FIELD NOTE

List of food plants of four sympatric Paradoxuriane civet species based on eight-year records on Borneo

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ABSTRACT
In this paper, I summarize the plant foods used by four sympatric Paradoxurinae civet species, based on data collected between May 2010 and June 2018, and consider their possible coexistence mechanisms on Borneo. I recorded the plants eaten by them, both by direct observation and fecal analysis, at four sites in Sabah, Malaysian Borneo. In total, I recorded 27, 27, 18, and 4 plant food items for common palm civets [Paradoxurus hermaphroditus], binturongs [Arctictis binturong], small-toothed palm civets [Arctogalidia trivirgata], and masked palm civets [Paguma larvata], respectively during the study period. The food plant species used by these species showed a large degree of overlap, especially among common palm civets, binturongs, and small-toothed palm civets. Based on the results of this study, differences among them in their degree of use of pioneer plant fruits and Ficus, and the acceptance of immature and unripe fruits, could enable these civets to coexist, even in a small area. However, there is no clear evidence for how they are able to coexist. This eight-year record is not enough to fully determine dietary similarities and dissimilarities or the coexistence mechanism of the four sympatric Paradoxurinae species on Borneo. More field observations with mechanical and chemical techniques are needed, not only to elucidate this mechanism but also to consider conservation of these animals and their habitats in a changing environment on Borneo.

Key words: coexistence mechanism, diet, civet, fecal analysis, behavioral observation

INTRODUCTION

Coexistence mechanisms are one of the biggest questions in tropical ecology. In Asian tropical rainforests, the number of sympatric mammalian carnivores is quite large compared with the numbers in the Afrotropics and the Neotropics (Corlett 2007). Generally, sympatric relative species differentiate their use of resources, such as food, active time, and habitat as a result of competition that occurred during their evolutionary process (McDonald 2002; Goulart et al. 2009). Many studies of the coexistence mechanisms of sympatric mammalian species have suggested that the differentiation of several ecological factors, such as diet, activity periods, and microhabitat preferences, enables their coexistence (Emmons 1980; Kronfeld-Schor and Dayan 2003). In mammalian carnivores, food niche separation, often associated with morphological dissimilarity, usually reduces intra-guild competition (Davies et al. 2007). However, the coexistence mechanisms of sympatric mammalian carnivores have only been studied for a few species in the Asian tropics.

Civets (Viverridae) are one of the most data deficient mammalian carnivores in the Asian tropics. They are generally nocturnal, solitary animals (Jennings and Veron 2009). Species belonging to the subfamily Paradoxurinae have similar ecology, being semi-arboreal and dependent on fruit for their diet. Up to four Paradoxurinae species occur sympatrically from Assam to Indochina and Peninsular Malaysia, and on Sumatra and Borneo (Jennings and Veron 2009). In Bornean rainforests, there are four sympatric Paradoxurinae species: common palm civets, [Paradoxurus hermaphroditus], binturongs, [Arctictis binturong], small-toothed palm civets, [Arctogalidia trivirgata], and masked palm civets, [Paguma larvata]. The home ranges of three species (common palm civets, small-toothed palm civets, and binturongs) exhibit considerable overlap, even in a small area (Nakabayashi et al. 2017). The largest species is the binturong (6-10 kg) followed by masked palm civets (2.5-3 kg), common palm civets (1.7-2.7 kg) and small-toothed palm civets (1.5-2.6 kg) (Yasuma and Andau 2000, Nakabayashi 2015, Nakabayashi unpublished data).

These large differences in body size suggest there could be differences in their food resource use. In mammalian carnivores, body size reflects prey size; small carnivores...
prey on relatively small preys but large species utilize from small to large preys (Sinclair et al. 2003). Therefore, the four sympatric Paradoxurinae species may differentiate their food fruit size according to their body size. Given that plant species diversity in tropical rainforests is higher than that of other terrestrial ecosystems (Wright 2002), animals living in such rainforests have a broad range of choice of food plants. The use of pioneer plant species would affect the habitat use of consumers, because these plants grow in environments with a high level of light, such as roadsides. Hence, the utilisation of different fruits may reduce interspecific competition among sympatric Paradoxurinae species. In this paper, I summarize the plant foods used by these four civet species on Borneo, based on data collected between May 2010 and June 2018, and consider their possible coexistence mechanisms on Borneo.

