

NATURE NOTES

First record of non-flying mammalian contributors to pollination in a tropical montane forest in Asia

Shun Kobayashi¹  | Somsak Panha^{2,3} | Teerapong Seesamut² | Nattawadee Nantarat⁴ | Natdanai Likhitrakarn⁵ | Tetsuo Denda¹ | Masako Izawa¹

¹Faculty of Science, University of the Ryukyus, Nishihara, Japan

²Department of Biology, Faculty of Science, Chulalongkorn University, Bangkok, Thailand

³Academy of Science, The Royal Society of Thailand, Bangkok, Thailand

⁴Department of Biology, Faculty of Science, Chiang Mai University, Chiang Mai, Thailand

⁵Faculty of Agricultural Production, Maejo University, Chiang Mai, Thailand

Correspondence

Shun Kobayashi, Faculty of Science, University of the Ryukyus, Nishihara, Okinawa, Japan.
Email: kobashun@sci.u-ryukyu.ac.jp

Present address

Masako Izawa, Kitakyushu Museum of Natural History and Human History, Kitakyushu, Japan

Funding information

Centre of Excellence on Biodiversity, Thailand, Grant/Award Number: BDC-PG2-159009; Japan Society for the Promotion of Science, Grant/Award Number: 16H05771 and 19K16215

Abstract

This study aims to identify the flower visitors of *Mucuna thilandica* (Fabaceae), endemic plant species in montane forests in Thailand, to determine their potential pollinators. The genus *Mucuna* produces papilionaceous flowers and has an explosive flower-opening step. Explosive opening rapidly exposes stamens and pistil from keel petals and releases pollen. The flower of this species depends completely on animals to perform this step, essential for pollination success. Using a camera trap survey, we revealed that non-flying mammals, such as squirrels (*Callosciurus* sp.) and masked palm civets (*Paguma larvata*), opened flowers explosively. Thus, these mammals contribute to the pollination of *M. thilandica*. This is the first report of non-flying mammals contributing to pollination in montane forests in tropical Asia.

KEYWORDS

montane forest, *Mucuna thilandica*, non-flying mammal, pollination, tropical Asia

1 | INTRODUCTION

Bird- and mammal-pollinated plants are recorded from 28 orders and 67 families in the world (Fleming & Kress, 2013). Most mammal-pollinated plants are pollinated by bats: however, non-flying mammals have also been recorded to pollinate some plant species (Carthew & Goldingay, 1998; Willmer, 2011). These plants are distributed across different regions, including semi-arid regions, shrublands, and montane grasslands in Africa (Hobbhahn et al., 2017; Kleizen et al., 2008; Payne et al., 2019; Steenhuisen et al., 2015;

Wester et al., 2019), cloud forests, rainforests, and alpine dry shrubland and grasslands in Central and South America (Amorim et al., 2020; Cárdenas et al., 2017; Cocucci & Sersic, 1998; Dellinger et al., 2019; Lumer, 1980), and heathland, dry woodland, and rain forests in Australia (Carpenter, 1978; Carthew, 1993; Goldingay et al., 1991; Quin et al., 1996; Wooller & Wooller, 2003). Such wide distribution of mammal-pollinated plants suggests that non-flying mammal-pollinated plants could exist in various habitats across these regions. However, only a few species of non-flying mammal-pollinated plants have been recorded in tropical Asia (Carthew & Goldingay, 1998;

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2021 The Authors. *Ecology and Evolution* published by John Wiley & Sons Ltd.

Willmer, 2011), and these records are limited to lowland evergreen forests (Ganesh & Devy, 2000, 2006; Kobayashi, Denda, et al., 2019; Yumoto et al., 2000).

In particular, non-flying mammal-pollinated plants have not been recorded in tropical Asian montane forests. In the aseasonal tropics in Asia, the difference in altitude between lowland and montane habitats ranges from 750 to 1300 m a.s.l. (Ashton, 2018). Montane areas can be classified into lower montane, upper montane, and subalpine areas where the tree line is above 3900–4000 m a.s.l. (Corlett, 2019). Bees are the most important pollinators in areas up to 1500 m a.s.l. (reviewed by Corlett, 2004).

