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A short note on extractive foraging behavior in gray snub-nosed monkeys

Zuofu XIANG,^{1,2} Wenbin LIANG,¹ Shuaiguo NIE¹ and Ming LI²

¹College of Life Science and Technology, Central South University of Forestry and Technology, Changsha, Hunan, China and ²Key Lab of Animal Ecology and Conservation Biology, Institute of Zoology, Chinese Academy of Sciences, Beijing, China

Abstract

Extractive foraging (EF) involves the exploitation of hidden or embedded foods, generally any food that is not visible to the naked eye. Therefore, EF is particularly important for survival in marginal habitats as it provides seasonal fallback foods in low food availability seasons. Although many studies consider primates' EF behavior and category, colobine species are usually categorized as non-extractive foragers and few studies quantitatively examine their EF behavior. In this study, we examined the EF behavior of one colobine species, the gray snub-nosed monkey (*Rhinopithecus brelichi*), at Yangaoping in Fanjingshan National Nature Reserve, Guizhou. We recorded 6 categories of EF behaviors. The most frequently sought-out foods were seeds, young bamboo and invertebrates. Extracted foods accounted for an average of 26.02% of feeding records. As the monkey engages in little EF behavior in the winter when the food availability is low, these results seem to do not support the hypothesis that EF serves to secure additional resources during lean times in marginal or seasonal habitats. According to these findings, we suggest *R. brelich* should be considered as an extractive forager. Our study also highlights the need for increased representation of colobines in the EF literature to better inform the discussion concerning its link to primate brain evolution.

Key words: extractive foraging, foraging behavior, primate intelligence, *Rhinopithecus brelichi*, snub-nosed monkey

INTRODUCTION

Extractive foraging (EF) involves the exploitation of hidden or embedded foods: generally any food that is not visible to the naked eye. Gibson (1986, p. 99) provides a helpful definition with examples:

Correspondence: Ming Li, Key laboratory of Animal Ecology and Conservation Biology, Institute of Zoology, Chinese Academy of Sciences, 1 Beichen West Road, Chaoyang, Beijing 100101, China. Email: lim@ioz.ac.cn Extractive foraging means feeding on foods that must first be removed from other matrices in which they are embedded or encased. Extractive foods include nut-meat, shellfish, snails, eggs, brains or bone marrow which must be removed from hard outer coverings, seeds and beans that must be removed from pods, tubers or roots that must be dug from the ground, ants and termites that must be removed from mounds or hills, insect larvae or pith that must be extracted from bark, and meat that is extracted from its hide prior to ingestion.

Extractive foraging behavior is particularly important for survival in marginal habitats as it provides seasonal fallback foods in low food availability seasons (Gibson 1986). Although many studies have concerned on the EF behavior of certain primate species and they are classified into 4 categories of EF ability (Gibson 1986), colobines are typically considered non-extractive foragers (Dunbar 1995). However, van Schaik *et al.* (1999) question this conclusion, highlighting the lack of studies quantitatively involve EF in any colobine species.

The gray or Guizhou snub-nosed monkey [Rhinopithecus brelichi (Thomas, 1903)] (Colobinae) is categorized as an endangered species by the World Conservation Union (IUCN 2010) and is listed as a Category I species under the Chinese Wild Animal Protection Law. Currently, R. brelichi is restricted to approximately 750 individuals living in a small region in the Mount Fanjing area in northwestern Guizhou, China (Xiang et al. 2009). The monkeys have a varied diet across the year, with flowers and young leaves in spring, young leaves and unripe seeds/fruits in summer, ripe seeds/fruits in autumn, and mature leaves and buds in winter. Its diet composition is 15.3% buds, 25.5% young leaves, 21.8% mature leaves, 9.4% flowers, 21.6% fruits/seeds and 6.3% other items (Xiang et al. 2012). Here, we quantitatively describe EF behavior in R. brelichi, a species adapted to extreme temporal variation in food availability, to bolster the data on the foraging techniques of colobines. We also test whether there is high EF behavior during the low food availability season, as EF is theorized to be particularly important for survival in marginal habitats (Gibson 1986).