**MATERIALS AND METHODS**

**Study sites**

I recorded the plants eaten by sympatric Paradoxurinae species, both by direct observation and fecal analysis, at four sites in Sabah, in the north-eastern part of Borneo: Tabin Wildlife Reserve, Imbak Canyon Conservation Area, Danum Valley Conservation Area, and Maliau Basin Conservation Area (Figure 1).

Tabin Wildlife Reserve (henceforth called Tabin) (5° 19’ N, 118° 50’ E) has an area of approximately 1225 km². The study was conducted around the western boundary of Tabin from August 2010 to November 2010 and from June 2011 to September 2011. The reserve is almost exclusively surrounded by large agricultural areas planted with oil
Food plants of four sympatric civet species on Borneo

Most parts of Tabin were heavily logged in the 1970 s and 1980 s and are dominated by pioneer species such as *Neolamarckia cadamba* around 120 m a.s.l. (Mitchell 1994). Danum Valley Conservation Area (hereafter called Danum) (4°57’ N, 117°48’ E) is a 438 km² protected area, and 90 % of this area consists of matured lowland evergreen dipterocarp forest between 180 and 900 m a.s.l. (Marsh and Greer 1992; Newbery et al. 1999). The study was conducted around the eastern boundary of Danum from June 2012 to May 2014. Maliau Basin Conservation Area (hereafter called Maliau) (4°49’ N, 116°54’ E) is a 588 km² protected area, including lowland dipterocarp rainforest and at least 12 forest types between 300 and 1675 m a.s.l. (Hazebrook et al. 2004). The study was conducted outside the basin in a selectively logged dipterocarp forest from February 2016 to June 2018 at around 300 m a.s.l. Some occasional observations of the frugivorous civets were conducted in Imbak Canyon Conservation Area (hereafter called Imbak) (5°6’ N, 117°2’ E) in June 2011. Imbak is 300 km² forest reserve which includes lowland dipterocarp rainforest and upper montane forest, including patches of montane heath forest between 250 and 1000 m a.s.l. (Sugau et al. 2012, Suleiman et al. 2012).

The identification of plant species, characterisation of fruit, and plant life form follows Berg and Corner (2005), Soepadmo and Wong (1995), Soepadmo et al. (1996, 2002, 2004, 2007, 2011), and Soepadmo and Saw (2000). The nomenclature of plant species follows WCSP (2020).

**Study animals**

I recorded food plants of four sympatric Paradoxurinae species: common palm civets, binturongs, small-toothed palm civets, and masked palm civets. These four species had been suggested to be widely distributed across South Asia and South-East Asia, but molecular studies revealed that Bornean populations of common palm civets, binturongs, and small-toothed palm civets should be separated at least from the Indochinese populations (Veron et al. 2015a, 2015b, 2020). Binturongs are generally solitary and nocturnal (Jennings & Veron 2009), but group feeding and diurnal activity has been reported (Nakabayashi 2015). This species is listed as Vulnerable by the IUCN (Wilcox et al. 2016). Bornean population of small-toothed palm civets has a different divergent clade from the Indochinese and the Sundaic regions (Veron et al. 2015b). There are no ecological studies on this species, but they often make a group of 2—4 adults (Nakabayashi 2015). There are no molecular studies on masked palm civets on Borneo, but population from Sundaic regions are genetically separated from Chinese population (Patou et al. 2009). This species is generally solitary and nocturnal (Nakabayashi personal observation).

**Fecal sampling and analysis**

I conducted fecal sampling and analysis of common palm civets from July to September 2011 in Tabin, and from June 2012 to September 2012 and from December 2012 to January 2013 in Danum. I searched for feces of common palm civets on gravel roads and forest transects, and recorded food items in the collected feces. In Tabin, I surveyed a 1-km-long forest transect and a 2-km-long gravel road early in the morning, two or three times a week. In Danum, I surveyed a 3-km-long forest transect and a 2-km-long gravel road in the same way. The census was not conducted if it rained heavily.

Based on DNA analysis, more than 90 % of civet-like feces in Tabin were from common palm civets (Nakashima et al. 2010). I conducted the fecal census in Danum after the census I carried out in Tabin; therefore, I had enough experience to identify feces by their shape and odor.

