

RESEARCH ARTICLE

Colobine forestomach anatomy and diet

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Abstract

Colobine monkeys have complex, multichambered, foregut-fermenting stomachs with either three (“tripartite”) or four (“quadripartite,” adding the praesaccus) chambers where a commensal microbiome digests plant cell walls and possibly detoxifies defensive plant chemicals. Although different potential functions for the praesaccus have been suggested, little evidence exists to support any of the proposed functions. To address the issue of the function of the praesaccus, we collated literature data on diet and compared tripartite and quadripartite species. Our results suggest that the praesaccus is an adaptation to a dietary niche with a particularly high reliance on leaves as fallback foods in colobine clades with quadripartite stomachs, and a higher reliance on fruits/seeds as foods at times of high fruit availability in clades with tripartite stomachs. This supports the notion that a large gut capacity is an important characteristic by which folivores survive on a high fiber diet, and that this large gut capacity may not be necessary for some species if there are seasonal peaks in fruit availability.

KEYWORDS

fallback food, forestomach, praesaccus, quadripartite, tripartite

1 | INTRODUCTION

Colobine monkeys differ from all other primates in having a foregut-fermentation digestive system (Bauchop & Martucci, 1968) with three (“tripartite”) or four (“quadripartite”) chambers in the forestomach (Chivers, 1994). Quadripartite stomachs are characterized by an additional blind sac or “pouch”; the praesaccus (Figure 1), which is lined with a stratified squamous epithelium and has a complete longitudinal muscle coat, representing an additional

chamber, prior to the three compartments common to all colobines (Langer, 1988).

Compilations of whether individual colobine species have three or four chambers have been published (Caton, 1998; Langer, 1988, 2017), but no comprehensive overview of the colobine group exists. Notably, the existing evidence does not rule out that there is variation in this trait (whether tripartite or quadripartite forestomach chambers) even within genera. To date, it appears that *Colobus*, *Semnopithecus*, *Trachypithecus*, and *Presbytis* represent taxa with a tripartite stomach,

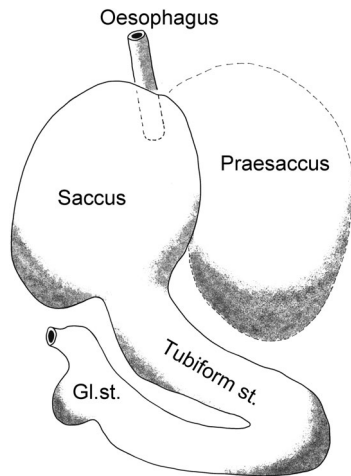


FIGURE 1 Schematic representation of the colobine stomach, illustrating the tripartite condition (with saccus, tubiform, and glandular stomach parts) and the quadripartite condition (with an additional praesaccus). Drawn after Langer (1988, p. 284) for *Colobus verus*. Note that the volumes, and the degree to which the praesaccus can be visually discerned from the saccus, may vary between species: Gl. st. = glandular stomach

whereas *Procolobus*, *Ptilocolobus*, *Rhinopithecus*, *Pygatrix*, and *Nasalis* represent taxa with a quadripartite stomach, with no information on *Simias* (Caton, 1998). Given the taxonomic distribution of this trait, it would seem that the praesaccus evolved in parallel both in some African and some Asian colobine clades. Therefore, it is tempting to assume that the praesaccus represents a functional adaptation, that is, convergent between the respective species. The alternative scenario would assume the praesaccus is an ancestral trait in both clades and was lost in parallel in some species in each group.

Different functions for the praesaccus have been proposed, but as of yet no evidence exists to support one proposal over another. Caton (1998), and subsequently Wright, Prodhon, Wright, and Nadler (2008), proposed that the praesaccus functions as a “gastric mill.” Chivers (1994) suggested it might be an adaptation to seed-eating, without providing a rationale or empirical data. In contrast, Langer (2017) considers the praesaccus an adaptation to folivory, based on the assumption that a large gastrointestinal capacity is a typical adaptation to a diet of low-digestibility items, such as leaves. This last explanation reverberates the finding of Chivers and Hladik (1980) that folivorous mammals generally have more gastrointestinal surface area in relation to metabolic body size than frugivorous and faunivorous mammals. This is because to derive a similar amount of energy from a diet of lower digestibility, more of that diet must be processed. Thus, the objective of our research was to test the prediction that colobines with a quadripartite stomach consume higher proportions of leaves than those with a tripartite stomach.

2 | MATERIALS AND METHODS

To address the question of the association between colobine praesaccus and the diets (i.e., fruit/seed- and leaf-eating), we collated

literature data on the natural diet of all colobine species for which the status of the number of forestomach chambers was known (according to Caton, 1998 as a starting point for our literature search). Most authors do not distinguish whether colobines consumed only seeds or fruits and consider both pulp and seed parts together. Therefore, we defined the amount of consumed seeds as that of consumed fruits and seeds. We obtained data on colobine natural diets, published by Fashing (1988), Kirkpatrick (2011), Sterck (1994) and added recently published literature (Table A1); these data represent the natural diet in percent of its various components, based on field observations that recorded the time spent feeding. If the values were not represented in the text, but were presented in figures, we measured the values using the Web Plot Digitizer ver. 4.1 (free software: <https://apps.automeris.io/wpd/>). An assessment of dietary variation has been demonstrated to be important for evaluating colobine foraging strategies (Harris & Chapman, 2018) and multiple diet descriptions were found for several taxa (Table A1). For each species, we calculated both the mean and the maximum percentage of fruits/seed and leaves in the diet based on annual averages, and additionally the maximum percentages based on monthly averages to better account for intra-annual variation.

