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Special issue

"The Frontline of the Researches on Conservation and Management of Japanese Macaques"

## Studies on primate crop feeding in Asian regions: A review

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Abstract. We reviewed previous literature on primate crop feeding in Asia. We found 134 reports from 14 different countries and regions. More than half of the crop feeding cases involved macaques, followed by colobines, especially common langurs, and to a lesser extent by orangutans. No crop feeding by gibbons, lorises, or tarsiers has been reported. Most reports obtained information about crop feeding through interviews with locals and recorded the crops damaged and troop composition, while a few recorded the activity of the target primates and their population parameters. Crop feeding increased when the field was located near the forest, and when natural food availability decreased. Most farmers used non-lethal countermeasures, while some farmers killed the monkeys, and a few used electrical fences to protect crops. In study sites inhabited by multiple animal species, primates are often the worst crop feeders. Human perception and attitudes toward crop feeding primates were affected by income, residential area, religion, and history of crop feeding. Recent studies have created models based on previous data to clarify the potential risk of crop feeding and to predict the monkeys' ranging patterns. To create models for reducing crop damage and to design conservation strategies, collecting fundamental information is necessary.

Key words: countermeasure, disease, Macaca, religion, seed dispersal.

Conflicts between humans and non-human primates (hereafter primates) that arise during crop feeding have become serious problems for farmers because their income decreases, and they are forced to spend extra time and energy to protect their crops (Hill 2004; Riley 2007; Marchal and Hill 2009). In Africa and Central/Southern America, studies aiming to decrease the degree of crop damage caused by primates have been conducted. For example, Naughton-Treves et al. (1998) and Chaves and Bicca-Marques (2017) found a positive correlation between the degree of crop damage by primates and the availability of preferred crops. These findings imply that farmers should intensively protect their crops during the harvest season. Such information is therefore useful for efficient damage control against crop feeding primates. Recent studies have also attempted to analyze the potential risk of crop damage (Siljander et al. 2020) and aimed

to create a scenario in which humans and primates can coexist while reducing crop damage (Hockings et al. 2009; Radhakrishna 2013; Taylor et al. 2016).

Primates in Asia are composed of five families, that is, Lorisidae (lorises), Tarsiidae (tarsiers), Cercopithecidae (macaques and colobines), Hylobatidae (gibbons), and Hominidae (orangutans). They inhabit almost every part of East and Southeast Asia, except for the Korean Peninsula and Mongolia (Corlett 2019). Several Asian primates inhabit areas close to human settlements (Aggimarangsee 1992; Watanabe and Muroyama 2005; Sha et al. 2009; Ilham et al. 2017). The close proximity between humans and primates is facilitated by cultural attitudes that imbue monkeys with religious and/or cultural symbolism, which likely translates into tolerance (Priston and McLennan 2013; Dore et al. 2017). However, the primate species in Asia are also known to frequently feed on crops (Chalise

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and Johnson 2005; Priston 2005; Riley 2007; Yamada and Muroyama 2010), and farmers often treat primates as pests (Agetsuma 2007; Nijman and Nekaris 2010b; Anand and Radhakrishna 2017). Depredation of crops by primates adversely affects local farmers, who sometimes respond by injuring or killing the animals (Hill 2004; Nyhus et al. 2005; Strum 2010; Anand et al. 2018). The repercussions of crop feeding are ultimately high for both humans and primates; therefore, aggregating local information and taking efficient countermeasures is necessary to reduce the damage caused by primates. Until recently, systematic reviews of primate crop feeding have been conducted in some countries and regions (India: Mariadoss et al. 2019; Sri Lanka: Cabral et al. 2018; Bangradesh: Uddin et al. 2020; Japan: Enari 2021), but studies covering the entire Asian region have never been conducted.

In this study, we review previous studies on crop feeding by primates in Asia. Specifically, we ascertain the countries that have reported the most intense crop feeding, document the kinds of countermeasures that have been used, and examine how economic, cultural, and religious backgrounds affect local people's perception of crop feeding primates. Gathering information from multiple study sites enables us to identify species-specific and/or site-specific factors causing human-primate conflict and to create models for reducing crop damage. This would be useful to foster the coexistence of humans and primates in a given area. Finally, we discuss the direction of future studies for researchers studying primate crop feeding in Asia.

### Materials and methods

We conducted a web-based search and collected case studies on primate crop feeding published since 1960s. We used 1) ISI Web of Science (http://apps.webofknowledge.com/), 2) Google Scholar (http://scholar.google.co.jp/), 3) Japan Science and Technology Information (J-STAGE, https://www.jstage.jst.go.jp/), and 4) Citation Information by the National Institute of Informatics (CINII, https://ci.nii.ac.jp/), and used the following key words: "Asia\*", "primate\*", "crop raid\*", "crop forage\*", and "conflict\*" (\*indicates a wildcard search). Since two out of the four search engines are managed by Japanese institutions, we accept the possibility that a disproportionate amount of the literature detected was written by Japanese researchers. We added information from the literature and books (published after 1960) stored at the libraries of the Pri-

mate Research Institute, Kyoto University, and Andalas University. In this study, we extracted only literature accessible to people of all countries and regions: articles, books, theses, and reports written in English. We excluded studies conducted at provisioned sites (Sha et al. 2009; Ilham et al. 2017), university campuses (Md-Zain et al. 2014), and temples (Buddhist and Hindu, Aggimarangsee 1992; Beisner et al. 2015) from the analyses because such "urban monkeys" feed almost entirely on provisioned foods and garbage rather than cultivated plants.

From the contents of the collected literature, we gathered the following information: 1) publication year (divided into ten-year increments for analysis), 2) publication media (categorized into international journals and other journals including reports, theses (both master's and doctoral), and book chapters), 3) primate species involved in the crop feeding, and 4) country where the study was conducted. We defined "international journals" (from step 2) as registered in the Journal Citation Reports (Web of Science JCR).

