I INTRODUCTION

1.1 Background

Feeding is an essential ecological aspect of primates and useful for understanding the animals' niche in a biological community (Hohmann *et al.* 2007), and, in the case of endangered species, to quantify their suitable habitat (Barnett 1995). Feeding also contributes to addressing scientific questions, such as foraging theory, nutritional condition, and carrying capacity (McGraw and Daegling 2012).

Primates' dietary characteristics, including the total number of food plant species, dietary composition, and dietary selection vary seasonally and geographically (Cui *et al.* 2018). Primates have coped with temporal and spatial variations in food availability to meet their requirements (including energy, protein, vitamins, and trace elements), and to minimize the intake of toxins and secondary compounds that inhibit digestion. To achieve these demands, each primate species has evolved different feeding strategies (Chapman *et al.* 2012).

A common trend in most colobine (Order: Cercopithecidae) diets, both Asian and African, is toward folivory (Davies and Oates 1994; Tsuji *et al.* 2013). Asian colobine diets consist primarily of foliage and unripe fruits, and sometimes these animals feed on seeds (Yeager and Kool 2000). For example, in Indonesia, Javan surili (*Presbytis comata*) feeds on leaves most frequently (64.7%) (Ruhiyat 1983). This trend is similar to that of Javan lutungs (*Trachypithecus auratus*); their diets were also dominated by foliage with the range from 46% to 94% (Beckwith 1995; Vogt 2003; Tsuji *et al.* 2019).

Recent studies found that they also have consumed a large number of non-leaf, such as fruits and seeds (Hadi 2011; Erb *et al.* 2012; Ehlers Smith *et al.* 2013). Therefore, the classical view of colobines as leaf specialists should be reconsidered, and we need to address the determinants of their feeding strategies (Sayers 2013). Black snub-nosed monkeys (*Rhinopithecus bieti*) are affected by seasonal differences: they preferentially feed on bamboo shoots and fruits in summer, young leaves in spring, and dried grass and bark in winter (Grueter *et al.* 2009, 2012; Xiang *et al.* 2007). Feeding of red colobus monkeys (*Procolobus rufomitratus*) is affected by habitat disturbance: individuals living in the logged areas ate the fruit, whereas individuals in the old-growth areas never did (Milich *et al.* 2014).

Trachypithecus cristatus, known as silvery lutung, is an Asian colobine species inhabiting Malaysia (Peninsular Malaysia and Borneo) and Indonesia (Sumatra and Kalimantan) (Roos *et al.* 2008). They have the widest distribution among *Trachypithecus* species (Nijman and Meijaard 2008), which implies that they have adapted to various kinds of environments. Therefore, silvery lutung also can be found on many types of habitat, including riverine, mangrove, swamp, montane, coastal and plantation (Furuya 1961; MacKinnon and MacKinnon 1987). Coastal is a typical habitat of silvery lutung in the western Sumatra, which has various type of vegetation and phenologies among each plant species. Previous studies on feeding of silvery lutung in coastal forest habitat are limited. Therefore, the further studies are needed to see the dietary dynamics of silvery lutung for their survival in their habitat.

1.2 Research Objectives

This study presents the first quantitative data on the diet of wild silvery lutung. The objectives of the study were 1) to investigate their dietary composition and its monthly change over the study period; 2) to examine the relationship between food items or dietary diversity and food availability.

1.3 Research Outcome

The research will be expected to provide an important contribution directly or indirectly towards the conservation and ecotourism management of silvery lutung in Gunung Padang, as a tourism area in Padang, which will help us to comprehensively understand ecological behavior and population existence.

II LITERATURE REVIEW

2.1 Taxonomy

The silvery lutung (*Trachypithecus cristatus*) (Figure 1) or *cingkuak* (Minangese, local name) is one of 16 primate species in Sumatra Island, Indonesia (Corbert and Hill 1992). The taxonomy of silvery lutung is (Mittemeier *et al.* 2013):

Kingdom	: Animalia
Phylum	: Chordata
Class	: Mammalia
Order	: Primate
Family	: Cercopithecidae
Sub Family	: Colobinae
Genera	: Trachypithecus
Species	: *Trachypithecus cristatus* Raffles 1821

Figure 2.1 Silvery lutung (*Trachypithecus cristatus*)
(photo by Akbar MA 2019)

2.2 Morphology

Trachypithecus cristatus is one of Colobine species which distinguishes them from Cercopithecines, does not have cheek pouches, the large stomach is sacculated, and lacks the ischial tuberosities (Napier 1985). Trachypithecus species are smaller and less sexually dimorphic in size than most other colobine genera, but more dimorphic than Presbytis (Pan and Groves 2004). Regardless of pelage color, some hairs are grayish-white and lighter distally, giving a silvered appearance. There are no white or pale facial markings, either pigment or hair, and pelage overall is uniform silvered gray, except for the white pubic patch of the female. There are a pointed crest and outward-projecting cheek hairs long enough to usually hide the ears when seen from the front (Harding 2010).

Trachypithecus cristatus is not sexually dimorphic except for irregular white patches on the inside flanks of females, females are 89% of the bodyweight of males (Roonwal and Mohnot 1977), and canine–sectoral teeth are considerably larger in the male (Groves 2001). Their mean body length (head-body length) of the adult male, adult females, juveniles, and infants are 750 mm, 751 mm, 500 mm, and 200 mm, respectively (Napier 1985), and their mean body weights are 6.6 kg, 5.7 kg, 1 – 3 kg, and 0.4 – 1 kg, respectively (Harding 2010). Neonates of this species have orange fur and white skin on hands, feet, and face (Bernstein 1968).

2.3 Biology

Almost all of Colobine species share the matrilineal-harem social system (one male-multifemale) (Newton and Dunbar 2001) with group sizes of 10 to 40 individuals. The composition of the group includes infants, juveniles, subadult, and adult. Although female dominance hierarchies have not been documented in the wild, *T. cristatus* does exhibit female-female affiliative behaviors such as allogrooming and sitting in proximity (Bernstein 1968). The female solicits copulation by making rhythmic, side-to-side head movements, and then presenting her hindquarters to the male; if he mounts, she continues head shaking during copulation (Roonwal and Mohnot 1977). Male mountings may be multiple, and if another female solicits simultaneously, the male mounts both in the same copulating sequence. Male masturbation is recorded (Bernstein 1968). There is no evidence of a breeding season (Medway 1970); reports of seasonal breeding (e.g., Fooden 1971) involved what is now recognized as other Trachypithecus species that live to the north in more seasonal environments.