One characteristic of mammal-pollinated plants is that they tend to have relatively large flowers or inflorescences compared to entomophilous (insect-pollinated) species (Fleming & Kress, 2013). Such plants can be found in lowlands and montane forests in tropical Asia. One of these species is *Mucuna thailandica* Niyomdham & Wilmot-Dear. *Mucuna thailandica*, an evergreen woody vine distributed in an altitude range of 1000–2400 m a.s.l. and endemic to Doi Inthanon, the highest mountain in Thailand (Wilmot-Dear, 2008). This species produces racemes with 18–45 pale green flowers that are more than 8 cm in length (Figure 1).

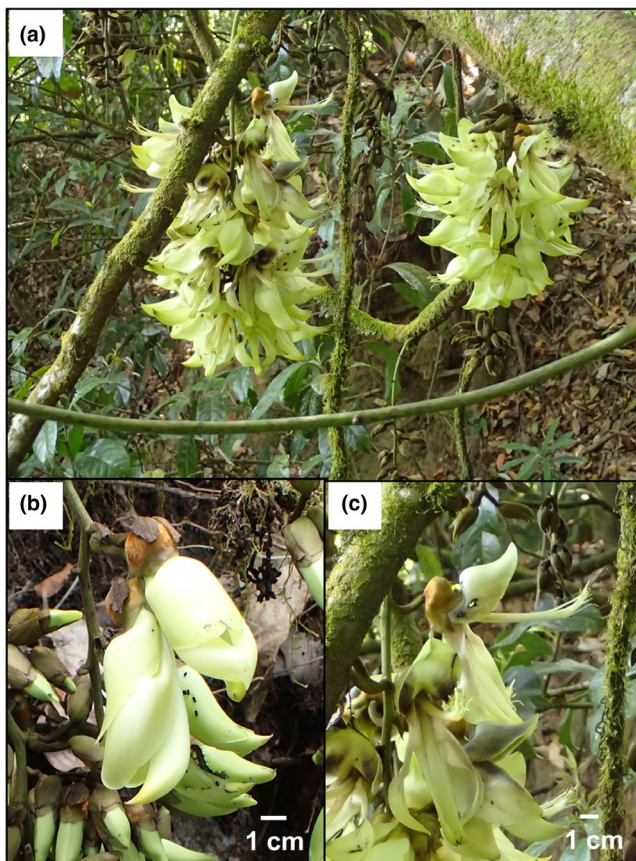


FIGURE 1 Inflorescences and flowers of *Mucuna thailandica*. (a) Inflorescences; (b) flowers before they were explosively opened, (c) flowers after they were explosively opened

Mucuna thailandica has a typical papilionaceous (butterfly-like) flower, consisting of a banner petal, a pair of wing petals, and a pair of keel petals that cover the stamens and pistils. Keel petal-opening is essential for pollination in this genus, but they do not open by themselves (Agostini et al., 2006; Kobayashi, Denda, et al., 2019; Kobayashi et al., 2021). Rather, when an animal pushes the banner petal and presses the wing petals downward, the keel petals are opened and the stamens and pistil are exposed, upon which the pollen grains splash. This essential step is called “explosive opening.” Once a flower explosively opens, the stamens and pistil remain exposed. *Mucuna macrocarpa* and *M. birdwoodiana*, two related species, cannot produce seeds without an explosive opening step (Kobayashi, Denda, et al., 2019). In addition, the flower opening strength, as measured using a digital force gauge, was found to be 16–409 times higher for the explosive opening of *M. macrocarpa*, which is pollinated by squirrels (*Callosciurus* spp.), flying foxes (*Pteropus dasymallus*), and macaques (*Macaca fuscata*), than for bee-pollinated plants (Kobayashi et al., 2018). These characteristics suggest that *M. thailandica* can be pollinated by mammals.

In this study, we identified flower visitors to the large flower plant *M. thailandica* in a montane forest in tropical Asia and recorded their flower-visiting behavior to determine the potential contribution of non-flying mammals to its pollination.