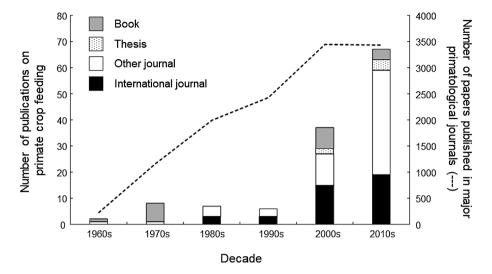
Besides collecting papers about primate crop feeding, we checked the number of papers (regardless of study field) published each year in the major primatological journals (*American Journal of Primatology, Folia Primatologica, International Journal of Primatology*, and *Primates*) for reference purposes. We conducted this search using Google Scholar in May 2019.

In order to address taxonomical variation in crop feeding cases, we compared composition of the case reports on the human-primate conflicts and composition of each taxonomic group, and tested by the Chi-square test of independence. Since there were no cases of crop feeding for the three primate groups (lorises, tarsiers, and gibbons), we omitted these groups from the statistical analysis. The analysis was conducted using R version 3.2.3 (R Developmental Core Team 2015). The statistical significance was set at 5%.

#### Results

Literature on primate crop feeding

We collected a total of 134 studies on primate crop feeding in Asia (Appendix 1). Figure 1 shows the number of publications every ten years. We found that the number of publications has increased rapidly since the 2000s. However, the percentage of publications on primate crop feeding within the broader primatological literature (calculated by the formula: [Number of publications on primate crop feeding]/[Number of papers published in major



**Fig. 1.** Temporal change (by ten-year increments) in the number and type of published reports on the conflict between human and non-human primates in Asia. Temporal changes in the number of reports published in the main international primatological journals (*American Journal of Primatology, Folia Primatologica, International Journal of Primatology, and Primates*) (dotted line) are also shown.

primatological journals] \* 100) has been consistently low (1.8% in the 1960s, 1.4% in the 1970s, 0.5% in the 1980s, 0.5% in the 1990s, 2.1% in the 2000s, and 3.9% in the 2010s). The percentage of international journals among the collected literature has also risen yearly, but it has remained at less than half of the total publication number. Theses on crop feeding first appeared in the 2000s and increased in the following decade (Fig. 1).

Crop feeding cases were reported from 14 different countries and regions throughout Asia (Fig. 2). The number of publications varied across countries and regions as follows: India had the highest number of reports (n = 37), followed by Indonesia (n = 27), Japan (n = 19), Nepal (n = 18), Bangladesh (n = 10), Sri Lanka (n = 8), and Thailand (n = 5). We found no reports from Indochinese countries (Vietnam, Laos, Cambodia, and Myanmar). In Singapore, there were several cases of macaques being a nuisance to people at tourism sites (e.g., Sha et al. 2009; Yeo and Neo 2010), but we found no publications on primate crop feeding.

## Primate species involved in crop feeding

Of the 134 studies, macaques (n = 94) were the most frequent primate species that fed on crops, followed by colobine monkeys (n = 10), such as *Semnopithecus* spp., *Trachypithecus* spp., and *Presbytis* spp. (Fig. 3). Twenty-six studies reported multiple primate species crop feeding (in most cases, two macaque species or one macaque one colobine species). The number of case studies on crop feeding by orangutans (*Pongo* spp.) was much

smaller (n = 3) than for macaques or colobines. We found no reports of crop feeding by lorises, tarsiers, or gibbons. Regarding species composition (macaques: 21 species, colobines: 44 species, lorises: 11 species, tarsiers: ten species, and orangutans: three species), the percentage of the crop feeding by macaques were higher, while that of the colobines was lower ( $\chi^2_2 = 44.6$ , P < 0.001).

#### Contents of the collected articles

a) Information on crop damages: Out of the 134 studies, 54 (41%) obtained information about crop feeding through interviews with local villagers (average number of interviews conducted: 387, range: 39-6983), while only nine studies (7%) conducted behavioral observations of the crop feeding monkeys (Appendix 1 and Supplementary Table S1). Seventeen out of 54 studies were review papers that included information collected from multiple study sites. As primary research articles, 62 studies (47%) listed specific crops damaged by primates. These records were mainly obtained by interviewing the occupants of local households. Chhangani and Mohnot (2004), for example, listed crops damaged by gray langurs (Semnopithecus entellus) based on interviews with local people, while Chalise (2003) evaluated the diets of Assamese macaques (Macaca assamensis) by behavioral observations (recorded by scan sampling method) and interviews with farmers. Twenty-seven studies (20%) evaluated the crop damage caused by primates. In villages near a protected area in Nepal, the annual crop damage caused by primates was estimated to be about

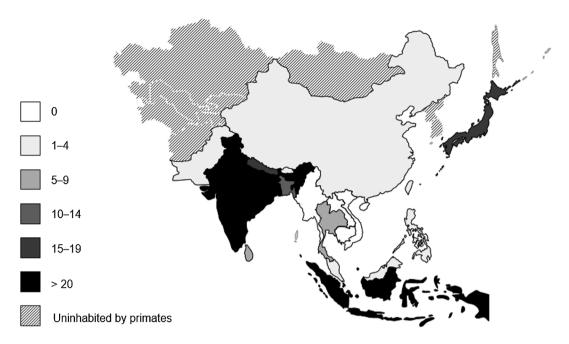
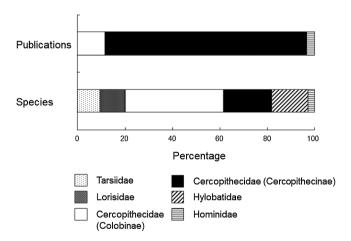


Fig. 2. A map showing the number of case reports on the conflict between human and non-human primates in Asia (n = 128). Saudi Arabia is not shown on the map.