In spite of the small number of species and the fact that the species with a quadripartite stomach in our data set were from the closely related odd-nosed colobine clade except *Ptilocolobus* and *Procolobus* (Sternner, Raaum, Zhang, Stewart, & Disotell, 2006), we accounted for the phylogenetic structure of the data set. For this purpose, analyses were performed on species means with generalized least squares (GLS) and with phylogenetic generalized least squares (PGLS). For PGLS, data were linked to a supertree of extant mammals (Fritz, Bininda-Emonds, & Purvis, 2009). The phylogenetic signal λ was estimated using maximum likelihood (Revell, 2010). λ can vary between 0 (no phylogenetic signal) and 1 (the observed pattern is predicted by the phylogeny; similarity among species scales in proportion to their shared evolutionary time; Freckleton, Harvey, & Pagel, 2002; Pagel, 1999). GLS and PGLS regression analyses were performed in R ver. 2.15.0 (R-Core-Development-Team, 2011) using the packages *caper* (Orme et al., 2010) and *nlme* (Pinheiro et al., 2011), and the significance level was set to .05, and results of $.05 < p < .10$ are discussed as trends. Due to the nature of the data set, with the majority of colobine species not having been classified with respect to their stomach anatomy (and therefore excluded), the analysis should be considered preliminary until more anatomical data becomes available.

3 | RESULTS

Time spent feeding on fruits/seeds by nine tripartite and five quadripartite species, including 33 and 25 populations, ranged from 0 to 84% (mean = $34.9 \pm$ standard deviation 20.8) and 6 to 50% (mean = 23.6 ± 13.0), respectively (Figure 2a), while the time spent feeding on leaves ranged from 10 to 88% (mean = 54.0 ± 21.4) and 31 to 88% (mean = 64.5 ± 15.6), respectively (Figure 1d). The mean maximum percentage of time devoted to feeding varied between tripartite and quadripartite species from 50.7 ± 17.8 to 37.8 ± 14.8 for fruit/seeds and 53.4