2 | MATERIALS AND METHODS

The study was conducted at the Kew Mae Pan Nature Trail in Doi Inthanon National Park, Thailand (18°33′20.63″N, 98°28′55.42″E, 2100 m a.s.l.). *Mucuna thailandica* has only been recorded in ten collections from Doi Inthanon and is thus very rare (Wilmot-Dear, 2008). Only one individual was selected because of the suitability for the camera trap survey. The studied plant was located near the office of the bushwalk tour. Although tourists were allowed to bushwalk near the study site, tourism decreased drastically at the end of the flowering season due to the COVID-19 pandemic, reducing the likely amount of disturbance. An automatic video camera trap (Ltl-6210; Shenzhen Ltl Acorn Electronics Co., Ltd., China) with a night vision recording function using an infrared lamp was set up to document seven inflorescences from January 20 to July 9, 2020. These inflorescences were located approximately 3.2 m above ground. The distance between the camera and inflorescences was approximately 1 m. The selected settings of the camera were 30 s video length, without intervals, and a normal sensor level. We monitored the plant from the bud stage to the end of the flowering phase. Flower-visiting behaviors were categorized based on Kobayashi et al. (2021) as: “explosive opening with no damage to the flower,” “visiting and feeding on the nectar of the opened flower,” “destruction of the flower without opening,” “nectar robbing from the unopened flower,” and “other non-specific behaviors and unknown.” Fruit availability on monitored inflorescences was checked when the camera trap was collected on August 29, 2020.

3 | RESULTS AND DISCUSSION

The first flower visitor was recorded on February 13, and all flowers dropped by March 31. In total, 173 shots were recorded. Animals were captured in 90 (52%) video shots, while the rest did not include animals. Tree squirrels (*Callosciurus* spp.), northern tree shrews (*Tupaia belangeri*), and masked palm civets (*Paguma larvata*) were recorded as flower visitors. Three *Callosciurus* species (*C. caniceps*, *C. erythraeus*, and *C. finlaysonii*) inhabit this area (Duckworth, 2016, 2017; Duckworth et al., 2017), but the flower-visiting squirrel could not be identified because we used camera traps with a night vision recording function using an infrared lamp and thus could not differentiate the color or detailed characteristics in some cases. *Callosciurus* squirrels visited all seven monitored inflorescences; on the other hand, the northern tree shrew and masked palm civet visited only two inflorescences. Giant squirrel (*Ratufa indica*), Asian red-cheeked squirrel (*Dremomys rufigenis*), bat sp., passerine birds, and sunbirds were also recorded in shots, but they did not visit the flowers.

Among these behaviors, “explosive opening with no damage to the flower” directly contributed to pollination success and was observed during visits by *Callosciurus* squirrels and masked palm civets. When the *Callosciurus* squirrels visited flowers, they frequently explosively opened flowers with no damage (5.0 ± 3.1 flowers per inflorescence; Figure 2). They grabbed a flower and then turned it upside down. After that, they opened the flower by holding it with their hands and pushing up the banner petal with their snout (Video S1). After the flower was opened, they fed on nectar stored inside the calyx. This was similar to the flower opening behavior previously reported for the squirrels *C. finlaysonii* and *C. caniceps* on *M. macrocarpa* (Kobayashi, Denda, et al., 2019). When the flowers were

opened upside down, the stamens and pistils attached to the throat and head of the squirrels. However, when they opened flowers in an upright manner, the stigma did not attach to visitors. This behavior was often observed in immature flowers.

The masked palm civet opened only three flowers (0.4 ± 1.1 flowers per inflorescence; Figure 2). The flower opening behavior was almost the same as that of squirrels: stamens and pistils were attached to the throat of the masked palm civet (Video 2). This explosive opening behavior of the masked palm civet was similar to that previously reported for *M. birdwoodiana* flowers (Kobayashi et al., 2019). Pollen grains may attach to the throat, although the details are not clear because of the recording mode of the camera trap.