MATERIALS AND METHODS

Study sites and animals

We conducted our study at Yangaoping (27°58'N, $108^{\circ}45'E$), an area that covers approximately $10-12 \text{ km}^2$ of temperate forest in the Fanjingshan National Nature Reserve, northeast of Guizhou. There are striking altitudinal changes in the vegetation, with subtropical broad leaf evergreen forest at low elevations and fir, hemlock and giant rhododendrons on the peaks (Zhu & Yang 1990). Only 2 distinct forest types appear within the study area (Xiang et al. 2010): (i) evergreen broadleaf forest (900-1300 m asl), in which the dominant species are Castanopsis spp., Asian oaks (Cyclobalanopsis spp.) and Lithocarpus spp. and (ii) evergreen-deciduous broadleaf forest (1300-2000 m asl), in which the dominant species are Fagus spp., Eurya spp. and Schima spp. Dwarf bamboo (Sinarundinaria spp.), at densities that can reach 1×10⁶/ha (Zhu & Yang 1990), forms a dense and nearly impenetrable ground cover in many areas.

The study animals form a fission-fusion band of approximately 450 individuals during spring, summer and early autumn (Xiang *et al.* 2009), splitting into 4 identified groups varying in size from 50 to 200 individuals in late autumn and winter (Nie *et al.* 2009). Due to difficult terrain and inclement weather, we observed the monkeys from 13 fixed observation sites within the Yangaoping area (Xiang *et al.* 2010). Therefore, the study subjects are also varied across the year (mean = 10.3, SD = 6.2, range = 1–38).

Data collection

We collected data on EF behavior by following the Yangaoping group from Jan 2006 to Jul 2008. We conducted instantaneous scan sampling (Altman 1974) at 15 min intervals. Individual feeding behavior was observed by SFS, scanning from either 1 of the 13 fixed stations with a field scope (APO-TELEVID 77, 20-60X) at distances between 50 and 1000 m (Xiang et al. 2010), or by AOB, approaching within approximately 15-50 m of the animals and observing them with or without binoculars (Xiang et al. 2012). At the beginning of each 15 min interval, the activity state (i.e. feed, travel, rest, groom, play or socialize) was recorded for each visible individual at the moment of detection. Once we spotted an individual processing a food item, we attempted to identify both the species and the food category. Then, food was sorted into extracted and non-extracted items (Tomasello & Call 1997). In our categorization scheme, extracted and non-extracted foods are mutually exclusive, with a given food type always falling into just 1 of the 2 groups. The 'extracted' food items were further subdivided according to the mode of Savers (2008): (i) removing the casing of a plant (e.g. peeling bamboo); (ii) excavation (i.e. digging or surface scratching); (iii) prying or picking (as in removing bark to reach objects underneath); and (iv) searching under obstacles (e.g. probing under or overturning rocks).

Temporal variation in food abundance was estimated by phenological sampling conducted via six 50×20 m quadrats at 1800 m asl (for details, see Xiang *et al.* 2012).

Data analysis

We used Spearman correlations to identify the relationship between EF in gray snub-nosed monkeys and the abundance or consumption frequency of types of plant parts. Plant part classes include evergreen mature leaves, deciduous young and mature leaves, leaf buds, unripe and ripe fruits, and flowers. The level of EF was measured as the percentage of individuals consuming extracted foods over all feeding records.

RESULTS

Frequency and category of extractive

foraging in snub-nosed monkeys

From Jan 2006 to Jul 2008, we were able to detect the monkeys for 682.5 h and directly observed them for 209.5 h, of which 21.5 h were AOB. We obtained a total of 1586 feeding records, 412 (26.02%) of which involved 'extracted' food items, such as seeds, bamboo, underground storage organs and invertebrates (Table 1). Feeding records with EF behavior observed within SFS and AOB are 311 and 101, respectively (Table 1).

The most frequent targets of extractive efforts were seeds (21.6% of overall diet and 83.01% of the EF records), invertebrates (2.03% of overall diet and 7.77% of the EF records) and young bamboo shoots (1.93% of overall diet and 7.52% of the EF records); underground storage organs were rarely utilized (Table 1 and Fig. 1). Monkeys were observed to forage on invertebrates throughout the year by overturning stones or decayed wood. The monkeys were never seen to use tools in the context of foraging.

Gray snub-nosed monkeys utilized 6 specific extractive actions, divided here into 4 general categories (Table 1):

1. *Removing plant casings*. The seeds of *Bothrocaryum controversum* (Cornaceae) and *Cyclobalanopsis, Quercus* (Fagaceae) were exposed using hands and teeth. Bamboo was processed by peeling the sheath.

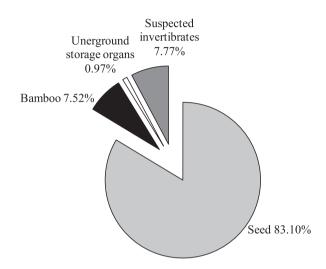


Figure 1 Percentage contribution of food types to extractive foraging in Mount Fanjing National Nature Reserve, China.

