on chiropterology in general.

- Acta Botanische Neerlandica 5:135-144.
34. Moura, T.M., Vatanparast, M., Tozzi, A.M.G.A., Forest, F., Wilmot-Deer, C.M., Simon, M.F., Mansano, V.F., Kajita, T. and Lewis, G.P. 2016. A molecular phylogeny and new infrageneric classification of *Mucuna* Adans. (Leguminosae-Papilionoideae) including insights from morphology and hypotheses about biogeography. *International Journal of Plant Sciences* 177:76-89.
  35. Corlett, R.T. 2007. What's so special about Asian tropical forests?. *Current Science* 93:1551-1557.
  36. Marshall, A.G. 1983. Bats, flowers and fruit: evolutionary relationships in the Old World. *Biological Journal of the Linnean Society* 20:115-135.
  37. Cox, P.A., Elmqvist, T., Pierson, E.D. and Rainey, W.E. 1991. Flying foxes as strong interactors in south pacific island ecosystems: A conservation hypothesis. *Conservation Biology* 5:448-454.
  38. Corlett, R.T. 2004. Flower visitors and pollination in the Oriental (Indomalayan) region. *Biological Review* 79:497-532.
  39. van der Pijl, L. 1961. Ecological aspects of flower evolution. II. Zoophilous flower classes. *Evolution* 15:44-59.
  40. McCann, C. 1934. The flying fox (*P. giganteus*) and the palm squirrel (*F. tristriatus*) as agents of pollinization in (*Grevillea robusta* A. Cunn.) the silky oak. *Journal of Bombay Natural History Society* 36:761-764.
  41. Yumoto, T., Momose, K. and Nagamasu, H. 2000. A new pollination syndrome-squirrel pollination in a tropical rain forest in Lambir Hills National Park, Sarawak, Malaysia. *Tropics* 9:147-151.
  42. Tandon, R., Shivanna, K.R. and Mohanram, H.Y. 2003. Reproductive biology of *Butea monosperma* (Fabaceae). *Annals of Botany* 92:715-723.
  43. Agostini, K., Sazima, M. and Galetto, L. 2011. Nectar production dynamics and sugar composition in two *Mucuna* species (Leguminosae, Faboideae) with different specialized pollinators. *Naturwissenschaften* 98:933-942.
  44. Rivera-Marchand, B. and Ackerman, J.D. 2006. Bat pollination breakdown in the Caribbean columnar cactus *Pilosocereus royenii*. *Biotropica* 38:635-642.
  45. Ollerton, J., Alarcón, R., Waser, N.M., Price, M.V., Watts, S., Cranmer, L., Hingston, A., Peter, C.I. and Rotenberry, J. 2009. A global test of the pollination syndrome hypothesis. *Annals of Botany* 103:1471-1480.
  46. Amorim, F.W., Galetto, L. and Sazima, M. 2013. Beyond the pollination syndrome: nectar ecology and the role of diurnal and nocturnal pollinators in the reproductive success of *Inga sessilis* (Fabaceae). *Plant Biology* 15:317-327.
  47. Johnson, S.D., Burgoyne, P.M., Harder, L.D. and Dötterl, S. 2011. Mammal pollinators lured by the scent of a parasitic plant. *Proceedings of the Royal Society B* 278:2303-2310.
  48. Johnson, S.D. 2010. The pollination niche and its role in the diversification and maintenance of the southern African flora. *Philosophical Transactions of the Royal Society of London, Series B* 365:499-516.
  49. Chen, G., Zhang, R., Dong, K., Gong, W. and Ma, Y. 2012. Scented nectar of *Mucuna sempervirens* and its ecological function. *Sheng Wu Duo Yang Xing* 20:360-367. In Chinese with English summary.
  50. Lau, M. 2004. Bat pollination in the climber *Mucuna birdwoodiana*. *Porcupine!* 30:11-12.
  51. Lau, M.W.N. 2012. Masked palm civet *Paguma larvata* apparently feeding on nectar of *Mucuna birdwoodiana*. *Small Carnivore Conservation* 47:79-81.
  52. Grünmeier, R. 1993. Bestäubung der Fabaceae *Mucuna* flagellipes durch flughunde in Kamerun. In: Barthlott, W., Naumann, C.M., Schmidt-Loske, K. and Schuchmann, K.-L. (eds.). *Animal-Plant Interactions in Tropical Environments*. Museum A. Koenig, Bonn, Germany. pp. 29-39. In Germany.
  53. Sazima, I. and Sazima, M. 1978. Polinização por morcegos em *Mucuna urens* (Leguminosae). In: Resumos da XXX Reunião da Sociedade Brasileira para o Progresso da Ciência. p. 419.
  54. Baker, H.G. 1970. Two cases of bat pollination in Central America. *Revista de Biología Tropical* 17:187-197.
  55. Cotton, P.A. 2001. The behavior and interactions of birds visiting *Erythrina fusca* flowers in the Colombian Amazon. *Biotropica* 33:662-669.
  56. Zies, P. 1999. Batty about sea-beans. *The Drifting Seed* 5:6-7.
  57. Stroo, A. 2000. Pollen morphological evolution in bat pollinated plants. *Plant Systematic and Evolution* 222:225-242.