2.4 Behavior

Trachypithecus cristatus is largely restricted to coastal and riverine forests and plantations, especially mangrove and palm (Davies and Oates 1994). Largely arboreal, *T. cristatus* rarely leaves the trees and retreats quickly if there is a threat of danger (Furuya 1961; Medway 1970). Home ranges averaged 43 ha and those of adjacent groups typically overlapped (Furuya 1961; Yeager and Kirkpatrick 1998). *Trachypithecus* feeds mainly in the middle and upper canopy (Napier and Napier 1985). *Trachypithecus cristatus* are mainly folivorous, spending more than 80% of their time feeding on foliage (Hock and Sasekumar 1979). Diets of *Trachypithecus cristatus* consisted of leaves, seeds, flowers, and fruits such as epiphytic figs (Roonwal and Mohnot 1977).

Trachypithecus cristatus is described as very shy and protective. In their group, they move silently and are generally quieter than other colobine monkeys (Roonwal and Mohnot 1977). Silvery lutungs appear to suffer low predation rates because individuals and brands are occasionally seen near fragmented areas, such as human settlements and on palm plantations. Predation rates are difficult to measure in primates, however, and maybe lower in habituated populations where predators are shy, and in fragmented areas where predator populations are reduced, than in undisturbed habitats (Hart 2007; Hill and Dunbar 1998; Hill and Lee 1998; Isbell 1994).

Males in silvery lutung groups will make threat calls then the group retreat quickly to the forest if they feel threatened (Bennett and Davies 1994; Bernstein 1970; Davies and Oates 1994).

Trachypithecus cristatus shows a low level of aggression and frequent sociosexual, gestural, and vocal interactions within the social group (Bernstein 1968; Furuya 1961; Supriatna *et al.* 1986; Wolf and Fleagle 1977). Silvery lutung is rarely sympatric with other colobines. Silvery lutung generally avoids interaction with their sympatric species in overlapped range and agonistic interactions are rare (Harding 2010). This may be due to the abundance of food in its habitat and its feeding behavior of facing toward the tree while eating, both of which decrease the frequency of interaction with other members of the group. But, among neighboring groups, *T. cristatus* exhibits both aggression and tolerance, according to the situation. (Roonwal and Mohnot 1977).

2.5 Distribution and Habitat

Indonesia is one of the biggest biodiversity hotspots in the world. Indonesia has two species of the genus Trachypithecus, *Trachypithecus auratus* is distributed majority in Java and *Trachypithecus cristatus* is distributed majority in Sumatera and Borneo (Fig. 2). According to Roos *et al.* (2008) *Trachypithecus cristatus* occurs on the Malay Peninsula, Borneo, Sumatra, the Natuna Islands, and adjacent, smaller islands. *T. c. selangorensis* occurs only on the Malay Peninsula. *T. c. cristatus* is found in other parts of the species' range (Roos *et al.* 2008), unless those from the Natuna Islands and Batam are distinct (Maryanto *et al.* 1997). Silvery lutung lives in a wide variety of habitat types. Mostly of silvery lutung groups live from riparian and mangrove forests in Peninsular Malaysia and Borneo, while in Sumatra they live in a variety of primary and secondary forest types, including riverine, mangrove, swamp, montane, and coastal, occasionally in plantations (Furuya 1961; MacKinnon and MacKinnon 1987).

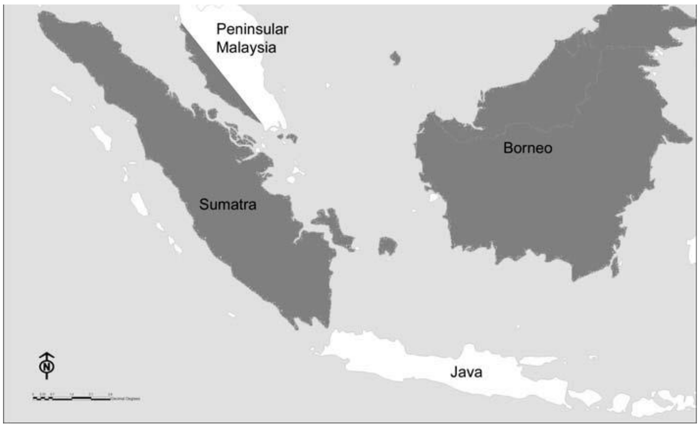

Figure 2.2 Distribution (dark gray) of *Trachypithecus cristatus*
Original figure from Harding (2010)

2.6 Conservation Status

International Union for Conservation of Nature and Natural Resources (IUCN) lists *T. cristatus* as Vulnerable (Meijaard and Nijman 2020). *T. cristatus*, as with other nonhuman primates, is threatened throughout its range by logging, hunting for meat and medicinal uses, and capture for the pet trade (Nijman 2008). For example, Bunguran Island, Indonesia, was until 1980 largely covered in primary forest habitat; however, by 2003 only small patches of primary forest remained within a matrix of logged forest covering. nearly 70% of the island (Lammertink *et al.* 2003). This is representative of habitat loss throughout the region (Meijaard *et al.* 2008).

III METHODS

3.1 Study Site and Subject Animals

We conducted the study at the Gunung Padang (GP) coastal area, Kampung Sebrang Pebayan, Batang Arau, Padang Selatan, Padang City, West Sumatra, Indonesia (100° 20′–100° 21′ E and 0° 57′–0° 58′ S). Mean temperature and precipitation during the study period ranged from 22 to 33 °C and 270–510 mm, respectively (www.weatherbase.com accessed on November 11, 2019). GP is a cape surrounded by the Indian Ocean. The GP area is approximately 20 ha, and the maximum elevation is up to 115 m above sea level (Fig 1).