**Fig. 3.** The top bar represents composition of the case reports on the conflict between human and non-human primates in Asia (n = 128) by primate families. Cases in which multiple species were included in the analyses were omitted. The bottom bar represents the proportion of the number of species in each taxonomic group (Kirkpatrick 2007). We separated Cercopithecidae into two ecologically and morphologically distinct subfamilies (Cercopithecinae and Colobinae).

183 kg/household, worth 75 USD/household (Paudel and Shrestha 2018). In Japan, the total agricultural damage over five years (2003–2007) caused by Japanese macaques (*M. fuscata*) was approximately 17.8 million USD (Suzuki and Muroyama 2010, see also Enari et al. 2021). A majority of these reports pooled the data across the study period, while several studies attempted to find sea-

sonal trends; Chhangani and Mohnot (2004) and Air (2015) conducted a field survey over a period of one year and found that crop feeding by langurs showed clear seasonality: crop feeding was proportional to the availability of crops. On the other hand, clear relationships between crop foraging and food availability in the forest were not always found (Riley 2007; Riley and Priston 2010). Across Asia, the crops damaged were mainly maize, potatoes, bananas, papayas, cacao, rice, and vegetables (Supplementary Table S1).

b) Group composition, home range, and activity of the crop feeders: The number of studies reporting activity budgets of the target primates (nine studies, 7%) or population parameters (such as group composition) (26 studies, 20%) was quite low. In addition, long-term monitoring of female reproductive ratio, infant survival ratio, and rate of natural increase of the target population have not been reported in Asian regions (but see Singh et al. 2016).

Crop feeding sometimes altered the daily travel distance and home-range size of the primates. Chhangani and Mohnot (2006) and Izumiyama et al. (2003) demonstrated that home-range sizes of crop feeding hanuman langurs (*S. entellus*) and Japanese macaques were much smaller than those of non-crop feeding groups, and that the home-range size increased proportionally with the number of group members. The former was attributed to the higher quality of food resources in the cropland, and

the latter was likely due to higher intra-group competi-

Accounts of crop feeding behavior by primates are site-specific and species-specific, and therefore, quantitative evaluation of the crop feeding requires all-day observation (Wallace and Hill 2012). Regmi et al. (2013) found that Assamese macaques visited the crop field in the early morning. Zak and Riley (2017), on the other hand, set camera traps in the farmland and evaluated the time when the moor macaques (*M. maura*) foraged in the crop field. Contrary to the farmers' impression that macagues visited the crop field early in the morning, the macaques entered the crop field in the afternoon and evening. Furthermore, Priston et al. (2012) reported intra-group variations in behavior among group members of crop feeders. They found that the number of co-feeding Buton macagues (M. ochreata) had a positive effect on the duration of time spent in the crop field, and the adult and subadult males took the lead when entering farms to forage on crops, while females and the dependent young were more likely to be observed crop foraging when people and dogs were absent from the farm.

c) Evaluation of crop quality: How valuable are crops to monkeys compared to foods in the forest? Several studies have evaluated the nutritional value of crops and compared them with that of natural foods. Riley et al. (2013) found that cultivated cacao fruits contained less fiber and higher energy than wild plants. Regmi et al. (2013) and Frondelius (2010) independently reported that maize and potatoes contained higher protein, lipids, and carbohydrates and deduced that the higher nutritional value of the crop was the main reason for primate crop feeding. At many sites, farmers experienced the highest levels of crop feeding on maize and (sweet) potato crops. It can be inferred that the nutritional value of these crops is likely responsible for attracting crop feeding.

d) Relationship between crop feeding and forest environment: Many studies have shown that crop fields located adjacent to the forest are at a greater risk of being visited by primates (e.g., Priston 2005; Adhikari et al. 2018a). The relationship between the crops' distance from the forest and the degree of crop feeding has been tested by several authors. Frondelius (2010) and Priston et al. (2012) found that papayas and sweet potato crops were mostly fed upon by Buton macaques located less than 10 m away from the forested border of the crop field, and foraging of sweet potatoes declined when the distance from the border increased to 25 m from the edge. Huang et al. (2018) demonstrated that the degree of crop

feeding by rhesus macaques (*M. mulatta*) was positively correlated with the number of croplands in the community and negatively correlated with distance from the nature reserve. These results corroborated those of Regmi et al. (2013), Wang et al. (2006), and Honda (2009), who found that crop feeding by Assamese macaques in Nepal, rhesus macaques in Bhutan, and Japanese macaques in Japan, occurred more frequently in crop fields located near the forest. These results imply that the monkeys do not like to stay out of the forest for a long time, and forests serve as their safe sites. In contrast, Air (2015) demonstrated that rhesus macaques fed on all the major crops, regardless of the distance from the national park. Thus, whether the forest serves as a refuge or not appears to be site- or species-specific.

e) Types of countermeasures: Thirty-five reports (26%) described the countermeasures used at the target study site (Supplementary Table S1). A variety of methods for reducing primate crop damage have been proposed by farmers. The most common methods were guarding, using dogs, and setting scarecrows. These are simple, involve low-technology, and do not incur additional costs. However, hunting, killing by poison, and fencing are also employed by some farmers. Rode-Margono et al. (2016) described in detail the protection measures employed by local people in Bawan Island, Indonesia and found that, while people mostly used poison and pesticides to get rid of rats and insects, they resorted to rock throwing, air pump guns, and noise making to protect crops against primates. Paudel (2016) showed that in Nepal, people guarded the crop fields by setting out scarecrows and releasing dogs. Farmers were forced to guard their crops even during the night. Priston (2009) tested the effectiveness of countermeasures (by evaluating the percentage of crops damaged) and found that setting up fences and mesh reduced the damage by up to 50%.