Flower-opening animals are considered pollinators because the pollen and stigma attach under their jaws (Kobayashi, Denda, et al., 2019; Kobayashi et al., 2021). This attachment position may be related to the behavior of the visitor in opening the flower. Effective pollinators in previous studies including flying foxes turned flowers upside down and then opened flowers (Kobayashi et al., 2017; Kobayashi, Denda, et al., 2019; Toyama et al., 2012). In addition, explosive opening is essential for fruit set in other *Mucuna* species, such as *M. macrocarpa* and *M. birdwoodiana* (Kobayashi, Denda, et al., 2019). Similar results were observed in this study; one fruit was produced from a flower that had been opened by *Callosciurus* squirrel. Thus, *Callosciurus* squirrels and masked palm civets, which opened flowers, contribute to the pollination success of *M. thailandica*, and *Callosciurus* squirrels were considered the main pollinators of this plant.

Plants with greenish petals are usually pollinated by bats (Lau, 2004; van der Pijl, 1941) and small non-flying mammals, for example, the case of mice and elephant-shrews pollinating plants with green petals in South Africa (Wester, 2011; Wester et al., 2019). The plants

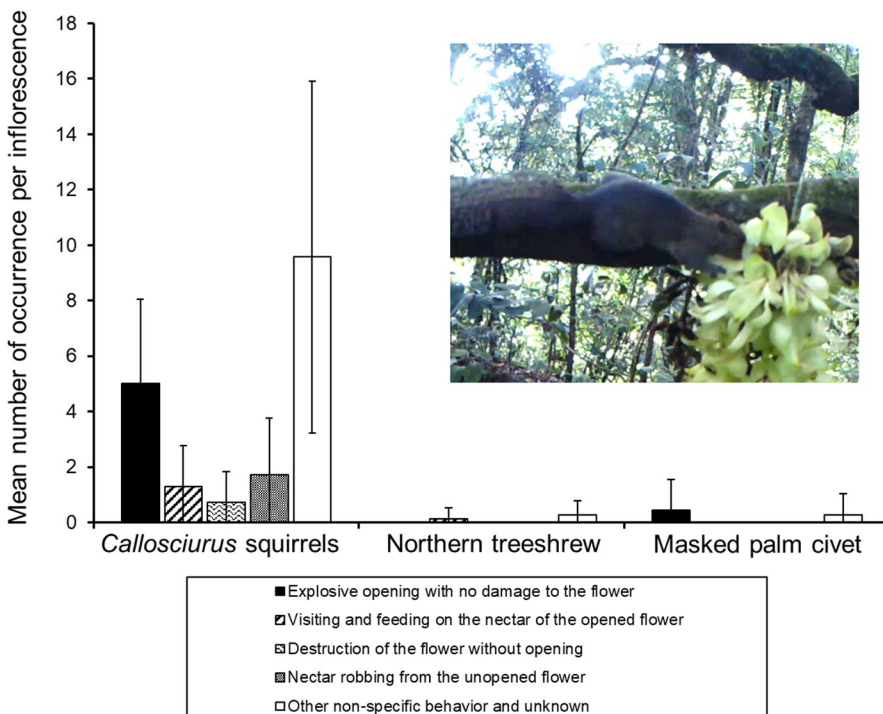


FIGURE 2 Flower visitors and their behaviors toward flowers. Photograph in the graph shows a *Callosciurus* squirrel holding a flower for explosive opening

in *Mucuna* are not always pollinated by bats, although bats inhabit the study site (Kobayashi, Gale, et al., 2019). In Doi Inthanon, at least one fruit bat species has been recorded (Thai National Parks, 2021), but no fruit bats visited *M. thailandica* flowers. Because the number of bat species is lower at higher elevations (McCain, 2011), relatively large flowers in such areas may be more likely to be pollinated by non-flying mammals.