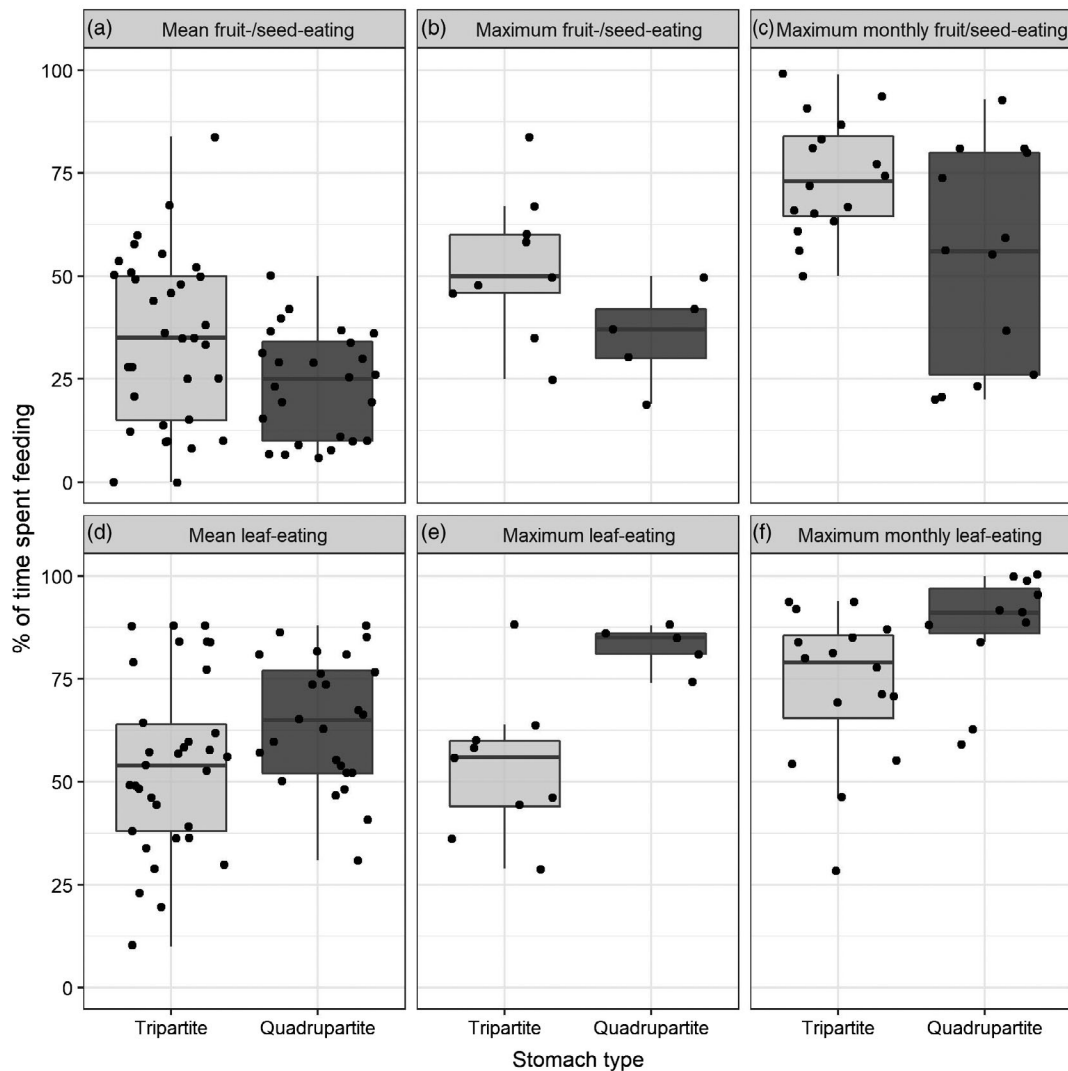


FIGURE 2 Boxplots illustrating dietary variation, with each point representing the percentage of time spent feeding on fruits/seeds (a, b, c) and leaves (d, e, f; of total feeding time) in natural habitats between colobine monkeys, with different forestomach anatomy, being represented by the central line, the extremes of the box representing the upper and lower quartile: Annual % in each population (a, d), maximum annual % within species (b, e) and monthly maximum % in each population (c, f). Species with a tripartite forestomach are *Colobus guereza*, *C. polykomos*, *Semnopithecus entellus*, *Trachypithecus vetulus*, *T. obscurus*, *Presbytis thomasi*, *P. femoralis*, *P. rubicunda*, *P. melalophos*; species with a quadrupartite forestomach are *Ptilocolobus badius* (formerly considered as *Procolobus badius*), *Procolobus verus*, *Rhinopithecus roxellana*, *Pygathrix nemaus*, *Nasalis larvatus*. Data from Table A1 (using all available data, that is, not species averages)

± 17.4 to 82.8 ± 5.54 for leaves, respectively (Figure 1b,e). Furthermore, the mean maximum monthly percentage of time devoted to feeding varied between tripartite and quadrupartite species from 74.1 ± 14.2 to 54.3 ± 26.4 for fruit/seeds and 73.1 ± 18.8 to 87.3 ± 14.0 for leaves, respectively (Figure 1c,f).

In the data set comprising all 14 species listed in the Table A1, the average percentage of fruits/seeds showed a negative relationship with the number of stomach compartments in GLS ($t = -2.687$, $p = 0.020$), with a similar trend in PGLS ($\lambda = 0.00$, $t = -2.065$, $p = .069$). The maximum percentage of fruits/seeds tended toward a significant, negative relationship with the number of stomach compartments in GLS ($t = -1.930$, $p = .078$), without an evident trend in PGLS ($\lambda = 0.00$, $t = -1.665$, $p = .130$). In contrast, the average percentage of leaves

showed a positive relationship in GLS ($t = 2.966$, $p = .012$) as well as in PGLS ($\lambda = 0.37$, $t = 2.524$, $p = .033$). The maximum percentage of leaves also showed a significant, positive relationship in GLS ($t = 3.614$, $p = .004$), indicating that quadrupartite species had a higher maximum percentage of leaves in their diet. This relationship was also significant in PGLS ($\lambda = 0.03$, $t = 2.945$, $p = .016$), indicating that the pattern occurred in parallel, or convergently, in the different colobine lineages. When using the more reduced data set (studies reporting monthly data, with three species less, that is, a total of 11 species only) for data on the maximum percentage of fruits/seeds or leaves on the basis of monthly data, considering the effects of intra-annual variation, there was again a negative relationship with the percentage of fruits/seeds in GLS ($t = -2.424$, $p = .038$) and a corresponding trend in PGLS ($\lambda = 1.00$, $t = -2.027$,

$p = .073$). For the percentage of leaves, however, no significant relationship with the number of stomach compartments could be ascertained in this reduced data set (GLS: $t = 1.586$, $p = .147$; PGLS: $\lambda = 1.00$, $t = 1.380$, $p = .201$).

4 | DISCUSSION

Our results indicate that the extremes of the natural diet might be more important in understanding morphophysiological adaptations than the averages, and the term “fallback food” has been used to explain such patterns (Lambert & Rothman, 2015; Marshall, Boyko, Feilen, Boyko, & Leighton, 2009; Marshall & Wrangham, 2007). Our similar results from both GLS and PGLS analyses, the general patterns of a positive relationship between consumption of leaves and the number of chambers, but a negative relationship with fruits/seeds, suggest that the praesaccus is an adaptation to a dietary niche with a particularly high reliance on leaves as a fallback food in certain colobine clades. A higher reliance on fruits/seeds as foods at times of high fruit availability in clades that do not have a praesaccus suggests that a praesaccus may not be required for this niche. The difference between tripartite and quadripartite stomachs and diet niches apparently evolved in both the African and the Asian colobine lineages, if our small sample is considered representative. However, the scope of the data sets submitted to statistical testing in this study—either 14 or 11 species—is limited. Until the anatomy of a larger number of colobine species has been described, these results must be considered preliminary.

