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Feeding Ecology of Red-Shanked Douc Langurs at Son Tra Nature Reserve, Da Nang, Vietnam

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Abstract: The first multi-year study of red-shanked doucs' (*Pygathrix nemaeus*) feeding ecology was conducted at Son Tra Nature Reserve, Danang City, Vietnam. Our goal was to discover the diet of red-shanked doucs at this nature reserve. Eleven years of data have been collected using scan sampling and video recording during group follows. Sixteen vegetation plots (50 m × 40 m) containing 160 trees from 60 species were established and monitored monthly for changes in fruit, flower, and young leaf production. A food calendar was constructed and used to estimate yearly food availability and abundance. Red-shanked doucs were found to depend primarily on buds and young leaves, while supplementing this intake with flowers, fruits, seeds, and bark. At least 226 plant species are used as food sources along with *Acacia pruinescens*, *Ficus racemosa*, *Ficus sumatrana*, *Millettia nigrescens*, and *Shorea guiso* that are consumed frequently. We found red-shanked doucs to be selective feeders since use of tree species was not based on relative density alone. The douc feeding strategy was to maintain a constant number of food resources monthly and seasonally while varying the plant species sources, resulting in dietary diversity. Our findings demonstrate that red-shanked doucs are more seasonally and dietarily flexible than was previously known, which may help explain why the species can survive in such a wide variety of forest habitats throughout its range.

Key words: *Pygathrix nemaeus*, feeding ecology, Son Tra Nature Reserve, conservation

Introduction

Red-shanked doucs (*Pygathrix nemaeus*) are colobine monkeys found in Vietnam, Laos, and Cambodia (Lippold 1995; Timmins and Duckworth 1999; Rawson and Roos 2008). They are classified as Critically Endangered in all habitats where they are found today (IUCN CR A2acd+3cd). with populations declining severely in Vietnam. High human population pressure resulting in habitat fragmentation and loss, hunting, and collection for the illegal animal trade are all major threats to the species' survival.

Red-shanked doucs have been studied for more than 50 years in the field and in captivity. The first field study took place at Son Tra in 1974, before it became a nature reserve (Lippold 1977). Data on taxonomy (Jablonski 1995, 1998), morphology (Canton 1998), gestation period (Lippold 1981), infant development (Lippold 1977), adoption (Lippold 1979), survivorship (Lippold 1989), care in captivity (Hick 1972; Ruempler 1998), status and distribution in the wild (Lippold 1995; Lippold and Vu 1996, 2008), and conservation (Lippold and Vu 1998, 2008) have been published. One major area that has been missing until now, however, is a multi-year study of red-shanked douc feeding ecology. Data presented in the current study now make it possible to elaborate red-shanked douc feeding ecology and compare it to studies of the black-shanked douc (*Pygathrix nigripes*) conducted by Hoang (2007; Hoang, Baxter and Page 2009) in Vietnam and Rawson (2009) in Cambodia, and the gray-shanked douc (*Pygathrix cinerea*) studied by Ha (2009) in Vietnam.

Son Tra Nature Reserve is an ideal location for this study, since it contains the largest known population of red-shanked doucs in Vietnam and is an essentially intact forest (Lippold and Vu 2008, 2018). We discovered this population in 2007 when we were asked by the Son Tra Forest Protection Department to determine if the red-shanked douc population continued to exist there (Lippold and Vu 2008). We discovered and reported a large douc population at that

time. The red-shanked douc population of Son Tra Nature Reserve provides an unequaled opportunity to describe feeding behavior along with many other aspects of red-shanked douc behavior. In addition, this douc population and reserve are actively protected by Army, Police, and Forest Protection Departments of both Danang and Son Tra districts. Recent infrastructure and road construction in support of resort development and organized tourism have made the reserve highly accessible.

Our first objective was to observe and quantify feeding behavior. We also collected botanical specimens of all plants that we observed doucs eating so that expert plant taxonomists at the National University Department of Botany and Plant Taxonomy in Hanoi, Vietnam, could identify the species.

Our second objective was to analyze each food species consumed by the doucs. Samples were collected, dried, and then submitted to the National Institute of Animal Husbandry Analysis Department in Hanoi, Vietnam. We submitted samples of all food items for analyses of a number of nutritional and chemical constituents including: crude protein, crude lipid, crude fiber, neutral detergent fiber, acid detergent fiber, carbohydrate, calcium, tannin, magnesium, iron, manganese, potassium, and zinc.

Our third objective included comparing the feeding behavior of Son Tra's red-shanked doucs to other studies of studies of the species (Ulabarri 2013; Otto 2005). Son Tra red-shanked douc feeding behavior will also be compared to black- and gray-shanked douc feeding behavior (Hoang 2007; Rawson 2009; Ha 2009). Our objective was to characterize red-shanked douc feeding behavior along with general douc feeding behavior, and to compare it with the dietary behavior of other Asian colobines, such as the white-headed langur (Li and Rogers 2009), the Tonkin snub-nosed monkey (Boonratana and Le 1998; Dang 2007), and the proboscis monkey (Sha *et al.* 2011; Yeager 1989).

Methods

Study area

We conducted our study in Son Tra Nature Reserve, a monsoon tropical evergreen forest approximately 10 km north-east of Danang City (16°06'–16°09'N, 108°13'–108°21'E) (Fig. 1). Established in 1977 as a cultural and historical site, in 1989 it was designated a nature reserve with a total of 4,437 ha, with 2,595 ha designated for strict protection and 1,844 ha for forest rehabilitation. It has been further reduced in size to 2,591 ha, just 58.4% of