**Behavioral observation**

I also recorded the diet of the four Paradoxurinae species by behavioral observations. I opportunistically searched for feeding Paradoxurinae species during the entire study period by thoroughly exploring the study areas of about 5 km² thoroughly or by using a car driving along the gravel roads. When I found civets feeding, I recorded the food species by focal sampling until I lost sight of the focal animals, it rained heavily, or the car needed to move. If the food item was fruit, I recorded the type of fruit, the color of the fruit when ripe, and the fruit diameter and length of the fruit. I also recorded whether civets fed on immature or unripe fruits; immature fruit indicates not
fully-grown one and unripe fruit indicates fully-grown but not yet ripe one. Most observations were conducted between 18:00 to 6:00, but I also conducted opportunistic observations during the daytime (6:00–18:00). All observations were aided by the use of 8 × 36-magnification binoculars (Nikon Monarch, Nikon Corp., Tokyo, Japan) and a 120-lumen headlamp (Black Diamond LED Headlamp, Black Diamond Equipment Ltd., Salt Lake City, UT, USA) with a red filter. I did not shine any lights continuously or directly onto a focal animal.

**Similarity analysis**

I evaluated the similarity of food plants eaten by Paradoxurinae civets using Jaccard’s similarity index (Jaccard 1912). The similarity between two civet species indicates the number of common foods divided by the total number of foods eaten by the two species. A value of zero indicates food plants are completely dissimilar between two species and a value of one indicates they are identical.

**RESULTS**

In total, I recorded 27, 27, 18, and 4 plant food items for common palm civets, binturongs, small-toothed palm civets, and masked palm civets, respectively during the study period (Table 1). Note that absence of records in this study does not indicate intrinsic avoidance of specific plant species. In the fecal census, I collected 55 fecal samples of common palm civets in Tabin, and 36 fecal samples in Danum. Fifty out of 55 (72.7%) and 22 out of 36 (61.1%) fecal samples were found on the gravel roads in Tabin, and in Danum, respectively. In total, I identified at least twelve food species of common palm civets by the fecal analysis. I excluded *Ficus* spp. from the total number because I could not identify them to species level. This study focused on plant foods only, but three common palm civet fecal samples included arthropod remains. I did not include these records in the results. By behavioral observation, I recorded 17, 27, 18, and 4 plant food items of common palm civets, binturongs, small-toothed palm civets, and masked palm civets, respectively. Feeding on *Endospermum diadenum* and *Solanum torvum* by common palm civets was recorded by both fecal census and behavioral observation.

Feeding on plant parts other than fruit, such as nectar and bark sap was only recorded for small-toothed palm civets. Also, only this species consumed completely immature and unripe fruits of four plant species, with the exception of *Ficus fistulosa*, as its immature fruits were also consumed by common palm civets. All the civet species observed in this study consumed *Ficus* fruits. Fourteen plant species were categorized as typical pioneer plants, and 10, 3, and 8 species of these species were consumed by common palm civets, binturongs and small-toothed palm civets, respectively (Table 1). I recorded 24, 8, 9, and 2 plant species, whose fruit types are categorized as syconium, drupes, berries, and nuts, respectively (Table 1). I recorded 16, 8, 1, 17, and 2 plant species that were categorized as trees, shrubs, herbs, hemi-epiphytes, and climbers, respectively (Table 1). No use of shrubs by binturongs or masked palm civets was recorded. I recorded red, orange, dark red, green, pale yellow, yellow, pale red, brown, and purple colored fruits when ripe (Table 1).

The mean ± SD of all recorded food fruits (mm, n = 39) was 22.9 ± 16.7 in diameter and 25.5 ± 19.3 in length. The mean ± SD diameters (mm) of fruits consumed by common palm civets (n = 19), binturongs (n = 25), small-toothed palm civets (n = 14), and masked palm civets (n = 4) were 20.0 ± 8.7, 25.9 ± 19.4, 20.1 ± 14.9, and 20.8 ± 15.9, respectively (Figure 2). The mean lengths (mm) of the fruits consumed by common palm civets, binturongs, small-toothed palm civets, and masked palm civets were 22.0 ± 11.1, 29.2 ± 22.2, 22.2 ± 20.3, and 20.8 ± 13.2, respectively (Figure 2). The largest diameters (mm) of fruit consumed by common palm civets, binturongs, small-toothed palm civets, and masked palm civets were 22.0 ± 11.1, 29.2 ± 22.2, 22.2 ± 20.3, and 20.8 ± 13.2, respectively (Figure 2). The mean diameters (mm) of fruit consumed by common palm civets, binturongs, and small-toothed palm civets, and masked palm civets were 40 (Ficus racemosa), 84.7 (Glenniea philippinensis), 66.5 (Ficus punctata), and 40 (Ficus racemosa), respectively. The mean lengths (mm) of fruit consumed by common palm civets, binturongs, small-toothed palm civets, and masked palm civets were 45.7 (Ficus annulata), 84.4 (Ficus punctata), 84.4 (Ficus punctata), and 35 (Ficus racemosa), respectively. The smallest diameters (mm) of fruit consumed by common palm civets, binturongs, small-toothed palm civets, and masked palm civets were 5.5 (Diospyros cauliflora and *Ficus caulocarpa*), 5.5 (Ficus caulocarpa), 5.5 (Ficus caulocarpa), and 7.3 (Ficus borneensis), respectively. The smallest lengths (mm) of fruit consumed by common palm civets, binturongs, small-toothed palm civets, and masked palm civets were 5.5 (Diospyros cauliflora), 5.6 (Ficus caulocarpa), 5.6 (Ficus caulocarpa) and 9.1 (Ficus borneensis), respectively.