Apart from the tourism area, GP contains fishermen settlements and a fresh-seafood market. GP is mainly composed of secondary forest, dominated by Apocynaceae (*Alstonia scholaris*), Arecacae (*Cocos nucifera* and *Arenga obstusifolia*), and Moraceae (*Ficus* spp.) (Ilham *et al.* 2018). In addition to the natural plants at GP, there are traditional agricultural plants, such as clove (*Syzygium aromaticum*) and cacao (*Theobroma cacao*). A detailed vegetation survey of GP has not been conducted.

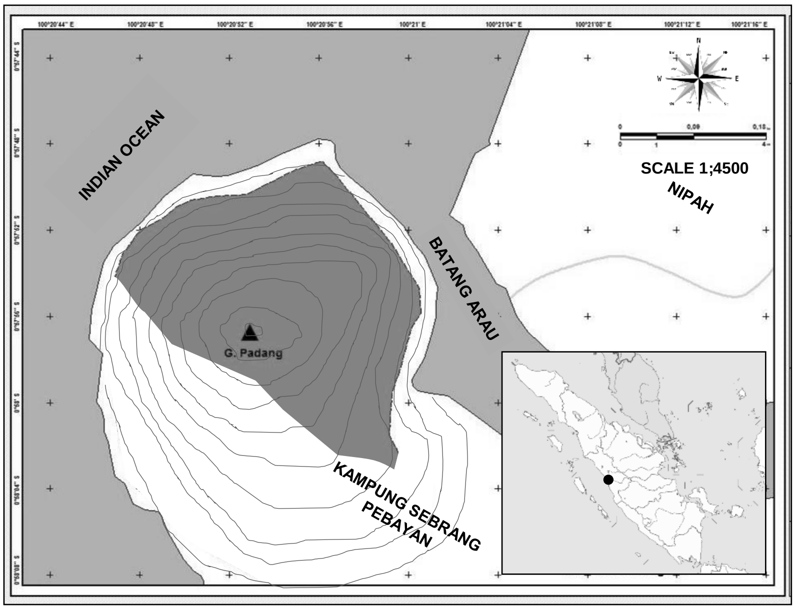

Figure 3.1 Maps of Gunung Padang, West Sumatra, Indonesia. (Shaded area represents the home range of the subject group of silvery lutung. A smaller map indicates Sumatra island and a dot mark represents Padang city)

Our study subjects were a group of silvery lutungs composed of 25 animals (one adult male, five nursing females, ten single females, and four juveniles; age-sex classes of the lutungs were defined based on Harding (2010)).

3.2 Feeding Observation

We observed the lutungs for 12 consecutive months between August 2018 and July 2019. We were able to observe the lutungs at a close distance (approximately 10 m). The total observation time was 481.6 h over 92 days (Table 1). Additionally, we used previous data covering July, August, and October 2016 (67.7 h over 15 days, Akbar *et al.* 2019).

Table 3.1 Observation time and results of scanning for a group of silvery lutungs at Gunung Padang

Year / Month	Observation		Total scan	Scanned animal		
	Day	Time (hr)		Total	Mean	Range
2016						
July[a]	5	18.3	220	1,017	4.6	4 – 15
August[a]	5	20.1	242	1,315	5.4	9 – 11
October[a]	5	23.3	280	1,560	5.6	11 – 18
2018						
August	7	27.1	163	965	5.9	1 – 15
September	3	7.3	44	197	4.5	1 – 12
October	3	7.0	42	329	7.8	7 – 14
November	5	15.3	92	683	7.4	7 – 20
December	4	12.1	73	424	5.8	2 – 17
2019						
January	7	31.3	188	1,114	5.9	4 – 14
February	5	32.3	194	1,305	6.7	11 – 20
March	3	71.8	431	2,448	5.7	5 – 19
April	15	108.5	651	3,544	5.4	8 – 23
May	10	72.3	434	2,171	5.0	8 – 23
June	10	52.3	314	1,536	4.9	6 – 17
July	10	50.3	302	1,683	5.6	6 – 23
Total	107	549.3	3669	20,291	5.8[b]	1 – 23

[a]Source: Akbar *et al.* (2019); [b]Grand mean

We observed the lutungs for as long as possible each day (range: 07:00–18:00) and recorded the feeding activity by using scan sampling as sampling rules and instantaneous scan sampling as recording rules (Martin and Bateson 1993) at 10-min intervals. For each scan, we spent 10 s on each visible individual to feeding activity recording. We checked each individual once in a single scan. We recorded the food items eaten by them.

Based on a previous study on lutung diets (Tsuji *et al.* 2013), the diets were classified into mature leaves, young leaves, ripe fruits, unripe fruits, flowers, and others (lianas, bark, stem, pith, and underground storage). When an individual fed on two or more parts of the plant during a single scan, we recorded only the first. When the lutungs fed on an unknown species, we collected specimens and identified them at the herbarium of Andalas University (ANDA).

Data on diets are expressed as a percentage of the feeding records. The measure was therefore of feeding effort rather than food intake. We calculated the feeding percentage of food item *i* using the following formula:

$$\frac{\text{Number of scanned animals feeding on food item (or species) } i}{\text{Total of number of scanned animals in feeding}} \times 100$$

Then, we used the Shannon-Wiener index (H') to examine (1) plant species diversity in GP and (2) plant species diversity in each group's diet. We calculated the diversity index H using the following formula:

$$H' = -\sum_{i=1}^{r}[p_i \times \log p_i],$$

where p_i is the feeding proportion of the plant part i (r types in total) (Tsuji *et al.* 2019).

In this study, we defined plant species (part combined) with > 1% usage and plant parts with > 1% usage over the study period as the main food plant species and main diet items, respectively.

3.3 Plant Phenology

In August 2018, we set 204 monitoring trees along a pre-existing forest path (ca. 1 km in length and ca. 5 m in width) inside the tourism area. The phenology of the monitoring trees was evaluated each month by examining each plant in the presence or absence of (1) mature leaves, (2) young leaves, (3) flowers, (4) mature fruits, and (5) young fruits. We calculated two different phenology indices: one across species and another for specific plant species. The proportion of trees on which the respective plant part was present represented the phenology index for that plant part in a given month (Tsuji *et al.* 2019).