The preliminary findings support the notion that a large gut capacity is an important characteristic by which herbivores survive on a leafy, high fiber diet (Müller et al., 2013), and that it may not be necessary for some species if there are strong seasonal peaks in fruit availability. A logical extension of our results is the prediction that the praesaccus will allow a higher food intake per feeding bout. Female tripartite and quadripartite colobines monkeys may not differ much in body mass (i.e., about <10 kg), though some male quadripartite species are substantially larger than tripartite ones (Table A1). Therefore, gut size relative to body mass might be greater in colobines with quadripartite stomachs, especially in females. This prediction needs to be tested with behavioral observations of colobines with quadripartite and tripartite stomachs. If our prediction is correct, this would suggest that species with a tripartite stomach would be constrained by the fact that they cannot ingest relatively large amounts, which would preclude them from occupying leaf-only niches. There are few examples that properly analyzed the fallback feeding behavior in species with a tripartite stomach, accounting for diet quality, abundance, and preference as recommended by Marshall et al. (2009). Hanya and Bernard (2007) describe young leaves of specific plant species as fallback foods for red leaf monkeys (*Presbytis rubicunda*) at Danum Valley, but they nevertheless rarely represent more than 60% of their diets. A further test of this relationship would involve examining if taxa with quadripartite stomachs are found in regions with a less reliable year-round supply of young leaves or fruits than species with tripartite

stomachs, and whether tripartite species occur in habitats where mature leaves represent the only food source for a certain part of the year.

In captivity, when animals are provided easily digestible diets, such as commercial foods, genera with a quadripartite stomach, such as *Nasalis*, *Pygathrix*, and *Ptilocolobus* (Hollihn, 1973; Matsuda et al., 2018; Struhsaker, 2010), are notoriously difficult to maintain and breed, compared to tripartite species. A potential reason for this could be that the higher intake capacity for species with a quadripartite stomach might be detrimental in the case of highly digestible diets that may lead to malfermentation (Claus & Dierenfeld, 2008). In comparison, species with a tripartite stomach might be less susceptible to extreme bouts of malfermentation when fed highly digestible diets due to a relatively reduced intake capacity.

To date, no physiological data exists that allows speculation on additional functions of the praesaccus. In particular, it is unclear why an additional stomach chamber would be necessary for an increase in capacity, rather than a more voluminous or expandable regular saccus. Unfortunately, the current information on stomach anatomy across colobine species is too limited to further test these predictions with respect to the relevance of the praesaccus with respect to a diet niche. Given our findings, one last prediction can be made. Associated with climate change, the fiber concentration in leaves consumed by colobines has increased and protein content has decreased over the past 30 years (Rothman et al., 2015). This leads to the prediction that tripartite species, possibly with a lower fiber tolerance, would be more vulnerable to climate change than quadripartite species.

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REFERENCES

- Bauchop, T., & Martucci, R. W. (1968). Ruminant-like digestion of the langur monkey. *Science*, 161(3842), 698–700. <https://doi.org/10.1126/science.161.3842.698>
- Bennett, E. L. (1983). *The banded Langur: Ecology of a Colobine in West Malaysian rainforest*. Cambridge, MA: University of Cambridge.
- Bennett, E. L., & Sebastian, A. C. (1988). Social organization and ecology of proboscis monkeys (*Nasalis larvatus*) in mixed coastal forest in