Information on plant-mammal interactions in montane forests, especially pollination-mediated relationships, is still lacking in tropical Asia (Corlett, 2004; Funamoto, 2019), although it has been reported that non-flying mammals contribute to pollination in other montane regions (Dellinger et al., 2019; Lumer, 1980). The present study showed that non-flying mammals may play an important role as pollinators in tropical montane forests, although the sample size was insufficient. Non-flying mammals are considered to be less important (Carthew & Goldingay, 1998; Willmer, 2011). Conversely, recent observations (Kobayashi, Denda, et al., 2019; Kobayashi et al., 2021) suggest that non-flying mammals play an important role as pollinators in Asia and other regions.

However, one caveat is that mammals with a high wariness probably did not visit the flowers as the study site was located near the office of the bushwalk tour, and human activity was relatively high. This suggests that pollinators and their actual contribution to pollination in this plant may differ in the natural environment, and thus, further observations in an environment with less human presence would be beneficial to support our conclusions. Overall, more studies on plant-animal interactions are needed in montane forests in tropical Asia.

ACKNOWLEDGMENTS

We express our gratitude for the permission to conduct this research in the Doi Inthanon National Park. This study was financially supported by JSPS KAKENHI (Grant No. 16H05771 and 19K16215) and the Centre of Excellence on Biodiversity, Thailand (BDC-PG2-159009).

CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest.

AUTHOR CONTRIBUTIONS

Shun Kobayashi: Conceptualization (equal); Data curation (equal); Funding acquisition (equal); Methodology (equal); Writing-original draft (lead); Writing-review & editing (equal). **Somsak Panha:** Conceptualization (equal); Funding acquisition (equal); Writing-original draft (equal); Writing-review & editing (equal). **Teerapong Seesamut:** Data curation (equal); Writing-original draft (equal). **Nattawadee Nantararat:** Data curation (equal); Writing-original draft (equal). **Natdainai Likhitrakarn:** Data curation (equal); Writing-original draft (equal). **Tetsuo Denda:** Conceptualization (equal); Writing-original draft (equal); Writing-review & editing (equal). **Masako Izawa:** Conceptualization (equal); Methodology (supporting); Writing-original draft (equal); Writing-review & editing (equal).

DATA AVAILABILITY STATEMENT

The raw data used in this study are publicly available in the Dryad: <https://orcid.org/0000-0003-3167-3358>.