3.4 Statistical Analyses

To examine how the lutungs responded to fluctuations in the availability of food resources, we conducted two types of analyses. First, for the plant-part category-based analyses, we conducted Spearman's correlation tests between the phenology index of each plant part eaten and the monthly percentage of feeding on the corresponding plant parts and dietary diversity index (*H'*). Second, for the species-based analyses, we conducted corresponding analyses between the phenology index of the main diet items and the monthly percentage of feeding on the target items.

We also examined how the percent of feeding by the lutungs for specific plant parts affects the percentage of feeding on other food types or dietary diversity. For these analyses, we did not use data collected in 2016 (Akbar *et al*. 2019), in which we did not conduct the phenology survey. We conducted all statistical analyses by R version 3.6.2 (R Development Core Team, 2020). The significance level (α) was $P < 0.05$.

IV RESULTS AND DISCUSSIONS

4.1 Dietary Composition

Over the study period, the silvery lutungs at GP fed on 37 different plant species from 20 families, of which 24 were tree species, followed by 10 shrub species, and 3 vine species (Table 2). Young leaves (68.3%) were dominant in their diet composition, followed by unripe fruits (21.1%), mature leaves (5.0%), ripe fruits (2.0%), and flowers (1.1%) (Table 4.1).

The diet of silvery lutungs encompassed 74 different diet items, most of which were leaves (mature leaves of 15 species and young leaves of 29 species), followed by fruits (ripe fruits of five species and unripe fruits of 14 species). The number of main diet items (> 1% annual feeding) was 23 (Table 4.1).

Table 4.1 Annual dietary composition of a group of silvery lutungs at Gunung Padang

Family / ***Species***	**Plant type**	**Eaten part**	**Annual feeding %**
Anacardiaceae			
Mangifera indica	Tree		
		ML	0.06
		YL	**1.05**
		UF	0.43
Araceae			
Colocasia esculenta	Shrub		
		ML	0.25
		YL	0.12
Arecaceae			
Arenga obtusifolia	Tree	UF	0.19
Bignoniaceae			
Spathodea campanulata	Tree		
		ML	0.56
		YL	0.12
		RF	0.19
		Fl.	0.74
Clusiaceae			
Calophyllum inophyllum	Tree		
		YL	**2.22**
		UF	0.62

Table 4.1 (*Continued*)

Family / ***Species***	**Plant type**	**Eaten part**	**Annual feeding %**
Combretaceae			
Terminalia catappa	Tree		
		ML	0.25
		YL	**3.64**
Compositae			
Chromolaena odorata	Shrub	YL	0.06
Wollastonia biflora	Shrub	YL	0.25
Mikania micrantha	Vine	O	0.56
Euphorbiaceae			
Excoecaria agallocha	Tree	YL	**1.17**
Homalanthus populneus	Tree	YL	**1.98**
Jatropha curcas	Shrub	YL	0.19
Macaranga tanarius	Tree	YL	**1.61**
Mallotus floribundus	Tree		
		ML	0.31
		YL	0.31
		UF	0.12
Hernandiaceae			
Hernandia nymphaeifolia	Tree	YL	0.49
Lamiaceae			
Vitex pinnata	Tree	YL	0.25
Volkameria inermis	Shrub	YL	0.06
Leguminosae			
Archidendron jiringa	Tree		
		ML	0.06
		YL	**1.24**
Crotalaria pallida	Shrub	YL	**2.66**
Pongamia pinnata	Tree		
		YL	0.19
		UF	0.06
Senna sophera	Shrub		
		ML	0.19
		YL	**1.91**
		RF	0.06
Malvaceae			
Commersonia bartramia	Shrub		
		ML	0.43
		YL	0.81

Table 4.1 (*Continued*)

Family / ***Species***	**Plant type**	**Eaten part**	**Annual feeding %**
Malvaceae			
Hibiscus tilliaceus	Tree		
		YL	0.06
		Fl	0.06
Theobroma cacao	Tree		
		YL	**2.35**
		UF	0.12
Meliaceae			
Xylocarpus rumphii	Tree		
		ML	0.19
		YL	**1.48**
		Fl.	0.12
Menispermaceae			
Cyclea barbata	Vine		**1.73**
Moraceae			
Ficus benjamina	Tree		
		YL	**1.36**
		UF	0.19
Ficus elastica	Tree		
		ML	**1.36**
		YL	**2.90**
		RF	0.37
		UF	**1.79**
Ficus fulva	Trees		
		ML	0.12
		YL	**2.16**
		UF	0.80
Ficus variegata	Tree		
		ML	0.93
		YL	**24.71**
		RF	**1.35**
		UF	**15.57**
Myrtaceae			
Eugenia polyantha	Tree		
		ML	0.06
		YL	**7.35**
		UF	0.74

Table 4.1 (*Continued*)

Family / ***Species***	**Plant type**	**Eaten part**	**Annual feeding %**
Myrtaceae			
Syzigium aromaticum	Tree		
		YL	0.12
		UF	0.37
Syzygium cumini	Tree		
		ML	0.06
		YL	**1.55**
		UF	0.06
Eurya acuminata	Tree		
		YL	**3.03**
		O	0.06
Piperaceae			
Piper aduncum	Shrub	YL	0.73
Rubiaceae			
Guettarda speciosa	Shrub		
		ML	0.19
		YL	0.19
		RF	0.06
		UF	0.06
Vitaceae			
Cissus hastata	Vine	O	0.12

ML: mature leaves, YL: young leaves, RF: ripe fruits, UF: unripe fruits, Fl.: flowers, O: Others. The species and parts eaten in bold letters represent main plant species (annual feeding percentage >1%, part combined) and main diet items (annual feeding percentage >1%), respectively.