Table 1 Categories and frequencies of extractive foraging of scanning with a field scope (SFS) and approach the monkey group and observe with or without binoculars (AOB) for gray snub-nosed monkey (*Rhinopithecus brelichi*) in Mount Fanjing Natural Nature Reserve, China

Category	Action(s)	Target	Season(s)	Frequencies			%
				SFS	AOB	Total	_
Removing plant cover	Casing or peeling seed cover	Seeds	Summer, Autumn	301	41	342	21.60
	Stripping husk	Young bamboo	Autumn	0	31	31	1.93
Excavation	Digging	USOs	Winter	0	4	4	0.28
	Surface scratching	Soft USOs	Winter	0	3	3	0.18
Prying and picking	Removing bark and dead wood	Suspected invertebrates	Yearly	10	9	19	1.20
Searching under obstacles	Probing under or turning over rocks	Suspected invertebrates	Yearly	0	13	13	0.83
			Total	311	101	412	26.02

USOs, underground storage organs. SFS, scanning with a field scope. AOB, approach the monkey group and observe with or without binoculars.

	Extractive foraging	Removing plant casings	Prying and picking
Evergreen mature leaf			
Abundance	0.417	0.103	-0.159
Consumption	0.662*	0.726**	0.828**
Deciduous mature leaf			
Abundance	0.005	0.239	-0.782**
Consumption	0.622*	0.732**	-0.342
Deciduous young leaf			
Abundance	-0.569	-0.317	-0.799**
Consumption	-0.656*	-0.812**	-0.847**
Bud			
Abundance	-0.571	-0.755**	0.375
Consumption	-0.621*	-0.815**	0.350
Ripe fruit			
Abundance	0.739**	0.775**	0.133
Consumption	0.756**	0.797**	0.134
Unripe fruit			
Abundance	-0.357	-0.146	-0.810**
Consumption	0.244	0.338	-0.434
Flower			
Abundance	-0.721**	-0.500	-0.681*
Consumption	-0.706*	-0.454	-0.777**

Table 2 Correlations between extractive foraging and phenology scores. Spearman rank correlation coefficients between extractive foraging, seed consumption and excavation with the abundance and consumption of plant part groups (N = 12)

*Indicates P < 0.05; ** indicates P < 0.01.

Leaves of young *Fargesia spathacea*, *Indocalamus tessellates* and *Phyllostachys sulphurea* (Gramineae) were accessed with teeth and/or hands.

- 2. *Excavation*. Underground organs from herbaceous plants or woody roots were dug up, pulled out, and either twisted out entirely and eaten by hand.
- 3. *Prying and picking*. Individuals (typically adults) were observed handling bark and dead wood and eating substances within. The food items sought in these cases were most likely invertebrates (Xiang *et al.* 2012).
- 4. Searching under obstacles. Monkeys uncovered invertebrates to consume by overturning wood, stones

and other debris. EF behavior appears to be a yearround phenomenon, but different types of EF behavior occur in different seasons, based on food availability. There is less EF frequency in winter than in other seasons.

Correlations between plant part abundance/ consumption and extractive foraging in gray snub-nosed monkeys

Correlations between EF and plant part abundance and consumption suggest seasonal trends in the types of EF behaviors displayed by the monkeys (Table 2).

The overall frequency of EF was not related to total vegetation abundance. It displayed a negative relationship with deciduous young leaf consumption $(r_s = -0.656, n = 12, P < 0.05)$, bud consumption $(r_s = -0.621, n = 12, P < 0.05)$, and the abundance $(r_s = -0.721, n = 12, P < 0.01)$ and consumption of flowers ($r_s = -0.706$, n = 12, P < 0.05). EF was positively correlated with the consumption of ripe fruits $(r_s = 0.739, n = 12, P < 0.01)$ and mature leaves $(r_s = 0.756, P < 0.01)$ n = 12, P < 0.01). Removal of plant casings was negatively correlated with deciduous young leaf consumption $(r_s = -0.812, n = 12, P < 0.01)$ and bud consumption $(r_s = -0.815, n = 12, P < 0.01)$, and positively correlated with ripe fruit abundance $(r_s = 0.755, n = 12,$ P < 0.05), ripe fruit consumption ($r_s = 0.797$, n = 12, P < 0.01) and the consumption of mature leaves (evergreen mature leaves: $r_s = -0.656$, n = 12, P < 0.05; deciduous mature leaves: $r_s = 0.732$, n = 12, P < 0.01). Prying and picking was negatively correlated with the abundance $(r_s = -0.799, n = 12, P < 0.01)$ and consumption of deciduous young leaves ($r_s = -0.847$, n = 12, P < 0.01), the abundance ($r_s = -0.681, n = 12$, P < 0.05) and consumption ($r_s = -0.777$, n = 12, P < 0.05) of flowers, and the abundance of unripe fruit $(r_s = -0.810, n = 12, P < 0.01)$. Prying and picking exhibited a positive relationship with consumption of mature evergreen leaves ($r_s = 0.828$, n = 12, P < 0.01).