In Japan, electric fencing and population control, conducted by the local government, have been used widely to protect crops against Japanese macaques (Honda et al. 2009; Muroyama and Yamada 2010). Maintenance of the electric fences by farmers, however, is often insufficient due to differences among farmers in their knowledge of the fence management and their willingness and motivation to maintain them (Suzuki and Muroyama 2010).

f) Relative importance of the primates as crop feeders: At many study sites, there are multiple animal species inhabiting there, and farmers need to protect their crops from these animals. Twenty-four studies (18%) have tried to evaluate the ranking of primates as crop feeders by

degree of crop damage. Awasthi and Singh (2015) found that primates (multiple species) were the worst crop feeders compared to other mammalian species (porcupine, goral, deer, jackal, bear, and several mouse species) in the Gaurishankar Conservation Area, Nepal, and Huang et al. (2018) (Daxueshan Nature Reserve, China) and Saraswat et al. (2015) and Anand et al. (2018) (Himachal Pradesh, northern India) found that rhesus macagues were the second-highest crop feeders among sympatric animals (wild boar, bear, porcupine, deer, nilgai, and several bird species). Campbell-Smith et al. (2010) demonstrated that Sumatran orangutans (Pongo pygmaeus) were not only ranked as the third most frequent and the fourth most destructive (17%) crop pest entering farmlands, but were also the most feared (31%) species. The damage caused by Japanese macaques was the third largest after sika deer (Cervus nippon) and wild boars (Sus scrofa) in Japan (Honda 2009; Suzuki and Muroyama 2010). In Kerinci Seblat National Park, Sumatra, crop feeding by southern pig-tailed macaques (M. nemestrina) was not as widespread as wild boars, but they caused much greater crop damage (73%) than wild boars (26%), contrary to farmers' perceptions (Linkie et al. 2007). In Lore Lindu National Park, Sulawesi, in contract to farmers' reports, forest mice were more destructive than macaques (Riley 2007). In this way, the relative threat level of the primates is site- and species-specific.

g) Human dimensions: In addition to the ecology of the crop feeding monkeys, 29 studies (22%) have investigated human perceptions of the crop feeding primates. Further, 22 studies (17%) discussed the effects of human activities on primate crop feeding. Aryal and Chalise (2013) and Kumara and Diandra (2018) interviewed the local communities in Nepal and India, respectively, and demonstrated that local people thought that the lack of food resources in the forest and the increasing size of the monkey populations were the proximate determinants of crop feeding. However, these speculations have rarely been confirmed. Nautiyal et al. (2020), on the other hand, argued that the economic background of local people is an indirect factor contributing to crop feeding; farmers with less agricultural productivity depend on livestock for extra income and thus rely on the neighboring forests for grazing and collecting fodder for their cattle. This consequently reduces the availability of natural foods eaten by the Himalayan langurs (S. schistaceus), and this consequently induces crop feeding. In Saudi Arabia, a decrease in predators was considered to affect the increase in crop feeding by hamadryas baboons (Papio hamadryas)

(Biguand et al. 1994). Several researchers have attempted to evaluate the effects of the social background of people on their attitudes toward primate crop feeding. Chauhan and Pirta (2010), for example, showed that residents (people living near a wildlife habitat) felt a greater need for its effective resolution than nonresidents (visitors or tourists). Furthermore, cultural and religious beliefs are likely to generate different perceptions of the crop feeding primates in many parts of Asia (Knight 1999; Khatun et al. 2013). For instance, Anand et al. (2018) compared people's attitudes in two locations in India (Solan and Kasaragod) and found that people in Kasaragod were less tolerant of crop feeding by macaques. This appears to arise from differing cultural backgrounds between the two regions, particularly with respect to perceptions regarding the role of forests and wildlife in human lives. In Bali, long-tailed macaques feed on crops frequently but the local people are relatively tolerant to the monkeys, and Loudon et al. (2006) interpreted this as attributable to Balinese Hinduism. Similarly, Tonkean macaques in central Sulawesi are culturally important to the local people and are afforded protection, even though they are known to forage on people's crops (Riley 2010).

In Japan, farming near the habitat of macaques is largely conducted as a low-profit, multipurpose activity, in which harvests are used for household consumption, gifts for relatives and neighbors, and a source of small additional income (Suzuki and Muroyama 2010). In such situations, even in the same village, some farmers have little motivation to protect their agricultural products from macaques, while others in the village depend mainly on the income generated from farm production. Suzuki and Muroyama (2010) point out that farmers' awareness of damages significantly affects the proper maintenance of the electrical fence.

h) Experimental and modeling approaches: Modeling is the best way to gauge the potential risk of crop feeding and to predict the home range of monkeys (Honda 2009). Enari and Suzuki (2010) created a risk map and potential habitat of monkeys in northern Japan to identify areas where precautionary actions should be taken to efficiently minimize the overall risk of damage. Linkie et al. (2007) developed models to predict the appearance of the target animals and found that most crop feeding occurred nearest to the forest edge and that the local guarding strategies used were ineffective. Priston and Underdown (2009) predicted the relative risk of primate crop feeding based on crops grown in the field, their availability within individual farms, and patterns of primate selectivity. Recently,

Honda et al. (2019) integrated field experiments and simulations and demonstrated that a high rate of guarding made the macaques less likely to feed crops, which has important implications for mitigating human-macaque conflicts.

#### Discussion

The number of studies on human-primate conflict is much smaller than that of publications in the field of primatology. Through web-based searching, we collected 134 studies (published between 1960 and 2020) on primate crop feeding in Asia, most of which were published in the past two decades. The rapid increase in publications since the 2000s is likely due to economic developments in Asian countries in the 21st century (Maddison 2009), which have enabled academics to turn their attention towards natural science, including primate ecology. Another likely reason for the recent increase in publications on crop feeding is the rise of "Ethnoprimatology" which examines interactions between humans and primates from biological, cultural, economic, and religious viewpoints (e.g., Knight 1999; Dore et al. 2017). In addition, recognition of the value of studying primate behavior in anthropogenic environments has grown (e.g., Suzuki and Muroyama 2010). The ethnoprimatology has provided the scientific basis for studies on crop feeding in Asia. However, as mentioned above, the percentage of crop feeding studies among primatology is still low. We hope that this applied field will attract the attention of more researchers in the future.