During the study period, foliage (both young and mature leaves) comprised the overwhelming majority of the silvery lutungs' diet (73.3%). Further, young leaves contributed the greatest proportion to the diet annually, and across months and seasons. However, the percentage of non-leaves, such as fruits (both ripe and unripe), flowers, and other parts of the plant was also considerable. The dietary composition of wild silvery lutungs has not been specified and these animals have been considered folivorous (Furuya 1961; Bernstein 1968; Subagyo 2008; Siburian 2018; Manalu 2020). We found that one-fourth of the diet was composed of non-leave items. The leaf-based diet is a common feature of the genus *Trachypithecus*.

The availability of leaves, especially young ones, can fulfill the nutritional requirement (Kumar and Solanki 2004) and indicates the quality of habitat that can support their population (Solanki *et al.* 2008). The consumption of fruits and flowers in silvery lutungs' diet is likely to obtain more energy. It was found by Solanki *et al.* (2007) that capped langurs (*Trachypithecus pileatus*) feed much on flowers during the reproductive season when they need extra energy. Moreover, Waterman *et al.* (1988) indicated that lutungs sustain themselves on fruits, seeds, and flowers as the dry season progresses.

Over the study period, 37 plant species were fed on at GP with a large number of plant species contributing to silvery lutungs' diet. It has been reported that nearly equal numbers of plant species comprise the diets of many other *Trachypithecus* species, such as 38 food plant species in *T. francoisi* diet (Hu 2011), 35 food plant species in *T. germaini* diet (Hoang *et al.* 2014), 34 food plant species in *T. johnii* diet (Kavana *et al.* 2015), and 33 -37 food plant species in *T. margarita* diet (Tran 2013; Monge 2016). However, there are several study sites where *Trachypithecus* species have been shown to feed on a large number of food plant species (Brotoisworo and Dirgayusa 1991; Sunderraj 2001; Fan *et al.* 2015). Dietary diversity was likely affected by observation time (Table 4.2).

The lutungs we studied spent much effort feeding on a limited number of plant species. This trend has been reported for other *Trachypithecus* species; the top 20 species, for example, occupied 95.1% for *T. francoisi* (Li *et al.* 2009), 910% for *T. delacouri* (Workman 2010), 93.2% for *T. geei* (Gupta and Chivers 2000), 92.0% for *T. germani* (Le *et al.* 2019), and 91.6% for *T. johnii* (Kavana *et al.* 2015). Thus, the number of key plant species that affect the activity, range, and inter-and intraspecific competition of the *Trachypithecus* species is limited and knowledge of the availability of such staple food plants is important to elucidate their feeding strategy.

Moraceae species, such as *Ficus elastica*, *F. variegata*, and *Eugenia polyantha* are the main dietary species of silvery lutungs in Gunung Padang. They may guarantee the availability of young leaves and other foods, and a healthy population of lutungs could be maintained. Thus, habitat restoration and further eco-tourism development within government authorities and stakeholders should pay more attention to trees that produce the staple diet of lutungs.

The silvery lutung group at GP fed on young leaves and unripe fruits of planted cacao trees (*Theobroma cacao*) as their main dietary species. During the colonization period, cacao trees, tea, and herb plants for condiments were planted; furthermore, they were also the leading commodities for export during Dutch colonialism around the 1700s–1900s and Japanese colonialism around the 1940s (Lerissa 2014). Dependence on the plantation food species by the *Trachypithecus* monkeys has been previously reported in *T. auratus* (Brotoisworo 1991; Djuwantoko 1991; Tsuji *et al.* 2019) and *T. vetulus* (Dela 2012). The dual characteristics of the strong dependence on specific tree species and the tolerance for new food plants may have enabled *Trachypithecus* monkeys to expand their distribution in Asian regions (Kirkpatrick 2011; Nijman 2014).

4.2 Seasonal Change in Diet and Relationship with Plant Phenology

The silvery lutungs at GP mainly fed on young leaves (mean over the study period, 67.3%), followed by unripe fruits (22.7%), mature leaves (5.1%), other parts of the plant (2.2%), and ripe fruits (1.8%). Flowers were the least consumed (0.9%). Young leaves formed the main component of the diet throughout the study period, but other items occasionally had a higher percentage, including mature leaves (August–September 2018 and June–July 2019) and unripe fruits (July 2016, October 2016, December 2018, February 2019, April 2019, July 2019). The percentage of ripe fruit feeding, flowers, and lianas was constantly low (Fig 2).

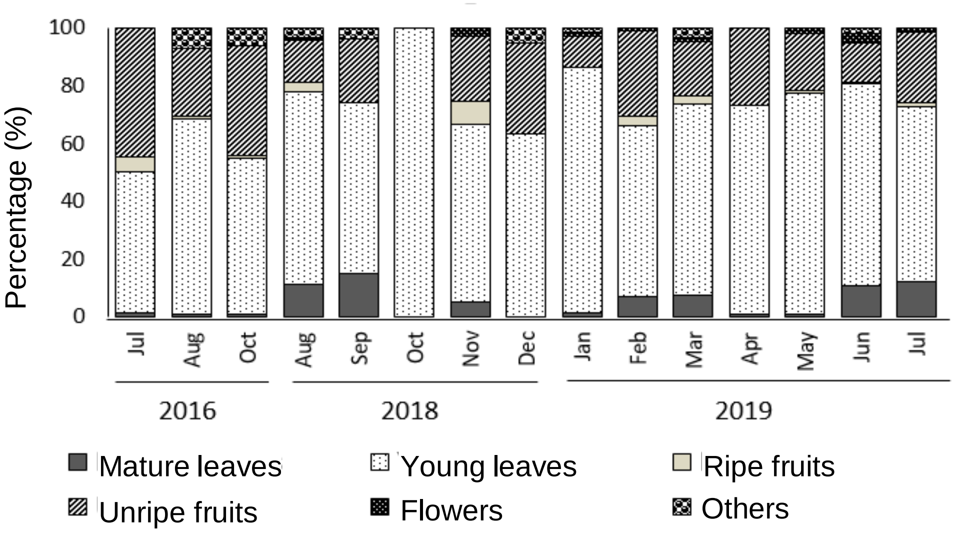

Figure 4.1 Monthly changes in the dietary composition of wild silvery lutungs at Gunung Padang, West Sumatra, Indonesia

The percentage of mature leaf feeding showed a significant positive correlation with dietary diversity (Spearman's correlation tests: $r_s = 0.792$, $P < 0.001$). A significant positive correlation was also found between the percentage of ripe fruit feeding with dietary diversity (Spearman's correlation tests: $r_s = 0.687$, $P = 0.005$). The percentage of young leaf feeding showed a significant negative correlation with the percentage of fruit feeding (ripe fruits - Spearman's correlation tests: $r_s = -0.560$, $P = 0.029$; unripe fruits - Spearman's correlation tests: $r_s = -0.761$, $P < 0.001$) and dietary diversity (Spearman's correlation tests: $r_s = -0.568$, $P = 0.029$). We also found a similar relationship between the percentage of unripe fruit feeding and the percentage of flower feeding (Spearman's correlation tests: $r_s = -0.553$, $P = 0.032$) (Table 4.3).