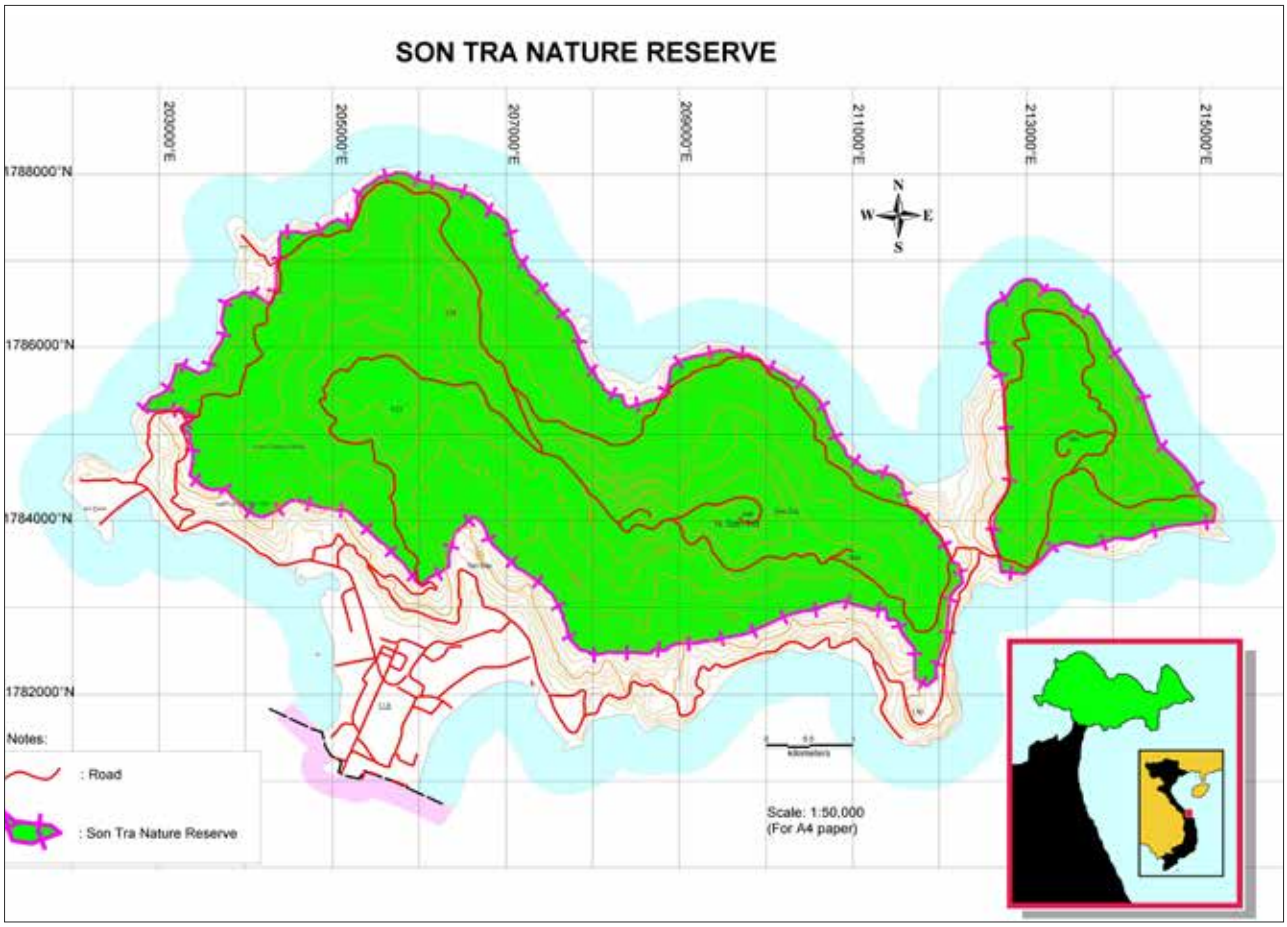

Figure 1. Son Tra Nature Reserve, coast of central Vietnam.

its original area by the Peoples Committee of Danang in a move to develop high end resorts for tourism. Son Tra covers a rocky peninsula and measures 7 km × 13 km, with the highest point being 696 m above sea level. According to the investment plan drawn up for the reserve in 1989, the nature reserve supports 400 ha of primary forest and 2,611 of secondary forest. Members of the Fagaceae, Dipterocarpaceae, Euphorbiaceae, Moraceae, and Sapindaceae families dominate the primary forest. There are also small areas that include scrub, grassland, and plantation forest. There are many microhabitats within the forest as a result of the complex topography, including many long, narrow valleys and steep hillsides (Lippold *et al.* 2018). Collection of non-timber forest products is widespread while tree cutting is occasional and selective. Douc groups were found in all major habitat types except scrub and grassland, and ranged from sea level to 696 m.

Subjects

More than 30 multi-male red-shanked douc groups and one all male group were the subjects of this study. We did not set out to habituate any of the groups because of the high frequency of hunting and trapping of all animals in the reserve. However, over the course of our study, groups started to recognize us and allowed us to observe them for long periods, sometimes for more than one hour. Groups were identified by the presence of individuals with distinctive markings and also by their age/sex composition. Some groups had infants of various ages while others did not. Red-shanked douc group sizes ranged from six to 24, with a mean group size of 14. We found that group size varied by season (Lippold and Thanh in prep.).

Forest analysis and phenology

Sixteen plots (50 m × 60 m) with 160 trees each were monitored for changes in fruit, flower, and young leaf production (Ganzhorn 2003). We also conducted phenological monitoring of 129 trees of 20 different species along five transects. We used these data to construct a douc food calendar (Fig. 2). This food calendar records edible plant species, edible parts of each species, and the period when each plant species is available for consumption according to our phenological studies. It also demonstrates the amount of variation in the douc's selected foods during each month of the year. In addition, the food calendar shows the availability of edible parts during all phenological periods. The calendar also points out the potential importance or level of contribution of each edible part of an individual plant species to the food base of the doucs. Finally, it is a useful tool because it allows us to predict the months when specific plants are available for consumption (the doucs already know this).

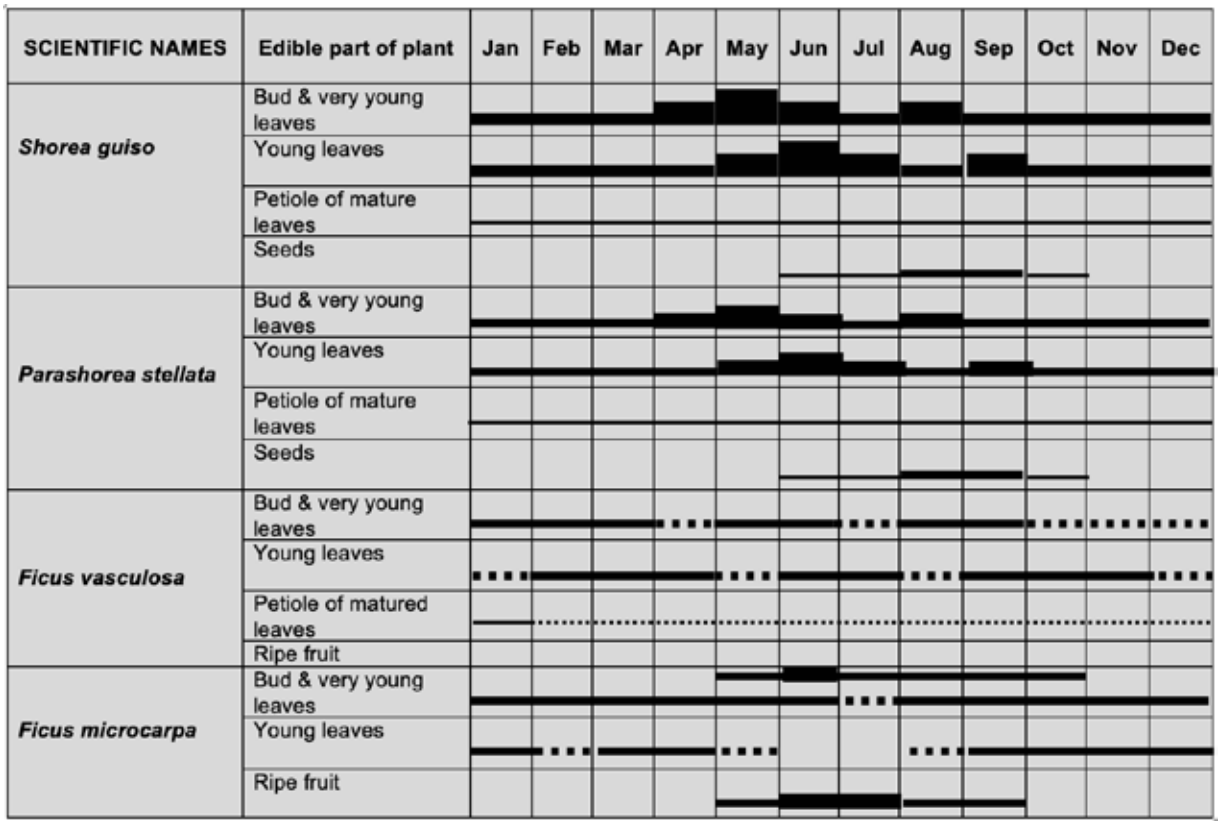

Figure 2. Red-shanked douc food calendar including species, plant part availability, and quantity during each month.

Data collection for feeding ecology

Data was collected on diet using scan sampling (Altmann 1974) and video recordings between the years 2009 and 2020. We started taking scans of all visible individuals every five minutes for 30 minutes per follow. Date, time, individual, GPS location, and food species eaten and part eaten were recorded. Since it was difficult to identify the specific part of the plant the doucs were consuming with either a spotting scope or binoculars, we documented the feeding behavior by video. A digital movie camera attached to a spotting scope was used to record all feeding bouts. These records allowed for exact identification of which tree species and plant parts were eaten. This technique also provided a permanent record of all feeding bouts, and these have been archived by specific douc group, location, and time of year.