It is noteworthy that the number of theses on primate crop feeding has increased since the 2000s (e.g., Priston 2005; Rijal 2015; Zak 2016). In spite of the limitations of a survey based on a review of published literature, our present results indicate that studies on primate crop feeding have become an important research topic, and such a trend is welcomed. In the next decade, the number of young researchers studying human-primate conflict is likely to increase further. Researchers in developed countries need to train students from developing countries as specialists in human-wildlife conflicts in their respective countries.

The percentage of studies published in international journals has increased; nonetheless, less than 50% of the total number of publications have been on primate crop feeding in Asia. Publishing research in international journals is invaluable as the knowledge gained from the provided research can easily be shared worldwide. In order

to publish research in international journals, researchers should collect sufficient high-quality data by using appropriate sampling methods, analyze the data with statistical tools, and prepare manuscripts with clear logic and hypotheses. It may be necessary to unify data sampling and analysis methods among researchers to allow clear comparisons of the results. Collaboration with researchers of fundamental primate ecology and behavior would be a good solution, but there are practical reasons that prevent joint research among researchers from different fields of study. For example, in Japan, countermeasure technology tends to be published with the aim of obtaining patents rather than research papers (Enari 2021). Further, damage management is often implemented with public budgets, requiring researchers to quickly provide results to local communities rather than publishing them in scientific journals. Thus, in order to share information by means of scientific papers, support from local governments would be essential.

In the Asian region, crop feeding is mainly done by macaques and, to a lesser extent, by colobines. The former is unsurprising because macaques are highly tolerant to environmental changes (Nijman and Nekaris 2010b; Tsuji et al. 2013) and even utilize human settlements as their habitats (Richard et al. 1989; Nijman and Nekaris 2010b). For macaques living in forests near human settlements, supplementing their diet with cultivated food is an adaptive strategy. However, it was unexpected that colobines were crop feeders as well. However, most of these cases were caused by Semnopithecus monkeys. Compared to other colobines in Asia (genera Trachypithecus, Presbytis, Rhinopithecus, and Pygathrix), Semnopithecus monkeys have a more omnivorous diet containing a lower proportion of leaves (Kirkpatrick 1999; Tsuji et al. 2013). In addition, Semnopithecus spp. have a higher tolerance than other colobines to environmental disturbances and can survive near human settlements (Minhas et al. 2010; Nautiyal et al. 2020). Generalist primates (such as genera Cercopithecus, Papio, and Sapajus) are often the crop feeders in Africa (Naughton-Treves 1998; Hill 2000; Nijman and Nekaris 2010b; Strum 2010) and Central/ South America (Spagnoletti et al. 2017). Therefore, crop feeding by generalist primates in Asia is expected. This implies that strategies for the management of primate crop feeding should target Macaca and Semnopithecus species.

Across Asia, India had the highest number of publications on crop feeding (n = 37), which is likely due to human population growth, deforestation, intense agricul-

tural practices, and urbanization (Mariadoss et al. 2019). In Indonesia (n = 27) and Nepal (n = 18), a majority of the reports were written by the same research group at the same study sites; thus, information from other groups/study sites is necessary to generalize their findings. The lack of information from Indochinese countries (Vietnam, Laos, Cambodia, and Myanmar) is likely due to the smaller number of researchers and shorter history of primatology in those countries, compared to other Asian countries.

Despite the considerable number of primate researchers and their respective country's economic scale, the number of case reports from Japan (n = 19) and China (n = 2) was small, because more scholars from these countries are publishing their research on crop feeding in non-English journals. We previously summarized the dietary habits of Japanese macaques feeding on crops (Tsuji et al. 2018) and found that almost all reports (> 90%) were written in Japanese (although several reports contained an English summary). Information written in native languages is useful to share among people within the country and to conduct rapid countermeasures locally. However, considering the globalization of the economy and academic activity, researchers should share with the world the information gained in their own country. This implies that researchers (especially in academia) need to write their reports in English. Reporting more studies from China and Japan on primate crop feeding cases, on effective countermeasures, and on mitigation programs would be useful models for other Asian countries suffering from primate crop feeding.

Crop damage levels depend on season, crop type, size, and location of the crop field, and the primate species involved. Multiple factors make it difficult to predict crop feeding accurately (Linkie et al. 2007; Nijman and Nekaris 2010b). As a next step, what should researchers in Asia do? First, they need to clarify the mechanisms driving the ranging behavior of crop feeding primates. For example, data on the population parameters of crop feeding primates should be systematically collected. Crop feeding often improves the nutritional condition of feeders and consequently increases their population size, which then escalates the crop feeding (Biquand et al. 1994). Collecting demographic data on crop feeders can be challenging and difficult if they are not habituated, and it might be unethical to habituate groups that regularly forage on crops (Riley and Bezanson 2018). Therefore, the use of technology such as sensor cameras (Zak and Riley 2017) and drones (Bonnin et al. 2018) should be

considered. Primate crop feeding behaviors cannot be understood solely in terms of animals shifting to crops to compensate for reduced forest food availability. Other possible reasons include the higher nutritional value of crops (Riley et al. 2013), behavioral tradeoff (primates may be weighing the risks and benefits, such that the benefits of crop feeding outweigh the risks) (McLennan and Hockings 2014), and a forest environment adjacent to the crop field (such as abundance and quality of natural foods and landscape structure) (Wang et al. 2006; Regmi et al. 2013; Hill 2017). In addition, extrinsic factors such as temperature, forest productivity, and snowfall also affect the distribution and ranging patterns of the crop feeding primates (Honda 2009). If we can evaluate the relative importance of each factor, we can provide a biological justification for the target primate's preference for crops.