- Sarawak. *International Journal of Primatology*, 9(3), 233–255. <https://doi.org/10.1007/bf02737402>
- Boonratana, R. (1993). *The ecology and behaviour of the proboscis monkey (Nasalis larvatus) in the lower Kinabatangan*. Thailand: Mahidol University.
- Caton, M. J. (1998). The morphology of the gastrointestinal tract of *Pygathrix nemaeus*. In N. G. Jablonski (Ed.), *Natural history of the doucs and snub-nosed monkeys* (pp. 129–149). Singapore: World Scientific.
- Chapman, C. A., & Pavelka, M. S. (2005). Group size in folivorous primates: Ecological constraints and the possible influence of social factors. *Primates*, 46(1), 1–9. <https://doi.org/10.1007/s10329-004-0093-9>
- Chivers, D. J. (1994). Functional anatomy of the gastrointestinal tract. In A. G. Davies & J. F. Oates (Eds.), *Colobine monkeys: Their ecology, behaviour and evolution* (pp. 205–257). Cambridge, UK: Cambridge University Press.
- Chivers, D. J., & Hladik, C. M. (1980). Morphology of the gastrointestinal tract in primates: Comparisons with other mammals in relation to diet. *Journal of Morphology*, 166(3), 337–386. <https://doi.org/10.1002/jmor.1051660306>
- Clauss, M., & Dierenfeld, E. S. (2008). The nutrition of browsers. In M. E. Fowler & R. E. Miller (Eds.), *Zoo and wild animal medicine: Current therapy* (6th ed., pp. 444–454). St. Louis: Saunders Elsevier.
- Curtin, S. H. (1980). Dusky and banded leaf monkeys. In D. J. Chivers (Ed.), *Malayan Forest primates* (pp. 107–146). Boston: Springer.
- Dasilva, G. L. (1994). Diet of *Colobus polykomos* on Tiwai Island: Selection of food in relation to its seasonal abundance and nutritional quality. *International Journal of Primatology*, 15(5), 655–680. <https://doi.org/10.1007/bf02737426>
- Davies, A. G., Bennett, E. L., & Waterman, P. G. (1988). Food selection by two South-east Asian colobine monkeys (*Presbytis rubicunda* and *Presbytis melalophos*) in relation to plant chemistry. *Biological Journal of the Linnean Society*, 34(1), 33–56. <https://doi.org/10.1111/j.1095-8312.1988.tb01947.x>
- Davies, A. G., Oates, J. F., & Dasilva, G. L. (1999). Patterns of Frugivory in three west African Colobine monkeys. *International Journal of Primatology*, 20(3), 327–357. <https://doi.org/10.1023/a:1020596503533>
- Davies, G. (1991). Seed-eating by red leaf monkeys (*Presbytis rubicunda*) in dipterocarp forest of northern borneo. *International Journal of Primatology*, 12(2), 119–144. <https://doi.org/10.1007/bf02547577>
- Dela, J. D. S. (2007). Seasonal food use strategies of *Semnopithecus vetulus nestor*, at Panadura and Piliyandala, Sri Lanka. *International Journal of Primatology*, 28, 607–626.
- Dunbar, R. I. M. (1987). Habitat quality, population dynamics, and group composition in Colobus monkeys (*Colobus guereza*). *International Journal of Primatology*, 8(4), 299–329. <https://doi.org/10.1007/bf02737386>
- Ehlers Smith, D. A., Husson, S. J., Ehlers Smith, Y. C., & Harrison, M. E. (2013). Feeding ecology of red langurs in Sabangau tropical peat-swamp forest, Indonesian Borneo: Extreme granivory in a non-masting forest. *American Journal of Primatology*, 75(8), 848–859. <https://doi.org/10.1002/ajp.22148>
- Fashing, P. J. (2001). Feeding ecology of guerezas in the Kakamega forest, Kenya: The importance of Moraceae fruit in their diet. *International Journal of Primatology*, 22(4), 579–609. <https://doi.org/10.1023/a:1010737601922>
- Fashing, P. J. (2011). African colobine monkeys: Their behavior, ecology, and conservation. In C. J. Campbell, A. Fuentes, K. C. MacKinnon, S. K. Bearder, & R. M. Stumpf (Eds.), *Primates in perspective* (2nd ed., pp. 203–229). Oxford, England: Oxford University Press.
- Freckleton, R. P., Harvey, P. H., & Pagel, M. (2002). Phylogenetic analysis and comparative data: A test and review of evidence. *American Naturalist*, 160(6), 712–726. <https://doi.org/10.1086/343873>
- Fritz, S. A., Bininda-Emonds, O. R., & Purvis, A. (2009). Geographical variation in predictors of mammalian extinction risk: Big is bad, but only in the tropics. *Ecology Letters*, 12(6), 538–549. <https://doi.org/10.1111/j.1461-0248.2009.01307.x>