Feeding included both manipulation and ingestion of food items. Food items were identified by species and plant parts. They included: young leaves, young leaves including buds and shoots, mature leaves, petioles, fruits (ripe and unripe), mature leaves, seeds, flowers, flower buds, branches, and bark.

In addition to scan samples and video analyses, we recorded all partially consumed and discarded foods on the forest floor with tooth marks or other signs of having been handled by the doucs. We used such feeding signs as additional evidence to estimate seasonal variance in diet.

General Results

Pygathrix nemaeus foraged in the trees; they only descend to the ground to cross roads or open areas on their way to feeding or sleeping trees. Their diet consisted of 503 plant items from 226 species (131 tree species, 19 shrub species, and 76 liana species), belonging to 65 families. The families with the most representatives were: Fabaceae (18 species), Moraceae (15 species), Euphorbiaceae (12 species), Myrtaceae (10 species), and Verbenaceae and Fagaceae (nine species), Lauraceae and Rubiaceae (seven species), and Annonaceae and Rutaceae (six species) (see Table 1)

The number of species that the doucs ate each month was high and stable throughout the year (mean 18: range 14–28). The number of vegetative parts consumed per species was also remarkably consistent from month to month (mean: 56.4 parts, range: 45–66). Table 2 lists the 25 most important food sources consumed throughout the year by red-shanked doucs at Son Tra Nature Reserve. Table 2 also includes the parts eaten and specifies if the food item is a tree, shrub, or liana. We found some differences in frequencies in food sources between the wet and dry season (Figs. 3 and 4).

Specific Results

Douc patterned resource collection

An analysis of each year confirmed that the doucs depend on a wide range of species each month. In 2019, for example, the number of species ranged from 14 in May to 24 in December. In addition to total feeding species, we found

Table 1. Number of families and species providing food for red-shanked Douc langurs at Son Tra Nature Reserve. Updated 7 August 2021.

TT	Family	No. of species	TT	Family	No of species
1	Fabaceae	19	34	Dilleniaceae	2
2	Moraceae	17	35	Combretaceae	2
3	Euphorbiaceae	13	36	Clusiaceae	2
4	Verbenaceae	11	37	Asclepiadaceae	2
5	Myrtaceae	11	38	Aquifoliaceae	2
6	Rubiaceae	9	39	Ancistrocladaceae	2
7	Fagaceae	9	40	Urticaceae	1
8	Lauraceae	8	41	Theaceae	1
9	Annonaceae	8	42	Smilacaceae	1
10	Tiliaceae	6	43	Simaroubaceae	1
11	Rutaceae	6	44	Rhamnaceae	1
12	Sterculiaceae	5	45	Proteaceae	1
13	Caesalpiniaceae	5	46	Piperaceae	1
14	Apocynaceae	5	47	Oleaceae	1
15	Vitaceae	4	48	Olacaceae	1
16	Loganiaceae	4	49	Lythraceae	1
17	Flacourtiaceae	4	50	Loranthaceae	1
18	Araliaceae	4	51	Leeaceae	1
19	Anacardiaceae	4	52	Lamiaceae	1
20	Ulmaceae	3	53	Juglandaceae	1
21	Sapindaceae	3	54	Icacinaceae	1
22	Myrsinaceae	3	55	Gnetaceae	1
23	Mimosaceae	3	56	Elaeocarpaceae	1
24	Menispermaceae	3	57	Cucurbitaceae	1
25	Dipterocarpaceae	3	58	Connaraceae	1
26	Convolvulaceae	3	59	Caprifoliaceae	1
27	Symplocaceae	2	60	Capparaceae	1
28	Sapotaceae	2	61	Boraginaceae	1
29	Rosaceae	2	62	Bignoniaceae	1
30	Ranunculaceae	2	63	Arecaceae	1
31	Lecythidaceae	2	64	Alangiaceae	2
32	Hypericaceae	2	65	Casuarinaceae	1
33	Ebenaceae	2		**Total**	**226**

Table 2. The most important food sources for *Pygathrix nemaeus* in Son Tra Nature Reserve, Vietnam.

No.	Family	Scientific name	Part Eaten[1]	Habit
1	Fabaceae	*Acacia pruinescens*	B, YL, ML, F,	Liana
2	Moraceae	*Ficus racemosa*	B, YL, YF, MF, B	Tree
3	Fabaceae	*Millettia nigresens*	B, YL, FL, YF, ML	Tree
4	Rutaceae	*Zanthoxylum avicennae*	B, YL, FL, YF, ML, Br, Bk	Tree
5	Fagaceae	*Castanopsis ceratacantha*	B, YL, ML, S	Tree
6	Moraceae	*Ficus sumatrana*	B, YL, ML	Tree
7	Moraceae	*Ficus vasculosa*	B, YL, P, RF	Tree
8	Verbanaceae	*Vitex quinata*	B, YL, ML, FL, F	Tree
9	Dipterocarpaceae	*Shorea guiso*	B, YL, P, ML, P, F, S	Tree
10	Moraceae	*Ficus annulata*	B, YL, F, P,	Tree
11	Convolvulaceae	*Ipomoea eberhardtii*	YL, M L	Liana
12	Myrtaceae	*Syzygium cumini*	B, YL, ML, YF, RF	Liana
13	Moraceae	*Ficus altissima*	B, YL, ML, F	Tree
14	Convolvulaceae	*Merremia boisiana*	YL, ML, P	Tree
15	Tiliaceae	*Brownlowia tabularis*	B, YL, ML, FL	Tree
16	Fabaceae	*Ormosia pinnata*	B, YL, ML, FL	Liana
17	Araliaceae	*Schefflera quangtriensis*	B, YL, ML	Tree
18	Sapotaceae	*Planchonella obovata*	B, YL, P, F, Br	Tree
19	Fabaceae	*Brauhinia touranesis*	B, YL, FL, Br	Tree
20	Hyperieaceae	*Cratoxylon formosum*	B, YL, ML	Tree
21	Tiliaceae	*Grewia bulot*	B, YL, ML, F	Tree
22	Leguminosae	*Peltophorhorum dasyrrhachis* var. *tonkinensis*	ML, FL	Tree
23	Fagaceae	*Quercus thorelli*	B, YL, ML, S	Tree
24	Euphorbiaceae	*Endospermum chinense*	B, YL, ML, P, FL, BR, S	Tree
25	Dipterocarpaceae	*Parashorea stellate*	B, YL, ML, P, F, S	Tree

[1] B = Buds, YL = Young Leaves, ML = Mature Leaves, P = Petioles of mature leaves, S = Seeds, F = Fruit, Bk = Bark, Br = Branch, Fl = Flowers

[2] T = Tree, L = Liana

that when we totaled the feeding minutes of each species each month it produced a consistent concentration of five species, which accounted for between 60 and 90 percent of the total observed feeding minutes.

Table 3 provides examples from 2019 of the consistent concentration of the five species primarily consumed by the doucs. As demonstrated below, *Acacia* occurred in every month and accounted for the highest total number of feeding minutes in 2019, followed by *Millettia* and then *Ficus racemosa.*

In 2020, the Danang city authorities closed the reserve during the months of April, June, and August due to a serious Covid-19 outbreak in Danang. The numbers of species used in each month ranged from 20 in July to 28 in February and November. *Ficus racemosa* was the most frequently eaten species by total percent of feeding minutes (118), followed by *Acacia* (88) and *Millettia* (76).

Son Tra Nature Reserve – Figs

This study is the first to document the importance of figs in the douc diet (Fig. 5). Their fig consumption is very consistent over the year. There are species of *Ficus* in the Son Tra forest, and the doucs ate the fruit, leaves, and flowers of all throughout the year. Examples of total percent of feeding minutes (tfm) of fig consumption in 2019 in each month are shown below in Table 4.

In 2020, figs continued to be important in the douc diet. Table 5 below documents the total feeding minutes of figs by the red-shanked doucs in Son Tra National Reserve. The reserve was closed in April, June, and August due to a Covid-19 outbreak in Danang.