ORCID

Shun Kobayashi  <https://orcid.org/0000-0003-3167-3358>

REFERENCES

- Agostini, K., Sazima, S. M., & Sazima, I. (2006). Bird pollination of explosive flowers while foraging for Nectar and Caterpillars1. *Biotropica*, 38(5), 674–678. <https://doi.org/10.1111/j.1744-7429.2006.00191.x>
- Amorim, F. W., Ballarin, C. S., Mariano, G., Lacerda-Barbosa, P. A., Costa, J. G., Hachuy-Filho, L., Zabin, D. A., Queiroz, H. G. D., Servilha, H., Moraes, A. P., & Morellato, L. P. C. (2020). Good heavens what animal can pollinate it? A fungus-like holoparasitic plant potentially pollinated by opossums. *Ecology*, 101, e03001. <https://doi.org/10.1002/ecy.3001>
- Ashton, P. S. (2018). Patterns of variation among forests of tropical Asian mountains, with some explanatory hypotheses. *Plant Ecology and Diversity*, 10, 361–377. <https://doi.org/10.1080/17550874.2018.1429028>
- Cárdenas, S., Niuevelo-Villavicencio, C., Cárdenas, J. D., Landázuri, O. P., & Tinoco, B. A. (2017). First record of flower visitation by a rodent in Neotropical Proteaceae, *Oreocallis grandiflora*. *Journal of Tropical Ecology*, 33, 174–177.
- Carpenter, F. L. (1978). Hooks for mammal pollination? *Oecologia*, 35, 123–132. <https://doi.org/10.1007/BF00344725>
- Carthew, S. M. (1993). An assessment of pollinator visitation to *Banksia spinulosa*. *Australian Journal of Ecology*, 18, 257–268. <https://doi.org/10.1111/j.1442-9993.1993.tb00453.x>
- Carthew, S. M., & Goldingay, R. L. (1998). Non-flying mammals as pollinators. *Trends in Ecology and Evolution*, 12, 104–108. [https://doi.org/10.1016/S0169-5347\(96\)10067-7](https://doi.org/10.1016/S0169-5347(96)10067-7)
- Cocucci, A. A., & Sersic, A. N. (1998). Evidence of rodent pollination in *Cajophora coronata* (Loasaceae). *Plant Systematics and Evolution*, 211, 113–128.
- Corlett, R. T. (2004). Flower visitors and pollination in the Oriental (Indomalayan) region. *Biological Reviews*, 79, 497–532. <https://doi.org/10.1017/S1464793103006341>
- Corlett, R. T. (2019). *The ecology of tropical East Asia* (3rd ed.). Oxford University Press.
- Dellinger, A. S., Scheer, L. M., Artuso, S., Fernández-Fernández, D., Sornoza, F., Penneys, D. S., Tenhaken, R., Dötterl, S., & Schönenberger, J. (2019). Bimodal pollination systems in Andean Melastomataceae involving birds, bats, and rodents. *The American Naturalist*, 194, 104–116. <https://doi.org/10.1086/703517>
- Duckworth, J. W. (2016). *Callosciurus caniceps*. The IUCN Red List of Threatened Species 2016: e.T3594A22254694. <https://doi.org/10.2305/IUCN.UK.2016-2.RLTS.T3594A22254694.en>
- Duckworth, J. W. (2017). *Callosciurus finlaysonii*. The IUCN Red List of Threatened Species 2017: e.T3596A22254494. <https://doi.org/10.2305/IUCN.UK.2017-2.RLTS.T3596A22254494.en>
- Duckworth, J. W., Timmins, R. J., & Molur, S. (2017). *Callosciurus erythraeus*. The IUCN Red List of Threatened Species 2017: e.T3595A22254356. <https://doi.org/10.2305/IUCN.UK.2017-2.RLTS.T3595A22254356.en>
- Fleming, T. H., & Kress, J. W. (2013). *The ornaments of life: Coevolution and conservation in the tropics*. University of Chicago Press.
- Funamoto, D. (2019). Plant-pollinator interactions in east Asia: A review. *Journal of Pollination Ecology*, 25, 46–68. [https://doi.org/10.26786/1920-7603\(2019\)532](https://doi.org/10.26786/1920-7603(2019)532)
- Ganesh, T., & Devy, M. S. (2000). Flower use by arboreal mammals in a wet evergreen forests, south Western Ghats. *Selbyana*, 21, 60–65.