DISCUSSION

Here we have provided preliminary data on EF behavior in a poorly known and endangered colobine species. We acknowledge that the EF behavior of *R. brelichi* remains incomplete, given the difficulties in directly observing groups in dense fog (Xiang *et al.* 2012). Our results show that gray snub-nosed monkeys at Yangaoping in Guizou engage in several types of extractive feeding. For example, the monkeys obtain seeds from acorns and peel off the bamboo leaf sheaths of young shoots. Monkeys dig up underground organs and other food, and find invertebrates in decaved wood and under rocks. According to the study results, EF behavior appears to be a year-round phenomenon. However, different types of EF behavior occur in different seasons, based on food availability. When seed-fruit is abundant, seed-eating occurs opportunistically on favored species. Excavation is uncommon during periods of high food availability of young leaves, buds and flowers. However, the monkey exhibits little EF behavior in the winter when the food availability is low (Xiang et al. 2012). Therefore, these results do not support the hypothesis that EF serves to secure additional resources during lean times in marginal or seasonal habitats (Gibson 1986). Our data are consistent with the recent findings on several types of EF behavior in Rhinopithecus spp. (R. bieti: Xiang et al. 2007, Xiang & Grueter 2007, Ren et al. 2010; R. roxellana: Li et al. 2010).

Seed is the most common EF food item, and represents 15% of the colobine diet (Sayers 2008). Seed consumption ranges from less than 1% of the diet in R. bieti (Xiang et al. 2007) to 51%, on average, in Colobus satanas Waterhouse, 1838 (Harrison 1986; Fleury & Gautier-Hion 1999). The second common EF food item could be considered hidden items, such as pith is the most common (Procolobus badius (Kerr, 1792) [Were 2000]; Procolobus kirkii [Siex 2003]: Colobus polykomos (Zimmermann, 1780) [Dasilva 1994]; C. satanas [Fleury & Gautier-Hion 1999]; Semnopithecus entellus (Dufresne, 1797) [Chalise 1995; Schülke et al. 2006; Savers & Norconk 2008]), followed by presumed or identified invertebrates (Procolobus badius (Kerr, 1792) [Struhsaker 1975]; S. entellus [Sayers & Norconk 2008]; R. bieti [Xiang et al. 2007]) and underground storage organs (S. entellus [Curtin 1975; Sayers & Norconk 2008]). Other extracted foods include soil located under the organic layer, peeled fruits, gum, vertebrate flesh and eggs (Sayers 2008). In light of this information, we recommend that some colobine monkeys should be classified as extractive foragers.

According to the extractive foraging hypothesis (Parker & Gibson 1977), more complicated extractive feeding will lead to larger brain size of primates or increase their complexity, and EF has been driving primate brain evolution. Therefore, we should also consider the colobines as extractive foragers when we use the EF hypothesis as an explanation for primate brain evolution. Our results indicate that a reevaluation of studies testing the putative relationship between EF and brain development may be prudent, and that more quantitative accounting of EF is necessary in primate field studies (King 1986; van Schaik *et al.* 1999). Although data is sparse, it is likely that most primates engage in EF at least occasionally, and that the complexity of such actions in many species has been underestimated. Therefore, similar work on other species, particularly from data-deficient clades, should be encouraged in the future.

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REFERENCES

- Altman J (1974). Observational study of behavior: sampling methods. *Behaviour* **49**, 227–67.
- Chalise MK (1995). Comparative study of feeding ecology and behaviour of male and female langurs (*Presbytis entellus*) (PhD dissertation). Tribhuvan University, Kathmandu.
- Curtin RA (1975). The socioecology of the common langur, *Presbytis entellus*, in the Nepal Himalaya (PhD dissertation). University of California, Berkeley, Berkeley.
- Dasilva GL (1994). Diet of *Colobus polykomos* on Tiwai Island: selection of food in relation to its seasonal abundance and nutritional quality. *International Journal Primatology* **15**, 655–80.
- Dunbar RIM (1995). Neocortex size and group size in primates: a test of the hypothesis. *Journal of Human Evolution* **28**, 287–96.
- Fleury MC, Gautier-Hion A (1999). Seminomadic ranging in a population of black colobus (*Colobus sata*nas) in Gabon and its ecological correlates. *International Journal of Primatology* **20**, 491–509.