Hill (2017) advocated the idea that crop feeding by primates should be treated as a feeding strategy (Stephens and Krebs 1986; Strum 2010). In this framework, not only crop fields but also the surrounding forest should be evaluated as the habitat of the target primate species, and the potential value of the crop fields (as feeding sites and refuge) should be assessed based on costs and benefits. This knowledge would be useful for controlling the determinants of crop feeding. Data accumulation enables models to simulate the monkeys' ranging and/or potential risk of crop damage, which is useful for both farmers and local governments to prepare countermeasures and to use their budgets and time efficiently. To fully understand why, how, and when primates incorporate crops into their dietary repertoire, researchers need to examine primate crop foraging behavior in the context of their feeding strategies (Strum 2010; MacLarnon et al. 2015; Hill 2017).

Furthermore, researchers should actively employ an experimental approach to confirm the efficiency of target countermeasures; Hill and Wallace (2012), for example, monitored primate crop feeding behavior prior to and after installing locally appropriate countermeasures (fences, alarms, repellents, and systematic guarding), developed by local farmers in Africa, and found that the incidence of feeding and crop loss decreased in almost all cases, often by shifting the feeding to unprotected fields or adjacent farms. Nijman and Nekaris (2010b) tested the applicability of a simple model for calculating the likelihood of crop damage by primates using crop susceptibility to predict the frequency of crop damage for individual farms and found that it works well for predicting crop feeding by langurs. In their study, farmers identified the

pros and cons of each countermeasure and considered which were the most effective and valuable. Unfortunately, such an approach has rarely been used in Asia (only five out of the 134 cases studied here), and many reports are just descriptions of the present situation.

Furthermore, in addition to damage control, researchers also need to evaluate how dependence on crops influences the ecological services of crop feeding primates. The ecological role of Asian primates as seed dispersers and their relationship with forest productivity has been previously revealed (McConkey 2018; Tsuji and Su 2018). Recent studies have shown that the ecological role of primates can be affected by human activity. Sengupta et al. (2015), for example, reported that a dependence on provisioned foods shifted the home range area of rhesus macagues to roadsides and consequently deteriorated their seed dispersal services. In Africa, Hockings et al. (2017) reported that chimpanzees dispersed seeds of cultivated cacao, but the cacao trees that grew in forests did not fruit. These results imply that when the range of primates is affected by human activity, seed dispersal characteristics and effectiveness are also affected. On the other hand, provisioning leads to decreased home range size (Chhangani and Mohnot 2006; Koganezawa and Imaki 1999), which might change the seed dispersal distance and direction. Research on crop feeding hitherto has paid little attention to this ecological perspective.

Additionally, researchers need to accumulate data on the effects of bites and illnesses inflicted upon people during crop feeding (none of the 134 collected studies identified this to be an issue). Engel et al. (2002) studied the infection risk of B virus from provisioned Balinese long-tailed macaques inhabiting a monkey park. Based on their report, more than half of the 105 staff members had been bitten or scratched by the park macaques, and the blood of 33 out of 38 tested monkeys showed a positive reaction to the B virus antibody. This implies that the risk of infection from monkeys to humans is high. At present, however, research on the risk of bite-borne infection is lacking.

It is difficult to balance the lives of farmers with primate conservation (Hockings and McLennan 2012; Hockings et al. 2020). Farmers often distrust local governments (Campbell-Smith et al. 2010; Enari 2021). In order to reach a consensus among stakeholders, researchers first need to show information on the ecological and conservation conditions of the target primate species to local people. Second, researchers need to advise local governments to suggest efficient countermeasures and

support local farmers to make them more likely to tolerate the primates (Campbell-Smith et al. 2010). The conservation initiatives provided by scientists would be useful for conducting damage control and environmental education, in terms of coexistence with wildlife.

Promoting research on crop feeding in Asian regions as applied science in the next few decades is the responsibility of researchers who study in Asia where sustainable development is strongly required.

## Supplementary data

Supplementary data are available at *Mammal Study* online. **Supplementary Table S1.** A summary of previous reports on the details of crop feeding by non-human primates in Asian region.

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Appendix 1.

A list of previous reports on the crop feeding by non-human primates in Asian region

