

Title: Prey capture and meat-eating by the wild colobus monkey *Rhinopithecus bieti* in Yunnan, China

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If it is true that extant primates evolved from an insectivorous ancestor¹, then primate entomophagy would be a primitive trait². Many taxa, however, have undergone a dietary shift from entomophagy to phytophagy, evolving a specialised gut³ and dentition¹ and becoming exclusive herbivores^{4, 5}. The exclusively herbivorous taxa are the Malagasy families Indriidae and Lepilemuridae, and the Old World Monkey subfamily Colobinae, and among these meat-eating has not been observed except as an anomaly², with the sole exception of the Hanuman langur (*Semnopithecus entellus*), which feeds on insects seasonally⁶, and a single observation of a nestling bird predated by wild Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*)⁷. Here, we describe the regular capture of warm-blooded animals and the eating of meat by a colobine, the critically endangered Yunnan snub-nosed monkey (*Rhinopithecus bieti*). This monkey engages in scavenge hunting⁸ as a male-biased activity that may, in fact, be related to group structure and spatial spread. In this context, meat-eating can be regarded as an energy/nutrient maximization feeding strategy rather than as a consequence of any special characteristic of meat itself⁹. The finding of meat-eating in forest-dwelling primates might provide new insights into the evolution of dietary habits in early humans.

Many primates supplement their plant-dominated diet with various faunal preys in the wild^{10,11,12}, whereas the Colobinae feed almost entirely on the foliage of trees, seeds, and occasional fruits and flowers¹³, and their diets conspicuously lack animal foods, even insects¹⁴. Their sacculated stomachs, which are adapted to folivory¹⁵, allow these monkeys a sluggish activity budget with an overwhelming amount of time spent in feeding or resting². Until now, active insect predation by wild Colobinae has been restricted to intermittent observations in a few langurs^{6, 9, 14}, despite decades of field observation. A record exists of the Sichuan snub-nosed monkey (*Rhinopithecus roxellana*) consuming a bird⁷, and several years ago faecal analysis suggested that the Yunnan snub-nosed monkey (*R. bieti*) may eat Yulungshan voles (*Eothenomys proditor*)¹⁶. Here, we describe regular prey capture and meat-eating by wild *R. bieti* at Xiangguqing (99°22'E, 27°37'N) in the Baimaxueshan National Nature Reserve in Yunnan province, China.

From March 2004 to January 2009, we conducted a long-term ecological study on a group of approximately 480 *R. bieti* that lived at elevations of 2800-3800 m. This large group consisted of >19 one-male units (OMUs) and 2 all-male units (AMUs)¹⁷, although, despite being unusually large, the group was cohesive¹⁸ and seldom split during its daily travel. The group confined its ranging area (ca. 50 km²) around three small villages (below 2600 m asl).

In this habitat, the mosaic vegetation is composed of a mixed coniferous and deciduous-broadleaf forest (*Sorbus* spp., *Betula alnoides*, *Acanthopanax evodiaefolius*, etc.), alpine fir (*Abies georgei*) forest, evergreen oak (*Cyclobalanopsis* spp. and *Quercus pannosa*) forests, and pine (*Pinus yunnanensis*) forest. Patches of bamboo (*Fargesia* spp.) and azaleas (*Rhododendron* spp.) occur between 2700 m and 3680 m asl, causing poor visibility in the habitat. Red-bellied tree squirrels (*Callosciurus flavimanus*), Swinhoe's striped squirrels (*Tamiops swinhoei*), Perny's long-nosed squirrels (*Dremomys pernyi*), at least three woodpecker species, including the white-bellied woodpecker (*Dryocopus javensis*), red-billed blue magpies (*Urocissa erythrorhyncha alticola*), Eurasian jays (*Garrulus glandarius*), black kites (*Milvus migrans*), bar-tailed tree-creepers (*Certhia himalayana*), and many tit-sized birds were commonly observed in the study site.

Lichens are the default food choice of *R. bieti*^{18,19}, and the discovery of regular carnivory was quite unexpected, although crumbling of rotted wood and branches by the monkeys was observed many times during our study period: searching in rotted wood indicates the possibility of insect larvae ingestion by *R. bieti*¹⁹.

Between 2004 and 2009, six instances of animal consumption by the Yunnan snub-nosed monkey were recorded *ad libitum* in this group at Xiangguqing (Table 1). All of the predatory behaviors occurred sporadically during the routine daily journey of the group. The capture of warm-blooded animals and meat-eating incidents suggest that *R. bieti* utilize scavenge hunting to capture prey since the prey was secured within a close range⁸. Evidently, the species exhibited characteristics of omnivorous primates²⁰ in animal prey procurement.

Although two cases of carnivory were observed by females, these involve scavenging. Only *R. bieti* males participated in active animal predation at the periphery of the group, where the AMUs are generally to be found. The AMU consists of ousted immature males and adult males that had been replaced in OMUs. Individuals in AMUs are compatible to each other (i.e. sitting together,

grooming each other, huddling when rest etc.) but strictly subordinate to those in OMUs and only move about around OMUs at the periphery of the whole group. As the group travels from one location to another day after day, the individuals on the fringe of the group encounter small animals at higher frequencies. As a result, the members of AMUs can more easily acquire more prey by hunting these animals.