Estimation of food value

Identifying the five most important food species each month and combining them with the analyzed nutritional

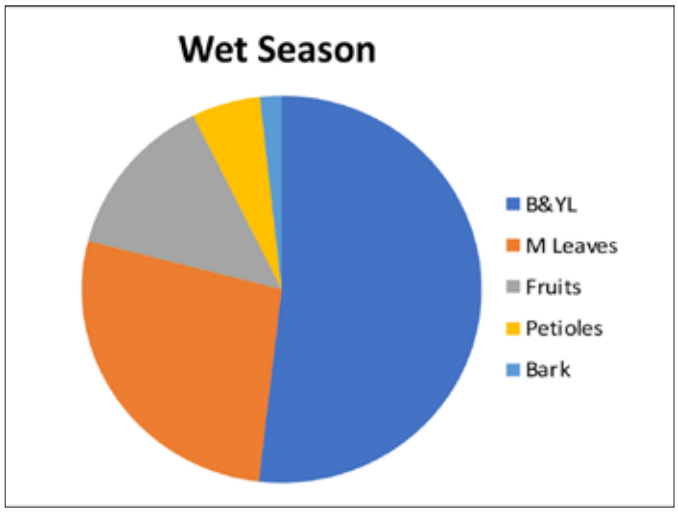

Figure 3. Wet season food consumption percentages. Buds and young leaves = 51.82%, mature leaves = 27.18, fruits=13.67%, petioles = 5.56%, and bark = 1.74%.

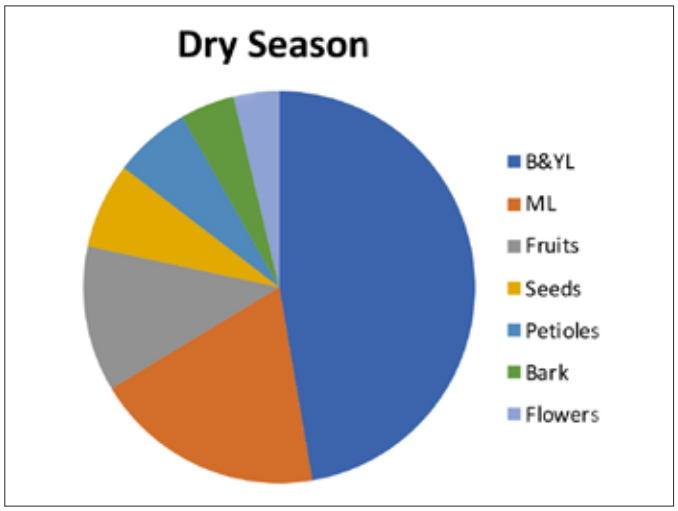

Figure 4. Dry season food consumption percentages. Buds and young leaves = 47.18, Mature leaves = 19.01, Fruits =11.97, Seeds =7.04, Petioles = 6.33, Bark = 4.46, Flowers = 3.75.

measures for each species allows an estimation of food value of these foods. These numbers are based on the nutritional analysis of more than 226 food plants that we observed the doucs eating. Each food item was assessed for crude protein, crude lipid, crude fiber, neutral detergent fiber (NDF), acid detergent fiber (ADF), carbohydrate, tannin, and several minerals, including iron.

For example, adding together the five top species in March 2020, which made up 78% of the douc feeding selection in that month, and then calculating the nutritional content of leaves) of each plant, produced the following results (Table 6): Mean values of protein are around 20%, fiber 18%, NDF 47%, ADF 8%, Cho (Carbohydrate) 13%, tannin 9%, and iron between 678 and 1576 mg/kg which was very high.

In our laboratory analyses of douc food items, we found consistent values of over 20% for protein for the douc's foods, followed by lower values for fiber, carbohydrates, and tannin. Iron is always very high (Lab data for 2020).

Discussion

Our first objective was to document the feeding ecology of the red-shanked douc langur at Son Tra Nature Reserve over the long term. A study of this duration had never been undertaken for doucs. It took us 11 years without interruption to accomplish this objective. Our teams were in the field continuously since 2007 collecting precise feeding observations. We have observed the doucs in all seasons, weather conditions, and in all habitats (Lippold *et al.* 2018). This study was planned to be of long duration, because we felt it was necessary to collect observations over many yearly cycles in order to identify the food species used by the doucs. Understanding the douc diet now has become critical due to the precipitous decline in douc populations all over Vietnam. Moreover, populations of all three douc species, *Pygathrix nigripes*, *P. cinerea*, and *P. nemaeus*, are now categorized as Critically Endangered on the IUCN Red List of Threatened Species because of their declining population in their home habitats (IUCN 2021). This decline is likely due to a combination of hunting and habitat loss.

We identified 226 plant species selected in the diet of the doucs. Direct observation and video recording of feeding bouts were used in order to differentiate the plant species and the exact parts of each plant consumed by the doucs. In our observations, we found that doucs concentrate on the young buds and young leaves of their favorite species. In fact, they seek out buds and young leaves in all seasons above all else. Buds and young leaves are combined seasonally with fruits and flowers during the dry season.

We found the doucs were highly folivorous: 54.8% of their feeding records comprised buds and young leaves, 22.6% mature leaves, 3.7% leaf petioles, and 18.9% other plant parts such as fruits, seeds, flowers, bark, and branches. There were seasonal variations in the doucs' reliance on different plant parts. Although the consumption of buds and young leaves occurred in both wet and dry seasons (wet season 51.82% versus dry season 47.18%), flowers and seeds were eaten primarily during the dry season (flowers 3.75%, seeds 7.04% respectively). Fruit was consumed in almost equal amounts during both seasons (dry season 11.97% and wet season 13.67%). At Son Tra, we also found that figs were selected all year, and they provided a basic and dependable food source for the doucs and many other mammals such as macaques, squirrels, deer and pigs.

A comparison of various colobine feeding patterns shows that they are similar. Leaves, fruit, flowers, seeds, and pith and bark (referred to as "Other") are categories of intake for all doucs and related species. Table 7 shows the results of colobine feeding patterns from several recent studies,

Table 3. Five-species patterns recorded during 2019 in Son Tra National Reserve, Vietnam.

Month	Total spp. in 2019	Top five Species in the diet	Total
January	14	*Acacia* 32% + *Zanthoxylum* 21% + *Ipomoea* 15% + *Ficus racemosa* 15% + *Clausena* 8%	91%
February	15	*Acacia* 31% + *Zanthoxylum* 20% + *Ficus racemosa* 15% + *Bauhinia* 9% + *Merremia* 8%	83%
March	N/A	Not available	-
April	14	*Ficus racemosa* 26% + *Acacia* 21% + *Milletia* 19% + *Ormosia* 8% + *Bauhinia* 7%	81%
May	14	*Acacia* 36% + *Millettia* 26% + *Ficus annulata* 10% + *Ficus racemosa* 9% + *Vitex* 4%	85%
June	18	*Acacia* 26% + *F. annulata* 21% + *Millettia* 11% + *Vitex* 10%, + *Bauhinia* 8%	76%
July	18	*Acacia* 26% + *Millettia* 24% + *Ficus racemosa* 17% + *Ficus annulata* 13% + *Quercus* 3%	83%
August	18	*Acacia* 23% + *Millettia* 20% + *Quercus* 9% + *Ficus sumatrana* 7% + *Zanthoxylum* 7%	66%
September	19	*Millettia* 36% + *Acacia* 18% + *Ficus altis* 10% + *Ficus annulata* 8% + *Vitex* 8%	80%
October	17	*Millettia* 31% + *Ficus racemosa* 13% + *Acacia* 11% + *Shorea* 10% +*Ormosia* 7%	72%
November	23	*Ficus racemosa* 19% + *Acacia* 18% + *Millettia* 11% + *Zanthoxylum* 9 % + *Syzygium cumini* 7%	64%
December	24	*Acacia* 23% + *Zanthoxylum* 15% + *Ficus racemosa* 12% + *Ipomoea* 9% + *Millettia* 6%	65%

Table 4. Monthly percentages of total feeding minutes on figs (*Ficus*) by red-shanked doucs in Son Tra National Reserve, Vietnam, in 2019.