Feeding on *Ficus borneensis* was recorded in all four Paradoxurinae species, and feeding on eight *Ficus* species was recorded in common palm civets, binturongs, and small-toothed palm civets in common. Similarly, feeding on *Ficus racemosa* was recorded in common palm civets, binturongs, and masked palm civets in common. The fruits
Food plants of four sympatric civet species on Borneo

Table 1. List of food plants eaten by the four Paradoxurinae civet species on Borneo

| plant part | Number of feeding patch | family | food species | pioneer | fruit type | growth form | color when ripe | fruit diameter \times length | immaturity/ unripeness |
|------------|--------------------------|--------|--------------|---------|-----------|-------------|-----------------|----------------------------|------------------------|
| C          | B                        | S       | M            |         |           |             |                 |                            |                        |
| fruit      | 1                        | Anacardiaceae | Koordersiodendron pinnatum | drupe | T         | green       | 17.6 \times 25.5 |                            |                        |
| 1          | (1)                      | Annonaceae | Desmos dorusus | berry | S         | yellow      | –               |                            |                        |
| 3          | Arecaeeae                | Elaeis guineensis (oil palm) | ○ | nut | T | dark red | 27.7 \times 43.5 |                            |                        |
| 2          | (2)                      | Cornaceae | Alangium javanicum | drupe | T | red | 20 \times 27.5 |                            |                        |
| 1          | (1)                      | Ebenaceae | Diospyros cauliflora | drupe | T | green | 5.5 \times 5.5 |                            |                        |
| 1          | (2)                      | Ebenaceae | Diospyros spp. | drupe | T | red | 32.3 \times 24.7 |                            |                        |
| 3          | (27)                     | Euphorbiaceae | Endospermum diademum | ○ | capsule | T | yellow | 15.6 \times 13.7 | unripe                |
| 2          | (2)                      | Fagaceae | Lithocarpus spp. | nut | T | brown | – |                            |                        |
| (32)       | Gentianaceae             | Fagraea cuspidata | ○ | berry | S | pale yellow | 15.7 \times 18 | unripe |                        |
| (1)        | Malvaceae                | Microcos fibrocarpa | drupe | T | yellow | 15.9 \times 20.4 |                       |                        |
| 1          | Melastomataceae          | Melastoma malabaricum | ○ | berry | S | red | 10.5 \times 11.4 |                       |                        |
| 1          | Melastomataceae          | Pterandra caerulescens | ○ | berry | T | purple | 12.3 \times 13 | unripe |                        |
| 1          | Meliaceae                | Aglaia. sp. | berry | T | orange | 30 \times 35.5 |                       |                        |
| (2)        | Meliaceae                | Aglaia. spp. | – | T | – | – |                        |                        |                        |
| 1          | 3                        | Moraceae | Ficus annulata | syconia | HE | orange | 32.6 \times 45.7 |                       |                        |
| 1          | 4                        | Moraceae | Ficus benjamina | syconia | HE | dark red | 16.9 \times 16.5 |                       |                        |
| 1          | 3                        | Moraceae | Ficus hitinjidi | syconia | HE | dark red | 20.8 \times 19.3 |                       |                        |
| 1          | 4                        | Moraceae | Ficus horneensis | syconia | HE | red | 7.3 \times 9.1 |                       |                        |
| 2          | Moraceae                | Ficus callophylla | syconia | HE | red | 10.5 \times 10.6 |                       |                        |
| 1          | Moraceae                | Ficus caudocarpa | syconia | HE | pale yellow | 5.5 \times 5.6 |                       |                        |
| 2          | Moraceae                | Ficus cucurbitina | syconia | HE | orange | 30.9 \times 37.5 |                       |                        |
| 1          | Moraceae                | Ficus delosyce | syconia | HE | pale yellow | 6.5 \times 7.5 |                       |                        |
| 1          | 1                       | Moraceae | Ficus dubia | syconia | HE | dark red | 27.7 \times 29.1 |                       |                        |
| 2          | 1                        | Moraceae | Ficus fistulosa | ○ | syconia | T | green | 15.4 \times 14.7 | immature |                        |
| 1          | 6                        | Moraceae | Ficus forstenii | syconia | HE | dark red | 20.9 \times 26.8 |                       |                        |