- Galat-Luong, A., & Galat, G. (2005). Conservation and survival adaptations of Temminck's red Colobus (*Procolobus badius temmincki*), in Senegal. *International Journal of Primatology*, 26(3), 585–603. <https://doi.org/10.1007/s10764-005-4367-x>
- Guo, S., Li, B., & Watanabe, K. (2007). Diet and activity budget of *Rhinopithecus roxellana* in the Qinling Mountains, China. *Primates*, 48(4), 268–276. <https://doi.org/10.1007/s10329-007-0048-z>
- Gurmaya, K. J. (1986). Ecology and behavior of *Presbytis thomasi* in northern Sumatra. *Primates*, 27(2), 151–172. <https://doi.org/10.1007/bf02382595>
- Hanya, G., & Bernard, H. (2012). Fallback foods of red leaf monkeys (*Presbytis rubicunda*) in Danum Valley, Borneo. *International Journal of Primatology*, 33(2), 322–337. <https://doi.org/10.1007/s10764-012-9580-9>
- Harris, T. R., & Chapman, C. A. (2007). Variation in diet and ranging of black and white colobus monkeys in Kibale National Park, Uganda. *Primates*, 48(3), 208–221. <https://doi.org/10.1007/s10329-006-0036-8>
- Hladik, C. M. (1977). A comparative study of two sympatric species of leaf monkeys: *Presbytis entellus* and *Presbytis senex*. In T. H. Clutton-Brock (Ed.), *Primate ecology: Studies of feeding and ranging behaviour in lemurs, monkeys, and apes* (pp. 323–353). London, England: Academic Press.
- Hollih, U. W. E. (1973). Remarks on the breeding and maintenance of Colobus monkeys *Colobus guereza*, proboscis monkeys *Nasalis larvatus* and douc langurs *Pygathrix nemaeus* in zoos. *International Zoo Yearbook*, 13(1), 185–188. <https://doi.org/10.1111/j.1748-1090.1973.tb02146.x>
- Hou, R., He, S., Wu, F., Chapman, C. A., Pan, R., Garber, P. A., ... Li, B. (2018). Seasonal variation in diet and nutrition of the northernmost population of *Rhinopithecus roxellana*. *American Journal of Primatology*, 80(4), e22755. <https://doi.org/10.1002/ajp.22755>
- Kirkpatrick, R. C. (2011). The Asian colobines: Diversity among leaf-eating monkeys. In C. J. Campbell, A. Fuentes, K. C. MacKinnon, S. K. Bearder, & R. M. Stumpf (Eds.), *Primates in perspective* (2nd ed., pp. 189–202). Oxford, England: Oxford University Press.
- Korstjens, A. H., Bergmann, K., Deffernez, C., Krebs, M., Nijssen, E., van Oirschot, B., ... Schippers, E. P. (2007). How small-scale differences in food competition lead to different social systems in three closely related sympatric colobines. In W. S. McGraw, K. Zuberbühler, & R. Noë (Eds.), *Monkeys of the Tai Forest: An African primate community*. Cambridge, MA: Cambridge University Press.
- Lambert, J. E., & Rothman, J. M. (2015). Fallback foods, optimal diets, and nutritional targets: Primate responses to varying food availability and quality. *Annual Review of Anthropology*, 44(1), 493–512. <https://doi.org/10.1146/annurev-anthro-102313-025928>
- Langer, P. (1988). *The mammalian herbivore stomach*. Stuttgart, Germany: Gustav Fischer Verlag.
- Langer, P. (2017). *Comparative anatomy of the gastrointestinal tract in Eutheria: Taxonomy, biogeography and food*. Berlin, Germany: De Gruyter.
- Liu, X., Stanford, C. B., Yang, J., Yao, H., & Li, Y. (2013). Foods eaten by the Sichuan snub-nosed monkey (*Rhinopithecus roxellana*) in Shennongjia National Nature Reserve, China, in relation to nutritional chemistry. *American Journal of Primatology*, 75(8), 860–871. <https://doi.org/10.1002/ajp.22149>
- Marshall, A. J., Boyko, C. M., Feilen, K. L., Boyko, R. H., & Leighton, M. (2009). Defining fallback foods and assessing their importance in primate ecology and evolution. *American Journal of Physical Anthropology*, 140(4), 603–614. <https://doi.org/10.1002/ajpa.21082>
- Marshall, A. J., & Wrangham, R. W. (2007). Evolutionary consequences of fallback foods. *International Journal of Primatology*, 28(6), 1219–1235. <https://doi.org/10.1007/s10764-007-9218-5>
- Matsuda, I., Bernard, H., Tuuga, A., Nathan, S. K. S., Sha, J. C. M., Osman, I., ... Clauss, M. (2018). Fecal nutrients suggest diets of higher fiber levels in free-ranging than in captive proboscis monkeys (*Nasalis larvatus*). *Frontiers in Veterinary Science*, 4, 246. <https://doi.org/10.3389/fvets.2017.00246>
- Matsuda, I., Tuuga, A., & Higashi, S. (2009). The feeding ecology and activity budget of proboscis monkeys. *American Journal of Primatology*, 71(6), 478–492. <https://doi.org/10.1002/ajp.20677>