Month - 2019	Percentage of total feeding minutes on each species	Total
January	*F. racemosa*	15%
February	*F. racemosa* 15% + *Ficus sumatrana* 2%	17%
April	*F. racemosa* 26% + *F. annulata* 1%	27%
May	*F. annulata* 10% + *F. racemosa* 9% + *Ficus sumatrana* 3% + *F. vasculosa* 1%	23%
June	*F. annulata* 21% + *F. racemosa* 6% + *F. vasculosa* 5%	32%
July	*F. racemosa* 17% + *F. annulata* 13% + *F. altissima* 2% + *F. sumatrana* 3%	35%
August	*F. sumatrana* 7% + *F. racemosa* 6% + *F. annulata* 2%	15%
September	*F. altissima* 10% + *F. annulata* 8% + *F. sumatrana* 4% + *F. racemosa* 2%	24%
October	*F. racemosa* 13% + *F. altissima* 4% + *F. sumatrana* 2%	19%
November	*F. racemosa* 19% + *F. sumatrana* 3% + *F. altissima* 2%	24%
December	*F. racemosa* 12% + *F. annulata* 5% + *F. altissima* 2%	19%

Table 5. Monthly percentages of total feeding minutes on figs (*Ficus*) by red-shanked doucs in Son Tra National Reserve, Vietnam in 2020.

Month - 2020	Percentage of total feeding minutes on each species	Total
January	*F. racemosa* 16% + *F. vasculosa* 8% + *F. sumatrana* 6%	30%
February	*F. racemosa* 15% + *F. vasculosa* 9%+ *F. sumatrana* 5%	29%
March	*F. racemosa* 17% + *F. vasculosa* 3% + *F. sumatrana* 3%	23%
May	*F. vasculosa* 11% + *F. racemosa* 5% + *F. sumatrana* 3%	19%
July	*F. racemosa* 18% + *F. annulata* 10% + *F. altissima* 6%	34%
September	*F. racemosa* 10% + *F. sumatrana* 6% + *F. annulata* 6%	22%
October	*F. racemosa* 11% + *F. sumatrana* 10% + *F. altissima* 7%	28%
November	*F. racemosa* 19% + *F. annulata* 9% + *F. altissima* 3%	31%
December	*F. racemosa* 12% + *F. annulata* 7% + *F. sumatrana* 6% + *F. altissima* 3%	28%

Table 6. Nutritional values (%) for the leaves of five species in the diet of the douc langurs: March 2020 at the Son Tra National Reserve, Vietnam.

Species	Protein %	Fiber %	NDF %	ADF %	Cho %	Tannin %	Iron mg/kg
Acacia	24	23	56	14	2	9	1576
Millettia	35	14	/	/	3	6	153
Ficus racemosa	20	16	67	7	8	2	678
Castanopsis	12	20	23	3	9	23	1130
Zanthoxylum	18	16	43	8	10	3	1312
Total	109	89	189	32	64	43	4849
Mean	21.8	17.8	47.25	8	12.8	8.6	969.8

Note. Percent of the feeding time of 24 species in the diet in March 2020 for *Acacia* 24% + *Millettia* 19% + *Ficus racemosa* 17% + *Castanopsis* 11% + *Zanthoxylum* 7% = 78% in total.

Table 7. Comparison of various colobine feeding patterns.

Species	Leaf	Fruit	Flower	Other	Seeds	References
Red-shanked douc	81.16	12.85	4.26	1.19	.54	Present study
Red-shanked douc	82	14	4	--	--	Lippold (1998)
Red-shanked douc	62	13	25	--	--	Otto (2005)
Black-shanked douc	54.60	19.78	14.56	1.51	9.56	Hoang Minh Duc (2009)
Black-shanked douc	39.90	11.40	8.80	.02	39.70	Rawson (2009)
Gray-shanked douc	58.9	41.0	0	.10	0	Ha Thang Long (2009)
Snub-nosed monkeys	38	47	0	0	15	Boonratana (1998)
Snub-nosed monkeys	53.1	25.0	12.2	0	7.2	Dong Thanh Hai (2008)
Proboscis monkey	41.0	41.0	3.0	0	15.0	Bennett and Sebastian (1988)
Proboscis monkey	52.0	40	3.0	0	5.0	Yeager (1989)
Proboscis monkey	66.0	26	0	8	0	Sha *et al.* (2011)
White-headed langur	89	5.7	2.7	0	0.4	Li and Rogers (2009)

comparing percentage of yearly intake of food items of several of the odd-nosed monkeys and the white-headed langur.

As shown in Table 7, only white-headed langurs (Li and Rogers, 2006) have higher values of leaf consumption. We found that red-shanked doucs maintain a folivorous diet throughout the year, with seasonal variation in species, and Son Tra doucs maintain their intake of young leaves over the year by increasing their intake of young leaves from a greater diversity of species.

Specific red-shanked douc comparisons

Ulibarri's (2013) single-year study of one group of red-shanked doucs at Son Tra listed 62 species in the diet. The study states that dietary diversity tends to be low and that there is a selection of feeding trees that are unrelated to tree densities, aside from the dipterocarps. He found that leaves were the most common resource (87.8%) followed by fruits and seeds (10.2%), flowers (1.6%), and bark and pith (0.4%). Ulibarri found that young leaves were selected over mature ones (68.6%), and whole leaves and petioles were selected over leaf parts. He said that food selection was not influenced by protein or fiber content. Ulabarri stated, without element analysis, that young leaves and mature leaves did not differ significantly in protein ratios.

In comparison, our long-term study of Son Tra doucs found dietary diversity to be very high and related to tree densities, especially the Moraceae. Our laboratory analysis of the protein content of young and old leaves demonstrated that young leaves do have significantly higher protein than old leaves. Our study demonstrated that doucs concentrate on protein rich food sources and select foods that are low in crude fiber and high in neutral detergent fiber. Moreover, Ulabarri (2013) missed the impact of figs as an important and stable food source.

Otto's (2005) study of red-shanked doucs took place in a semi-free enclosure at Cuc Phuong National Park, Vietnam,

located outside of the northern range of red-shanked doucs. Even though the site was outside the usual range of doucs, the Cuc Phuong red-shanked doucs chose many of the same genera of the plants as those consumed by the doucs at Son Tra. While the genera were the same, the species were different due to the more northerly location of Cuc Phuong. Twenty-two of the same plant genera were consumed by red-shanked doucs at Cuc Phuong and Son Tra. While there were differences in plant consumption, due to the variation in flora, the pattern of plant consumption was the same. In the semi-free enclosure at Cuc Phuong, Otto (2005) found that doucs consumed a large quantity of young leaves and demonstrated a high degree of specialization to folivory. Leaves accounted for a very large proportion of their diet. Otto (2005) also found that doucs demonstrate selectivity when feeding on leaves—her observations were virtually identical to the dietary characteristics that we have identified for the red-shanked doucs of the Son Tra Nature Reserve.

Further douc comparisons

Recent studies of black-shanked doucs further illuminate the dietary flexibility of the doucs as a group. Hoang's (2007) study of black-shanked doucs took place in southern Vietnam at two sites, Nua Chua National Park and Phuoc Binh National Park. The frequency of leaf items in Hoang's black-shanked douc samples was over 50%. In Rawson's (2009) study of black-shanked doucs at Keo Semia in Mondulkiri Province, Cambodia, the frequency of leaf consumption was lower than 40%. In both studies of red shanked doucs, the frequency of leaf consumption was over 60%: Son Tra doucs were over 80 % and in Otto's (2005) study the frequency was over 60%.