| 2          | 3                        | Moraceae | Ficus kerkhovieni | syconia | HE | dark red | 14.4 \times 13.8 |                       |                        |
| 1          | Moraceae                | Ficus lawesii | syconia | HE | green | 8.3 \times 10 |                       |                        |
| 1          | Moraceae                | Ficus lepicarpa | ○ | syconia | S | pale red | 15.4 \times 17.1 |                       |                        |
| 1          | Moraceae                | Ficus pisocarpa | syconia | HE | yellow | 15.3 \times 13.3 |                       |                        |
| 4          | Moraceae                | Ficus punctata | syconia | C | red | 66.5 \times 84.4 |                       |                        |
| 1          | 1                       | Moraceae | Ficus racemosa | syconia | T | red | 40 \times 35 |                       |                        |
| 2          | Moraceae                | Ficus sestica | ○ | syconia | S | green | 30 \times 25 |                       |                        |
| 7          | Moraceae                | Ficus stipenda | syconia | HE | orange | 58.5 \times 72.6 |                       |                        |
| 2          | Moraceae                | Ficus subcordata | syconia | HE | red | 42.1 \times 51.4 |                       |                        |
| 1          | Moraceae                | Ficus sundaica | syconia | HE | orange | 15.5 \times 17.3 |                       |                        |
| 1          | Moraceae                | Ficus trichocarpa | syconia | C | orange | 13.9 \times 18.1 |                       |                        |
| 3          | 1                       | Moraceae | Ficus variegata | ○ | syconia | T | red | 22.7 \times 17.2 |                       |                        |
| 1          | Moraceae                | Ficus xylaphyla | syconia | HE | dark red | 23.6 \times 32.1 |                       |                        |
| (16)       | Moraceae                | Ficus spp. | – | – | – | – |                      |                        |                        |
| 1          | 2                       | Pentaphylacaceae | Adinandra sp. | ○ | berry | T | green | – | – | unripe |                        |
| 1          | Rubiaceae               | Neonauclea sp. | ○ | capsule | T | green | 17.9 \times 17.3 |                       |                        |
| (1)        | Rubiaceae               | Praravinia suberosa | berry | S | – | – |                      |                        |                        |
| (1)        | Rutaceae                | Glycosmis sp. | berry | S | green | – |                      |                        |                        |
| 1          | Sapindaceae             | Glenniea philippinensis | drupe | T | yellow | 84.7 \times 81.5 |                       |                        |
| 1          | 5                       | Solanaceae | Solanum torvum | ○ | berry | H | yellow | 10 \times 10.7 |                       |                        |
| pith       | 1                       | Arecaeeae | Elaeis guineensis (oil palm) | ○ | T | – | – |                       |                        |
| nectar     | 1                       | Malvaceae | Durio sp. | – | T | – | – |                       |                        |
| bark sap   | 2                       | Rubiaceae | Neolamarckia cadamba | ○ | T | – | – |                       |                        |

a: Numbers in parenthesis indicate the number of collected feces by fecal census. C, common palm civets; B, binturongs; S, small-toothed palm civets; M, masked palm civet
b: T, tree; S, shrub; H, herb; HE, semi-epiphyte; C, climber
c: data collected only for small-toothed palm civets
of 15 out of 18 plant species that were recorded to be consumed by at least two civet species belonged to *Ficus* spp.

In each fruiting tree, civets sniffed individual fruits and never ate fruit without sniffing it first. They selected only one fruit from a bunch and swallowed the fruit whole after chewed it. I observed small-toothed palm civets squeezing juice by chewing a whole fruit, and letting the squashed residues of rind drop, with fruiting *Endospermum diadenum*, *Ficus racemosa*, *Ficus punctata*, *Ficus annulata*, and *Fagraea cuspidata* and immature stage of a *Ficus fistulosa* tree. A common palm civet did the same one time, feeding on immature figs of *Ficus fistulosa*. Similarly, small-toothed palm civets chewed the pith of an oil palm tree and the inner bark of a *Neolamarckia cadamba* tree, and let the residue of pith or bark drop from their mouth. I observed them defaecating in a fruiting *Ficus fistulosa* during foraging, and their egesta was almost completely liquid containing a small quantity of seeds and pulp residue.