- Megantara, E. N. (1989). Ecology, behavior and sociality of *Presbytis femoralis* in east Central Sumatra. *Comparative Primatology Monographs*, 2, 171–301.
- Mittermeier, R. A., Rylands, A. B., & Wilson, D. E. (2013). *Handbook of the mammals of the world* (Vol. 3). Barcelona, Spain: Lynx Edicions.
- Müller, D. W., Codron, D., Meloro, C., Munn, A., Schwarm, A., Hummel, J., & Clauss, M. (2013). Assessing the Jarman-Bell Principle: Scaling of intake, digestibility, retention time and gut fill with body mass in mammalian herbivores. *Comparative Biochemistry and Physiology. Part A, Molecular & Integrative Physiology*, 164(1), 129–140. <https://doi.org/10.1016/j.cbpa.2012.09.018>
- Newton, P. (1992). Feeding and ranging patterns of forest hanuman langurs (*Presbytis entellus*). *International Journal of Primatology*, 13(3), 245–285. <https://doi.org/10.1007/bf02547816>
- Oates, J. F. (1977). The Guereza and its food. In T. H. Clutton-Brock (Ed.), *Primate ecology: Studies of feeding and ranging behaviour in lemurs, monkeys and apes* (pp. 276–319). New York, NY: Academic Press.
- Oates, J. F. (1988). The diet of the olive colobus monkey, *Procolobus verus*, in Sierra Leone. *International Journal of Primatology*, 9(5), 457–478. <https://doi.org/10.1007/bf02736220>
- Oates, J. F. (1994). The natural history of African colobines. In A. G. Davies & J. F. Oates (Eds.), *Colobine monkeys: Their ecology, behaviour and evolution* (pp. 75–129). New York, NY: Cambridge University Press.
- Orme, D., Freckleton, R., Thomas, G., Petzoldt, T., Fritz, S., & Isaac, N. (2010). Caper: Comparative analyses of phylogenetics and evolution in R. R package version 0.4/r71. Retrieved from <http://caper.r-forge.r-project.org/>
- Pagel, M. (1999). Inferring the historical patterns of biological evolution. *Nature*, 401(6756), 877–884. <https://doi.org/10.1038/44766>
- Pham, N. (1993). First results of the diet of the red-shanked douc langur, *Pygathrix nemaeus*. *Australian Primatology*, 8, 5–6.
- Pham, N. (1994). Preliminary results on the diet of the red-shanked douc langur (*Pygathrix nemaeus*). *Asian Primates Journal*, 4, 9–11.
- Phiapalath, P., Borries, C., & Suwanwaree, P. (2011). Seasonality of group size, feeding, and breeding in wild red-shanked douc langurs (Lao PDR). *American Journal of Primatology*, 73(11), 1134–1144. <https://doi.org/10.1002/ajp.20980>
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & R Development Core Team. (2011). nlme: Linear and nonlinear mixed effects models. *R Package Version*, 3, 1–102 Retrieved from <https://cran.r-project.org/web/packages/nlme/>
- Plumptre, A. J. (2006). The diets, preferences, and overlap of the primate community in the Budongo Forest Reserve, Uganda. In N. Newton-Fisher, H. Notman, J. Paterson, & V. Reynolds (Eds.), *Primates of Western Uganda* (pp. 345–371). New York, NY: Springer.
- R Core Development Team. (2011). *R: A language and environment for statistical computing*. Vienna, Austria: Foundation for Statistical Computing Retrieved from <https://www.R-project.org/>
- Revell, L. J. (2010). Phylogenetic signal and linear regression on species data. *Methods in Ecology and Evolution*, 1(4), 319–329. <https://doi.org/10.1111/j.2041-210X.2010.00044.x>
- Rothman, J. M., Chapman, C. A., Struhsaker, T. T., Raubenheimer, D., Twinomugisha, D., & Waterman, P. G. (2015). Long-term declines in nutritional quality of tropical leaves. *Ecology*, 96(3), 873–878. <https://doi.org/10.1890/14-0391.1>
- Sayers, K., & Norconk, M. A. (2008). Himalayan *Semnopithecus entellus* at Langtang National Park, Nepal: Diet, activity patterns, and resources. *International Journal of Primatology*, 29, 509–530.
- Sterck, E. H. M. (2012). The behavioral ecology of Colobine monkeys. In J. C. Mitani, J. Call, P. M. Kappeler, R. A. Palombit, & J. B. Silk (Eds.), *The evolution of primate societies* (pp. 65–90). Chicago, IL: The University of Chicago Press.
- Sterner, K. N., Raaum, R. L., Zhang, Y. P., Stewart, C. B., & Disotell, T. R. (2006). Mitochondrial data support an odd-nosed colobine clade. *Molecular Phylogenetics and Evolution*, 40(1), 1–7. <https://doi.org/10.1016/j.ympev.2006.01.017>
- Struhsaker, T. T. (2010). *The red Colobus monkeys: Variation in demography, behavior, and ecology of endangered species*. New York, NY: Oxford University Press.
- Supriatna, J., Manullang, B. O., & Soekara, E. (1986). Group composition, home range, and diet of the maroon leaf monkey (*Presbytis rubicunda*) at Tanjung Puting Reserve, Central Kalimantan, Indonesia. *Primates*, 27, 185–190.
- Ulibarri, L. (2013). *The socioecology of red-shanked doucs (Pygathrix nemaeus) in son Tra nature reserve, Vietnam*. Colorado: University of Colorado.
- Wachter, B., Schabel, M., & Noë, R. (1997). Diet overlap and polyspecific associations of red Colobus and Diana monkeys in the Tai National Park, Ivory Coast. *Ethology*, 103(6), 514–526. <https://doi.org/10.1111/j.1439-0310.1997.tb00164.x>
- Wasserman, M. D., & Chapman, C. A. (2003). Determinants of colobine monkey abundance: The importance of food energy, protein and fibre content. *Journal of Animal Ecology*, 72(4), 650–659. <https://doi.org/10.1046/j.1365-2656.2003.00736.x>
- Wright, B. W., Prodhon, R., Wright, K., & Nadler, T. (2008). Mandibular morphology as it relates to ingestive and digestive folivory in *Trachypithecus* and *Pygathrix*. *Vietnamese Journal of Primatology*, 2, 25–32.
- Yeager, C. P. (1989). Feeding ecology of the proboscis monkey (*Nasalis larvatus*). *International Journal of Primatology*, 10(6), 497–530. <https://doi.org/10.1007/bf02739363>
- Yiming, L. (2006). Seasonal variation of diet and food availability in a group of Sichuan snub-nosed monkeys in Shennongjia Nature Reserve, China. *American Journal of Primatology*, 68(3), 217–233. <https://doi.org/10.1002/ajp.20220>
- Zhao, H., Dang, G., Wang, C., Wang, X., Guo, D., Luo, X., ... Li, B. (2015). Diet and seasonal changes in Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*) in the southern Qinling mountains in China. *Acta Theriologica Sinica*, 35(2), 130–137.