		a) Listu	a) List up of crops damaged	lamaged	<ul> <li>b) Group composition, home range, and activity of the crop-feeders</li> </ul>			d) Relationship		f) Relative	g) Humar.	g) Human dimension	h) experiments and models		
# Country/region	Primate species performing crop feeding	Interview (N)	Damaged crops	Danaged Evaluation Population crops of damage parameters	Population parameters t	of eys	c) Evaluation of crop quality	between crop damage and environment	e) Type of countermeasure	of the primates as crop-feeders	Perception/ opinion of local people toward primates	Effects of human characteristics: Age-sex/ Religion/City	Experiments Model	Type of article <sup>a</sup>	Reference
1 All Asia	Macaques			*					*		*	*		В	Lee and Priston (2005)
2 All Asia	Macaques		-											В	Priston and McLennan (2013)
3 All Asia	Multiple species						-							-	Richard et al. (1989)
4 Banglades	Bangladesh M. mulatta	* (40)	*											0	Ahsan and Uddin (2014)
5 Banglades	Bangladesh M. mulatta	* (No data)	*	*						*				0	Aziz and Feeroz (2007)
6 Bangladesh	sh M. mulatta		*		*	*								Т	Jaman and Huffman (2013)
7 Bangladesh		* (410)							*		*	*		0	Khatun et al. (2012)
8 Bangladesh	S. entellus	* (410)									*	*		0	Khatun et al. (2013)
		* (70)	*	*										0	Miah et al. (2001)
10 Bangladesh	sh M. mulatta, Trachypithecus pileatus		*											0	Naher et al. (2017)
11 Bangladesh						*								0	Rahman et al. (2015)
12 Banglades	Bangladesh M. mulatta, S. entellus, T. pileatus	* (40)	*											0	Uddin and Ahsan (2018)
13 Bangladesh	sh M. mulatta, S. entellus, T. pileatus													0	Uddin et al. (2020)
14 Buhtan		* (274)	*					*	*					0	Wang et al. (2006)
15 China	M. mulatta		*					*		*			*	-	Huang et al. (2018)
16 China	M. mulatta		*											-	Poirier and Hu (1983)
17 India	M. mulatta, M. radiata	(926) *									*	*		-	Anand et al. (2018)
18 India	Multiple species (mainly M. mulatta)									*				0	Anand and Radhakrishna (2017)
19 India	M. radiata	·	*		*				*					В	Chakravarthy and Thyagaraj (2005)
20 India	M. mulatta, S. entellus													0	Chaturvedi and Mishra (2014)
21 India	M. mulatta	* (400)					-							0	Chauhan and Pirta (2010)
22 India	S. entellus	* (no data)	*	*	*		-		*					0	Chhangani and Mohnot (2004)
23 India	S. entellus		*		*									0	Chhangani and Mohnot (2006)
24 India	M. nemestrina		*											0	Choudhury (2003)
25 India	M. mulatta	* (no data)			*									0	Das and Mandal (2015)
26 India	Multiple species (mainly M. mulatta)	* (120)	*											0	Devi and Radhakrishna (2013)
27 India	M. mulatta	(809) *			*				*		*	*		0	Ganguly and Chauhan (2019)
28 India	Multiple species (mainly M. mulatta)	*	*				- 4		*					0	Hanse et al. (2015)
29 India	M. mulatta	* (300)										*		0	Imam and Ahmad (2013)
30 India	M. radiata		*	*					*	*				0	Jayson (1999)
31 India	M. radiata, S. entellus	* (47)	*	*					*	*	*			0	Kumara and Diandra (2018)
32 India	M. mulatta		*											В	Lindburg (1977)
33 India	M. mulatta, M. assamensis, M. radiata, S. entellus								*					0	Mariadoss et al. (2019)
34 India	M. arctoides		*											0	McCann (1933)
35 India	Semnop ithecus schistaceus	* (215)						*				*		-	Nautiyal et al. (2020)
36 India	M. mulatta, S. entellus	*	*		*				*		*			Т	Pirta et al. (1997)
37 India	Multiple species			*										0	Radhakrishna and Sinha (2010)
38 India	S. entellus			*						*				-	Rao et al. (2002)
39 India	M. mulatta													В	Rattan (2011)
40 India	M. radiata													В	Roonwal and Mohnot (1977)
41 India	M. mulatta, S. emtellus	* (380)								*	*			Н	Sabic (2011)
42 India	M. mulatta	* (54)		*					*	*	*			Т	Saraswat et al. (2015)
43 India	M. mulatta, S. entellus	* (180)		*			-		*					-	Sekhar (1998)
44 India	M. radiata, Semnopithecus hypoleucos	* (50)			*					*				0	Sengupta and Radhakrishna (2013)
45 India	M. mulatta				*									0	Sharma et al. (2011)
A6 Tradio	C autollin	* (100)	*								*			c	Sharma of al. (2010)

Appendix 1. (continued)

	a)	a) List up of crops damaged	damaged	home range, and activity	home range, and activity of the crop-feeders		d) Relationshin		f) Relative	g) Human	g) Human dimension	n) experiments and models	is and		
Country/ Primate species performing region crop feeding	ning Interview (N)		Damaged Evaluation crops of damage	Pop	Activity of the monkeys	c) Evaluation of crop quality	d) Ketationsinp between crop damage and environment	e) Type of countermeasure	importance of the primates as crop-feeders	Perception/ opinion of local people toward primates	Effects of human characteristics: Age-sex/ Religion/City	Experiments	Model	Type of article <sup>a</sup>	Reference
India M. mulatta										ļ					Singh (2019)
India M. mulatta		*		*										0	Singh et al. (2016)
India M. mulatta, S. entellus	* (3243)	43)												0	Singh and Thakur (2012)
														-	Singh and Thalour (2017)
														, n	Southwick of al (2005)
nela M. matana															Southwick et al. (2002)
		*													Wada (1984a)
India M. mulatta		*		-										0	Wada (1984b)
Indonesia P. abelii	* (822)	22)							*	*		*		-	Campbell-Smith et al. (2010)
Indonesia M. fascicularis, M. nemestrina		*		*										В	Crockett and Wilson (1980)
1		*											-		Di Bitetti (2019)
1		*												В	Fittinghoff and Lindburg (1980)
1		*				*	*				*			-	Frondelins (2010)
				*											Hadi et al. (2012)
	the Care Antes	John		,				4							Handwick et al (2013)
	(no) *			K-				K-							Hardwick et al. (2017)
	* (20)	*	*						*						Linkie et al. (2007)
Indonesia M. fascicularis	* (153)	53)		-							*			0	Loudon et al. (2006)
Indonesia M. fascicularis, Presbytis. thomasii,	masii, * (98)	*						*	*					0	Marchal and Hill (2009)
Indonesia P momans	(£869) *	83)												-	Meijaard et al. (2011)
-										-8	-36				Deterson and Rilay (2013)
	70.7			4	4		4	4					-		reteison and Aney (2013)
	(122)		¢ -	6	6		6	•	6	F	F				FTISION (2002)
1			6									6			FTISION (2009)
													W-	-	Priston and Underdown (2009)
Indonesia M. ochreata		*			*		_	_						-	Priston et al. (2012)
			*						*					-	Riley (2007)
Indonesia M. tonkeana														_	Riley (2008)
Indonesia M. tonkeana				-			-				*			_	Riley (2010)
Indonesia M. tonkeana, M. fascicularis		*	*							*	*			_	Riley and Fuentes (2011)
Indonesia M. tonkeana										*				-	Riley and Priston (2010)
M. tonkeana		*				*								-	Riley et al. (2013)
		*						*	*	*				0	Rode-Margono et al. (2016)
1		*												1	Supriatna et al. (1992)
1		*												-	Wheatley (1980)
-	+	_					4			+	÷				** Incaring (17.00)
	* (no data)	data)					K-		K	K-	K-			-	Zak (2010)
Sia	* (no data)	data)												7	Zak and Kiley (2017)
Japan <i>M. fuscata</i>			*				*	*		*	*			-	Enari (2021)
Japan M. fuscata													*	_	Enari and Suzuki (2010)
Japan M. fuscata		*												В	Hill (1974)
Japan M. fuscata							*		*				*	-	Honda (2009)
								*	*			*		-	Honda et al. (2011)
								-*	20			*			Honda et al. (2011)
Japan M. fiscata								,	+				×		Honda et al. (2003)
												ţ	6	- ,	HOnda et al. (2012)
				*										-	Izumiyama et al. (2003)
Japan M. fuscata			*								*			_	Knight (1999)
Japan M. fuscata							*						*	-	Mochizuki and Murakami (2011)
							*						*	1	Mochizuki and Murakami (2013)
				*			*			*	*			В	Murovama and Yamada (2010)
													-	-	
														_	Sprague (2002)