In the category-based analyses, we found that an increase in young leaf-feeding coincided with a decrease in fruits feeding (both ripe and unripe) and dietary diversity and that an increase in mature leaves and ripe fruits feeding coincided with an increase in dietary diversity. This implies that the category-based dietary composition of the lutungs is characterized by foliage.

We found a significant negative relationship between the phenology score of young leaves and the percentage of ripe fruit feeding (Spearman's correlation tests: r_s = -0.761, P = 0.004). The phenology of flowers showed a significant positive relationship with the percentage of mature leaf feeding (Spearman's correlation tests: r_s = 0.610, P = 0.03) (Table 4.4).

In contrast, forest phenology did not affect whether lutungs fed on specific diet categories. Thus, lutungs' feeding is not affected by the availability of whole plant items. Rather, we found several significant positive relationships between the monthly feeding of specific plant items and their availability. Therefore, to understand the feeding strategy of colobines, researchers need to evaluate how they select dietary items at a fine-scale (species-based) as we have demonstrated.

As for the species-based analyses, conversely, three of the 17 main diet items had a significant positive correlation with their availability: flowers of *Spathodea campanulata* (Spearman's correlation tests: r_s = 0.608, P = 0.036), young leaves of *Homalanthus populneus* (Spearman's correlation tests: r_s = 0.708, P = 0.010), and unripe fruits of *Ficus elastica* (Spearman's correlation tests: r_s = 0.803, P = 0.002) (Table 4.5).

Regarding plant species, we found several significant positive relationships between monthly feeding and plant availability. These relationships likely determine the feeding behavior of lutungs to seasonal changes in diet, and perhaps activity budgets, ranging patterns, and inter-group competition over food resources.

Table 4.2 Comparison of diet composition in the genus Trachypithecus

Species / Study site	#Ot (hr.)	Composition of diet (%)								#Fps	Fc (%)		
		Foliage			Fruits			Fl.	O		Top 5	Top 10	Top 20
		ML	YL	#	RF	UF	#	#	#				
T. cristatus													
Gunung Padang, West Sumatra[1]	549.3	5	68.3	73.3	2	21.1	23.1	1.1	2.5	37	67.2	77.3	93.3
T. auratus													
Pangandaran (GRP3)[2]	726			46			27	21	6	88	44.9	61.1	77.1
Pangandaran (GRP21)[2]	726			48			37	7	8	49	38.4	60.9	80.4
Pangandaran, West Java[3]	612			80			10	10		94	n.a.	n.a.	n.a.
Cibodas, West Java[4]	n.a.	2	62	64			17[b]	16	3	90	34.0	46.1	63.3
West Bali NP (Group A)[5]	n.a.			46			42	6	6	50	52.9	77.3	88.2
West Bali NP (Group B)[5]	n.a.			58			32	8	2	46	46.2	71.9	87.8
Pangandaran, West Java[6]	622.4	0.8	69.9	70.7			21.2			85	43.4	63.8	81.2
T. crepusculus													
Wuliangshan, Yunnan, China[7]	1,738	29	25	54			32	6	8	148	32.0	43.7	59.4

Table 4.2 (*Continued*)

Species / Study site	**#Ot (hr.)**	**Composition of diet (%)**								**#Fps**	**Fc (%)**		
		Foliage			**Fruits**			**Fl.**	**O**		**Top 5**	**Top 10**	**Top 20**
		ML	**YL**	**#**	**RF**	**UF**	**#**	**#**	**#**				
T. delacouri													
Van Long NR, Vietnam[8]	372	20.4	59.3	79.7			9.9[b]	5.1	5.3	42	62.0	82.0	91.0
T. francoisi													
Nonggang, China[9]	739			56.9[a]			31.4[b]	11.6[c]	0.1	90	41.2	62.2	79.9
Fusui, China[10]	680			86.9			9.3	0.6	3.1	40	70.2	85.3	95.0
Nonggang, China[11]	n.a.			75.4			13.7	8	2.9	56	34.5	54.3	n.a.
Mayanghe, China[12]	759			66.3			32.2	1.1	0.4	38	32.6	44.0	n.a.
Fusui, China[13]	n.a.	12.1	58.5	70.6			23[b]	4.3	2.4	44	54.1	74.3	93.4
T. geei													
Sepahijala, India[14]	304			43.8			46.9	9	0.3	53	42.5	71.6	93.2
T. germaini													
Kien Luong, Vietnam[15]	312	5.3	71.8	77.1			18.4	3.3[c]	1.2	35	n.a.	n.a.	n.a.
Kien Luong, Vietnam[16]	320.4	9.5	58	67.7[a]			22.7	8[c]	1.6	58	53.1	76.8	92.0
T. johnii													
Mundanthurai, Western Ghats, India[17]	n.a.	4.2	44.1	48.3	4.6	10.5	33.7[b]	8.4	9.6	102	n.a.	55.7	n.a.