- Ganesh, T., & Devy, M. S. (2006). Interactions between non-flying mammals and flowers of *Cullenia exarillata* Robyns (Bombacaceae), a canopy tree from the wet forests of Western Ghats, India. *Current Science*, 90, 1674–1679.
- Goldingay, R. L., Carthew, S. M., & Whelan, R. J. (1991). The importance of non-flying mammals in pollination. *Oikos*, 61, 79–87. <https://doi.org/10.2307/3545409>
- Hobbhahn, N., Steenhuisen, S.-L., Olsen, T., Midgley, J. J., & 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.
- Kleizen, C., Midgley, J., & Johnson, S. D. (2008). Pollination systems of *Colchicum* (Colchicaceae) in Southern Africa: Evidence for rodent pollination. *Annals of Botany*, 102, 747–755. <https://doi.org/10.1093/aob/mcn157>
- Kobayashi, S., Denda, T., Liao, C.-C., Wu, S.-H., Lin, Y.-H., & Izawa, M. (2017). Squirrel pollination of *Mucuna macrocarpa* (Fabaceae) in Taiwan. *Journal of Mammalogy*, 98, 533–541.
- Kobayashi, S., Denda, T., Placksanoi, J., Waengsothorn, S., Aryuthaka, C., Panha, S., & Izawa, M. (2019). The pollination system of the widely distributed mammal-pollinated *Mucuna macrocarpa* (Fabaceae) in the tropics. *Ecology and Evolution*, 9, 6276–6286.
- Kobayashi, S., Gale, S. W., Denda, T., & Izawa, M. (2019). Civet pollination in *Mucuna birdwoodiana* (Fabaceae: Papilionoideae). *Plant Ecology*, 220, 457–466. <https://doi.org/10.1007/s11258-019-00927-y>
- Kobayashi, S., Gale, S. W., Denda, T., & Izawa, M. (2021). Rat- and bat pollination of *Mucuna championii* (Fabaceae) in Hong Kong. *Plant Species Biology*, 36, 84–93.
- Kobayashi, S., Hirose, E., Denda, T., & Izawa, M. (2018). Who can open the flower? Assessment of the flower opening force of mammal-pollinated *Mucuna macrocarpa*. *Plant Species Biology*, 33, 312–316.
- Lau, M. (2004). Bat pollination in the climber *Mucuna birdwoodiana*. *Porcupine*, 30, 11–12.
- Lumer, C. (1980). Rodent pollination of *Blakea* (Melastomataceae) in a Costa Rican cloud forest. *Biotropica*, 32, 512–517.
- McCain, C. M. (2011). Could temperature and water availability drive elevational species richness patterns? A global case study for bats. *Global Ecology and Biogeography*, 16, 1–13. <https://doi.org/10.1111/j.1466-8238.2006.00263.x>
- Payne, S. L., Witkowski, E. T. F., & Symes, C. T. (2019). Good times, bad times: Inter-annual reproductive output in a montane endemic succulent (*Aloe peglerae*; Asphodelaceae) driven by contrasting visitor responses of small mammals and birds. *Australian Journal of Botany*, 67, 116–127. <https://doi.org/10.1071/BT18163>
- Quin, D., Goldingay, R., Churchill, S., & Engel, D. (1996). Feeding behaviour and food availability of the yellow-bellied glider in North Queensland. *Wildlife Research*, 23, 637–646. <https://doi.org/10.1071/WR9960637>
- Steenhuisen, S., Balmer, A., Zoeller, K., Kuhn, N., Midgley, J., Hansen, D., & Johnson, S. D. (2015). Carnivorous mammals feed on nectar of *Protea* species (Proteaceae) in South Africa and likely contribute to their pollination. *African Journal of Ecology*, 53, 602–605.
- Thai National Parks. (2021). *Wildlife in Doi Inthanon*. <https://www.thainationalparks.com/doi-inthanon-national-park/wildlife>
- 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.
- 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.
- Wester, P. (2011). Nectar feeding by the Cape rock elephant-shrew *Elephantulus edwardii* (Macroscelidea) – A primarily insectivorous mammal pollinates the parasite *Hyobanche atropurpurea* (Orobanchaceae). *Flora - Morphology, Distribution, Functional Ecology of Plants*, 206, 997–1001. <https://doi.org/10.1016/j.flora.2011.05.010>
- Wester, P., Johnson, S. D., & Pauw, A. (2019). Scent chemistry is key in the evolutionary transition between insect and mammal pollination in African pineapple lilies. *New Phytologist*, 222, 1624–1637. <https://doi.org/10.1111/nph.15671>
- Willmer, P. (2011). *Pollination and floral ecology*. Princeton University Press.
- Wilmot-Dear, C. M. (2008). *Mucuna* Adans. (Leguminosae) in Thailand. *Thailand Forest Bulletin*, 36, 114–139.
- Wooller, R. D., & Wooller, S. J. (2003). The role of non-flying animals in the pollination of *Banksia nutans*. *Australian Journal of Botany*, 51, 503–507. <https://doi.org/10.1071/BT02063>
- Yumoto, T., Momose, K., & 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. <https://doi.org/10.3759/tropics.9.147>

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Kobayashi, S., Panha, S., Seesamut, T., Nantarat, N., Likhitrakarn, N., Denda, T., & Izawa, M. (2021). First record of non-flying mammalian contributors to pollination in a tropical montane forest in Asia. *Ecology and Evolution*, 11, 17604–17608. <https://doi.org/10.1002/ece3.8361>