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TABLE A1 Variation in the percentage of natural dietary components (per observed feeding time) in 13 colobine species known forestomach type (i.e., tripartite or quadripartite)

Forestomach type	Species	Body mass (male/female) ^a	Mature leaf	Young leaf	Total leaf/lichen ^b	Max seasonal leaf %	Seed + fruit	Max seasonal fruit %	Flower	Others	References
Tripartite	<i>Colobus guereza</i>	8–13.5/5.5–10.2			54	81	28	56	1		Dunbar (1987)
			20	33	53	71	46	77	8	3	Plumptre (2006)
			25	37	62	94	38	61	9	4	Plumptre (2006)
			4	30	58	-	25	-	3	15	Fashing (2011)
			5	24	48	69	44	81	1	7	Fashing (2001)
			9	23	57	80	33	67	0	9	Fashing (2001)
			6	78	84	-	10	-	0	1	Wasserman and Chapman (2003)
			14	65	79	-	12	-	6	2	Wasserman and Chapman (2003)
			12	62	77	-	14	-	2	8	Oates (1977)
			5	78	84	-	10	-	3	3	Wasserman and Chapman (2003)
			4	84	88	-	0	-	2	1	Wasserman and Chapman (2003)
			4	84	88	-	0	-	2	9	Chapman and Pavelka (2005)
			6	78	84	-	10	-	0	2	Chapman and Pavelka (2005)
23	60	88	94	8	-	2	3	Harris and Chapman (2007)			
Tripartite	<i>Colobus polykomos</i>	6.6–10/6.7–8.3	20	28	49	92	48	83	3	1	Fashing (2011); Korstjens et al. (2007)
			26	30	56	-	35	63	2	6	Dasilva (1994); Davies, Oates, and Dasilva (1999)
Tripartite	<i>Semnopithecus entellus</i>	16.9–19.5/9.5–16.1	25	10	57	78	21	50	7	15	Sayers and Norconk (2008)
			40	8	64	-	15	-	6	15	Sterck (2012)
			35	4	49	84	25	72	10	16	Newton (1992)
Tripartite	<i>Semnopithecus (Trachypithecus) vetulus</i>	3.4–9.4/3.8–9.3	40	20	60	87	28	66	12	-	Hladik (1977)
			8	22	30	46	54	65	8	8	Dela (2007)

(Continues)

TABLE A1 (Continued)

Forestomach type	Species	Body mass (male/female) ^a	Mature leaf	Young leaf	Total leaf/lichen ^b	Max seasonal leaf %	Seed + fruit	Max seasonal fruit %	Flower	Others	References
Tripartite	<i>Trachypithecus obscurus</i>	6.1–9.1/5.0–8.6	4	17	20	54	60	74	4	16	Dela (2007) Curtin (1980)
Tripartite	<i>Presbytis thomasi</i>	7.0–8.0 (no sexual dimorphism in size)	22	36	58	-	35	-	7	3	Gurmaya (1986)
Tripartite	<i>Presbytis femoralis</i>	5.9–8.2 (sexual dimorphism in size is unknown)	3	26	29	-	58	-	<1	13	Megantara (1989)
Tripartite	<i>Presbytis rubicunda</i>	6–7/5.5–6	1	37	38	71	49	87	11	11	Davies (1991) Supriatna, Manullang, and Soekara (1986) Hanya and Bernard (2012) Ehlers Smith, Husson, Ehlers Smith, and Harrison (2013)
Tripartite	<i>Presbytis melalophos</i>	5.9–9.0/5.2–8.9	8	28	36	55	50	94	12	3	Bennett (1983); Davies, Bennett, and Waterman (1988)
Quadripartite	<i>Ptilocolobus badius</i> ^c	9–12.5/6.0–9.0	12	35	47	42	42	9	9	3	Fashing (2011) Oates (1994) Galat-Luong and Galat (2005) Galat-Luong and Galat (2005) Wachter, Schabel, and Noë (1997) Fashing (2011); Korstjens et al. (2007) Davies et al. (1999) Waterman and Chapman (2003)
			7	42	48	-	36	-	9	7	
			6	70	76	-	19	-	1	4	
			20	45	65	-	10	-	14	11	
			7	24	31	-	37	-	30	2	
			4	46	50	63	29	59	20	1	
			20	32	52	-	31	23	16	1	
			6	76	81	-	7	-	4	8	

(Continues)

TABLE A1 (Continued)

Forestomach type	Species	Body mass (male/female) ^a	Mature leaf	Young leaf	Total leaf/lichen ^b	Max seasonal leaf %	Seed + fruit	Max seasonal fruit %	Flower	Others	References
			13	64	77	-	9	-	1	13	Wasserman and Chapman (2003)
			22	60	82	-	7	-	2	8	Wasserman and Chapman (2003)
			7	79	86	-	6	-	2	9	Wasserman and Chapman (2003)
Quadripartite	<i>Procolobus verus</i>	4.0–5.7/3.0–4.2	1	83	85	95	8	21	4	3	Fashing (2011); Korstjens et al. (2007)
Quadripartite	<i>Rhinopithecus roxellana</i>	15–19/6–10	11	59	74	-	19	20	7		Davies et al. (1999); Oates (1988)
				4	57	84 ^d	29	74 ^d	11	13	Guo, Li, and Watanabe (2007)
			17	36	54	59 ^d	23	37 ^d	2	21	Hou et al. (2018)
			11	9	60	99	25	93		15	Zhao et al. (2015)
			4	34	81	100	15	81	1	3	Yiming (2006)
			9	19	67	-	30	-	1	1	Liu, Stanford, Yang, Yao, and Li (2013)
Quadripartite	<i>Pygathrix nemaeus</i>	8–11.6/6.0–8.0	28	60	88	100	10	55	1.5	0.5	Ulibarri (2013)
					63		37				Pham (1993, 1994)
					55	88	34	80	4	8	Phiapalath, Borries, and Suwanwaree (2011)
Quadripartite	<i>Nasalis larvatus</i>	20–24/10	0	73	74	91	11	26	8	8	Boonratana (1993)
			0	66	66	92	26	56	8	1	Matsuda, Tuuga, and Higashi (2009)
			3	38	41	-	50	-	3	6	Bennett and Sebastian (1988)
			10	42	52	89	40	81	3	5	Yeager (1989)

^aBody mass from Mittermeier, Rylands, and Wilson (2013).^bCombining the value of mature, young, and unknown leaves and lichen.^cPreviously considered as *Procolobus badius*.^dMaximum values among four seasons.