I excluded masked palm civets from this analysis because of their small sample size. The Jaccard’s index between common palm civets and binturongs was 0.71, between common palm civets and small-toothed palm was 0.71, and between binturongs and small-toothed palm civets was 0.68.

**DISCUSSION**

The food plant species used by the sympatric Paradoxurinae species studied showed a large degree of overlap, especially among common palm civets, binturongs, and small-toothed palm civets. Similarly, food fruit diameter and length were highly overlapped among the four species, and therefore it was impossible to clarify the relevance of body size for food fruit size at this time. Based on Jaccard’s index, the food plants of these species were quite similar. Feeding on plant parts besides fruit was observed only in small-toothed palm civets here, but feeding on nectar by masked palm civets (Lau 2012; Kobayashi et al. 2019) and on flowers by common palm civets (Nakashima et al. 2010) has been reported. Therefore, if no specific foods for a civet species are found, their food items are similar.

There were clear differences among common palm civets, binturongs, and small-toothed palm civets in feeding on pioneer plants and preference for *Ficus*. These species consumed pioneer plants in common, but the numbers of species and feeding patches on these plants were much larger for common palm civets and small-toothed palm civets than binturongs. This result was corroborated by their habitat use. Common palm civets and small-toothed palm civets preferentially use roadside and riverine forests, where their food pioneer plants such as *Adinandra* and *Pternandra* naturally grow (Metcalfe et al. 1998), while binturongs have no preference for these habitats (Nakabayashi et al. 2017). Although *Ficus* is one of the most important foods for all four civet species, binturongs are highly dependent on it (Nakabayashi et al. 2016; Nakabayashi and Ahmad 2018). *Ficus* includes both typical pioneers such as *Ficus fistulosa* and non-pioneers such as hemiepiphytes (Berg and Corner 2005), so binturong habitat use also corroborates their feeding habits. Therefore, the degree of dependence on pioneer plants and *Ficus* could be a factor in the food niche separation among the four sympatric civet species.

Feeding on immature and unripe fruits also differed among the four civet species. All of them consumed mature fruits, but only small-toothed palm civets fed on completely immature fruits of more than two plant species. They
squeezed fruit juice by mastication and let the squashed residue of rind drop. This feeding technique has been reported in Thailand (Duckworth and Nettelbeck 2007) and is also quite similar to that of fruit bats (Wendeln et al. 2000). Fruits consumed by small-toothed palm civets, such as Fagraea cuspidata and Pterandra coerulescens are typical “bat fruits”; they are green in color, have a musty odor, and project out from the foliage (Fleming 1979). Generally, immature and/or unripe fruits are avoided because they often contain toxic or distasteful secondary compounds, and they are structurally difficult to process and nutrient-poor (Swain 1977). Some consumers of immature fruits, such as colobine monkeys, have specialized stomachs to digest them (Lambert 1998), but civets do not (Jinhui et al. 1997). Given that they imbibed nectar and squeezed bark sap, small-toothed palm civets intentionally consumed liquid matter with soluble sugars, and not fruit pulp, from fruits including both immature and unripe ones. Thus, the acceptance of immature and unripe fruits relevant to the feeding technique may also affect their coexistence mechanism.

This is the first report on plant food items of the four sympatric Paradoxurinae civet species living on Borneo. Based on the results of this study, differences among them in their degree of use of pioneer plant fruits and Ficus, and the acceptance of immature and unripe fruits, could enable these civets to coexist, even in a small area. However, there is no clear evidence for how they are able to coexist. Differences in the use of Ficus and unripe fruits have also been reported among four sympatric frugivorous primates on Sumatra (Ungar 1995). Compared with these primates that can consume other plant parts, such as leaves, Paradoxurinae civets have limitations on digestible plant foods because of their morpho-physiological disadvantages for digesting plant materials (Anders 2005; Lambert et al. 2014). Therefore, differences in the use of food types should be critically important factors for their coexistence. This eight-year record is not enough to fully determine dietary similarities and dissimilarities or the coexistence mechanism of the four sympatric Paradoxurinae species on Borneo. More field observations with mechanical and chemical techniques such as automatic video recorders, stable isotope analysis, and DNA barcoding are needed, not only to elucidate this mechanism but also to consider conservation of these animals and their habitats in a changing environment on Borneo.

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