Comparing red and black-shanked doucs' consumption of fruit, flowers, and seeds indicates that both red and black-shanked douc diets include fruit seasonally. However, in Hoang's (2007) black-shanked douc study, fruits, flowers, and seeds all exhibit higher frequencies than those at Son Tra. These frequencies might reflect genuine black-shanked douc specific dietary characteristics, or they may represent

Figure 5. Fig heaven for the red-shanked doucs, *Pygathrix nemaeus*, in the Son Tra Nature Reserve, Vietnam. Photograph by Lois K. Lippold.

the differences in the forests of Son Tra and Nua Chua. The forests of Nua Chua produce a large crop of flowers, fruits, and seeds as a result of the minimal seasonal temperature and weather differences in southern Vietnam. At Son Tra Nature Reserve, seasons are highly differentiated by the cold winds of the north. It is possible that, because of this seasonality, the flower, fruit, and seed crops are not as abundant (Lippold *et al*. 2018).

The red-shanked doucs at Son Tra were similar to black-shanked doucs at Nua Chua in the proportions of leaves consumed before and after mid-day. Similar to black-shanked doucs, the red-shanked doucs tended to eat fruit and flowers in the morning. This pattern is consistent with suggestions by Oates (1987) that leaf monkeys consume fruits mainly in the morning perhaps because they can provide readily accessible energy needed after a night's rest (Oates 1987). Doucs at Son Tra ate leaves the first thing in the morning and the last thing in the evening before moving to trees where they spent the night.

Hoang (2007) found that black-shanked doucs exhibit seasonal variation in their diet based on the availability of food species. In southern Vietnam, tree species flower from the mid dry season to the early wet season and bear fruit in the wet season. The wet season at Nua Chua provides more fruit than in the dry season. Hoang observed an activity pattern that he termed "dietary switching" as a way for the black-shanked doucs to cope with food availability. In the dry season, the doucs reduced their movement and spent more time feeding and less time resting. Proportions of leaf consumption increased while dietary diversity decreased (Hoang 2007). In the wet season, the black-shanked doucs increased their resting rate, movement rate, and reduced their feeding rate. The proportion of fruits increased and dietary diversity increased. When the plant species consumed at Nua Chua are compared with the plant species consumed at Son Tra, we found at least 20 of the same genera including: *Mangifera*, *Semecarpus*, *Uvaria*, *Melodinus*, *Schefflera*, *Sindora*, *Dillenia*, *Artocarpus*, *Ficus*, *Syzygium*, *Antidesma*, *Mallotus*, *Castanopsis*, *Gnetum*, *Garcinia*, *Dalbergia*, *Millettia*, *Ormosia*, *Zanthoxylum*, and *Vitex*.

Rawson's study (2009) of black-shanked doucs at the Keo Semia Biodiversity area in Cambodia reports another feeding adaptation for black-shanked doucs. Rawson described the forests as similar to those of Cat Tien National Park in southern Vietnam, where the forest lost leaves near the end of the dry season from January through March. In Cambodia, the new leaf flush occurs prior to the beginning of the wet season. New fruit production, however, showed no clear temporal pattern. Rawson found that the top five species constituted more than 43% of the feeding records. In general, flowers were consumed at high levels when in abundance. Rawson found that doucs at Semia ate seeds at a higher rate than at any other site where douc feeding ecology has been reported. He also reported that seeds were consumed in higher frequencies in the wet season and eaten in the morning. Rawson, in fact, characterizes black-shanked doucs at Keo Semia as seed predators. We did not find that Son Tra doucs consumed seeds at a high rate in any season. However, the Son Tra douc diet did include nine genera of the same plants found at Rawson's site, and these include: *Ilex*, *Dillenia*, *Acacia*, *Millettia*, *Sindora*, *Vitex*, *Syzygium*, *Ficus*, and *Ziziphus*.

Each forest in Vietnam can be characterized as having a dominant suite of trees, and exactly which species remains depends on its logging history. All forests in Vietnam have been selectively harvested in the past and many are the sites of recent (past 10 years) or active logging operations, such as Kon Ka Kinh and Kon Cha Rang National Park, where grey-shanked doucs were recently reported by Ha (2009). The logging history of each forest makes it difficult to compare the specific food species in the diets of red, grey, and black-shanked doucs. In addition, seasonal variations appear quite pronounced at Son Tra while there is less seasonal variation at Keo Semia in the Cambodia site or in Nua Chua in southern Vietnam. The Son Tra forest is influenced by the cold winds of the north which make for a wet season that lasts from October to January. Little if any fruit (except figs) is produced during the wet season. By comparison, fruiting can occur all year in the southern forests of Vietnam and Cambodia because there is little seasonal temperature variation in comparison to Son Tra.

Regardless of seasonal differences, the feeding strategy of the doucs is clear. Red-shanked doucs depend on buds and young leaves all year round. They maintain this high frequency by using a variety of species throughout the year. Red-shanked doucs at Son Tra maintain a consistent number of food species monthly from a large variety of species. Even though the red-shanked doucs of Otto's (2005) study were outside of their normal distributional range, they also exhibited a high frequency of leaf eating over any other food source when given free choice in a semi-captive situation. The black-shanked doucs at Nua Chua and Binh Phuoc also exhibited a high frequency of leaf eating. Only the black-shanked doucs of Rawson's (2009) research were characterized by a noticeable divergence in feeding strategy. This may be related to the forests where they are found.

More on protein and patterns

The length and depth of our study allowed for component analyses of the species selected by the doucs. A publication in preparation (Lippold and Thanh in prep.) will present a detailed discussion of these analyses. We can generalize here, however, that the species selected by the doucs at Son Tra have all of the characteristics that several authors (Lambert 2007; Milton 1979; Oates *et al.* 1980; Otto 2005) have suggested. We have found that young leaves generally have higher nutritional quality, and they are higher in protein and lower in fiber and secondary compounds. We found this to be true for the food species that we have submitted for analyses. For example, in the March 2020 diet, the protein value of the five selected food items added up to more than 20% protein. This protein value is consistent throughout the

year. Results obtained for *Ficus* from Son Tra demonstrated that young leaves contained twice as much protein, half as much fiber, and twice as much iron as mature leaves of the same species (Lippold and Vu in prep.). When calculating the food value of the five species concentration, we found that they delivered 20% protein consistently, low fiber, high NDF, low ADF, low carbohydrate, and high iron. Also, the five top species provided 47–82% of the total intake each month.

We have been able to demonstrate that doucs depend on high protein gathered from buds and young leaves throughout the year. We have analyzed all of the 226 species for a constellation of characteristics, which included high protein, low carbohydrate, low fiber, high neutral detergent fiber (NDF), low acid detergent fiber (ADF), and a suite of minerals, including a very high concentration of iron.

Doucs' patterned concentration

Many years of data collection have also allowed us to delineate a patterned concentration of five species per month. Although red-shanked doucs consume between 14 and 25 species per month, we found that they concentrate on five for up to 47–82 % of the food intake. This combination of food species assures that their intake of protein remains above 20%.

Figs

This study demonstrated that the Son Tra doucs depend on a wide variety of fruits seasonally from April to October. An entirely new finding was the degree with which the doucs feed on figs, the consumption of which delivers a substantial source of nutrition to the doucs. There are at least 13 fig species in the Son Tra forest, and the doucs feed on them every month of the year. For example, figs accounted for 15–36 % of food per month in 2019. In January 2019, one fig species accounted for 14% of the total feeding time, and in July four species of fig accounted for 35% of total feeding time. In May 2020, three fig species accounted for 19% of the total feeding minutes and in July three fig species accounted for 34% of total feeding minutes. Clearly, figs are important at Son Tra every month.