Appendix 1. (continued)

		a) Listı	a) List up of crops damaged	amaged	<ul> <li>b) Group composition, home range, and activit of the crop-feeders</li> </ul>	b) Group composition, home range, and activity of the crop-feeders		d) Relationship		f) Relative		g) Human dimension	h) experiments and models	s and		
Country/region	Primate species performing crop feeding	Interview (N)	Damaged Evaluation crops of damage	Evaluation of damage	Population	Activity of the monkeys	c) Evaluation of crop quality	between crop damage and environment	e) Type of countermeasure	of the primates as crop-feeders	Perception/ opinion of local people toward primates	Effects of human characteristics: Age-sex/ Religion/City	Experiments Model	1	Type of article <sup>a</sup>	Reference
Japan	M. fuscata														I	Sprague et al. (2004)
Japan	M. fuscata	* (182)		*					*		*	*			В	Suzuki and Muroyama (2010)
Japan	M. fuscata	ļ							*			*			ا ا	Ueda et al. (2018)
98 Japan	M. fuscata														В	Watanabe and Muroyama (2005)
99 Japan	M. fuscata		*		*			*							-	Yamada and Muroyama (2010)
100 Malaysia	M. fascicularis	* (46)			*				*		*	*			0	Hambali et al. (2012)
101 Nepal	M. mulatta, S. entellus	* (100)		*				*		*						Adhikari et al. (2018a)
102 Nepal	M. assamensis	* (100)	*		*	*									-	Adhikari et al. (2018b)
103 Nepal	M. mulatta	* (100)							*						Į.	Air (2015)
104 Nepal	M. mulatta, S. entellus	* (155)	*		*				*		*				0	Aryal and Chalise (2013)
105 Nepal	Unknown	*(202)		*						*						Awasthi and Singh (2015)
106 Nepal	M. mulatta, M. assamensis, S. entellus		*	*						*					0	Chalise (2000)
107 Nepal	M. assamensis		*		*	*									0	Chalise (2003)
108 Nepal	M. mulatta, M. assamensis	* (267)									*				В	Chalise and Johnson (2005)
109 Nepal	M. mulatta		*													Ghimire (2001)
110 Nepal	M. mulatta	* (> 200)	*	*							-					Ghimire and Chalise (2016)
111 Nepal	M. assamensis		*					-							0	Ghimire and Chalise (2019)
112 Nepal	M. assamensis	* (39)	*	*				-			-					Ghimirey et al. (2018)
113 Nepal	Multiple species?	* (100)	*	*				*			*					Paudel and Shrestha (2018)
114 Nepal	M. assamensis		*		*	*		-	*							Paudel (2013)
115 Nepal	M. assamensis	(96) *	*	*				-	*							Paudel (2016)
116 Nepal	M. assamensis	* (120)	*		*		*	*	*							Regmi et al. (2013)
117 Nepal	M. assamensis	* (375)	*		*	*			*		*					Rijal (2015)
118 Nepal	M. mulatta	(09) *	*	*					*							Sharma and Acharya (2017)
	M. mulatta		*													Siddiqi and Southwick (1977)
S	M. fascicularis	* (303)	*						*							Gamalo et al. (2019)
121 Sri Lanka	M. sinica, S. priam thersites, T. vetulus									*						Cabral et al. (2018)
Sri Lanka	S. vetulus	* (110)									*				0	Dela (2011)
Sri Lanka	Multiple species (mainly M. sinica, Sennopithecus sp.)	* (150)	*		*				*		*	*				Dittus et al. (2019)
124 Sri Lanka	M. sinica			_		-			*	*					1	Horgan and Kudavidanage (2020)
125 Sri Lanka	M. sinica	* (307)							*						В	Nahallage and Huffman (2012)
126 Sri Lanka	M. sinica, S. priam thersites, T. vetulus															Nahallage et al. (2008)
127 Sri Lanka	M. sinica, T. velulus	* (48)									*					Nijman and Nekaris (2010a)
128 Sri Lanka	M. sinica, T. velulus							*							_	Nijman and Nekaris (2010b)
129 Taiwan	M. cyclopis		*												П	Poirier (1986)
130 Thailand	M. arctoides		*					-								Bertrand (1969)
131 Thailand	M. assamensis		*					-								Eudey (1987)
132 Thailand	M. assamensis		*					-			- 1				0	Fooden (1971)
	M. assamensis		*													Fooden (1982)
134 Thailand	M faccionlasie	× (1417)		-		-										

<sup>a</sup> B: book and book chapter, I: international journal, O: other journals including reports, T: theses