Table 4.2 (*Continued*)

Species / Study site	**#Ot (hr.)**	**Composition of diet (%)**								**#Fps**	**Fc (%)**		
		Foliage			**Fruits**			**Fl.**	**O**		**Top 5**	**Top 10**	**Top 20**
		ML	**YL**	**#**	**RF**	**UF**	**#**	**#**	**#**				
T. johnii													
Wayanad, Western Ghats, India[18]	n.a.			28.6			57.1[b]	14.3		21	n.a.	n.a.	n.a.
Nilgiri Hills, South India[19]	110			80.7[a]			8.9	9.3	0.8	34	45.0	68.7	91.6
T. leucocephalus													
Fusui, China[20]	982			89			6.1	2.7	1	50	47.9	69.1	93.6
Fusui, China[21]	1,553			91.6			4.2	0.3	3.9	109	74.3	83.9	n.a.
Chongzuo NR, Guangxi, China (Group 1)[22]	607	16.5	55.7	72.2			22.8	3.1	1.9	97	34.1	56.0	74.1
Chongzuo NR, Guangxi, China (Group 2)[22]	594	13.6	66.4	80.7			11.4	5.8	2.1	97	34.1	56.0	74.1
T. margarita													
Takou NR, Binh Thuan, Vietnam[23]	n.a.	7.1	54.5	61.6			29.9	7.7	0.7	33	64.3	83.2	92.9
Veun Sai Siem Pang, Ratanakiri, Cambodia[24]	n.a.			8.2			89.6	0.7	1.5	37	68.1	90.7	n.a.
T. obscurus													
Penang, Malaysia[25]	n.a.			63.0			19.9	13.5	3.6	56	n.a.	n.a.	n.a.

Table 4.2 (*Continued*)

Species / Study site	#Ot (hr.)	Composition of diet (%)								#Fps	Fc (%)		
		Foliage			Fruits			Fl.	O		Top 5	Top 10	Top 20
		ML	YL	#	RF	UF	#	#	#				
T. phayrei													
Gumti Wildlife Sanctuary, India[26]	n.a.	0.1	48.5	48.6	1.5	5.2	29.9[b]		20.6	18	78.4	n.a.	n.a.
Phu Kieo Wildlife Sanctuary, Thailand[27]	n.a.			39.4			35.6	6.4	18.6	n.a.	n.a.	n.a.	n.a.
Lawachara, Bangladesh[28]	n.a.	47		51[a]			14	16	19	29	n.a.	n.a.	n.a.
T. phayrei													
Phu Kieo Wildlife Sanctuary, Thailand[29]	n.a.	12.4	31.3		12.6	23.9		8.9	10.9	117	33.6	51.8	n.a.
T. pileatus													
Madhupur, Bangladesh[30]	n.a.	61		68[a]			26[b]	4	2	26	n.a.	n.a.	n.a.
Madhupur, Bangladesh[31]	1,400	57.8					33.7	7		28	54.0	73.9	n.a.
Pakhui, India[32]	n.a.	68					16	16		52	57.1	73.9	88.2
T. vetulus													
Panadura, Sri Lanka (PT1)[33]	n.a.	8	21.7	31.7[a]			53.7[b]	7.6		22	51.2	65.6	n.a.
Piliyandala, Sri Lanka (R1)[33]	n.a.	3.8	16.5	29.4[a]			60.1[b]	4		14	69.3	75.5	n.a.

ML: mature leaves, YL: young leaves, [a]: including petioles, RF: ripe fruits, UF: unripe fruits, [b]: including seeds Fl: flowers, [c]: including flower buds, O: other parts. Ot (hr.): observation time (in hour), Fps: food plant species Fc: food contribution, #: total, n.a.: not available.

Sources:

[1]This study
[2]Kool (1993)
[3]Brotoisworo and Dirgayusa (1991)
[4]Beckwith (1995)
[5]Vogt (2003)
[6]Tsuji *et al.* (2019)
[7]Fan *et al.* (2015)
[8]Workman (2010)
[9]Zhou *et al.* (2006)
[10]Li *et al.* (2009)
[11]Zhou *et al.* (2009)
[12]Hu (2011)
[13]Huang *et al.* (2015)
[14]Gupta and Chivers (2000)
[15]Hoang *et al.* (2014)
[16]Le *et al.* (2019)
[17]Sunderraj (2001)
[18]Sivaperuman and Kumar (2012)
[19]Kavana *et al.* (2015)
[20]Li *et al.* (2003)
[21]Zhou *et al.* (2013)
[22]Dayong *et al.* (2015)
[23]Tran (2013)
[24]Monge (2016)
[25]Leen *et al.* (2019)
[26]Gupta and Kumar (1994)
[27]Koenig *et al.* (2004)
[28]Aziz and Feeroz (2009)
[29]Suarez (2013)
[30]Islam and Husain (1982)
[31]Stanford (1991)
[32]Solanki *et al.* (2008)
[33]Dela (2007)

Table 4.3 Summary of Spearman's rank correlation tests between monthly feeding percentages and dietary diversity (H') of silvery lutungs at Gunung Padang

Feeding % (range)	Feeding % YL	RF	UF	Fl.	*H'*
ML (0-14.81)	r_s = -0.429 p = 0.110	r_s = 0.395 p = 0.145	r_s = - 0.107 p = 0.703	r_s = 0.312 p = 0.257	r_s = 0.792 p < 0.001**
YL (48.95-100)		r_s = -0.560 p = 0.029*	r_s = -0.761 p < 0.001**	r_s = 0.318 p = 0.249	r_s = -0.568 p = 0.029*
RF (0-8.08)			r_s = 0.273 p = 0.325	r_s = 0.239 p = 0.392	r_s = 0.687 p = 0.005*
UF (0-44.76)				r_s = -0.553 p = 0.032*	r_s = 0.066 p = 0.815
Fl. (0-3.23)					r_s = 0.329 p = 0.231

ML: mature leaves, YL: young leaves, RF: ripe fruits, UF: unripe fruits, Fl.: flowers, *H'*: dietary diversity. + p < 0.1, * p < 0.05, ** p < 0.001.