In addition, we found that doucs concentrate on habitats 3, 4, and 5 of the tropical evergreen broad-leafed forest found from sea level to 200 m. in the reserve (Lippold *et al* 2018). Doucs also take advantage of sources from secondary vegetation (such as lianas and figs), which are common in areas where there has been road building and other environmental disturbance. There has been an increase in the number of fig species utilized in recent years. As a result of the construction of the Tensa Road in 2010, more food sources that flourish in open habitats have become available to doucs. We have observed that doucs readily adopt new food sources. Our early studies concentrated on the primary forest where *Parashorea* and *Shorea* are dominant, and these important food sources were preferred by doucs. As the years have passed the primary forest continues to be lost or damaged through tree falls, human destruction and weather-related events such as typhoons. The richness of the Son Tra forest has provided additional food sources, and doucs have turned to a younger forest at a lower level of the reserve. Figs abound at the lower altitudes of the forest as do lianas.

The red-shanked douc feeding strategy clearly emphasizes buds and young leaves over all other food resources (more than 54% of intake is buds and young leaves). Since these resources are not confined to a single location in the forest, the doucs must move every few days to find new sources of such as young leaves. In the forests of Son Tra, the doucs can rely on a number of tree species that produce young leaves throughout the year. It, therefore, appears that tree species that will produce a number of crops of young leaves each year are critical components of this specialized feeding strategy. *Parashorea* and *Shorea* trees are common throughout the forest and this condition allows the doucs to move from one location to another to feed from these trees. Not only are they common but they also respond to the douc's consistent feeding on them by producing several crops of new buds and young leaves each year. This is a unique characteristic of *Parashorea* and *Shorea* at Son Tra and illustrates a basic symbiotic interaction between the doucs and the trees. In other forests, such as Phong Nha National Park in Quang Binh Province, *Parashorea* and *Shorea* only one crop of buds and young leaves are produced each year (T. D. Nghia, pers. obs.).

Regardless of seasonal differences, the feeding strategy of the doucs is clear. Red-shanked doucs depend on buds and young leaves all year round. They maintain this high frequency by using a variety of species throughout the year. They maintain a consistent number of food species each month from a large variety of species at Son Tra. Even though the red-shanked doucs studied by Otto (2005) were outside their normal distributional range, they also exhibited a high frequency of leaf-eating over any other food source when given free choice in a semi-captive situation. The black-shanked doucs at Nua Chua and Binh Phuoc also exhibited a high frequency of leaf eating. As stated above, only the black-shanked doucs of Rawson's (2009) study were characterized by a noticeable divergence in feeding strategy. This may be related to the forests in which they are found.

Our long-term study of the red-shanked douc langurs of Son Tra provides an important piece of the puzzle to understanding douc langur feeding ecology. We found that the doucs exhibit dietary flexibility in the numbers and concentrations of the species that they consume. We also discovered that they are characterized by their ability to add new species to the inventory of their diet. Any new species planted in the Son Tra forest by tourist operations or in reforest operations were readily consumed by the doucs. They added *Iponema*, an African liana, for example, which

has become the scourge of Son Tra entirely covering parts of the forest. This dietary flexibility is imperative for their survival.

Summary

Son Tra is an exceptional habitat for the red-shanked douc because it has a unique forest characterized by a high frequency of species such as *Parashorea* and *Shorea* in the primary forest and figs and lianas in the secondary forest. Since Son Tra provides an ideal habitat for doucs, it is also a perfect site to undertake the first multi-year study of their feeding ecology. Our 11-year study provided a depth of knowledge not obtainable in a single year study, and it took all of those years to discover and identify the 226 food species consumed by the red-shanked doucs. Not only did this study reveal a high number of species selected by the doucs, but it also demonstrated their selective and flexible dietary choices. We found doucs to be selective feeders because they preferred only 226 species as food items from a total of 1,048 species at Son Tra.

Thirty multi-male red-shanked douc groups and one all male group were the subjects of our research. We collected data on diet using scan sampling (Altmann 1974) and video recording between the years of 2009 and 2020. We started taking scans of all visible individuals every five minutes for 30 minutes per follow. Date, time, individual, GPS location, and food species eaten and partly eaten were recorded. Sixteen plots (50 × 60 m) with 160 trees each for changes in fruit, flower, and young leaf production were monitored (Ganzhorn 2003). We also conducted phenological monitoring of 129 trees of 20 different species along five transects. We used these data to construct a douc food calendar (see Fig. 2).

We found the doucs were highly folivorous: 54.8% of their feeding records comprised of buds and young leaves, 22.6% mature leaves, 3.7% leaf petioles, and 18.9% other plant parts, such as fruits, seeds, flowers, bark, and branches. There were seasonal variations in the doucs' reliance on different plant parts. Although consumption of buds and young leaves occurred in both wet and dry seasons (wet season 51.82% versus dry season 47.18%), flowers and seeds were consumed primarily during the dry season (flowers 3.75%, seeds 7.04% respectively). In addition, fruit was consumed in almost equal amounts during both seasons (dry season 11.97% and wet season 13.67%).

Figs were selected all year round, and they provided a basic dependable food source for doucs and other animal species—they are plentiful in Son Tra, numbering at least 13 varieties and the doucs consumed one to several species of fig every month of the year. Our observations are the first to establish the importance of figs in the douc diet. Fig trees produce fruit all year round and doucs eat hard, unripe figs which provide a substantial source of nutrition.

Doucs use between 14 and 28 species each month. However, within each month they spend more than 50% of their feeding time on just five species. The species may change each month, but the concentration on five species remains over the year. In fact, in some months, up to 80% of the feeding minutes are spent on the five species with the remaining species accounting for a very low percentage of minutes. This patterned feeding was consistent over the years studied.

Red-shanked doucs are like other doucs in selecting especially young leaves and buds. All doucs show dietary flexibility as a group, and buds and young leaves comprise a large proportion of their diet. They maintain this high frequency by using a variety of species throughout the year, maintaining a consistent number of food species monthly from the large variety of species at Son Tra, patterning their use of resources in a distinctive fashion.

A long-term feeding study of red-shanked doucs is long overdue. The decline in population over the last 15 years has been significant. In fact, none have been found from some sites where we studied doucs just 10 years ago (Lippold and Vu field notes). This precipitous decline in all douc populations has moved the population status from Endangered to Critically Endangered. The three species are found only east of the Mekong River, an area experiencing one of the highest rates of deforestation in the world,.

Time to save doucs is running out, and we are only now finding out what they eat! We have been studying this Son Tra douc population since we discovered them in 2007 (Lippold *et al* 2008), and have spent the last 14 years trying to save the Son Tra Nature Reserve itself from massive and destructive development (Lippold *et al*. 2018). It took 11 years to understand the unique way in which the doucs utilize the flora of Son Tra Nature Reserve, establishing that they depend on high protein intake, gathered from buds and young leaves throughout the year. We have analyzed all of the 226 species for a constellation of characteristics—high protein, low carbohydrate, low fiber, high neutral detergent fiber, low acid detergent fiber, and a suite of minerals, including a very high concentration of iron.

One of the unexpected benefits of our research is that the findings of this study may impact the the diets provided for doucs in captivity. Doucs have been very challenging to maintain in captivity due to complex feeding protocols. We believe this is because doucs depend heavily on buds and young leaves of a large number of species along with unripe figs and other fruits and flowers. Doucs readily adapt to new species and add many introduced plants to their menu at Son Tra, and we believe that local species of plants around zoos can be utilized to feed them. This dietary flexibility further defines another douc adaptation.

The fig-rich forest of Son Tra provides doucs with an opportunity to expand beyond the folivore niche and subsist on large quantities of unripe fruit when available. The dietary flexibility may be a major reason why doucs are able to inhabit such a wide variety of habitat types in Vietnam.

Son Tra is an ideal place for doucs not only because of the rich flora but also because of its complex topography.