- Gibson K (1986). Cognition, brain size and the extraction of embedded food resources. In: Else JG, Lee PC, eds, *Primate Ontogeny, Cognition and Social Behavior*. Cambridge University Press, Cambridge, pp. 93–103.
- Harrison M (1986). Feeding ecology of black colobus, *Colobus satanas*, in central Gabon. In: Else JG, Lee PC, eds, *Primate Ontogeny, Cognition and Social Behavior*. Cambridge University Press, Cambridge, pp. 31–7.
- IUCN (2010). IUCN Red List of Threatened Species. IUCN, Gland, Switzerland & Cambridge, UK. [Cited 20 Feb 2011.] Available from URL: http://www.iucnredlist.org
- King BJ (1986). Extractive foraging and the evolution of primate intelligence. *Human Evolution* **1**, 361–72.
- Li YK, Jiang ZG, Li CW, Grueter CC (2010). Effects of seasonal folivory and frugivory on ranging patterns in *Rhinopithecus roxellana*. *International Journal of Primatology* **31**, 609–26.
- Nie S, Xiang Z, Li M (2009). Preliminary report on the diet and social structure of gray snub-nosed monkeys (*Rhinopithecus brelichi*) at Yangaoping, Guizhou, China. *Acta Theriologica Sinica* **29**, 326–31.
- Parker ST, Gibson KR (1977). Object manipulation, tool use and sensorimotor intelligence as feeding adaptations in Cebus monkeys and great apes. *Journal of Human Evolution* **6**, 623–41.
- Ren B, Li D, Liu Z, Li B, Wei F, Li M (2010). First evidence of prey capture and meat eating by wild Yunnan snub-nosed monkeys *Rhinopithecus bieti* in Yunnan. *Current Zoology* **56**, 227–31.
- Sayers K, Norconk M (2008). Himalayan Semnopithecus entellus at Langtang National Park. Nepal: diet, activity patterns, and resources. International Journal of Primatology 29, 509–30.
- Sayers KA (2008). Optimal foraging on the roof of the world: a field study of Himalayan langurs (PhD dissertation). Kent State University, Kent, OH.
- Schülke O, Chalise M, Koenig A (2006). The importance of ingestion rates for estimating food quality and energy intake. *American Journal Primatology* 68, 951–65.

- Siex KS (2003). Effects of population compression on the demography, ecology, and behavior of the Zanzibar red colobus monkey (*Procolobus kirkii*) (PhD dissertation). Duke University, Durham.
- Struhsaker, TT (1975). *The Red Colobus Monkey*. University of Chicago Press, Chicago.
- Tomasello M, Call J (1997). *Primate Cognition*. Oxford University Press, Oxford.
- van Schaik CP, Deaner RO, Merrill MY (1999). The conditions for tool use in primates: implications for the evolution of material culture. *Journal of Human Evolution* **36**, 719–41.
- Werre JLR (2000). Ecology and behavior of the Niger Delta red colobus monkey (*Procolobus badius epieni*) (PhD dissertation). City University of New York, New York.
- Xiang ZF, Grueter CC (2007). First direct evidence of infanticide and cannibalism in wild snub-nosed monkeys (*Rhinopithecus bieti*). *American Journal Primatology* **69**, 249–54.
- Xiang ZF, Huo H, Xiao W, Quan R, Grueter C (2007). Diet and feeding behavior of *Rhinopithecus bieti* at Xiaochangdu, Tibet: adaptations to a marginal environment. *American Journal Primatology* **69**, 1141– 58.
- Xiang ZF, Nie SG, Chang ZF, Wei FW, Li M (2009). Current status and conservation off the gray snubnosed monkey *Rhinopithecus brelichi* (Colobinae) in Guizhou, China. *Biological Conservation* **142**, 469– 76.
- Xiang ZF, Nie SG, Chang ZF, Wei FW, Li M (2010). Sleeping sites of *Rhinopithecus brelichi* at Yangaoping, Guizhou. *International Journal Primatology* 31, 59–71.
- Xiang ZF, Liang WB, Nie SG, Li M (2012). Diet and feeding behavior of *Rhinopithecus brelichi* at Yangaoping, Guizhou. *American Journal of Primatology* **74**, 551–60.
- Zhu SQ, Yang YQ (1990). Forest types of Mt Fanjing. In: Zhou ZX, Yang YQ, eds. *Research on the Mt Fanjing*. Guizhou People's Publishing House, Guiyang, pp. 95–222 (In Chinese).