R. bieti killed its animal prey by biting the head and neck off of their prey, as is usual among omnivorous primates². Even when the prey was already dead, as in the case of the red-billed blue magpie, the juvenile female picked the animal up and ate its head and neck first (Fig.1: A,B). This mechanism of killing animal prey benefits the predator by protecting the predator from the bite of the prey, ending the prey's struggle more quickly, and allowing easy killing of the prey while the predator holds the prey by the back and legs. *R. bieti* males killed their captured prey immediately by biting the animal to death in contrast to other primates who carry the prey away to kill them (e.g. *Cercopithecus ascanius*²¹, *Macaca silenus*⁸, and *Nomascus concolor jingdongensis*²²). Even the related *R. roxellana*, in the sole observation of predation in this species, tore the nestling Eurasian blackbird (*Turdus merula*) to death when the male grabbed the bird from the nook and ate the prey at another site⁷. *R. bieti*, on the other hand, ate its prey at the location where he killed the animal or she picked it up (Fig.1).

Meat-eating occurrences were entirely sporadic for *R. bieti* because all prey was encountered opportunistically while foraging for plant foods. Although prey capture is, according to our observations up to now, a male-biased activity in *R. bieti*, two females were observed to possess meat (Fig. 1); these, however, were scavenging of dead magpies; one adult female obtained the bird after the predator male discarded it to escape from possible attack from the dominant male in her OMU, and a juvenile female just happened to acquire a dead bird in a leafless shrub. Only a few males in the study group took part in animal predation while most of the others showed indifference. Interestingly, when one would catch an animal, the others did not try to snatch it but, instead, actively gave up the chase, and the catcher would always eat the prey alone. Beggars existed and were eager to tentatively get the predator monkey to share his catch; no meat-sharing was observed, however, because the meat possessors did not permit the beggars to approach them closely. Avoidance of the other individuals nearby was the only response. We did not observe more than two males chasing a single prey animal at the same time. In all

instances, the individual that killed the prey ate the animal without delay.

Only chimpanzees, among nonhuman primates, have developed social meat-eating by sharing hunted animal carcasses with others inside the same group. This sharing reinforces social bonds within a group and attracts estrous females¹¹. If cooperative hunting and meat-sharing in non-human primates is characteristic of high cognition, then predation on animals and meat-eating in *R. bieti* occur at a lower level of cognition. Meat-eating, in this way, can be regarded as an energy/nutrient maximization feeding strategy, rather than as a consequence of any special characteristic of meat itself⁹.

Evidence for prey capture meat-eating by the Yunnan snub-nosed monkey confirm this species an omnivorous colobus monkey but not a complete herbivore. Poor visibility in the habitats and short-term study period might be the main reason to exclude colobines out of primate meat-eaters. The present findings cast light upon dietary diversity and the ability of *R. bieti* to expand the spectrum of prey. Definitely, diet influenced human evolution, but trends in the evolution of the human diet and the role of meat in it are still unclear. Study on patterns of meat-getting and meat-eating in colobines might help us better understand feeding habits and dietary niche of early tropic forest-dwelling humans. Given gender division of meat-getting in *R. bieti* is noticeable, further study can allow us to pose more theoretical questions relating to the ecology of meat procurement.

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Acknowledgements The present research was granted by the key project of Natural Science Foundation of China (No.30630016), China Program of The Nature Conservancy and the National Basic Research Program of China (973 Program: 2007CB411600). Many thanks to our field assistants Mr. Yu Zhonghua, Mr. He Xinmin, and Mr. Yu Jianhua. Permission to work in the Baimaxueshan National Nature Reserve was provided by Mr. Liu Sikang, director of Weixi Nature Reserve Branch Bureau. We are especially indebted to Mr. Shen Yongsheng, Mr. Zhao Weidong, and Mr. Mao Wei for their generous help in local accommodation at Tacheng and Diqing prefecture on all aspects of this project. Also thanks to Professor Colin Groves for English revision and comments.

Author contributions BP. R. and M.L. designed the project. BP. R and DY. L conducted the field work. BP. R. analyzed these data. BP. R. and M..L. wrote the manuscript. M.L. supervised the project. All authors edited and commented on the manuscript.

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Figure legends

Fig. 1. Females are eating red-billed blue magpies (*Urocissa erythrorhyncha alticola*) and carcass parts rejected(C, F) at Xiangguqing. Picture A and B are juvenile female in November 2008, and picture D and F are adult female in January 2009.

Table 1. Predatory episodes and preys consumed by *Rhinopithecus bieti* in Yunnan, China (2004-2009).

Date	Prey species	Age class of preys	Age-sex of predators	Beggars	Carcass rejected
18.06.2004	Swinhoe's striped squirrel <i>Tamias swinhoi</i>	Adult	AM	Two ADMs	Tail
10.08.2005	Eurasian Jay <i>Garrulus landarius</i>	Fledgling	AM	One SAM	None
08.06.2006	White-bellied Woodpecker <i>Dryocopus javensis</i>	Nestling	AM	None	None
03.07.2008	Black kite <i>Milvus migrans?</i>	Fledgling	AM	None	None
30.11.2008	Red-billed Blue Magpie <i>Urocissa erythrorhyncha</i>	Adult	AF	One J and one AF	Wings feathers
02.01.2009	Red-billed Blue Magpie <i>Urocissa erythrorhyncha</i>	Adult	J	None	Wings, feathers and legs

Notes:

Age definitions of *R. bieti*: Juvenile : 1.5-2.5 years old, sex is not clear; Adolescent: 2.5-4 years old for female and 2.5-6.5 years old for male; Subadult: 4-5 years old for female and 6.5-8 years old for male. Youngster: <1.5 years old. Adult: >5 years old for female and >8 years old for male.

Age-sex of *R. bieti*: AM: adult male; AF: adult female; ADM: adolescent male; SAM: subadult male; J: Juvenile.

? We did not identify the bird species but a young kite. Predators in the table mean meat possessors *per ce*.



A



B



C



D



E



F