Son Tra is characterized by a large number of microhabitats that contain complex and rich plant resources with deep valleys that shelter and protect the doucs from frequent typhoons and monsoon rains (Lippold *et al.* 2018). The survival of these Critically Endangered doucs depends upon active protection of the Son Tra Nature Reserve in terms of proactive law enforcement regarding hunting, logging, and development encroachment, now and in the future.

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Literature Cited

Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour* 49: 227–267.

Bennett, E. L. and A. G. Davies. 1994. The ecology of Asian colobines. In: *Colobine Monkeys: Their Ecology, Behavior and Evolution*, A. G. Davies and J. F. Oates (eds.), pp.129–171. Cambridge University Press, Cambridge, UK.

Bennett, E. L. and A. C. Sebastian. 1988. Social organization and ecology of proboscis monkeys (*Nasalis larvatus*) in mixed coastal forest in Sarawak. *Int. J. Primatol*. 9: 233–255.

Boonratana, R. and X. C. Le. 1998. Preliminary observations of the ecology and behavior of the Tonkin snub-nosed monkey (*Rhinopithecus avunculus*) in northern Vietnam. In: *The Natural History of the Doucs and Snub-nosed Monkeys*, N. G. Jablonski (ed.). pp.207–215. World Scientific Publishing, Singapore.

Canton, J. 1998. The morphology of the gastrointestinal tract of *Pygathrix nemaeus* (Linnaeus 1771). In: *The Natural History of the Doucs and Snub-nosed Monkeys*, N. G. Jablonski (ed.). World Scientific Publishing, Singapore.

Dong Thang Hai. 2007. Ecological Behavior and Conservation of *Rhinopithecus avunculus* in Vietnam. *Final Report*. Rufford Small Grants and the Australian National University, Canberra.

Ganzhorn, J. 2003. Habitat description and phenology. In: *Field and Laboratory Methods in Primatology*, J. M. Setchell and D. J. Curtis (eds.), pp.40–56. Cambridge University Press, Cambridge, UK.

Ha, T. L. 2009. Behavioral Ecology of Gray-shanked Douc Monkey (*Pygathrix cinerea*) in Vietnam. PhD thesis, University of Cambridge, Cambridge, UK.

Hick, U. 1972. Breeding and maintenance of douc langurs *Pygathrix nemaeus* at Cologne Zoo. *Int. Zoo Yearb.* 12: 98–103.

Hoang, D. 2007. Ecology and Conservation Status of the Black-shanked Douc (*Pygathrix nigripes*) in Nui Chua and Phuoc Binh National Parks, Ninh Thuan Province, Vietnam. PhD thesis, University of Queensland. Australia.

Hoang, M. D., G. S. Baxter and M. J. Page. 2009. Diet of *Pygathrix nigripes* in southern Vietnam. *Int. J. Primatol.* 30: 15–28.

IUCN. 2021. The IUCN Red List of Threatened Species. International Union for Conservation of Nature (IUCN), Gland, Switzerland, and Cambridge, UK. Website: <www. iucnredlist.org>.

Jablonski, N. G. 1995. The phyletic position and systematics of the douc langurs of Southeast Asia. *Am. J. Primatol*. 35: 185–205.

Jablonski, N. G. 1998. The evolution of the doucs and snub-nosed monkeys and the question of phyletic unity of the odd-nosed colobines. In: *The Natural History of the Doucs and Snub-nosed Monkeys*. N. G. Jablonski (ed.), pp.13–52. World Scientific Publishing, Singapore.

Lambert, J. A. 2007. Primate nutritional ecology: feeding biology and diet at ecological and evolutionary scales. In: *Primates in Perspective*, C. J. Campbell, A. Fuentes, K. MacKinnon, M. Panger and S. K. Bearder (eds.), pp.482–495. Oxford University Press, Oxford, UK.

Li, Z., and E. Rogers. 2009. Food consumed by white-headed langurs in Fusui, China. *Int. J Primatol*. 27: 1551–1567.

Lippold, L. K. 1977. The douc langur: a time for conservation. In: *Primate Conservation*, H. S. H. Prince Rainier III of Monaco and G. H. Bourne (eds.), pp.513–538. Academic Press, New York.

Lippold, L. K. 1979. Uta and Jack: adoption in douc langurs. *Zoonooz* 18(3): 7–9.

Lippold, L. K. 1981. Monitoring female reproductive status in the douc langur (*Pygathrix nemaeus*) at the San Diego Zoo. *Int. Zoo Yearb.* 21: 184–187.

Lippold, L. K. 1989. Reproduction and survivorship in douc langurs *(Pygathrix nemaeus*) in zoos. *Int. Zoo Yearb*. 28: 252–255.

Lippold, L. K. 1995. Distribution and conservation status of douc langurs in Vietnam. *Asian Prim*ates 4: 4–6.

Lippold, L. K. 1998. Natural history of douc langurs. In: *The Natural History of the Doucs and Snub-nosed Monkeys*, N. G. Jablonski (ed.), pp.191–206. World Scientific Publishing. Singapore.

Lippold, L. K. and, N. T. Vu. 1996. Douc langur variety in the Central Highlands of Vietnam. *Asian Primates* 5(1–2): 6–8.

Lippold, L. K. and N. T. Vu. 1998. Primate conservation in Vietnam. In: *The Natural History of the Doucs and Snub-nosed Monkeys*, N. G. Jablonski N (ed.), pp.293–300. World Scientific Publishing, Singapore.

Lippold, L. K. and N. T. Vu. 2008. The time is now: survival of the douc langurs of Son Tra, Vietnam. *Primate Conserv*: (23): 1–5.

Lippold, L. K., N. T, Vu, and T. D. Nghia. 2018. Resource assessment and development impact on douc population at Son Tra Nature Reserve, Vietnam. *Primate Conserv*. (32): 167–174.

Milton, K. 1979. Factors influencing leaf choice by howler monkeys: a test of some hypotheses of food selection by generalist herbivores. *Am. Nat*. 114: 362–378.

Oates J. F., P. Waterman and G. Choo. 1980. Food selection by the South-Indian leaf monkey *Presbytis johnii* in relation to leaf chemistry. *Oecologia* 45: 45–56.

Oates, J. F. 1987. Food distribution and foraging behavior. In: *Primate Societies*, B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham and T. T. Struhsaker (eds.), pp.197–209. University of Chicago Press, Chicago, IL.

Otto, C. 2005. *Food Intake, Nutrient Intake and Food Selection in Captive and Semi-Free Douc Langurs*. Schüling Verlag, Munster.

Rawson, B. and C. Roos. 2008. A new primate species record for Cambodia: *Pygathrix nemaeus*. *Cambodian J. Nat. Hist.* 1(1): 7–11.

Rawson, B. 2009. The Socioecology of the Black-shanked Douc (*Pygathrix nigripes*) in Mondulkiri Province, Cambodia. PhD thesis, Australian National University, Canberra, Australia.

Ruempler, U. 1998. Husbandry and breeding of douc langurs *Pygathrix nemaeus nemaeus* at Cologne Zoo. *Int. Zoo Yearb.* 36: 73–81.

Sha, J. C. M., I. Matsuda and H. Bernard. 2011. *The Natural History of the Proboscis Monkey*. Natural History Publications. Sabah, Malaysia.

Timmins R. and J. Duckworth. 1999. Status and conservation of douc langurs (*Pygathrix nemaeus*) in Laos. *Int. J. Primatol*. 20: 469–489.

Ulibarri, L. R. 2013. The Socioecology of Red-shanked Doucs (*Pygathrix nemaeus*) in Son Tra Nature Reserve. PhD thesis, University of Colorado, Boulder, CO.

Yeager, C. 1989. Feeding ecology of the proboscis monkey (*Nasalis larvatus*). *Int. J. Primatol.* 10: 497–530.

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