Table 4.4 Summary of Spearman's rank correlation tests between monthly phenology index and monthly feeding percentage and dietary diversity (H') of silvery lutung at Gunung Padang

Food types (range)	**Feeding % (range)**					***H'***
	ML (0-14.81)	**YL (59.18-100)**	**RF (0-8.08)**	**UF (0-31.58)**	**Fl (0-3.23)**	**(0-0.37)**
ML (37.67 - 37.99)	r_s = -0.279	r_s = 0.129	r_s = -0.022	r_s = -0.127	r_s = -0.022	r_s = -0.147
	p = 0.379	p = 0.688	p = 0.946	p = 0.695	p = 0.946	p = 0.648
YL (14.71 - 21.78)	r_s = -0.193	r_s = 0.154	r_s = -0.761	r_s = 0.018	r_s = -0.203	r_s = -0.552
	p = 0.549	p = 0.635	p = 0.004**	p = 0.957	p = 0.527	$p = 0.066^{+}$
RF(0.67 - 3.96)	r_s = -0.140	r_s = 0.312	r_s = -0.054	r_s = -0.132	r_s = -0.305	r_s = -0.035
	p = 0.664	p = 0.324	p = 0.867	p = 0.684	p = 0.335	p = 0.291
UF (1.63 - 7.35)	r_s = 0.221	r_s = 0.034	r_s = 0.051	r_s = -0.322	r_s = -0.254	r_s = -0.182
	p = 0.491	p = 0.921	p = 0.876	p = 0.307	p = 0.426	p = 0.921
Fl. (2.48 - 8.70)	r_s = 0.610	r_s = -0.273	r_s = 0.341	r_s = -0.372	r_s = -0.043	r_s = 0.517
	p = 0.035*	p = 0.391	p = 0.278	p = 0.235	p = 0.893	$p = 0.089^{+}$

ML: mature leaves, YL: young leaves, RF: ripe fruits, UF: unripe fruits, Fl: flowers, H': dietary diversity.
+ $p < 0.1$, ** $p < 0.01$.

Table 4.5 Summary of Spearman's rank correlation tests between phenology index and monthly feeding of silvery lutungs at Gunung Padang on the main diet items.

Species	**Family**	**Eaten part**	**Annual feeding (%)**	r_s	***p-value***	
Mangifera indica (N = 9)	Anacardiaceae	YL	1.20	0.019	0.954	n.s
Spathodea campanulata (N =4)	Bignoniaceae	Fl.	1.02	0.608	0.036	*
Calophyllum inophyllum (N = 1)	Clusiaceae	YL	3.05	0.569	0.053	+
Terminalia catappa (N = 4)	Combretaceae	YL	4.76	0.486	0.109	n.s
Excoecaria agallocha (N = 1)	Euphorbiaceae	YL	1.61	0.315	0.319	n.s.
Homalanthus populneus (N = 1)	Euphorbiaceae	YL	2.37	0.708	0.010	*
Macaranga tanarius (N = 1)	Euphorbiaceae	YL	2.20	0.167	0.605	n.s
Archidendron jiringa (N = 1)	Leguminosae	YL	1.70	0.398	0.200	n.s
Theobroma cacao(N = 7)	Malvaceae	YL	3.22	0.093	0.774	n.s
Xylocarpus rumphii (N = 2)	Meliaceae	YL	2.04	-0.326	0.301	n.s
Ficus elastica (N = 3)	Moraceae	ML	1.86	-	-	-
Ficus elastica (N = 3)	Moraceae	YL	3.98	-0.443	0.149	n.s
Ficus elastica (N = 3)	Moraceae	UF	2.46	0.803	0.002	**
Ficus variegata (N = 9)	Moraceae	YL	19.92	-0.452	0.140	n.s
Ficus variegata (N = 9)	Moraceae	UF	15.34	-0.377	0.2261	n.s
Eugenia polyantha (N = 17)	Myrtaceae	YL	5.34	0.489	0.107	n.s
Eurya acuminata (N = 1)	Pentaphylacaceae	YL	3.81	0.536	0.073	+

ML: mature leaves, YL: young leaves, RF: ripe fruits, UF: unripe fruits, Fl: fowers; $^{+}p < 0.10$, * $p < 0.05$, ** $p < 0.01$, n.s.: not significant. N = number of monitoring trees within the home range.

V CONCLUSIONS

Lutungs fed on 74 items (foliage, fruits, flowers, and other items) from 37 different plant species (24 tree species, 10 shrub species, and three vine species) during the study period, dominated by young leaves (68.3%) which is also as the main component of the diet throughout the study period, but other items sometimes had a higher percentage. There were 19 main plant species (>1% usage) in the lutungs' diet at Gunung Padang.

The percentage of mature leaves feeding showed a significant positive correlation with their dietary diversity, and between the percentage of ripe fruits feeding with their dietary diversity as well. The percentage of young leaves feeding showed a significant negative correlation with percentages of fruits feeding and between the percentage of unripe fruits feeding with the percentage of flower feeding. As to species-based analyses, flowers of *Spathodea campanulata,* young leaves of *Homalanthus populneus*, and unripe fruits of *Ficus elastica* had a significant positive correlation with their availability.

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BIOGRAPHY

The author was born in Jakarta on August 4, 1994, to the couple Mr. Muhammad Zaki and Mrs. Nurazizah, as the first child of six siblings. The author graduated from SMAN 2 Payakumbuh, West Sumatra in 2012, and the same year was accepted as a Biology undergraduate student, Faculty of Mathematics and Natural Sciences, Andalas University (UNAND), Padang, West Sumatra through the *SNMPTN* track. In 2017, the bachelor program was completed with a study entitled "*Aktivitas Harian dan Makanan Lutung Kelabu* (*Trachypithecus cristatus* Raffles, 1821) *di Gunung Padang, Sumatra Barat* [Undergraduate thesis in Indonesia]"

The author was accepted as a master's program student in the Animal Bioscience study program, Department of Biology, Faculty of Mathematics and Natural Sciences, Bogor Agricultural University in 2017 through a *Pendidikan Magister Menuju Doktor untuk Sarjana Unggul (PMDSU)* Batch 3 from Ministry of Research and Technology (*Kemenristekdikti*). While becoming a master's student, the author participated as a surveyor in Mentawai primate observation program by Siberut National Park and researcher by the Cooperative Research Fund of Primate Research Institute, Kyoto University, and KAKENHI, JSPS Bilateral Open Partnership Joint Research, Future Development Funding Program of Kyoto University Research Coordination Alliance, JSPS Core-to-Core Program

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